VARIATION IN
NUTRIENT DYNAMICS
AND
SECONDARY ECOSYSTEM
DEVELOPMENT
IN
SUBALPINE EU CAL YPT
FORESTS AND WOODLANDS

by

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Thesis submitted for the Degree of
Doctor of Philosophy
in the
Australian National University

(1 February 1975)
"One may be sceptical of the idealisation of the natural state. In the forest as well as elsewhere, virginity is not accompanied by excessive virtue. The harmony-of-nature concept romanticises a status-quo in which man plays no part, and doubtless it holds more charm for those who lack untouched vegetation than for those of us who can go out and see (frequently with dismay) what theory assures us ought to be a beautifully balanced condition, healthy, harmonious and in every way ideal."

- J.S. Rowe
The determination of the following nutrient groups,

(i) total cations
(ii) total nitrogen, total phosphorus
(iii) exchangeable cations

and extraction of (i) and (ii) was carried out by the staff of the Soil and Plant Analytical Laboratory, Department of Forestry, A.N.U., on automated instruments.

Unless otherwise stated, all field work, sample preparation, extraction and analysis was by myself.

Except where specific reference is made to the work of another author, all work in this Thesis is original and was done without collaboration.

Geoffrey Park
(1 February 1975)
I owe a debt of gratitude to Tony Druce and Ian Atkinson whose guidance in the understanding of ecological patterns and processes, and the fundamental importance of *time*, in the mountains of New Zealand has been a constant source of inspiration.

For the opportunity to carry out the research which forms the basis of this thesis I am indebted to the Commonwealth Scholarship and Fellowship Plan and the Australian National University who financed the project.

I would like to thank Dr. Peter Stevens, now at the School of Australian Environmental Studies, Griffith University, who was my supervisor for the duration of the project. His own work in primary ecosystem development in New Zealand did much to open my eyes to the complexity of nutrient dynamics in forest ecosystems.

To Professor J. D. Ovington, Dept. of Forestry, A.N.U., I am indebted for the provision of technical facilities. Dr. R. G. Florence helped me with critical reading of draft material.

I owe special thanks to Dr. Ken Eldridge, Forest Research Institute, Canberra, for his interest in the project, his ability to point out the problems of Ph.D. research before they became too severe, and for criticisms of the manuscript.

For advice during my introduction to the Australian high country, I would like to thank Professor L. D. Pryor, Botany Dept. A.N.U., Mr. D. J. Wimbush C.S.I.R.O., Jindabyne, and district officers of the Forests Commissions of Victoria and New South Wales.

I would like to acknowledge helpful discussion and correspondence with the following people: Mr. J. Bailey, C.S.I.R.O. Division of Soils; Drs. P. Walker and M. P. Austin, C.S.I.R.O. Division of Land Research; Dr. A. B. Costin, C.S.I.R.O. Division of Plant Industry; Prof. W. D. Jackson, Botany Dept., University of Tasmania; Dr. M. Gilbert and Mr. N. Johnson, Forests Commission of Tasmania; Dr. R. J. Grose, Forests Commission of Victoria; Dr. Truda Howard, Botany Dept., University of N.S.W.; Dr. P. Attiwill, Botany Dept., University of Melbourne; Dr. J. M. Flood, Dept. of Prehistory, R.S.Pac.S., A.N.U.; Dr. S. Barker, Dr. B. McCauley and Mr. C. E. Harwood, Dept. of Environmental Biology, A.N.U.; Dr. T. J. Blake and Mr. J. C. G. Banks, Dept. of Forestry, A.N.U.; Dr. M. Owens, Bureau of Mineral Resources; and Dr. G. E. Likens, Cornell University, New York.

The Forests Commissions of Victoria and Tasmania, and the National Park and Wildlife Services of N.S.W. and Tasmania provided assistance with field transport, and permission to collect sample material.

C.S.I.R.O. Division of Plant Industry provided the facilities for grinding the tonnes of forest floor samples. Dr. J. Jennings, Dept. of Biogeography and Geomorphology, A.N.U., provided a laboratory for the physical fractionation of soil samples.

The reproduction of the considerable number of figures in this thesis was carried out by the Visual Aids Section, A.N.U.
The assistance of Mr. Terry Johnson was invaluable in the writing of numerous computer programmes.

I owe special thanks to Mr. Frank Darlington for his assistance and tolerance during my occupation of the Soil and Plant Analytical Laboratory, Dept. of Forestry, A.N.U.

I should thank members of the Banks and Park families for their field assistance during visits to Australia.

To Ann Howarth and Sandra Thomas I am very grateful for typing through the holiday period, and Ann and Peter Wellman for proof-reading.

Finally, I would like to thank Lindsay, Turi and Matiu for making available that most precious of all commodities "time" during the long periods when the Ph.D. has taken precedence over our other activities.
TAXONOMIC NOTE

The names, *Eucalyptus delegatensis* and *Eucalyptus pauciflora* have been used throughout this thesis to define the dominants of two major subalpine communities. There is some contention on the validity of these names. My usage is as follows:

*Eucalyptus delegatensis*  

*Eucalyptus delegatensis* was considered to be the correct name by Cameron (1946), "The species is usually referred to *E. gigantea* Hook. f. (1847), a composite species which, as originally described, included *E. obliqua* L'Herit. The name, however, is already preoccupied by *E. gigantea* Dehn. (1822) - a synonym of *E. globulus* Labill. (1799). *E. gigantea* Hook. f. must therefore fail, and *E. delegatensis* be retained as the specific name of this important tree. (N.B. Baker's use of the "a" in spelling Delegete is perhaps questionable.)"

*Eucalyptus pauciflora*  

Green (1967) provides a taxonomic chronology of 13 published taxa related to *E. pauciflora* Sieb. ex Spreng. The original name was proposed for populations on the mainland and Tasmania extending up to an altitude of 4000 ft. (Green, loc cit). Four varieties and two additional species were validly published for populations thought to differ in some way from *E. pauciflora* Sieb. ex Spreng. Those given specific rank (*E. de Beuzevillei* Maiden (1920) J. Roy. Soc. N.S.W. 54:68 and *E. niphophila* Maiden and Blakely (1933) Maid. Crit. Rev. 8:34) were high altitude populations unknown at the time of the original description, while the four varieties were minor variants discovered within the originally known geographic range (Green, 1967). In the present thesis, only a specific ecotypic component of the broad species *E. pauciflora* was studied (where the species forms a contiguous boundary with *E. delegatensis*) and the conclusion of Green (1967) was assumed,

"... There was no evidence of significant grouping within the broad species *E. pauciflora* sufficient to justify strict adherence to the formal varieties and species segregates so far published"
ABSTRACT

Studies have been made of nutrient dynamics in the forest floor and surface soil layers of subalpine eucalypt ecosystems, particularly those dominated by *Eucalyptus delegatensis* and *E. pauciflora*.

Field studies of the commonly contiguous limits of distribution of eucalypt species in the montane - subalpine zones suggest that the primary factor in distribution is topography, largely because of the topographic control of microclimatic extremes, Quaternary landscape-forming processes, pedogenesis and the frequency of fires. Many of the ecotones between eucalypt-dominated communities represent discontinuities in community structure, suggesting considerable thresholds in the quantity and quality of the nutrient pools of the ecosystems at their distribution limits.

The preliminary analytical results reported in this thesis suggest that the soils supporting *E. delegatensis* contain greater concentrations and quantities of nutrients than the soils supporting eucalypt species forming the adjacent communities. However, detailed analyses of the forest floors and the uppermost 5 cm of soil indicate greater concentration and accumulation beneath *E. pauciflora* forest. In most cases the difference is slight, as a proportion of the mean weight or concentration, and is sensitive to changes in the secondary successional status of the forest floor.

The monitoring of the seasonal fluxes of nutrients in the ecosystems of *E. delegatensis* and *E. pauciflora*, in an ecotonal situation, indicated that the quantities of all nutrients tended to converge in the litter-fall of the two systems, compared to the differences in dry-weight of the biomass and total litter-fall. This convergence was increased in the decomposing
litter to the extent that within a few months on the forest floor, there were greater quantities of nutrients in the leaf litter of *E. pauciflora*. This difference prevails in the standing-state of nutrients in the forest floor layers. A comparison of turnover rates showed that there is preferential accumulation of all nutrients, except perhaps K and Na, in the forest floor layers of *E. pauciflora* ecosystems. Despite the constancy of the physical environment, the ecosystems showed considerable divergence in the rates of nutrient mobility.

The results suggest that the differences in the morphology of decomposing leaves, and the nature of the forest floors, in the respective ecosystems are more important determinants of the long-term processes of decomposition, mobilization and net accumulation of nutrients in the detrital layers, than are differences in community structure.

Whilst there are clear differences in the rate of long-term flux of nutrients in the forest floor and surface soil between the two ecosystems, the integration of the nutrient data as differential functions of the net accumulation of the forest floor in time, suggest that the process of flux is similar.

Although there are clear successional trends in the dynamics of nutrients and understorey vegetation, the quadratic functions defining the trends are often non-significant because of considerable variation between the 46 ecosystems selected for the study.

While the study of seasonal fluxes of nutrients has shown that the mobility of most nutrient elements is somewhat independent of fluxes in organic matter, the long-term overview is that the weight-distributions of nutrients show marked correspondence to the equivalent distributions for total organic matter. Monitoring of the quantities and flux-rates of nutrients immediately after a wildfire, and for the following 10 months,
showed that very large amounts of carbon are lost from the ecosystems during, and after, a perturbation of this nature. The loss of carbon, and the concomitant de-structuring of organic matter:nutrient ion complexes appears to be critical in determining the flux of nutrients out of the forest floor and surface soil layers.

Recovery of forest floor and understorey-vegetation properties, following a perturbation, proceeds initially to a point of maximum storage of nutrients and energy in the forest floor following homeostatic adjustment to the immediate effect of the perturbation. The process is estimated to take about 55 years in *E. pauciflora* ecosystems and about 35 years in *E. delegatensis* ecosystems for organic matter, and proportionately different periods for individual nutrient-elements. Beyond this point it appears that declining litter production related to structural changes in the community is concomitant with increased decomposition. The mass of the forest floor is reduced and the organic matter becomes endorganic in marked contrast to an earlier sharply differentiated ectorganic distribution.

The phasic replacement of understorey shrub vegetation is also a readily observable phenomenon of 'recovery' in the earlier stages of the secondary succession in the subalpine eucalypt ecosystems, whilst later stages showed apparent steady-state in composition. The data support long-term observations of earlier workers that a period of about 40 years is required for the general vegetation succession from a shrub to grass-herb understorey. This includes a very distinct trend in understorey species diversity during the most intensive period of recovery from perturbation.

In the discussion, I have developed some general models of long-term ecosystem development in the subalpine eucalypt biome, by integrating the studies of the dynamics of understorey vegetation and the nutrients...
of the forest floor and surface soil layers with the anthropomorphic history of the subalpine zone, the palaeoecology of the biota and comparative analyses of the responses of the current vegetation-dominants to fire.

Finally, in the form of a coda, I discuss the present-day state of the subalpine ecosystems in terms of the problems of conservation of diversity of 'natural' patterns and processes.
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"THE tendency toward the development of steady-state functions, applying to different processes on different levels is one of the most general characteristics of ecosystems .... The steady-state magnitudes of communities seem not to be directly selected for, but to be resultants of processes which tend, by some mode of growth until input and output are equal, to balance themselves.

We conclude that community characteristics are to be understood as cumulative effects of species evolution and multiple steady-state processes. We should like, though, in scrutinising some traditional ideas to comment on one, the balance of nature. This expression is as common in the popular literature of conservation as it is unpopular among scientists - though it may be conceived as the tendency of populations and communities to compensate for perturbations (Slobodkin et al., 1967).

What is the truth? We suggest that it is the intuitive perception of the steady-state function of populations, ecosystems and the biosphere by naturalists to whom the steady-state concept as such was mostly unknown. It is the inference that, underlying the relative constancy of the biological world from year to year, there must exist functional balances and regulatory processes. The perception - of communities as tending toward self-stabilization involving steady-state function, and of the biosphere as a great steady-state system of interconnected steady-state systems - was not false. The emergence of loosely ordered and imperfect steady-state functions is a most general feature of the evolution of ecosystems. A technological civilization might make no greater mistake than to think that the balance of nature is irrelevant to human affairs, ..... it is in our interest to protect what is left of this balance if we can, for we cannot adequately foresee the disadvantages to us of further disturbances. Man is now at a turning point in history where he has the power to change not only the functions of particular ecosystems, but the characteristics of the biosphere as a whole. It seems a fateful turning."

Whittaker and Woodwell (1972)

PROLOGUE

I have two reasons for choosing Whittaker and Woodwell's conclusions to introduce this thesis about the eucalypt ecosystems of
high-country Australia. Firstly, from the enormity of contemporary information on ecological principles and processes, these eminent ecologists consider the tendency toward the steady-state function the most fundamental and unifying. Secondly, it is the implications for management within the steady-state function that evokes a contrariety of understanding of the ecological patterns and processes in the high-country forests and woodlands. This understanding must be said to come as much from the analyses of nutrient pools, and the photosynthetic/respiratory balance of snow gum woodlands and alpine ash forests as from the generations of 'burning-off', grazing and droving cattle, and destruction of property by wildfire both within the high country and at lower altitudes.

It is not uncommon for the ecologist to set himself certain long-term aims, that is, one sets a framework of understanding within a field such that when confronted with an unfamiliar ecosystem or landscape, this framework serves as a plane of reference. My own plane of reference may be defined as 'the strategy of ecosystem development' (Odum, 1969). Perhaps because of research origins in temperate rainforest in New Zealand, I am immediately concerned with the nature of the steady-state function and ascertaining the inertia of evolutionarily determined development. I am then concerned with the qualitative and quantitative amplitudes of a 'new' ecological situation.

I have referred to contrariety in our understanding of the processes in high altitude eucalypt ecosystem. The contrariety will remain as long as the reference framework of the Kosciusko National Park Ranger is Kosciusko National Park, that of the Hume-Snowy Bushfire Prevention Scheme is fuel reduction and the 'uniqueness' of eucalypt forest succession, and that of the ecosystem ecologist, the validity of the primeval ecosystem.
The preservation of "a status-quo ... a beautifully balanced condition, healthy, harmonious and in every way ideal" (Rowe, 1961, Frontispiece) does not follow from the perspective of forest ecosystem dynamics, with regards to formulation of an ecologically determined policy of conservation. Nor, however do the widely used concepts of "overmaturity", or a national park as "a potential powder keg in the eyes of its neighbours ... [whereby] ... the use of control burning for hazard reduction on a broad scale sets the framework within which the [National Parks and Wildlife] Service can, with safety carry out some more intensive burning for ecological management of the Park" (N.S.W., 1970).

The question is no longer "Was fire a natural factor before the white man came?" It is becoming increasingly crucial that now we ask, "How much, and what kinds of fire were natural, and were there changes associated with the build up of human populations, with the arrival of the white man, and with inter- and post-glacial climatic fluctuations?" (Heinselman, 1971). These are the immediate problems of the field ecologist, and it is towards these ends that this study has been undertaken.

Is a theory of long-term ecosystem development valid and applicable to the planning of conservation policies in the subalpine forests and woodlands of Eucalyptus through which passes the most important water on the continent? Is the investigation and conservation of biological time-scales and the few remaining near-primeval ecosystems an international scientific obligation? Or, will management practice continue to condone a century old tradition in attitudes to fire in these ecosystems? What is the truth?
"For the Earth, our mother, at last has found a master; She was slow and kindly, she laughed and lay in the sun - Time strapped to his wrist, he made the old girl work faster, Stripping her naked and shouting to make her run.

He cracked his stockwhip; that characteristic gesture Made dust of the plains and the hurricane bore it away, A thousand years had gone to make the pasture Which the wind or the flood destroyed in a single day."

- from "Toast for a Golden Age"

(A. D. Hope)

1.1 INTRODUCTION

The quantitative study of the dynamics of nutrient elements has become one of the major thrusts of current ecological thought (Likens and Bormann, 1972). It is now clear that an understanding of nutrient cycles is fundamental to understanding the long-term welfare of man. There is a finite quantity of certain essential minerals or nutrients available to terrestrial plants in the biosphere, particularly nutrients such as phosphorus which naturally occur only in very small quantities in the atmosphere and must be provided from soil or rock sources. It is estimated (Cole, 1958) that annually, some 8 million tonnes of $P_4$ are transported to the sea. Only a fraction of this is returned annually to the land.

One of the basic ideas of ecosystem theory is that the cycling of nutrients, and the evolutionary development of the whole ecosystem and its component parts, reach a kind of dynamic equilibrium suitable to an open system. Within forest ecosystems, the rates at which ecosystem components reach equilibrium are, for any one system, extremely variable (Park, 1970; Stevens and Walker, 1971). It becomes difficult for one who has observed the variable rates of change of a group of apparently related ecosystem parameters within a time-based sequence, to accept the notions of the plant association (Clements, 1936; Braun-Blanquet, 1932) and the
genetic soil profile (Taylor and Pohlen, 1962; U.S.D.A., 1960). Ecosystems are polythetic structures, their development proceeding directly and inevitably towards a state of dynamic equilibrium. This dynamic equilibrium must be defined, for individual ecosystem components, within the limits of an open system (Bertalanffy, 1950; Nikiforoff, 1959). Fundamental to the meaning of such an equilibrium, or steady-state, is a minimum of continuous variation within and between all parts of the ecosystem; that every variable is, and is part of, a continuum (Webster, 1968; Park 1970, 1972) in time and space.

In defining my ecological philosophy and the objectives of this study, I make three general hypotheses, namely:

1. The successional development of subalpine eucalypt ecosystems will tend to proceed directly and inevitably towards a state of dynamic equilibrium, following a perturbation. The process, whilst proceeding continuously in an environment with a high probability of disturbance will be truncated according to the frequency of disturbance.

2. Two elements of the subalpine landscape differentiate it from the landscapes of lower altitudes, in terms of the quantity and quality of nutrients available to the forest ecosystem, and the dynamics and time-scale of successional processes.

(a) the geomorphic groundsurfaces are predominantly recent and support comparatively young, fertile soils.

(b) the vegetation, whilst dominated by *Eucalyptus*, appears to have evolved in a comparatively low-fire-frequency

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* A feature of ecological literature is the imprecision and variability of definition of terms and concepts. Steady-state is an important concept in this thesis; it is used throughout in this sense.
3. The current assumptions by conservation management of the incidence of fire in subalpine eucalypt ecosystems have homocentric origins, and are at variance with the evolutionary incidence of fire in these ecosystems. It is likely that the contemporary pattern of fire in the subalpine zone is more a result of the time-scale of European man than of the biological time scale of succession in the component ecosystems.

My aim in this thesis has been to achieve some understanding of the dynamics of secondary succession in subalpine eucalypt vegetation, in the context of:

(i) the palaeo-ecology of the biota,
(ii) the recent anthropomorphic history,
(iii) the general theories of forest ecosystem development, particularly the concepts of inertia-of-development and steady-state,
(iv) nutrient cycling, particularly the nutrient dynamics of the forest floor/soil surface,
(v) a future policy of rational conservation of ecological diversity, including the unique features of long-term succession in these ecosystems.

To complement investigations of nutrient cycling in successional development, I have,

(a) examined the nutrient status of the forest floors and surface soils of a large number of sites where there is a very narrow ecotone between two communities dominated, very exclusively, by *Eucalyptus delegatensis* and *E. pauciflora*, at the upper
altitudinal limit of the former. There is a considerable difference between the quantities of above-ground biomass of the two communities. This admirably suits the purposes of an assessment of the importance of nutrients in the determination of eucalypt distribution in the subalpine zone.

(b) examined the seasonal fluxes in leaf fall, nutrient concentration and accession to the forest floor, and between the L and F/H components of the forest floor, in one of these narrow ecotones.

To date, any quantitative understanding of nutrient cycling on an ecosystem basis in Australian forests has been restricted to either plantations of exotic species (reviewed by Lamb, 1972) or natural forests of Eucalyptus on old infertile soils, subjected to numerous weathering cycles in the lowlands and lower montane zone (Hatch, 1955; Ashton, 1956; Attiwill, 1964). There are no comparable studies of forests or woodlands on the young and relatively fertile soils of the subalpine or upper montane zone. Even in the absence of ecosystem data, there is little understanding of the changing quantitative relationships between the major site variables and dependent ecosystem parameters during secondary succession. In terms of the modern importance of these ecosystems to the human population, succession is the singularly important principle on which to base an ecologically determined policy for their management and conservation. Land unit surveys are essentially concerned with the static characteristics of soils and vegetation, and have proceeded little beyond the heuristic and predictive value of their classification. In upland forest soils the single most important measure of soil fertility is the amount of organic matter. In most undisturbed forest ecosystems, certainly in the Australian subalpine region, organic matter, total nitrogen, phosphorus, and the exchangeable cations tend to accumulate in
the surface soil or the overlying litter and biomass, where they can attain considerable quantities under steady-state conditions. There is mounting evidence from recent research that these nutrients are rapidly depleted, redistributed or changed in state as soon as the biomass, forest floor or soil surface is disturbed (Stone, 1973).

A corollary of this is that the forest floor/soil surface interface is the single most important component of the ecosystem from which to ascertain the nature and degree of stress being placed upon the natural inertia of forest ecosystem nutrient cycles, by the various management options (Stevens, 1974, *pers. comm*). These constraints include:

1. Relatively large unweathered reserves of "non-available" nutrients are held within the root range in even the poorest forest soils. For example, in the present study, the proportion by weight of unweathered stones greater than 2 mm diameter in the surface 5 cm varies from 5-95% under vegetation dominated by only two eucalypt species on different parent materials. In comparative studies, particularly where there are pedogenetic differences in the physical form of the soil, it is of critical importance to define nutrient parameters in terms of weight per unit area, or unit volume. Usually only the fraction passing a 2 mm mesh is retained for analysis, and even then, considerable unweathered material will be analysed. On this basis in many upland forest soils, particularly lithosolic phases, well over half the solum will not be analysed. However, the ecological and land management literature is full of impossible figures on amounts of 'available nutrients' in soils (Major, 1969), usually because nutrient concentration data have been used without reference to the physical character of the profile, or because nutrient
weights have been derived from the bulk density of an entire sampling depth. If concentration, energy or mass units alone, without reference to areal or volumetric units, are used to describe an ecosystem much of the potential information of changes in components of the ecosystem is lost. The ecosystem may be oversimplified, misunderstood, and in fact, unrecognisable in terms of quantitative results.

2. "Available" nutrients are often in short supply. Even if there are abundant reserves of a particular element, the ratio of exchangeable ion unit to total ion unit in surface soil is invariably narrow. Total analyses are to be interpreted with caution, even in plant tissues, primarily because considerable and unknown proportions may be held in biochemical and geochemical fixation. Nutrients form often complex gradients of availability dependent on their solubility at the root-hair surface. The 'available' component of any nutrient can only be arbitrarily determined by the ecosystem chemist, who formulates suitable extract solutions. The solubility gradient of phosphorus, for example, has received much attention (Chang and Jackson 1957; Williams, 1967). In soils from most parent materials only a small proportion of the total phosphorus is within the solubility range enabling plant uptake (Humphreys, 1969; White, 1972; Daughtrey et al., 1973a, 1973b). Of this, a considerable proportion is either recycled within the biomass, particularly in eucalypt forests (Attiwill, 1964) or returned to the forest floor bound to organic complexes. It may remain for an extremely long time in organic form in the forest floor and soil (Stevens, 1968) and even mineralisation does not mean it will be converted
to plant-available form, as large amounts of unavailable inorganic phosphorus, and other nutrients, can accumulate in deep forest floor layers, as will be shown in this study. Mineralisation of nutrients returned to the forest floor from the living biomass is dependent on the degree of biological activity at the forest floor/surface soil interface. The forest floor can, in some forests, represent a significant proportion of the total nutrient pool and organic matter (Olsen, 1963; Reiners and Reiners, 1970).

3. The weakest link in nutrient cycles of forest ecosystems may be the transfer of nutrients from the forest floor to the mineral soil, about which there is little specific knowledge (McColl and Grier, 1972) apart from recognition of the importance in mobilising cations of certain anions (e.g. $\text{HCO}_3^-$, $\text{NO}_3^-$) resulting from respiration in the forest floor and interaction with rainfall (Gessel et al., 1973; Bormann and Likens, 1972). There is little information on the possibility of an eventual equilibrium process of nutrient transfer between the forest floor and the mineral soil.

4. A major gap in our knowledge of eucalypt forest ecology which restricts constructive criticism of current management assumptions is a lack of quantitative information on the relationship between the variable balance of soil weathering of primary parent materials, and nutrient losses by leaching, erosion and long-term ecosystem development. Man can now influence the nutrient cycles of these ecosystems by managing some inputs (fertilizers, sprays, changing the composition and structure of the biomass), outputs (harvesting of plants and animals, soil disturbance, fire, maximum biomass protec-
tion for catchment values), redistributions (disturbance of forest floor and soil) and numerous natural feedbacks and perturbations. Recently, many commentators (Kimmins, 1972) have critically considered the ecological consequences of management stresses on forest ecosystems with widely varying thresholds to stress, in the northern boreal and temperate forest biomes.

Considerable recent appraisal of the effect of forest disturbance on nutrient fluxes has been made in response to public and political demands for information on clear-felling in the U.S.A. (Curry, 1973; Gessel et al., 1973; Stone, 1973). It can be concluded that in the long term any erosion of forest floor and/or soil materials, especially organic matter and the fine mineral fractions reduces soil and site productivity. Changes in the physical form of the solum may be negligible, whilst erosion of the pool of plant-available ions is proceeding at the soil surface by solution. If one considers only the observed increases in nutrient outflows and specific conductivity of water draining disturbed areas reviewed by these authors, it is possible to predict that soil productivity will decline to the extent that nutrient outflow exceeds natural primary mineral weathering and atmospheric inputs.

Recently, some of the same data have been effectively, but also somewhat uncritically applied (Routley and Routley, 1974) and subsequently disputed, in the context of the clear-felling of eucalypt forests in Australia. There is simply inadequate information on the dynamics of nutrients in the eucalypt biome for an equivalent critique to be made in this country. The disturbance of the forest floor and deflation of the soil surface in the subalpine forests and woodlands consequent upon the post-European history of land use practices in the Australian high country have been described in numerous surveys of catchment conditions (Byles,
1932; Costin, 1954, 1957; Morland, 1958, 1959, 1960; Rowe, 1967) and cannot be disputed. Such deterioration may be slow and not obviously apparent for years after the disturbance event. However, once the soil physical equilibrium has been upset, deterioration tends to be self-perpetuating until new equilibrium conditions are attained, often under a quite different community type (Costin, 1969). There are some data, besides that of the forementioned surveys, to suggest that in upland forests, perturbations to nutrient cycling occur simply as a result of regular burning reducing the mass of the understorey and forest floor. The burning of the same country by graziers in the past would have had similar accumulative effects, and it would appear that this practice has created a syndrome of truncated secondary succession, hence the current need of National Park and Forestry Commission personnel to regularly burn the dense, microphyllous shrub understories that result.

These perturbations are significant in the short-term (Rowe and Hagel, 1974) and are balanced against inputs from atmospheric and weathering sources in the long term, primarily because in these soils the forest floor and the soil surface are the sites where most nutrients accumulate and are mobilised in plant available form. The majority of nutrients accumulated and recycled in the biomass must enter via the pool of available nutrients, and eventually be returned to it.

From successional studies of nutrient dynamics in the eastern U.S.A. (Marks, 1974) it seems likely that during the first year or so following disturbance, particularly heavy cutting, some increase in net nutrient losses (compared to the undisturbed system) is inevitable, but in amounts less than the extreme, maintained case at Hubbard Brook (Likens et al., 1970). Curtailment of nutrient losses would be promoted by early attainment of full occupancy, maximum net production, and subsequent rapid accumulation of biomass and nutrients (Marks and Bormann, 1972).
As a forest develops, the quantities of nutrients withdrawn from the soil and atmosphere, and accumulated and returned from the biomass, increases. However, there is little evidence that the resultant net decrease of available cations and anions will proceed to a stage of declining productivity within the stand (Ovington, 1959). It appears that there is a significant decline in the available nutrient pool only during the relatively short period of the productivity optimum, often when a secondary forest is of pole form (Remezov, 1964; Attiwill, 1964), when most nutrients are fixed in the biomass. As natural forest development proceeds this disequilibrium is minimised. It should be noted that in cool superhumid climates, in Australia restricted to S.W. Tasmania (Jackson, 1965), the environmental stresses inducing considerable net nutrient losses by leaching lead to a protracted decline in the available nutrient pool to such a degree, that eventually there is a threshold to self-maintenance of a forest ecosystem (Park, 1972; Stevens, 1968; Walker, 1965).

In general, the soils of the subalpine region of Australia are young and have formed in a cold, but relatively dry climate. There is some agreement that *Eucalyptus* as a whole evolved in conditions of relative aridity and infertility (Burbidge, 1959; Wood, 1959) but whilst these criteria apply to the present distribution of many lowland forests and woodlands, the subalpine forests and woodlands, in the main, do not occur on soils of obvious infertility in the pedogenetic sense. However, as the current study suggests, there are nutrient gradients, particularly of phosphorus, corresponding to the severity of recent disturbance and declining to levels that would be considered low in lowland dry sclerophyll forests. There are also catenary sequences which show consistent parallels in discontinuities of nutrients and of eucalypt species. It may appear contradictory that the same eucalypt species occupies a range of sites
in which there is an enormous range in nutrient supply characteristics, for example 200-4000 ppm of total phosphorus in the surface soil of *E. pauciflora*. Likewise there is a similar range in uptake and mobilisation within the biomass as shown by the concentration of individual ions in the undecomposed litter of different subalpine species on similar parent materials, and that of the same species on different parent materials.

Only a few studies (Ashton, 1954; Attiwill, 1964) have measured the quantities and proportions of nutrients in the biomass of upland eucalypt forests, and perhaps only Attiwill, (1964, 1971) has viewed the nutrients in the biomass in terms of their critical quantities in the "available" component of the soil. Attiwill has emphasised the very low phosphorus status of the soils, the low concentrations of phosphorus in a highly productive biomass despite wide biomass P/soil P ratios, and the efficient redistribution of P within the biomass to the extent that in relation to other elements, only a very small quantity is returned to the soil in litter or organically fixed within old wood tissue (Table 1).

<table>
<thead>
<tr>
<th>TABLE 1 RATIOS OF RELATIVE DISTRIBUTIONS OF ELEMENTS IN A <em>Eucalyptus obliqua</em> FOREST ECOSYSTEM (after Attiwill, 1964)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accumulation of nutrients in the biomass relative to soil <em>⁺</em> (biomass/soil)</td>
</tr>
<tr>
<td>P</td>
</tr>
<tr>
<td>0-30 cm</td>
</tr>
<tr>
<td>0-60 cm</td>
</tr>
<tr>
<td>0-90 cm</td>
</tr>
<tr>
<td>Return of nutrients to soil from the biomass (litter/biomass (%))</td>
</tr>
<tr>
<td>2.9</td>
</tr>
</tbody>
</table>

(⁺ = "available")
From this and other information, Attiwill predicted ultimate restriction of regeneration growth by phosphorus in particular, within a very few 50-60 year harvesting cycles in *E. obliqua* forests, allowing for future weathering rates and presumably assuming little disturbance to the surface soils in the interim.*

Although harvesting of a forest by clear-felling is extreme, in the sense of the current study of perturbations to the forest floor/surface soil, both inevitably result in some depletion of the nutrient capital of the ecosystem through losses in harvested or incinerated minerals (Rennie, 1957; Weetman and Weber, 1972; Floyd, 1966; Harwood and Jackson, *pers. comm.*, 1974), as the result of disruption of nutrient retention mechanisms (Bormann and Likens, 1970; Bormann, Likens and Eaton, 1969; Marks and Bormann, 1972; Rowe and Hagel, 1974). The extreme case is where entire boles are removed and the area either completely scarified (Kimmins, 1973) or secondary succession prohibited by herbicide treatment (Likens *et al.*, 1970), thereby creating an "open" system of nutrient dynamics, rich in potential plant nutrients relative to organically bound forms, and initially occupied only by small organisms with simple life histories or by the seedlings of forest trees. Neither of these growth forms are

*Attiwill concluded that the majority of available phosphorus in the *E. obliqua* ecosystem is held within the biomass, at least up until the age 50-60. At this age the return of cations exceeded the mean rate of accumulation, such that there was a progressive increase in the surface soil. The cations in Attiwill's study were all subject to rapid initial uptake relative to return, resulting in net accumulation in the biomass and a decline in the pool of available nutrients in the soil. The capacity of the biomass for high rates of dry matter production is apparently dependent on the supply of phosphorus at the time of re-establishment of the ecosystem, which determines the level of the cycle of redistribution of phosphorus within the biomass and the ratio of uptake to return. Thus the concentration of phosphorus in the surface soil may be a critical factor in the re-establishment of the particular ecosystem. Attiwill postulated that phosphorus is returned in greater amounts in old undisturbed stands and may actually accumulate in the surface soil.*
able to fix or accumulate much of the inorganic ions which tend to be rapidly flushed from the forest ecosystem by the increased quantities of water resulting from reduced transpiration, producing attendant perturbations in aquatic ecosystems (Odum, 1968; White, 1972). Increasing biotic regulation of function diminishes losses of particulate matter and inorganic dissolved substances and promotes the kind of steady-state buffering that is a feature of undisturbed ecosystems.

Fire, in any form, directly removes small amounts of some nutrients from the ecosystem via vapourisation and particulate ash (Harwood and Jackson, loc cit), but converts large quantities into available form at the soil surface. High temperatures can increase the availability of primary surface-bound forms of soil phosphorus, for example (Humphreys, 1969). The degree of indirect losses is a function of the retentive ability of a particular ecosystem under the stresses of post-fire weather patterns.

Rowe and Hagel (1974) demonstrated the initial surge in exchange-ability of cations and their subsequent decline due to leaching and biogeochemical fixing in upland forests of *Eucalyptus bicostata* in N.E. Victoria immediately following "fuel reduction burning". The forest is somewhat similar in biomass, structure and composition of understorey to that studied by Attiwill (loc cit). In conjunction, the two studies suggest a probable scale of long term losses of cations from the forest floor/soil surface following any disturbance or removal of these ecosystems components. One is led to conclude that repeated re-establishment of a disequilibrium in the cycling of nutrients in these forests will promote both rapid uptake and initial leaching from the pool of available nutrients with a progressive, but stepwise, decline in the total pool of available nutrients, and a decrease in ecosystem stability (Figure 1).

The concept of ecosystem stability has two components:
1) a capacity of the system to resist change or disturbance (Bormann et al., 1969; Marks and Bormann, 1972; Marks, 1974; Park, 1970); and

2) a capacity of the system to recover from disturbance, once the limits of resistance have been exceeded (Marks, 1974).

The relative importance of each component depends primarily on the magnitude and frequency of the disturbance; the capacity to resist change becoming less effective as the disturbance becomes more severe (Marks, 1974) and the net effect of a series of disturbances becomes magnified (Kimmins, 1973; Jordan, Kline and Sasscer, 1972).

Although different specific concepts of stability need to be applied to different parts of the biosphere (Preston, 1969) the inertia within an ecosystem to restore itself to a steady-state function (Whittaker, 1972) is fundamental. Steady-state systems (Figure 1) can be either stable, unstable but bounded, or unstable (Jordan, Kline, and Sasscer, 1972). Figures 1 and 2 show how each of these systems reacts differently to a perturbation of the steady-state. A stable system returns monotonically (Figure 1, line a) or with decreasing oscillations (Figure 2, line a) toward the steady-state. An unstable system continues to depart from the steady-state, either monotonically (Figure 1, line c) or with increasing oscillations (Figure 2, line c). An unstable but bounded system either assumes a new steady-state level (Figure 1, line b) or oscillates with the amplitude of the oscillations remaining constant (Figure 2, line b).

Forest ecosystems may be defined according to their stage of successionary development. Of the subalpine ecosystems in Australia, perhaps only Nothofagus rainforest and the coniferous forest in western and central Tasmania and some of the very old Eucalyptus pauciflora

* and are represented by Figure 1.
woodlands, for example in the N.W. Snowy Mountains, are stable in the sense of Figure 1, a. Mineral cycles in ecosystems which remain intact (Jordan, Kline and Sasscer, 1972) are all monotonically stable (Figure 1, line a). If the ecosystem does not remain intact, i.e., it is clearfelled or the forest floor is disturbed, then the mineral cycle may become unstable, to the extent of Figure 1, line c. Examples of unstable, but bounded systems (Figure 1, line b) in forests are the conversion of *Eucalyptus* forest to *Pinus radiata* plantation (Hamilton, 1964) and the alteration of *Nothofagus* forests throughout New Zealand following the introduction and stabilising of red deer populations.

![Figure 1: Monotonic Response of a stable system (a), unstable system (c) and an unstable but bounded system (b) to a perturbation](after Jordan, Kline and Sasscer, 1972)

![Figure 2: Oscillating Response of a stable system (a), unstable system (c), and an unstable but bounded system (b) to a perturbation](after Jordan, Kline and Sasscer, 1972)
We have seen that in drier montane eucalypt forests in S.E. Australia, the natural cycle of nutrients may lead to relatively low concentrations of phosphorus and high concentrations of cations in the surface soil within 50-60 years from establishment. It is in this position in the ecosystem that nutrient ions are most susceptible to perturbation. It follows that an examination of nutrient fluxes between different components of an ecosystem and between successionaly related ecosystems will obtain a maximum of information from the forest floor/soil surface interface.

One aspect of this study is to ascertain the scale of difference in the rates of litter fall, nutrient transfer to the forest floor from litter, and release of nutrients from decomposing litter between adjoining *E. delegatensis* forest and *E. pauciflora* woodland. It is known that some related eucalypt species vary in their need for a particular element (Moore, 1959; McColl, 1967) and in their ability to extract it from the litter and soil. In the case of these particular species, the discontinuities in distribution appear to be expressions of the topographic and pedological patterns of an area. *E. delegatensis* and *E. pauciflora* are in taxonomic proximity and although introgression has been observed in disturbed situations (Pryor, 1954) the species possess very efficient genetic barriers (Barber, 1965). Physiognomically, the two species form communities of very distinct structure, notably in older stands, and it is quite feasible to expect a threshold in the rates of biomass accumulation, nutrient cycling and secondary ecosystem development at the sharp ecotone between their respective ecosystems. Nothing is known of their relative efficiencies in mobilising and accumulating nutrients, and there has been no integration of successional botanical studies in these ecosystems, apart from the revegetation analyses of Costin and co-workers (Bryant 1971a, b; Costin 1966) in the higher altitude *E. pauciflora* (*E. niphophila*) woodlands. The role of successional species in the maintenance of
stability can be important, particularly as disturbances become more severe and more frequent (Marks, 1974). Quantitatively, the sequence patterns of the numerous understorey types, in the Snowy Mountains forests alone, are complex and need examination.

My impression is that there is a basic philosophical dilemma facing those responsible for the conservation of ecological patterns and processes in national parks and other reserves of similar purpose in the high country of Australia, particularly within the concept of 'wilderness'. Because of decades of burning by graziers, and for fire protection in recent years, vegetation patterns have been altered to the extent that it is virtually impossible to observe entire ecosystems that pre-date European man. The goal of conservation of biological time-scales of ecosystem development has been compromised. Concurrent with these changes in the biological systems are impacts on the variety of human users. The way these problems are currently dealt with, and will most likely continue to be, reflects the philosophy that explicitly or implicitly underlies the predominant policy of different management agencies. In the coda following the results of this thesis in the significance of the results to conservation planning, two mutually exclusive philosophies - homocentric and biocentric - are identified, and discussed in terms of their long-term effects in conserving ecological patterns and processes in a fire-environment. The difference lies in the degree to which the benefits of 'wilderness' and other 'natural' areas are viewed as being dependent on maintaining the biological integrity of ecosystems.

At the root of the management dilemma is the fact that a wildfire has traditionally been viewed as (a) a negative and destructive force, or (b) at best, a transitory disturbance in forest ecosystems, or (c) a 'tool of management'. In view of our conditioned attitudes towards fire, we may be suggesting solutions to ecosystem functions and land-management
and conservation problems that disregard fundamental relationships and because we have not asked the right question, or we have asked it from the point-of-view of human demands, human time-scales, and human biases for the validity of specific stages of forest succession.

1.2 THE STUDY

The study examines the forest floor and surface soil of subalpine eucalypt forest and woodlands to determine whether nutrient-pool thresholds are likely factors in the discontinuous distribution of certain eucalypt species, and whether a theory of the long-term development of these ecosystems can be formulated from an examination of the long-term dynamics of nutrients at the forest floor/surface soil interface, and the patterns of understorey species composition.

The initial studies in Chapter 4 examine the disjunct distributions of subalpine and montane eucalypt species, particularly *E. delegatensis* and *E. pauciflora*, throughout the Australian region utilising published data as well as the field observations of the author. A preliminary study of some of the soil physical and nutrient factors considered likely to influence locally discontinuous distributions is described.

Studies of the various situations in which forests and woodlands of *E. delegatensis* and *E. pauciflora* form sharp compositional ecotones are described. These attempt to qualify nutrient concentrations in terms of the different rates of turnover and accumulation of these two eucalypts and the proportion of nutrient exchange surfaces in the surface in the surface soil. The problems inherent in determining nutrient

* on the assumption that an environmental factor critical to the distribution of a species is best examined at the distributional limit of that species.
weight parameters in often lithosolic soils, from a wide range of parent materials, are discussed as they preclude the collection of large numbers of samples per site. Consequently, within the limits of this study, only consistent trends emergent from the data can be interpreted with any significance to discontinuous forest patterns. Other studies measure the structure and composition of the understorey and ground cover in these ecotonal situations.

Together with data from single stands, the data from the ecotonal study are amalgated in a study of long-term secondary succession, following perturbations to the soil surface/forest floor and understorey components of the ecosystems. The large number of sites studied, particularly in the northern part of the subalpine zone, permitted the construction of probability distributions showing patterns of change in the form of the forest floor and the surface soil. Consideration is given to the likely trends of ecosystem development following the inevitable, but rarely observed, decline in production and biomass accumulation as the eucalypt canopy opens and the ecosystem shifts towards self-maintenance. The role of fire, in an evolutionary as well as short-term context, is discussed. A 12 month study of the fluxes in nutrients and dry matter, via litter fall and litter decomposition in adjacent *E. delegatensis* and *E. pauciflora* ecosystems is described. The purpose of the study was to support the interpretation of the ecotonal and successional studies.

Finally, the significance of the results to an understanding of the evolutionary development of these ecosystems, in relation to the palaeoecology of the Australian upland region, is discussed in the light of present-day distributions. Some of the ecological processes critical to the conservation of evolutionarily realistic diversity, and the past, present and future policies of management and conservation of the subalpine landscape are reviewed. A large and important part of the
The landscape of upland south-east Australia is one of the nature surfaces on which youthful features and processes have been superimposed. The formation of the present landscape has been a synthesis of the altitudinal, physiographic, climatic and biotic changes following the consequent uplift and related ecogeons (Costin, 1956; 61) and Sharp, 1954; Kable, 1954). In the northern part of the uplands Costin (1956), differentiated the region into four broad but ecologically well-defined environments.

Subalpine: The land between 6000 and 9000 altitude. In the main a rolling landscape with much of the Tertiary surface intact.

Alpine: The land between 900 and 1500 altitude. A landscape of deeply entrenched drainage systems, and steep slopes in which only a few remnants of the Tertiary landscape exist.

Subalpine: Although glacial drainage and physiography result in the depression of a subalpine environment to an ice age Tertiary altitude, the subalpine zone mainly consists of Tertiary plateau and slopes much dissected by post-glacial fluvial erosion, with large areas showing periglacial effects, between 1500 and 2000 altitude.

Alpine: Restricted to the land above tree line. the landscape is a result of Pleistocene glacial processes and some stream erosion.

For general description, the montane, subalpine and alpine
CHAPTER 2
THE AUSTRALIAN SUBALPINE ENVIRONMENT

2.1 INTRODUCTION

The landscape of upland southeast Australia is one of the mature surfaces on which youthful features and processes have been superimposed. The formation of the present landscape has been a synthesis of the altitudinal, physiographic, climatic and biotic changes following the Kosciusko Uplift and related orogenies (Costin, 1954; Gill and Sharp, 1956; Keble, 1954). In the northern part of the uplands Costin (1954), differentiated the region into four broad but ecologically well-defined environments:

- **Tableland** The land between 600m and 900m altitude, in the main a rolling landscape with much of the Tertiary surface intact.
- **Montane** The land between 900 and 1500m altitude; a landscape of deeply entrenched drainage systems, and steep slopes in which only a few remnants of the Tertiary landscape exist.
- **Subalpine** Although cold-air drainage and physiography result in the depression of a subalpine environment to as low as 1200m altitude, the subalpine zone mainly consists of Tertiary plateaux and slopes much dissected by post-Kosciusko Uplift erosion, with large areas showing periglacial effects, between 1500m and 2000m altitude.
- **Alpine** Restricted to the land above tree-line; the landscape is a result of Pleistocene glacial processes and some stream erosion.

For general description, the montane, subalpine and alpine
environments of Costin may be adhered to throughout S.E. Australia, with lowered altitudinal limits at southern latitudes. The ecosystems examined in detail in the present study, *Eucalyptus delegatensis* and *E. pauciflora* open forest and woodland, correlate with the upper part of Costin's montane zone and the lower part of his subalpine zone respectively. The distribution of vegetation within these types forms a distinct zone (Figure 4), and for simplicity and consistency throughout this thesis this zone is referred to as the subalpine. It may be defined as the zone between 1450m and 1850m in the Snowy Mountains declining, with increasing latitude, to 650m to 1050m in Tasmania.

The subalpine regions of Tasmania contain a complex eucalypt vegetation, as well as coniferous forest and cold temperature rainforest, pertinent to understanding the evolutionary ecology of subalpine eucalypt ecosystems throughout the Australian region. However they differ in several respects from the subalpine regions of the mainland. Most of the Tasmanian subalpine zone consists of a central plateau of resistant dolerite, bounded by precipitous 'tiers', the climate is more oceanic than equivalent areas of the mainland, and the soils stonier in drier sites and peaty, with gleyed and well podzolised elements in wetter situations. The flora is richer, notably the eucalypt community dominants, and contains a number of relict monogeneric conifers (Jackson 1965). In many cases the subalpine and alpine flora of Tasmania bears closer relationships to New Zealand, southern South America and the subantarctic islands than to the Australian mainland.

Because the sites described in this study have been selected from throughout the Australian subalpine zone, it is necessary to describe, in some detail, the variation in subalpine environments, particularly the distribution and geochemistry of parent materials and the patterns of vegetation and soil distribution.
The main features of the subalpine and adjoining zones are summarised in Figure 3.

2.2 FEATURES OF THE SUBALPINE ENVIRONMENT

2.2.1 LANDFORMS

The regional topography has a fundamental influence on the regional and local climatic, soil and vegetation patterns particularly the discontinuous distributions of the species and ecotypes of *Eucalyptus* which invariably dominate the biotic environment.

Although plateaux with undulating to rolling surfaces are a notable feature of the subalpine environment, slopes of from 25% to 50% are common, as are differences in altitude from 100 to 1000m between valley bottom and adjacent interfluve (Rowe, 1967).

In Tasmania the subalpine zone containing eucalypt vegetation is restricted to the central plateau with a few outliers such as Mts. Field, Barrow and Ben Lomond and the Hartz Mountains. The subalpine zone in the west is virtually all rainforest. In the southern part on the mainland, the subalpine zone is restricted to isolated plateau remnants of generally conformable height. In southeast Victoria the plateau remnant, the Baw Baw surface, has restricted extent. It includes the mildly to deeply dissected high plateaux of the Acheron and Baw Baw Ranges and the relatively flat Macedon Range. Outlying remnants occur toward the major ranges in the northeast, at Mts. Useful, Selma, Matlock and Terrible. The surface gradually rises to the east and north from about 1000m at Mt. Macedon, to 1250m at Mt. Donna Buang, 1500m at Mt. Torbreck and 1550m at Mt. Baw Baw. The main subalpine areas in N.E. Victoria are plateau structures, the Bogong High Plains, Dargo High
Plains, and their adjoining upper slopes, the Bennison-Mt. Wellington-Mt. Arbuckle area, Mt. Skene, the Mt. Loch-Mt. Feathertop-Mt. Hotham area, the arc of mountains from Mt. Cobbler near the N.S.W. border, to The Bluff and individual subalpine areas within the main ranges on Mts. Bogong, Wills, Stirling, Gibbo, Pinnabar and the Cobberas. A well separated subalpine area in N.E. Victoria is the Mt. Buffalo plateau.

The Snowy Mountains in N.S.W. lie on the margin of a moderately dissected plateau, which rises from a general altitude of 1350m in the north to over 2100m in the vicinity of the peaks of Kosciusko, Abbott, Townsend and Jagungal. Relief is low to moderate except at the margins, for example the steep fall of the upper Geehi, and where drainage systems such as the Tumut penetrate the high plateau country. The characteristic landforms are rounded ridges and broad shallow valleys. The plateau falls gradually eastward to about 900m on the Monaro tableland, with a few higher subalpine remnants, Mts. Delegate and Tingiringi and the Tinderry Mountains, and sharply to the west and north in the form of steep-sided gorges separated by narrow ridges of which the most prominent are the Bogong and Fiery Ranges and the Bimberi-Brindabella Range forming the western border of the A.C.T.

The geographic form of the uplands of S.E. Australia are indicated in Figure 5.

2.2.2 CLIMATE

Introduction

The climate of the subalpine areas of the Australian mainland, and the central plateau and N.E. mountains of Tasmania, is cold and dry in relation to other subalpine areas in the southern temperate latitudes. The patterns of soil and vegetation strongly reflect the very close
relationships of climate to the physiography of the region (Costin, 1954; Rowe, 1967) and the local topography. Like most of the Australian continent, there are considerable fluctuations in mean and extreme annual temperature and annual precipitation. It is probably these fluctuations, particularly during the short and sharply defined period of growth, that more than any other singular factor, exert the greatest control on the distribution of the subalpine vegetation. According to the classification of Thornthwaite (1931) the climate is of the sub-humid meothermal type. In looser terms, the climate has been described as "counterpart to that of dry Mexican regions, with sections of France and the British Isles and specks of Norway" (de Beuzeville, 1943).

2.2.2.2 Weather Patterns

The pattern of weather is approximately continental, even on the central plateau of Tasmania, modified by oceanic elements in the highlands of southern Victoria and most of Tasmania. In these areas the long periods of dry weather broken by summer thunderstorm activity, are not so marked.

The plateaux mountains form natural obstacles to the cool westerly wind system which brings a succession of depressions and frontal disturbances to the region in winter and spring. Much of the moisture is deposited on the plateaux, and adjoining catchments and some is lost to evaporation on the drier, warmer coastal region to the east. In early summer, the anticyclonic belt moves south from the subtropics and the weather becomes more settled with an easterly flow of air over the southern subalpine areas, the Baw Baw Plateau and Tasmania. The anticyclonic path moves further south to include these areas during mid and late summer. The movement of air masses is controlled by the rapidity with which the anticyclones move; the weather conditions conducive to
wildfires, an important element in the vegetation/soil pattern, occurring when an anticyclone becomes stationary over S.E. Australia and hot dry air comes down from the semi-arid interior. Convective diurnal patterns occur regularly during the summer.

2.2.2.3 Temperature

Aspect and topography influence temperature over small areas. Northern aspects are warmer than southern. These effects are important in explaining the distribution of eucalypts, particularly the site sensitive species such as *E. delegatensis*, which are absent from sites subject to relatively wide temperature extremes.

Temperature inversions can result from the drainage of cold air from slopes into hollows, particularly during the early evening. The low temperatures in such frost hollows or cold-air-drainage valleys, common in the northern part of the Snowy Mountains, can be severe enough to prevent the establishment of trees and shrubs (Costin, 1954, 1957). The summer months, December to February, are the warmest and driest for all areas. The mean maximum temperature in January, the hottest month, is about 24-30°C. Extreme maximum temperatures may be over 40°C. In winter the mean maximum temperatures are about 4-8°C. The minimum summer temperatures in the subalpine areas vary from about 12°C in the Snowy Mountains to about 5°C in the southern highlands of Victoria and Tasmania, and the winter minimum from -2°C to about -5° in southern latitudes. Extreme winter minima of -18°C have been recorded in grassland, at the margin of open eucalypt forest, in cold-air-drainage hollows.

2.2.2.4 Precipitation

The distribution of the plateaux mountains regulates the local precipitation, to the extent that there are numerous rainshadow subalpine areas in the east of the region. This is reflected in the soils and
vegetation, particularly the density and species of tree cover. In areas where soil moisture may frequently become limiting the subalpine vegetation is usually open forest or woodland of either *E. pauciflora*, *E. dalrympleana* or *E. rubida* over wide areas.

Above 1450m annual precipitation is usually above 1250 mm and less than 1750 mm although from the few long-term rainfall stations and the considerable fluctuations in the annual amount it is difficult to generalise. Carr and Turner (1959) for example, quote an average annual precipitation for the alpine zone Bogong High Plains in N.E. Victoria of 2500 mm and a variance of 700 mm. Areas with highest elevation and those in the southern, more maritime, region have the highest precipitations. Throughout the subalpine zone, a considerable amount of the winter precipitation is snow. Fog drip may produce increases in precipitation under trees, particularly where low cloud is common, but there have been few measurements of this. Costin and Wimbush (1961) have measured interception by *E. pauciflora* above 1200m in the Snowy Mountains and suggest that 25-120 mm may be added to annual precipitation by this means. In all seasons the highest rainfalls occur along the main divide, although the western and southern Tasmanian mountains and the Baw Baw Plateau also have high rainfalls, receiving in excess of 300 mm in summer. Heavy falls from thunderstorms may occur in late summer. Winter is usually the wettest season. High potential evapo-transpiration values of 400 mm reported by Rowe (1967) from the Bogong High Plains and the Mt. Hotham area in Victoria.
FIGURE 3  Climate, Soils and Vegetation in the Monaro (after Costin 1959:435).
### 2.2.3 SOIL PARENT MATERIALS

**Geological formations**

The dissected plateaux surfaces are situated chiefly in resistant Upper Devonian and Silurian volcanics and granites. The stratigraphic pattern is in general, one of folded Ordovician sediments, deformed by the Benambran Orogeny (Packham 1970), beneath Silurian volcanics (mainly thick sequences of acid volcanics) both of which were displaced by extensive granite batholiths during the late Silurian and early Devonian.

As a result of the instability and batholith emplacement, the present plateaux areas were uplifted during the Devonian, dissected after vertical movements during the Mesozoic and again uplifted during the Tertiary, when the present surfaces were formed and local basalts extruded.

In the central plateau of Tasmania, comprising much of the subalpine zone relevant to this study, the older Palaeozoic rocks are covered by Permian and Triassic sediments into which dolerite has been intruded to form sheets which tend to be horizontal. The resistant dolerite dominates the subalpine and montane landscape, capping plateau-like residuals and forming massive scarps, resulting from Mesozoic erosion.

In mountain areas where dissection and degradation processes are still very active soils are invariably young, often lithic and under strong micro-topographic control (Costin and Polach, 1971). It is to be expected therefore that soil variation will reflect the dynamics of initial physical and chemical weathering of the various parent materials. Throughout the subalpine of the mainland, soil parent materials derived from acid igneous and sedimentary rocks, and their metamorphosed
derivatives predominate. Granites, adamellites, granodiorites and quartz porphyrys forming the massive batholiths occur over considerable areas. Smaller areas of dacites and rhyolites, often in the form of tuffs, are associated with these batholithic materials as are folded sediments, mainly shales and fine sandstones, occasionally altered to schists and quartzites in metamorphic zones. Basic igneous parent materials are not extensive in area, occurring locally associated with Tertiary plateau surfaces or as isolated residuals on ridges. The rocks are Tertiary, either flow basalt or tuffs. There are small areas of Palaeozoic limestones throughout the subalpine zone.

Few of the drainage systems in the subalpine zone are of sufficient size to contain large areas of alluvial parent materials. The most extensive areas of alluvial parent materials occur in the broad subalpine valleys of the northern plateaux. The margin of alluvials with basement materials is often associated with major vegetation and soil discontinuities.

**Palaeoclimate and the origin of surficial soil parent materials.**

Whilst there is evidence of palaeoclimatic fluctuations in the mountains of S.E. Australia, pointing to previously colder climates (Carr and Costin, 1955; Talent, 1965; Costin et al., 1967; Caine, 1967) the time of formation of features and their specific climatic connotations are insufficiently known for accurate deductions (Galloway, 1971). Similarly although there are cases of geographic disjunctions in the distribution of some of the more site-sensitive upland eucalypts (Costin, 1954, 1971) this evidence alone cannot be applied uncritically, in the absence of palynological evidence for example, to measure palaeoclimatic variation. Nevertheless some important periglacial evidence does suggest that a long, cold unstable period appears to have lasted from
32,000 to 10,000 BP in S.E. Australia. This period correlates with the last Wurm/Wisconsin glaciation (Galloway, 1965; Davies 1967) well documented for the temperate latitudes in both hemispheres. The area in the Australian region that was actually glaciated is small (some 50 km\(^2\) in the Snowy Mountains, Galloway, (1963), but a much larger area down to the lower limit of the present montane zone would have been subject to periglacial conditions (Costin, 1973).

Periglacial evidence of severe former frost action such as large scale solifluction rubble mantles, patterned ground and block-streams has been found throughout the alpine and subalpine zones (Caine and Jennings, 1968; Costin et al., 1967). Recent work by Costin (1973) on the extensive slope deposits of 590m on the lower slopes of Black Mountain, Canberra, suggests that they indicate earlier periglacial conditions. Wood fragments dated at 27,930\(^\pm\)2,690 years BP, suggests an age not significantly different from the mean age of slope deposits in the Snowy Mountains, 31,000\(^\pm\)1,700 years BP (Costin and Polach, 1971). There is also agreement with the maximum age of the oldest slope deposits found in the Lake George basin in the southern highlands of N.S.W. (Coventry, 1973) and the oldest terrace in the Shoalhaven Valley (Walker, 1962).

Costin and Polach (1971) suggested that on the basis of present-day temperatures in the Snowy Mountains, the minimum lowering in mean annual temperature required to produce the periglacial deposits in the region down to 1000m would be approximately 8°-10°C. Such low temperatures would have ensured an absence of tree-growth from the vast majority of the present alpine and subalpine zones. The slope deposits are major landscape features, not confined to depressions and drainage lines (Costin and Polach, 1971) although tending to be absent from interfluves, which in the main have deflated ground surfaces. They have formed on a wide range of parent materials, on slopes of less than 5° to nearly 25°, and consist
of fines with gravel and angular stones showing preferred downslope orientation up to depths of 6 meters. Soil development, mainly of transitional alpine humus soils and brown podzolics (Costin, 1954) is in the surface meter.

On the basis of woody material in the slope deposits in the Snowy Mountains from a number of sites at 1200-1400 m, and the 35,000 years old *Nothofagus* aff. *cunninghamii* stump beneath a block stream in the Toolong Range (Jennings and Caine, 1968), Costin (1971) has concluded that prior to the onset of general instability, conditions whilst not greatly different from those of today, were somewhat cooler in summer. This conclusion was based on the observation that the present distribution of the Australian species of *Nothofagus* is associated with cool summers and frequent afternoon cloud and fog, as, for example on Lake Mountain and the Baw Baw Plateau in Southern Victoria, Tasmania, and on the Barrington Tops in Northern N.S.W.

Within the Holocene there is some evidence of climatic oscillations (from sphagnum and snowpatch peats, stone lines and solifluxion terraces) for a slightly colder period between 3000 and 1500 years ago, following generally mild conditions. In the Snowy Mountains and the Brindabella Range, A.C.T., these conditions could have led to considerable soil and vegetation instability in the subalpine zone, particularly at the limits of the more site-sensitive eucalypt species, for example *E. delegatensis* and *E. fastigata*, and at the limits of temperate rainforest.

There is evidence of very recent ground surface deflation in the form of a concentration of small stones at the surface of virtually all the soils, on a variety of rock types, examined in this study. Costin (pers. comm.) has attributed much of the deflation of the grassland soils of the subalpine valleys and tablelands to post-settlement land use, and
it is not unlikely that the deflation of the subalpine forest soils has a similar explanation. Rowe (1967) considered man-induced erosion not to be part of a normal cycle of landscape development. The pattern and history of the soils of the tablelands below the subalpine zone have received much attention in the development of a theory of phasic or cyclic landscape development, viz. the K-cycles of Butler (1958, 1959) and van Dijk (1959). Rowe (1967) considered that all the subalpine soils have developed in groundsurfaces produced during a single recent K-cycle.

**Geochemical variation**

Because of the youth of the soils, the concentration of essential elements in the parent materials has a considerable effect on nutrient concentrations. Although no analyses are available for sedimentary rocks, the concentrations of the essential elements in the igneous and metamorphic rocks vary considerably. As described in Chapters 4 and 5, this variation must be considered when discussing the relationships of the vegetation to nutrient supply. A list of chemical analyses from the major rock types encountered in this study are tabled in Appendix IV.

### 2.2.4 SOILS

The importance of the early chemical and physical weathering of the range of parent materials has already been referred to in understanding the soil pattern in mountainous forested areas. In describing such soils in the Australian region, it is also important to ascertain the length of time during which a ground surface has been subject to soil-forming processes, (Rowe, 1967) for there is much in the pedogenesis of the youthful subalpine and alpine soils that distinguishes them from the soils of lower altitudes, where the one ground surface may have been subject to several cycles of aridity, laterisation, solonization etc..
In the following general descriptions of subalpine soils I am indebted to the extensive information provided by R. K. Rowe in "A Study of the Land in the Victorian Catchment of Lake Hume" (1967) and A. B. Costin in "Ecosystems of the Monaro" (1954).

Any description of entire soil profiles in this thesis will be restricted to this introductory chapter. The present study was concerned with the dynamics of the forest floor and the soil surface (0-5 cm depth) only; a soil profile description of each site was beyond the scope of this study.

**Classification and distribution of the soils**

The soils of the subalpine zone form an altitudinal continuum from the cryptopodzols, with a wider occurrence at the warmer, relatively dry northern end of the zone, through acid brown earths and transitional alpine humus soils to alpine humus soils at the cool higher altitudes and in the more southern latitudes (Figure 3) (Costin, 1961). Lithosols may occur at all altitudes on steep and exposed slopes, and fen and bog peats may occur at higher altitudes associated with alpine humus soils and transitional alpine humus soils. The complex pattern of alpine soils (Costin, 1954, 1961) is not described. The soils associated with subalpine forests and woodland are summarised in Table 2. The table is constructed from the detailed information provided in Costin (1954) and Rowe (1967), for the Snowy Mountains and N.E. Victoria respectively, with some reference to Tasmania (Nicolls and Dimmock, 1965), and does not closely correspond to the broader classification of The Atlas of Australian Soils (C.S.I.R.O., 1966).

Although there are podzols and gley podzols associated with the mixed woodlands of *E. pauciflora* and *E. stellulata*, and most of the eucalypts in the subalpine zone of Tasmania, the great majority of the
soils associated with the upper limits of *E. delegatensis* and the lower
limits of *E. pauciflora* are soils in which the profile is acid to
strongly acid in the surface and shows no eluviation of sesquioxides.
In the southern areas of higher rainfall, or on the slopes of sheltered
aspect favoured by *E. delegatensis*, throughout its range, the greater
availability of soil moisture induces vigorous growth of understorey and
ground plants, such that multilayered communities predominate. Mature
soils in these situations, usually acid brown earths, are more deeply
weathered, have a greater accumulation of organic matter in the surface,
and show little evidence of clay or iron eluviation. Rowe (1967) has
suggested that despite the large quantities of water which pass through
these soils podzolisation is limited by the vigour of the vegetation in
recycling cations, particularly calcium and iron and aluminium from the
subsoil to the surface. In the mature alpine humus soils under *E.
pauciflora* woodland towards the upper limit of the subalpine zone, the
lowered temperatures become the dominant climatic factor in soil formation.
Organic matter decay and mineralisation are slower (cf. Wood, 1971) and
organic matter accumulation at the soil surface is therefore greater.

The transitional alpine humus soils occur between these two groups,
and have some features of both, namely a deep organic horizon similar to
the alpine humus soil and a deep clayey horizon similar to the acid brown
earth.

At lower elevations, where temperatures are milder and rainfall
lower, the acid brown earths grade into cryptopodzols. These soils
resemble acid brown earths in colour and texture. However they have a
weakly bleached A2 horizon which is usually masked by organic colouring.
There is less organic matter accumulation than in the acid brown earths,
and structure is not as well developed.
<table>
<thead>
<tr>
<th>Soil Group</th>
<th>Profile features</th>
<th>Vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alpine humus soil</td>
<td>very friable organic profile grading rapidly to weathering parent material.</td>
<td>higher altitude <em>E. coccifera</em>, <em>E. archeri</em>, <em>E. gunnii</em>, <em>E. pauciflora</em> woodland and rarely upperlimit of older <em>E. delegatensis</em> forests.</td>
</tr>
<tr>
<td>Transitional alpine humus</td>
<td>well weathered profile up to 1.5m deep; abundant organic matter in the top 10 cm; mineral soil, reddish brown to black, very friable loam to clay loam.</td>
<td>wet sclerophyll forest (<em>E. delegatensis</em>, <em>E. dalrympleana</em>, <em>E. urginera</em>, <em>E. johnstonii</em>), and occasionally <em>E. pauciflora</em> forest. Best development under broadleaved shrub understories.</td>
</tr>
<tr>
<td>Acid brown earth</td>
<td>similar to above, but less organic matter within mineral soil which is more clayey and compacted.</td>
<td>similar to above, but restricted to dryer climates with microphyllous shrub and snow grass understories; grade to above at later stages of secondary ecosystem development.</td>
</tr>
<tr>
<td>Cryptopodzol</td>
<td>moderate deep to shallow brown to yellowish-brown loam to clay loam, often somewhat lithosolic. Little humus, weak podzolisation is usually masked by organic matter in the surface 10-20 cm.</td>
<td>dryer mixed wet sclerophyll forest; on steep exposed slopes; moisture availability lower than optimum for <em>E. delegatensis</em>; mixed forests of <em>E. dalrympleana</em>, <em>E. rubida</em>, and <em>E. pauciflora</em>. Some <em>E. pauciflora-E. stellulata</em> woodlands.</td>
</tr>
<tr>
<td>Soil Group</td>
<td>Profile features</td>
<td>Vegetation</td>
</tr>
<tr>
<td>-----------------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Krasnozems</td>
<td>deep permeable profile of strong crumb structure; high clay content but loamy due to flocculation of clay by high content of sesquioxides. Profile entirely eluvial, brown to brownish-red at surface to red with depth. Very localised.</td>
<td>wet sclerophyll forest (<em>E. delegatensis</em>): restricted to basic igneous rocks.</td>
</tr>
<tr>
<td>Meadow soils</td>
<td>profile is a function of a seasonal water table; greyish-brown loam at surface, apedal with depth; some gleying and iron-staining.</td>
<td>common in <em>E. pauciflora</em>-<em>E. stellulata</em> woodland, often adjacent to wet sclerophyll forest, at the margins of subalpine valleys.</td>
</tr>
<tr>
<td>Podzols</td>
<td>moderate differentiation into an upper A1 horizon, greyish black to ashy grey in colour, and a lower bleached A2 horizon. Development of a distinct A0 horizon under dense broadleaved shrub understoreys. A B horizon of accumulation of humus and sesquioxides, is often masked under grass/herb understoreys.</td>
<td>wet sclerophyll forest (<em>E. delegatensis</em>); best developed in wetter more southern latitudes where succession to grass/herb understoreys does not offset podzolisation, as it does in the above groups of soils; also <em>E. urarinera</em> and <em>E. coccifera</em> in Tasmania.</td>
</tr>
<tr>
<td>Gley podzols</td>
<td>profile is a function of a seasonal water table; a grey to black A1 horizon and a lighter coloured A2 overlain by a brownish-black A0; humus and sesquioxides accumulate in a heavy subsoil; gleying in lower subsoil.</td>
<td>very occasionally associated with <em>E. pauciflora</em>-<em>E. stellulata</em> woodland in wetter sites of subalpine valleys.</td>
</tr>
<tr>
<td>Soil Group</td>
<td>Profile features</td>
<td>Vegetation</td>
</tr>
<tr>
<td>------------------</td>
<td>----------------------------------------------------------------------------------</td>
<td>---------------------------------</td>
</tr>
<tr>
<td>Peats (humified)</td>
<td>organically dominated profile, associated with bog peats and alpine humus soils.</td>
<td>higher altitude <em>E. pauciflora</em> woodlands.</td>
</tr>
<tr>
<td>Lithosols</td>
<td>profiles consist almost entirely of rock fragments; lithosolic phases of the majority of soil groups occur if sufficient fines for pedogensis; usually shallow profiles, restricted to steep exposed slopes.</td>
<td>all vegetation types.</td>
</tr>
</tbody>
</table>
The broad altitudinal pattern of the major soil groups (Figure 3) is generally paralleled in topographic sequences throughout the same part of the subalpine zone. A common sequence is either alpine humus soils or strongly lithic transitional alpine humus soils, with shallow deflated profiles, under *E. pauciflora* open-forest or woodland on the cold exposed ridge, and transitional alpine humus or acid brown earth beneath (*E. delegatensis* forest, with some *E. dalrympleana* on the slope. These soils grade to cryptopodzols at lower altitudes under the same forest type but with a greater proportion of *E. dalrympleana*. As can be seen from Figure 4, *E. delegatensis* is often absent from the altitudinal and topographic sequences. In these situations, there is minimal development of both transitional alpine humus soils and acid brown earths, and instead, more widespread cryptopodzols and lithosolic soils, beneath mixed open forests of *E. pauciflora* and various other species, mainly *E. dalrympleana*, *E. rubida*, *E. chapmaniana*.

Chemical and Physical Features of the Soils

In this section, properties of the various groups will be discussed in general terms, to illustrate trends relevant to an expansion of the results reported later in this thesis, that are concerned with the distributions of nutrients in the forest floor and the soil surface. The following is, in the main, summarised from Costin (1954) and Rowe (1967).

In virtually all soils the proportion of clay in the surface soil is less than 25% of the soil fines, and there is less clay in the surface than elsewhere in the solum. Bulk density as an indicator of total pore space is difficult to assess in the majority of soils because of the large amount and variability of stones. The A-horizons of the alpine humus soils, transitional alpine humus soils, the acid brown earths and the few subalpine krasnozems have bulk densities of less than 1.0. These
are highly structured, organic soils. However most of the other soils, especially lithosolic phases and those subject to severe disturbance, have bulk densities of between 1.0 and 1.5.

The alpine humus soil has by far the most available water of the subalpine soils, because of high field capacity and low wilting point. Mature transitional alpine humus soils, acid brown earths and the cryptopodzols also have relatively high available water capacities, compared to the soils of lower altitudes.

All of the soils are acid throughout the profile, the most strongly acid being the alpine humus soils and the transitional alpine humus soils which have pH values of 4.5 or less in the surface 15 cm rising to about pH 5.5 below 30 cm. The acid brown earths and cryptopodzols have surface values of pH 5.0-5.5 with minimal trend down the profile.

The nitrogen and organic carbon levels, the C/N ratio, and the ratios of nitrogen and carbon with other nutrients show very considerable variation according to the diversity of land management histories, principally involving fire, and the history of wildfire. As it is the relative rates in the accumulation and mineralisation that control the ultimate amount of organic matter involved in pedogenesis, the major present-day variables controlling soil formation are climate and the processes of secondary succession defining the nature of the forest floor and decomposer organisms. Rowe (1967) has demonstrated the strong positive relationship between organic matter in the surface soil and elevation from dry sclerophyll forest to subalpine woodland. Organic carbon % increases from less than 2% to 8% in the upper mineral soils along the altitudinal sequence.

In all soils organic matter is concentrated in the surface 5-15 cm, and except in the alpine humus soils and transitional alpine humus soils,
decreases rapidly with depth. The soils under forest vegetation, particularly where this is a low ground cover of herbs and grasses, have high C/N ratios often greater than 50. Pure eucalypt litter has very high C/N ratios (Leeper, 1952), and as a result the soils under forest have C/N ratios of about 20 or higher (Gibbons and Downes, 1964; Rowe, 1967).

Most of the soils have less than 0.10% (or 1000 ppm) total phosphorus in the surface except for some transitional alpine humus soils under *E. delegatensis* forest and the krasnozem-like soils on basaltic parent materials which may attain higher levels. Except for those soils with a severely disturbed profile, most of the subalpine soils have higher values of total phosphorus than the amphipodzols, red podzolic soils and regosols at lower altitudes under wet sclerophyll forest, dry sclerophyll forest and woodland, savanna woodland and grassland. Phosphorus is an element that must be almost completely provided by the weathering of the parent material, and undoubtedly the relatively high phosphorus levels of the subalpine soils is a function of their comparative youth. Certainly, the extremely low phosphorus levels reported by Beadle (1962) in a discussion of the eucalypt/sub-tropical rainforest margin, and Attiwill (1962) in a study of nutrient cycling in *Eucalyptus obliqua*, have few parallels in all but the most disturbed subalpine surface soils.

'Available' phosphorus forms about 20-30% of the total phosphorus in nearly all the soils and shows similar quantitative trends, although a greater response to pertubations of the forest floor. Despite the differences with the soils of the adjacent lowlands, phosphorus levels are generally low if the comparison is made with soils of wooded regions elsewhere in the temperate zone.

With few exceptions, the cation exchange capacity (C.E.C.) is high at the surface and in the lower forest floor, indicating a close relation-
ship with the organic matter in these layers. The C.E.C. of the subalpine soils is considerably higher than the soils of the adjacent lowlands (Rowe, 1967).

Exchangeable Ca and Mg are concentrated at the soil surface and in the forest floor, but the subalpine soils, in general, are lower in both of these cations than the dryer soils at lower altitudes. There are higher levels of exchangeable K in comparison with the lower altitude soils, possibly because K tends to cycle predominantly in rainfall and through fall, whereas Ca and Mg cycle more in plant litter (Attiwill, 1971). Sodium is only a minor ion in the exchange complex, occupying less than 1% of the C.E.C..

Compared to the lower altitude soils, the proportion of the cation exchange complex (% saturation) occupied by metal ions is low in the alpine humus soils, transitional alpine humus soils, acid brown earths and crytopodzols, where it is as low as 1% in some subsoils.

2.2.5 VEGETATION

Introduction

Apart from some very small areas in northern N.S.W., southern Victoria and much of southern and western Tasmania the subalpine forest and woodland vegetation of Australia is almost exclusively dominated by Eucalyptus (Table 3). The eucalypt ecosystems are floristically poor. Most understorey species are common to the entire subalpine zone, and very few have restricted local distributions. Fire, largely through an evolutionary interaction with summer rainfall (Jackson, 1968), must be accepted as one of the major influences controlling the broad aspects of ecological distribution in the subalpine zone, as it is throughout the wooded regions of Australia. The sclerophyll species show marked adaption
to its influence, and in the geographic absence of non-sclerophyll dominants, for example Nothofagus, the entire process of successional development of a forest or woodland ecosystem is dominated by the species which originally occupies the site following fire. The evolutionary ecology and the results of the present study suggest a long-term process of successional development in the subalpine eucalypt ecosystems with low fire frequency. In Tasmania, where 'there would appear to be no aspect, soil-type, or edaphic situation .... which cannot be occupied by cold temperate rainforest' (Jackson, 1968), studies of forest succession and the likely evolutionary mechanisms show a strong feed-back reaction between fire-frequency and vegetation type, with a second feed-back between fire-frequency and vegetation type determined by the interaction between soil fertility and vegetation (Jackson, 1968). A considerable portion of the entire subalpine zone is occupied by species of Eucalyptus common to Tasmania and the mainland, and the same species of Nothofagus is known to have been present as far north as the northern Snowy Mountains as recently as the late Pleistocene (Jennings and Caine, 1968). Another species of Nothofagus occurs in association with similar eucalypt species in a small area of subalpine vegetation in northern N.S.W. (Table 3). The successional dynamics of subalpine eucalypt forest, would appear, on this basis, to be largely a function of the evolutionary pressures of competition with mesic vegetation which is now relic in the subalpine zone of the mainland. In Tasmania, Jackson (1965) has referred to all 'wet sclerophyll forest' as disclimax, in relation to cold temperate rainforest.

A Classification of Subalpine Vegetation.

The IBP classification of Australian vegetation that is the basis of the recently published survey of vegetation in conservation reserves (Specht et al., 1974) has been followed in this description and all
<table>
<thead>
<tr>
<th>Height</th>
<th>Cover</th>
<th>Physiognomy</th>
<th>Composition of dominants</th>
<th>Distribution</th>
</tr>
</thead>
</table>
| > 30m | 30-70%| Tall open forest | 1. *E. delegatensis* + *E. dairympleana*  
(E. dairympleana may be replaced by spp listed under Open-forest, locally)  
2. *E. delegatensis*; *E. delegatensis*- *E. dairympleana* | Tasmania (except S.W.) |
| > 30m | 10-30%| Tall woodland | 1. *E. delegatensis*  
2. *E. delegatensis* - *E. dairympleana* | E. Highlands (Vic.), Snowy Mountains (N.S.W.), A.C.T. |
| 10-30m| 70-100%| Closed forest | 1. *Arthrotaxis selaginoides*- *A. cuneata*  
2. *Phyllocladus aspleniifolius* + *Nothofagus cunninghamii*  
3. *Nothofagus cunninghamii*- *Eucryphia milligani*  
4. *Nothofagus cunninghamii* + *Leptospermum lanigerum*  
5. *Leptospermum lanigerum*  
6. *Nothofagus moorei*- *Orites excoelia*- *Eucryphia moorei* | Tasmania (1) except S.W.,  
E. Highlands (Vic.), Snowy Mountains (N.S.W.) (in all cases, local)  
Tas. (W., C. plateau, S.W., S.E.)  
Tas. (N.W., W., Central plateau, S.W., N.E.)  
Tas. (W., S.W.)  
Baw Baw Plateau (Vic.)  
Tas. (N.E., E., C., S.E.);  
Vic., N.S.W. (Loc),  
Barrington Tops (N. N.S.W.) |
<table>
<thead>
<tr>
<th>Height</th>
<th>Cover</th>
<th>Physiognomy</th>
<th>Composition of dominants</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-30m</td>
<td>30-70%</td>
<td>Open forest</td>
<td>1. <strong>E. delegatensis</strong></td>
<td>both types: Tas., except S.W., E. Highlands (Vic.), Snowy Mountains (N.S.W.), A.C.T.</td>
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<td></td>
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<td></td>
<td>2. <strong>E. delegatensis</strong>-<em>E. dalympleana</em>*</td>
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<td></td>
<td></td>
<td></td>
<td>5. <strong>E. gunnii</strong></td>
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<td>6. <strong>E. archeri</strong></td>
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<td>7. <strong>E. urginera</strong></td>
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<td>8. <strong>E. subcrenulata</strong></td>
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<td>9. <strong>E. rodwayi</strong></td>
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<td>10. <strong>E. pauciflora</strong></td>
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<td></td>
<td></td>
<td>11. <strong>E. pauciflora</strong>-<em>E. dalympleana</em>*</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>Cover</td>
<td>Physiognomy</td>
<td>Composition of dominants</td>
<td>Distribution</td>
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<tr>
<td>10-30m</td>
<td>10-30%</td>
<td>Woodland</td>
<td>1. <em>E. occipiter</em> ± <em>E. pauciflora</em></td>
<td>Tas. (Central plateau)</td>
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<td></td>
<td></td>
<td></td>
<td>2. <em>E. gunnii</em></td>
<td>Tas. (Central plateau)</td>
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<td>3. <em>E. subcrenulata</em></td>
<td>Tas. (Central plateau)</td>
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<td>4. <em>E. aggregata</em></td>
<td>Tas. (Central plateau, E.)</td>
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<td></td>
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<td></td>
<td>5. <em>E. pauciflora</em></td>
<td>E. Highlands (Vic.);</td>
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<td>Snowy Mountains,</td>
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<td>Barrington Tops (N.S.W.):</td>
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<td>A.C.T.</td>
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<td></td>
<td>6. <em>E. pauciflora</em> - <em>E. dalrympleana</em></td>
<td>N.E. Highlands (Vic.);</td>
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<td></td>
<td></td>
<td></td>
<td>Snowy Mountains (N.S.W.):</td>
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<td>A.C.T.</td>
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<tr>
<td>5-10m</td>
<td>70-100%</td>
<td>Low closed forest</td>
<td>1. <em>Nothofagus cunninghamii</em></td>
<td>Tas. (S.W., W., C. plateau,</td>
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<td></td>
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<td></td>
<td></td>
<td>N.E. S.E.)</td>
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<td></td>
<td>2. <em>Eucryphiya milliganii</em> ±</td>
<td>Tas. (W., S.W., S.E.)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td><em>Nothofagus cunninghamii</em></td>
<td></td>
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<td></td>
<td>3. <em>Phyllocladus aspleniifolius-Anodopetalum biglandulosum</em></td>
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<td>4. <em>Nothofagus cunninghamii-Leptospermum lanigerum</em></td>
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<td></td>
<td>5. <em>Podocarpus lawrencei</em></td>
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<td>6. <em>Nothofagus moorei-Crataceae-Eucryphiya moorei</em></td>
<td>Baw Baw plateau (Vic.)</td>
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<td></td>
<td>Errinundra plateau (Vic.)</td>
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<td></td>
<td>Barrington Tops (N. N.S.W.)</td>
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<tr>
<td>Height</td>
<td>Cover</td>
<td>Physiognomy</td>
<td>Composition of dominants</td>
<td>Distribution</td>
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<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>5-10m</td>
<td>30-70%</td>
<td>Low open forest</td>
<td>1. <em>E. coccifera</em></td>
<td>Tas. (Central plateau)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>2. <em>E. subcrenulata</em></td>
<td>Tas. (W., Central plateau, S.W., S.E.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3. <em>E. gunnii</em></td>
<td>Tas. (Central plateau)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4. <em>E. rodesayi</em></td>
<td>Tas. (Central plateau, N.E.)</td>
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<td></td>
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<td>5. <em>E. urginera</em></td>
<td>Tas. (S.E.)</td>
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<td></td>
<td></td>
<td></td>
<td>6. <em>E. nitida</em></td>
<td>Tas. (N.W., W., S.W., S.E.)</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>7. <em>E. archeri</em></td>
<td>Tas. (Central plateau, N.E.)</td>
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<tr>
<td></td>
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<td>8. <em>E. pauciflora</em></td>
<td>Tas. (Central plateau, E.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>E. Highlands (Vic.); Snowy Mountains, Barrington Tops (N.S.W.); A.C.T.</td>
</tr>
<tr>
<td></td>
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<td>9. <em>E. pauciflora-E. dives</em></td>
<td>N.E. Highlands (Vic.); Snowy Mountains (N.S.W.; A.C.T.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(in all cases, local)</td>
</tr>
</tbody>
</table>

<p>| 5-10m  | 10-30%  | Low woodland | 1. <em>E. coccifera</em> | Tas. (Central plateau, S.W., S.E.)                                      |
|        |         |              | 2. <em>E. subcrenulata</em> | Tas. (W., Central plateau, S.W., S.E.)                                      |
|        |         |              | 3. <em>E. gunnii</em> | Tas. (Central plateau)                                                     |
|        |         |              | 4. <em>E. urginera</em> | Tas. (S.E.)                                                                |
|        |         |              | 5. <em>E. archeri</em> | Tas. (N.E.)                                                                |
|        |         |              | 6. <em>E. rodesayi</em> | Tas. (Central plateau, E., N.E.)                                           |</p>
<table>
<thead>
<tr>
<th>Height</th>
<th>Cover</th>
<th>Physiognomy</th>
<th>Composition of dominants</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>5-10m</td>
<td>&lt;10%</td>
<td>Low open woodland</td>
<td>1. <em>E. pauciflora</em> (subsp. <em>niphophila</em>)</td>
<td>E. Highlands (Vic.); Snowy Mountains (N.S.W.); A.C.T.</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td></td>
<td>2. <em>E. pauciflora</em></td>
<td>Tas. (N.W., W., S.W., S.E.)</td>
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<td></td>
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<td>3. <em>E. pauciflora</em> - <em>E. stellulata</em></td>
<td>Tas. (Central plateau, E.) E. Highlands (Vic.); Snowy Mountains, Barrington Tops (N.S.W.); A.C.T.</td>
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<tr>
<td>7</td>
<td></td>
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<td><em>E. nitida</em></td>
<td>N.E. Highlands (Vic.); Snowy Mountains, Barrington Tops (N.S.W.); A.C.T.</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>10. <em>E. pauciflora</em> (subsp. <em>niphophila</em>)</td>
<td>E. Highlands (Vic.); Snowy Mountains (N.S.W.); A.C.T.</td>
</tr>
</tbody>
</table>

examined in this study.
subsequent vegetation terms in this thesis. The classification system used in Table 3 has essentially been extracted from the comprehensive classification of the contributors to Specht et al., (loc. cit.). The system supports the earlier Australian ecological literature, and regional colloquialisms, in making the forest/woodland division (Specht, 1970) and is based on two primary parameters, projective foliage cover and height/life-form of the tallest stratum. Forest is subdivided into dense or closed forest* with a coverage of 70-100% and open forest with a coverage of 30-70%; the very broad term, woodland is subdivided into woodland with 10-30% cover, and open woodland with 0-10%. Further division can be made on height, e.g. tall open forest, † with trees greater than 30 m in height, open forest, ✦ with trees 10-30 m and low open forest, ✦ with trees 5-10 m (Specht, 1970). In the subalpine zone, there is a more meaningful correspondence with the successional changes in vegetation structure, and less restriction on one species occupying more than one classification unit. This is particularly so when only one or two vegetation types are examined over a range of ecological situations. For example, E. pauciflora can form open forest, woodland and open woodland, and low vegetation of the same densities, throughout the subalpine. In the previously accepted classifications this range would include wet sclerophyll forest, dry sclerophyll forest and subalpine woodland. Because in the latter, reference is made to environmental features, implications which are not necessarily accurate are made about the species distribution.

Distribution and genealogy of the upland eucalypts

As Pryor (1954) noted, the altitudinal range in climate from 600 m to over 2000 m in the Australian Capital Territory would in many parts of

* formerly rainforest.
† formerly wet sclerophyll forest.
✦ formerly dry sclerophyll forest.
the world, bring about major changes in the genera of the dominants, but
this area, like virtually all of upland Australia, is covered entirely
by about 20 species of *Eucalyptus*. The dominants of each community type
are either a single species or a vicarious pair of non-interbreeding
species, each from a separate subgenus (Table 4). Interbreeding species
are separated by environmental discontinuities or out-of-phase reproductive
periods. *E. pauciflora* is ecologically, and genetically, extremely
restricted in the subalpine of Tasmania compared to a widespread clinal
and ecotypic distribution on the mainland. The present distribution of
*E. delegatensis* on the mainland, suggests that it is a relic species in
the northern part of the subalpine zone. The disjunct nature of its
distribution has been attributed to the warm, moist conditions during
the Pleistocene, at least, enabling a greater competitive success in the
intervening country (Costin, 1954; 1971). The distribution of *E.
delegatensis* (Figure 5) is semi-continuous throughout the main divide of
the eastern highlands of Victoria and the Snowy Mountains, but markedly
disjunct populations occur on Mt. Macedon, the Nunniong Plateau, and Mt.
Delegate in Victoria and Mt. Tingiringi, the Bobeyan divide, Robert's Mt.,
Mt. Clear and possibly in hybrid form on the Tinderry Mts. in southern
N.S.W.. In the Cotter catchment (A.C.T.) at the northern limit of the
species there are numerous locally disjunct stands of *E. delegatensis*,
often of no more than a few trees (Figure 4). The disjunct populations
cited above are in association with both the upper limits of montane
species and *E. pauciflora* and/or *E. dalrympleana*. There are a few disjunct
stands associated with only montane species, notably on Talbingo Mt.,
N.S.W., with *E. radiata*, and the Errinundra Plateau, N.E. Victoria, with
*E. fastigata* and *E. nitens*.

In the subalpine and montane zones, the major feature of eucalypt
distribution, apart from the sheer number of species, is their strikingly
consistent and predictable distribution in relation to local environment discontinuities. The upland eucalypts differ markedly in their genetic response to environmental stresses of the kind likely to lead to speciation. This variation in response is possibly a function of the relative genetic and ecological 'space' available to interbreeding taxa. Some species display a number of ecotypes over a wide ecological range e.g. *E. pauciflora* (Pryor, 1956; Green, 1967); many are clinal, e.g. *E. delegatensis* (Grose, 1960); *E. regnans* (Ashton, 1956; Eldridge, 1966); *E. urginera* (Barber and Jackson, 1962; Thomas and Barber, 1974) and *E. pauciflora* (Green, 1967); most are extremely sensitive to changes in the micro-environment. A steep environmental gradient such as the margin of a cold-air-drainage valley (Costin, 1954; p. 646; Barber, 1955) will produce a series of sharply defined bands of vegetation dominated by different eucalypts.

The primary element in eucalypt distribution in the subalpine zone is topographic, largely because of the topographic control of micro-climatic extremes, Quaternary landscape processes, pedogenesis, and of course the frequency of fire. However, the physical form of individuals themselves and the physiognomy of the communities they produce, differ considerably, such that it is difficult to examine the differentials of the physical environment alone. At this stage in our knowledge of the determinants of the distribution of upland eucalypts, it is only speculative to assume the nature of inter-relationships.

If the distribution of *Eucalyptus delegatensis*, for example, is examined in relation to ecologically associated species with which it forms invariably sharp ecotones (Table 5) there is a clear declaration of the relative sensitivity of this single species. The nature of the physical environment essential to the distribution of *E. delegatensis* is obvious, but nutritional variation across what is certainly a highly
selective series of genetic barriers and competition interfaces, can only be inferred. Understanding of the role of nutrients in the origins of the various discontinuities is still little more than intuitive even with information on the concentration of nutrients in the soil, until this information is looked at in combination with biomass weights, production rates, rates of accession to the forest floor and degradation there of nutrients as well as dry matter, and the relative fluxes and redistribution of different nutrients through the ecosystem.

It is probable that virtually all the environmental factors (Table 5) will effect a discontinuity in the rate and quality of nutrient supply from the physical environment to the biomass. We can also expect fluxes in nutrient dynamics at the ecotones attributable to the differences in biomass of all communities dominated by species in Table 5.

In this sense nutritional thresholds, not absolute (cf. Beadle, 1962) but pertaining to a zone of high genetic selection and interspecific competition, may be pertinent to any consideration of the evolution of the present distribution of eucalypts in the region. There is support for such an argument in successional sequences, which include non-eucalypts in Tasmania (Howard, 1974; Jackson, 1968).

Part of this present study has examined the different topographic and altitudinal situations in which there is an ecotone between *Eucalyptus delegatensis* and other species. In a preliminary study,* the topographic, altitudinal, soil physical and soil nutrient concentration fluxes were examined in a range of ecotones throughout the altitudinal range of *E. delegatensis*. Subsequently the ecotonal study was restricted to comparing the nutrient weights and concentrations of the forest floor and surface.

*See Chapter 4.*
soil in various ecotones between *E. delegatensis* and *E. pauciflora*, over a range of successional stages. Although the two communities often adjoin in the landscape mosaic, they represent, as encompassed in this study, a large extent of the range of forest and woodland ecosystem structure in the upper montane-subalpine zone. The distribution of these two species and the ecotone between them is described in Chapter 4.

*The altitudinal distribution of upland vegetation*

The altitudinal relationship of major vegetation types in the Snowy Mountains, A.C.T., and the N.E. Highlands of Victoria are summarised in Table 4.

Compared to the subalpine zone of the mainland the montane forests vary considerably with latitude in the composition of the dominants. Each species usually is co-dominant with another from a different subgeneric group (Pryor, 1954) (Table 4) and the ecotone between the communities is usually sharp and clearly observable, particularly at topographical discontinuities. In the A.C.T. mountains the altitudinal distribution can be summarised as follows:

<table>
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<tr>
<td>drier, exposed slopes</td>
<td>moister, sheltered slopes</td>
</tr>
<tr>
<td>2000m</td>
<td></td>
</tr>
<tr>
<td>pauciflora</td>
<td>pauciflora</td>
</tr>
<tr>
<td>pauciflora-rubida</td>
<td>pauciflora-rubida</td>
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<tr>
<td>dives-rubida</td>
<td>dives-rubida</td>
</tr>
<tr>
<td>dives-dalrympleana</td>
<td>dives-dalrympleana</td>
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<tr>
<td>1500m</td>
<td></td>
</tr>
<tr>
<td>rossii-mannifera-dives-mannifera</td>
<td>rossii-mannifera-dives-mannifera</td>
</tr>
<tr>
<td>rossii-mannifera</td>
<td>rossii-mannifera</td>
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<tr>
<td>manifera</td>
<td>manifera</td>
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<tr>
<td>viminalis</td>
<td>viminalis</td>
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</tbody>
</table>
The altitude of the transition from tall open forest (dominated by *E. delegatensis*) to low open forest (*E. pauciflora*) ranges between 1350 m and 1500 m, throughout the mainland mountains, descending lower on the cold and more exposed slopes, and with latitude, for example the Baw Baw Plateau. There is no truly continuous 'tree-line' in the Australian mountains, except perhaps on steep continuous slopes, e.g. the N.W. slopes of Mt. Feathertop in the Victorian mountains and the N.W. slopes of Mts. Kosciusko, Abbott and Townsend in the Snowy Mountains, N.S.W.. In nearly all cases the alpine eucalypt cover (mainly *E. pauciflora* subsp. *niphophila* on the mainland, and *E. occidentalis* in Tasmania) becomes increasingly open until an altitudinal limit at about 2000 m, although various environmental factors may prohibit tree growth at lower altitudes, such as the woodland and forest margins to cold-air-drainage valleys.

Tall forest of *E. delegatensis* dominates the altitudinal belt between 1200 m and 1500 m in N.E. Victoria and throughout the Snowy Mountains and the A.C.T., and between about 1050 m and 1350 m in the southern mountains of Victoria, with other eucalypts replacing *E. delegatensis* in a manner very similar to the pattern on the A.C.T. (Table 4). Woodlands of *E. rubida* and *E. pauciflora* dominate cold, dry environments.

The usual pattern in the montaine forests in the eastern highlands of Victoria is *E. obliqua* and occasionally *E. cypellocarpa* and *E. nitens* on the moister slopes, with *E. viminalis* in valleys and *E. macrocarpha*, *E. radiata*, and *E. dives* on drier slopes, on the northern side of the highlands. A few species are localised e.g., *E. bicostata* (also in the Snowy Mountains), *E. chapmaniana* and *E. obliqua* dominates the montane zone on the eastern side of the highlands, also usually with *E. radiata*, *E. nitens* and *E. viminalis* on their respective sites. However in some of the wetter areas in this region e.g. Acheron Divide and Baw Baw Plateau
and much of Tasmania, *E. regnans* is predominant at altitudes below *E. delegatensis*, with the above species restricted to dryer sites. In the gullies, *Nothofagus cunninghamii* and *Atherosperma moschatum* in the understorey result in a multilayered forest.

There is a trend toward denser and more mesic understories with increasing latitude in the upland forests, particularly in the southern mountains of Victoria and throughout Tasmania where the more maritime climate results in wetter summers, and has enabled the region to avoid the palaeoclimatic aridity of the northern mountains, resulting in a far greater number of understorey shrub species.

2.2.6 A SUMMARY OF THE ENVIRONMENTAL FEATURES OF THE SUBALPINE ZONE

1. The landforms are mature dissected plateaux.

2. The subalpine climate is predominantly cold and dry (sub-humid mesothermal) and reflects the regional topography. There are considerable fluctuations in mean and extreme annual temperatures and annual precipitation.

3. The predominant soil parent materials are late Silurian and early Devonian granites which have displaced and altered Ordovician sediments and Silurian volcanics.

4. A long cold period between 32,000 and 100,000 years BP altered vegetation patterns, notably the distribution of cold-temperate rainforest (dominated by *Nothofagus*) and produced extensive slope deposits. These are major groundsurface features, but usually absent from interfluvies, which have deflated groundsurfaces.

5. There is evidence of groundsurface deflation since the onset of European settlement.
6. There is much in the pedogenesis of the youthful subalpine soils that distinguishes them from the soils at lower altitudes, where one groundsurface may have been subject to several cycles of aridity, laterisation, etc.

7. The subalpine soils form a continuum with altitude from crytopodzols, through acid brown earths, transitional alpine humus soils and alpine humus soils. There is often a parallel in topographical sequences.

8. The soils are low in clay and are acid, particularly in the upper horizons. Organic matter and available nutrients are concentrated at the soil surface, the degree of concentration varying with the frequency and intensity of disturbance.

9. Except for marginal zones of cool temperate rainforest, the subalpine vegetation is almost exclusively dominated by *Eucalyptus* forming forest or woodland communities. The dominants of each community type are either a single species or a vicarious pair of non-interbreeding species.

10. The eucalypt dominants show marked and consistent changes in composition in relation to local environmental discontinuities, mainly topography and microclimate. The structure of the communities and the time-scale of successional changes are a function of the frequency and intensity of wildfires. It is probable that the environmental discontinuities and the pattern of fires effect changes in the rate and quality of nutrient supply to the resultant ecosystems.
CHAPTER 3

FIELD, LABORATORY AND DATA-INTERPRETATION METHODS

3.1 INTRODUCTION

All methods of sample selection, collection and treatment and laboratory analysis of all samples are described in this Chapter, rather than in the sections preceding the descriptions of different groups of results.

From the outset, the entire study was defined as one of a predominantly field nature, with subsequent laboratory analysis of samples. It appeared that whilst an experimental study of the critical establishment characteristics of subalpine eucalypts was an important prerequisite to a knowledge of their distribution, a field-ecological knowledge of their site-nutritional characteristics and the process of succession was more important to the problems of conservation of diversity in the ecosystems that they dominate.

3.2 PRELIMINARY FIELDWORK AND ANALYSIS

During the first summer of fieldwork, a sampling survey of soil nutrients was made at the limits to the distribution of a number of montane and subalpine species of *Eucalyptus*, particularly *E. delegatensis* throughout S.E. Australia. Sites were selected from topographic maps and local knowledge of eucalypt distribution. About 8500 km were travelled between sites, allowing only brief sampling.

The vegetation profile, particularly the understorey and forest floor was noted and unknown species retained for identification. The altitudes of the absolute upper and lower limits of *E. delegatensis* in
an area were recorded as well as the altitudinal limits to the dominance of this species on most aspects. Where possible the entire altitudinal range was traversed by 4-wheel drive vehicle, and occasionally on foot. 'Grab-samples' of the surface soil were collected from most sites.

Soil samples were stored in heavy paper bags, air-dried, weighed, sieved to retain particles less than 2 mm diameter, after light grinding to break up aggregates and stored in aluminium cans for determination of nitrogen, phosphorus and total cations.

3.3 SAMPLING AND SAMPLE PREPARATION

The variation established in the preliminary study demanded a somewhat more rigorous approach to the problems of sampling to ascertain discontinuities in the nutrient pools between ecosystems.

3.3.1 SAMPLE LOCATION

Sites were selected to encompass the geographic range from the Australian Capital Territory to southern Tasmania, and within the A.C.T.-Snowy Mountains area to encompass topographic, geological and fire history variation. Site location was also governed by the physical problem of transporting soils and sampling equipment between the site and access.

Within a stand, pit sites were located by random table co-ordinates, allowing for stem bases, dense patches of shrubs, rock outcrops and other apparent irregularities. If an outcrop was encountered immediately below the soil surface during sampling the sample was discarded and another pit sampled. A major criterion for site location was a similar fire history throughout the area covered by the ecotone, usually a zone 30-40 metres wide. For this reason, situations where a road traversed the ecotone were
avoided. Intra-ecotone discontinuities in parent material and topography were included in the sampling design.

3.3.2 SAMPLING TIME

Sampling was undertaken in late summer-early autumn 1973, immediately following the main period of litter fall. Winter sampling, when the mass of the forest floor was at a seasonal minimum (Reiners and Reiners, 1970) was prevented by problems of access to high altitude areas because of snow and poor roads. Late summer sampling also enabled the maximum seasonal development of herbaceous annuals to be included in the analysis of the species composition of the forest floor.

3.3.3 SAMPLE SIZE

Vegetation

Shrub understorey and forest floor cover was measured by a method of point analysis (Park, 1973). In all cases the size of the sample was 200 sampling stations allowing for multiple cover repetition (Goodall, 1952; Park, 1972) where shrubs occurred in the understorey.

Forest floor and surface soil

Although different scales of variation were anticipated on different parent materials, and for different paramenters, it was decided within the scope of this study to retain a constant sample size so that for the total number of soil pits excavated (140) in the entire study, the environmental variation was maximised at the expense of a high degree of statistical definition for individual sites. The results of this study can thus only be interpreted in terms of trends of change.

Unfortunately, very few definitive studies of forest floor
availability have been made. Studies usually show a wide range in sample weights despite the care taken by the observer. This variation may be attributed to differences in litter fall, rates of decomposition, and climatological and ecological factors. The scale of variation in subsequent nutrient weights based upon these data can be expected to be greater than the variation in the sample weights themselves. Only the most exhaustive sampling could determine the extent of this variation. In second growth Douglas fir in western Washington, Grier and McColl (1972) found that at least 30 samples of 560 m² surface area needed to account for most of the variation in total dry weight. Bourn and Brown (1971), in a study of mixed oak forest floors on Rhode Island, showed that 168 samples, each with an area of 0.202 m² were adequate to determine litter weight within 5% of the mean, and considered precise determinations likely to be too time consuming and expensive. Few, if any, studies of forest floors have included anything approaching this number. In the present study, the time available allowed only a brief study of forest floor variation. This was undertaken in each ecotonal situation where selected nutrient flux studies were made. In this separate study, 10 samples of both the litter (L) and fermentation/humus (F/H) layers in both the *E. delegatensis* and *E. pauciflora* ecosystems were collected. In all other sites, 3 samples of the L and F/H litter layers and 3 volumetric cores of the 0-5 cm soil depth each 0.102 m² were collected.

### 3.3.4 SAMPLE COLLECTION

**Vegetation**

In order to relate structure and function of secondary successional understorey and forest floor vascular plant species to nutrient dynamics, basic data on plant populations were collected by point analysis and species listing. The method of point analysis used (Atkinson, 1962) has
been widely used by the present author in vegetation survey in New Zealand forests. It has the advantage that measurement of herbaceous and graminoid species does not demand counting of individuals. The method involves a vertically descending 'point' attached to a pole held at arms length. Sampling stations were located with random table co-ordinates and bias was virtually eliminated at each station by rotating the pole horizontally prior to descent. Only the descent was observed and the species identity of any intercept recorded. Although the great majority of intercepts were of the forest floor, in some stands shrubs were encountered, and recorded as multiple cover repetition. Litter, bare soil, and rock outcrops were included in the sample.

Collections of species that could not be identified in the field were made, together with a list of all vascular plant species in the stand.

**Forest floor and surface soil**

The L, and F/H layers and the 0-5 cm soil depth were removed from three randomly placed 36 cm diameter pits defined by a cylindrical steel corer. The corer was 15 cm in depth, with an etched graduation 5.0 cm from the bevelled cutting edge. The corer was driven into the soil by blows of a sledge hammer on a 5 mm thick circular metal plate placed on the upper edge of the corer. Such a method was found to be necessary in a range of soils where the > 2 mm fraction varied from 5-95% of the entire weight of the 0-5 cm depth. It was preferred to a large number of smaller core samples for this reason, although it also provided considerable manual problems for the single field worker.

The forest floor was defined as all organic matter lying upon the mineral soil including ground vegetation (Gessel et al., 1971). The same authors have drawn attention to the major problem of the contribution
of large branches and logs to the forest floor. This is often an important component of the forest floor in some forests, and it is very difficult to collect adequate samples. In this study the term 'forest floor' pertains to all bark material, leaves and all woody material less than 5 cm diameter, as well as living ground plants. The L litter layer was defined as undecomposed plant detritus. Decomposition studies (see Chapter 6) would suggest that this definition restricts the L layer to litter fall of at least the preceding 12 months, for both *E. delegatensis* and *E. pauciflora*. The F/H layer comprised all decomposing organic matter that could be separated from the mineral soil and small roots by hand scraping. The 0-5 soil depth was removed, with the aid of the etched graduations on the coring cylinder, by careful excavation with sharp knives and a trowel. All unweathered parent material within the core was retained.

Samples were placed in airtight plastic bags, sealed and transported to the laboratory. They were dried at 45°C in paper bags in a forced air oven, and weighed.

### 3.2.5 SAMPLE PREPARATION

*Vegetation*

After all vascular species had been identified, point analysis data was tabulated and, with the list of all species in the stand, entered on cards. For the calculation of cover values and species diversity indices, the procedure was as follows:

Each point intercept in the 200 sampling positions of the sample for an individual stand was assigned a value of 5. Thus, in a stand with no shrub understory intercepted, i.e. no cover repetition point intercepts, the cover values would total 1000. For stands with dense shrub understories
the cover value would be appreciably more than 1000. Species listed as present in the stand but not encountered in the point analysis sample were assigned a value of 1 on the same scale. The data was punched on cards for the calculation of cover values of shrubs (including a separate value for shrub species of the Leguminosae), herbs and grasses, and the species diversity indices of Brillouin (1962), McIntosh (1967), and Pielou (1966).

Forest floor and surface soil

After drying, L and F/H samples were ground in a large Christy and Norris mill (Courtesy of Dept. of Plant Industry, C.S.I.R.O.). The entire sample was retained in ground form and completely mixed before a small portion was stored in screw-top glass phials. The remainder of each sample was stored in paper bags in a dry atmosphere at constant temperature.

The portion of the large volumetric 0-5 cm soil depth sample (often exceeding 5000 g in weight) retained for preparation for chemical analysis was sub-sampled during the physical analysis of soils (see below). The sub-sample was lightly ground to break up soil aggregates and sieved to retain all material passing a 2 mm square mesh. This material was further hand ground and stored in screw-top glass phials.

160 L litter samples, 180 F/H litter samples and 140 soil samples were prepared for chemical analysis for the study of site variation at the *E. delegatensis/E. pauciflora* ecotone throughout the Australian subalpine zone.
3.4 COLLECTION OF FOREST FLOOR SAMPLES FOR NUTRIENT FLUX STUDIES

3.4.1 INTRODUCTION

These studies were conducted in a typical ecotone situation where, on a sheltered S.W. slope, *E. delegatensis* is sharply replaced by *E. pauciflora* with increasing altitude. The study site was located on shallow, but of variable depth, soils formed from adamelite of the Bendora batholith formation in the Brindabella Range, Australian Capital Territory. The site is included in the major study of this project and its environmental and community features are described in Chapter 6 (section 2. The site is termed Brindabella Range in Figure 23, Appendix I.

The two studies on the fluxes in nutrients from the biomass to the complex soil surface interface, were designed to obtain information on the scales of mobilisation of nutrients that take place annually in these ecosystem types. In this way it should be possible to ascertain the relative importance of individual elements in the diverse range of *E. delegatensis/E. pauciflora* ecotone types that have been surveyed in this project. Few management recommendations may be made from analytical data on the static nutrient quantities and concentrations of soils and forest floors in isolated sites without some knowledge of the dynamics of nutrients between components of representative ecosystem types.

3.4.2 TRANSFER OF ELEMENTS FROM BIOMASS TO FOREST FLOOR

The only transfer that was monitored was litter-fall. All litter components were collected at two week intervals from 15 sieves in both the *E. delegatensis* and *E. pauciflora* ecosystems. Each of the 30 sieves had a collection area of 0.258 m², with a 2 mm square mesh, contained within a 10 cm tall wall and raised 2 cm above the forest floor to prevent
decomposition from that source. The sieves were randomly located in each stand in October 1972 and during the peak leaf-fall period of the following summer, variation in litter-fall was assessed each week. Some sieves, at first randomly located beneath large canopy gaps or beneath clumps of tall *Acacia dealbata*, were later re-located to more representative sites. Litter-fall was recorded, every two weeks, from mid-February 1973 to early April 1974. At each collection, samples from the 30 sieves were transferred to labelled paper bags and air-dried. The weight of each sample was recorded and the 15 samples from each stand were pooled and sorted into the categories; leaves, bark, branches, seeds/reproductive tissue, and assorted comminuted tissue (chaff). Each category was weighed and the entire collection pooled and stored in sealed plastic bags prior to grinding in a large Christy and Norris mill. The entire collection for each two-week period was milled, thoroughly mixed and a sub-sample stored in a screw-top glass phial, prior to analysis for total nitrogen, total phosphorus and the total content of each of the cations calcium, iron, magnesium, manganese, potassium, sodium and zinc.

3.4.3 TRANSFER OF ELEMENTS FROM LITTER TO THE SOIL SURFACE

Large quantities of the oldest series of leaves were collected from branches of canopy foliage removed with a 0.222 rifle and fresh litter from supplementary plastic sheets, during a 7-day period at the time of maximum leaf-fall in late February 1973. The leaves were air-dried and thoroughly mixed. About 20 g (8-12 leaves) was accurately weighed and placed in a labelled 35 cm x 30 cm terylene mesh bag that was subsequently sealed. The three dimensions of the meshes in the terylene were 3 x 10 mm, 3 x 3 mm and 0.3 x 1.0 mm allowing access to most microfauna and the penetration of vascular plants, whilst maximising the retention of leaf fragments.
In late March 1973, a total of 208 mesh bags containing leaves were set in stratified design in the two ecosystem types; 104 in each stand, as close as possible to the ecotone but beneath a 100% *E. delegatensis* and 100% *E. pauciflora* canopy respectively. The L and F/H layers and plant ground cover were removed, and the mesh bags attached to the soil surface by wire staples. The bags were placed on an even soil surface in numerical order and throughout the following year removed in this same order; 4 bags per two week collection from each stand. Litter falling on the mesh bags during the year was not removed.

At each collection, the bags were carefully removed from the soil surface, with the aid of secateurs during the second half of the year, and placed in heavy flat paper bags for transport to the laboratory. Most contaminating foliage was removed in the field, the remainder in the laboratory. The decomposed leaves were air-dried, removed from the bag, weighed and stored in sealed paper bags until grinding. Ground samples were stored in screw-top glass phials for chemical analysis. Analyses were made of total nitrogen, total phosphorus and the total content of the cations calcium, iron, magnesium, manganese, potassium, sodium and zinc. A few analyses were made of the exchangeable components of calcium, magnesium, potassium and sodium, and some phosphorus fractions.

A computer program was written for the calculation of loss in dry weight and net and cumulative changes in the weights and concentrations of separate elements, as well as the calculation of annual decomposition constants.

Collections were made from March 1973 to March 1974.

3.4.4 COLLECTION OF ENVIRONMENTAL DATA

Weekly visits were made to three sites in the Brindabella Range,
A.C.T. to monitor temperature, rainfall and moisture variation on various soil surfaces within *E. delegatensis/E. pauciflora* ecotones, throughout all of 1973 and the first three months of 1974. Temperature was measured by three maximum/minimum thermometers in each ecosystem at each ecotone. Rainfall reaching the forest floor was measured with a standard gauge of 1000 point capacity. Soil surface moisture was measured by a Nuclear Enterprises neutron moisture probe in a surface shield. Some measurements of soil moisture were made during the dry months of the 1972-73 summer, but were discontinued during 1973 when it was found that the soil surface was at or above field capacity almost continuously, and that the labour of transporting equipment some 150 metres upslope from a road was not commensurate with results achieved.

In the site at which nutrient flux measurements were being made, the meteorological instruments were placed near the decomposition experiment, and read regularly every seven days for the duration of the study.

3.5 PHYSICAL ANALYSIS OF SURFACE SOILS

3.5.1 INTRODUCTION

It was early realised that accurate measurement of nutrient pools at the soil surface was dependent on a knowledge of the portion of the soil volume containing ion-exchange surfaces available to plant nutrient uptake processes. This is critical in the range of soils encountered in this study, which are predominantly lithic, particularly if derived from sediments, where the proportion of primary particles greater than 2 mm diameter could be as great as 95% of the soil weight. Furthermore, the majority of the soils contained a concentration of stones at the surface,
possibly as a consequence of the intensified disturbance to the forest floors of these ecosystems in the last 100 years. The concentration of stones at the soil surface is not to be confused with the widespread phenomenon of slope-deposits. Costin and Polach (1971) drew attention to the occurrence of slope deposits, often of angular rock particles, on steeper slopes in the region, with local dates in the vicinity of 35,000 years BP. They have a probable soliflual origin, and often occur in the sites included in this study, particularly in the sheltered valleys occupied by *E. delegatensis*. The physical analysis of soils concentrated on the separation of particles less than 2 mm diameter. The resultant parameters were used as independent variables in ecosystem identification, but their primary function was in the calculation of coefficients for the computation of nutrient results in the form: kilogram/0-5 cm depth/hectare.

3.5.2 PROCEDURE

Soil physical analyses were made in the sedimentology laboratory, Dept. of Biogeography and Geomorphology, Research School of Pacific Studies, A.N.U..

The entire air-dry 0-5 cm depth sample from each 36.0 cm diameter core was weighed for the determination of bulk density, then mixed and sub-sampled using apparatus that retained any particles greater than 15 mm diameter. Two 50 g sub-samples of material passing the sieve were retained for chemical analysis and the separation of finer particles. One subsample was weighed accurately in a beaker, 25 ml of 5% NaOH and 25 ml of 10% Calgon added to disperse primary soil particles, and dislodge organic and clay colloids from unweathered particles, the suspension stood overnight and then agitated mechanically for 15 minutes. The mixture was wet-seived through a 2 mm square mesh. The coarser particles were dried
at 105°C within the sieve, which was placed on filter paper in an oven, and weighed. The suspension passing the sieve was evaporated to dryness on a deep sand bath, and weighed.

Both the difference between the weights of the sample prior to dispersion and the particles > 2 mm, and between the weight of the former and the < 2 mm particles evaporated to dryness, were used in calculation of soil physical parameters. In the cases of discrepancies, the former was used, allowing for the possible volatisation of organic matter from 'hotspots' during evaporation. This appeared to occur in the more organic soils.

A computer program was written to calculate soil physical parameters and volume weight coefficients (kg/0.5 cm/ha) from the weight data.

### 3.6 CHEMICAL ANALYSIS OF FOREST FLOORS, FOLIAGE AND SURFACE SOILS

#### 3.6.1 INTRODUCTION

Apart from preliminary analyses, all analyses were made in duplicate and the mean used in subsequent calculations. The methods of analysis were identical for all materials.

#### 3.6.2 DETERMINATION OF TOTAL CATIONS

Total cations were determined by a Techtron atomic absorption spectrophotometer (AAS) in the Soil and Plant Analytical Laboratory at the Department of Forestry, A.N.U., after wet-digestion of 0.5 g oven-dried samples in conical flasks by 5 ml of digestion mixture (7:1 concentrated perchloric and sulphuric acids) and 15 ml of concentrated
nitric acid. This was carefully digested on a hotplate until the perchloric and nitric acids were driven off, a little distilled water was added after cooling and the solution filtered, with repeated washing, into a 100 ml volumetric flask. The solution was then made up to 100 ml with distilled water. The extract could be used directly for determination of potassium, manganese, iron, sodium and zinc, but sometimes required further dilution.

To eliminate interference by aluminium (in soil samples) and phosphorus (in organic material) calcium must be determined in the presence of a high concentration of sulphate and magnesium ions. Samples and standards were suitably diluted with $\text{H}_2\text{SO}_4$ and $\text{MgCl}_2$ to give 2% $\text{H}_2\text{SO}_4$ and 6000 ppm Mg in the final solution. Lanthanum oxide ($\text{La}_2\text{O}_3$) at 1% concentration was added for determination of magnesium.

3.6.3 DETERMINATION OF TOTAL NITROGEN AND TOTAL PHOSPHORUS

Total nitrogen and phosphorus were simultaneously determined by a Technicon AutoAnalyser (ascorbic acid/ammonium molybdate method) in extracts prepared by wet-ashing 0.5g oven-dried samples in conical flasks with 6.0 ml of digestion mixture (200 g of potassium sulphate and 1.0 g of selenium powder dissolved in 1 litre of concentrated sulphuric acid at about 250°C). The sample was digested until the solution became a light straw colour, the solution diluted, filtered and washed into a 100 ml volumetric flask, and made up to 100 ml.

3.6.4 DETERMINATION OF EXCHANGEABLE CATIONS AND CATION EXCHANGE CAPACITY (C.E.C.)

Oven-dried, finely ground material of either soil, litter or foliage was analysed using a procedure modified from a number of methods by staff of the Canberra analytical section, C.S.I.R.O. Division of Soils.
It was considered appropriate for the analysis of a large number of soils and forest floor samples from a diverse range of parent materials and soil types.

Approximately 2.0 g of sample was accurately weighed into a 100 ml centrifuge tube, 80 ml of neutral 1N ammonium chloride was added, the mixture shaken for 4 hours end-over-end and centrifuged for 15 minutes at 2000. The two supernatants were combined and analysed for the individual concentrations of exchangeable calcium, potassium, magnesium and sodium, using the AAS as described above.

The sample was then washed out with 150-200 ml of 99% isopropyl alcohol, and the soil allowed to drain thoroughly in a filter funnel. The ammonium-saturated soil was slowly leached with 10% acidified NaCl until 225 ml had passed through the sample, and the leachate made up to 250 ml with the acidified NaCl solution. A 2 ml aliquot (greater if C.E.C. was low) was then diluted to 100 ml, ensuring that the final acidity was compatible with the AutoAnalyser method for the determination. All determinations for C.E.C. were made on the basis that the value obtained for nitrogen represented the nitrogen in the $\text{NH}_4^+$ ion.

3.6.6 DETERMINATION OF NON-OCCULDED INORGANIC PHOSPHORUS.

The method of Petersen and Corey (1966) for the analysis of 'easily soluble-P', 'Al-P', and 'Fe-P', with some modifications after the more detailed method of Williams et al., (1967) was used. The fractions extracted are considered to be surface forms of soil phosphorus (Stevens, 1968) and it is generally assumed that they represent a large component of the phosphorus available to the plant uptake processes. The literature on phosphorus fractionation and plant phosphorus availability is considerable and will not be discussed here. The terminology of the
forms of phosphorus should be defined by the means of analysis and for this reason the terminology of Petersen and Corey (1966) has been avoided. The following step-wise procedure extracted three fractions.

1. $P_{NH_4Cl}$: An oven-dried sample was weighed to exactly 1.00 g in a polypropylene 100 ml centrifuge tube, 50 ml of 1N ammonium chloride added, the mixture shaken end-over-end for 30 minutes, and centrifuged for 15 minutes at 200. Preliminary analyses showed negligible P in this extract and so for soil samples the supernatant was discarded. The supernatant of F/H samples was retained for analysis, as Williams et al. (1967) found that very large amounts of $P_{NH_4Cl}$ were removed by repeated extraction of F/H layers in podzolised and gleyed New Zealand soils. Although the present author did not attempt repeated extraction of this fraction in F/H layers, there was evidence that the deeper, more organic layers contained higher amounts of $P_{NH_4Cl}$ than other layers.

2. $P_{NH_4F}$: 50 ml of 5N ammonium fluoride (pH 8.2) was added to the sample residue from the previous extraction, the mixture shaken end-over-end for 24 hours and centrifuged for 15 minutes at 2000. In all cases, except a few soils on which secondary forest understorey development was just commencing, the solution was highly coloured by organic matter, which was removed by repeated filtration through about 0.5 g of activated charcoal on filter paper. The solution, when clear was retained for phosphorus determination. The resorption of phosphorus during the extraction was checked by a simultaneous replicate extraction with 0.5N ammonium fluoride (pH 8.2) plus 100 ppm solution of phosphorus as potassium dihydrogen phosphate (Smith, 1965; Williams et al., 1967)

3. $P_{NaOH}$: In the P fractionation scheme of Williams et al. (1967)
which involves nine consecutive steps of adding extractant, shaking, centrifuging, taking an aliquot, removing supernatant and washing residue; there are two extractions using NaOH. The extraction used in this study is the '1st NaOH-P' of Williams et al. (1967) in which the phosphorus extracted is primarily surface-bound to iron complexes (Chang and Jackson, 1957; Petersen and Corey, 1966). The residue from the previous extraction was washed twice with 25 ml portions of saturated NaCl by centrifugation at 2000 for 5 minutes. The supernatant was discarded. 50 ml of 0.1N sodium hydroxide was added and the mixture shaken end-over-end for 17 hours and centrifuged at 2000 for 15 minutes. The supernatant was decanted into a volumetric flask, 10 drops of concentrated sulphuric acid added and the solution swirled to flocculate the organic matter. Where the colour was not removed by this method some of the extract was filtered through charcoal and filter paper.

Following all phosphorus extractions, the supernatant was carefully withdrawn by suction using a finely tapered glass tube to facilitate maximum retention of the residue for subsequent extractions.

Phosphorus was determined in all extracts by the method of Dickman and Bray (1940) as modified by Fife (1959), measuring the absorbance with a colorimetric spectrophotometer. Standards were prepared from dried potassium dihydrogen phosphate.

3.6.7 DETERMINATION OF ORGANIC PHOSPHORUS

The ignition method (Saunders and Williams, 1955; Walker and Adams, 1958) was used. Ignited and non-ignited (550°C for one hour) 2.0 g samples of oven-dried ground material were extracted with 0.2N sulphuric acid by 16 hours shaking. The phosphorus content of extracts was
determined by Autoanalyser as previously described.

3.6.8 DETERMINATION OF OXIDISABLE CARBON

The absorptiometric modification of the method of Walkley and Black (1934) and Walkley (1947) described by A. J. Metson (pers. comm.) Soil Bureau, D.S.I.R., New Zealand was used. 0.2 g or 0.5 g of sample was weighed into a 200 ml conical flask, 30 ml of concentrated sulphuric acid added and the flask occasionally swirled over 10 minutes. 15 ml of 4N sodium dichromate was added with constant mixing, to promote rapid and vigorous oxidation. The mixture was diluted to nearly 200 ml with distilled water and left overnight, thoroughly mixed and made up to 200 ml. Aliquots of the supernatant were centrifuged for 15 minutes at 2000. The intensity of colour was read on a colorimetric spectrophotometer at a wave length of 600M. The oxidisable carbon values were read from curves prepared from standards equivalent to 0, 20, 40, 60, 80 and 100 mg of soil carbon, treated in the same way as the soil.

3.6.9 CALCULATION OF THE SAMPLE VALUES FROM AAS AUTOANALYSER AND COLORIMETRIC SPECTROPHOTOMETER OUTPUT

Sample and standard values from the AAS were printed onto paper tape, from the AutoAnalyser on a continuous chart, and results from the colorimetric spectrophotometer were recorded manually. A Fortran program, PEANUT 7, originally developed by M. T. Tanton and A. V. Spain of the Department of Forestry, A.N.U., was used to calculate the concentrations (PPM for nutrient ions, and percentage content for oxidisable carbon) of each element in the original sample. The program derived the curve of best fit for a set of standards and then compared the sample determination with this regression, combining dilution factor, concentrations, values of blanks and sample weight to calculate the final
sample concentrations.

3.6.10 DETERMINATION OF ORGANIC MATTER BY LOSS ON IGNITION (LOI%)

Ground soil and F/H litter material was oven-dried and weighed in silicon crucibles. This sample was then brought to 550°C and ignited for 1 hour to determine the LOI%. The ignition was made in conjunction with organic phosphorus sample preparation.

3.6.11 DETERMINATION OF SOIL REACTION

A soil/distilled water suspension (1:2.5) was stirred and intermittently shaken over 24 hours in sealed containers. Immediately before measurement the sample was shaken again. Duplicate measurements of pH were made 5 minutes apart.

3.7 STATISTICAL TREATMENT OF FOREST FLOOR AND SOIL SURFACE DATA

The degree of inherent variation that can be expected in forest floor and soil surface sampling has been discussed. The primary function of this study has been to describe and measure the nature of environmental variation, particularly as it pertains to the development of nutrient pools, in a successional sense. It has not been possible to approach the sampling design of such a study by way of a statistical definition of sample size for individual stands. In a separate study of the degree of variation in the forest floor of one two-stand ecotonal situation in the Brindabella Range, A.C.T., 10 samples of the L and F/H layers were sampled per stand. In other cases, 3 samples were taken per stand.

Duplicate chemical analyses were made for each sample and only the mean used. Calculation of kg/ha, kg/0-5 cm/ha, tonnes/ha etc.
parameters for each sample was from these means.

Calculation of single parameter values for individual stands was made on a program, GRUPSTATS, a modification of the BASTATS program developed by M. T. Tanton of the Department of Forestry, A.N.U.. This provided the values of means, standard error of the mean and the 95% confidence limits of the means that have been used in the presentation and plotting of results.
CHAPTER 4
ECOTONAL RELATIONSHIPS BETWEEN NUTRIENT POOLS AND THE DISTRIBUTION OF UPLAND EUCALYPTS

4.1 INTRODUCTION

The quantities of nutrients and their interactions have been suggested as important factors in any explanation of the site-specific distributions of Eucalyptus species and the discontinuities of eucalypt forest and rainforest (Beadle 1962; Florence, 1969; McColl, 1969; Moore, 1959, 1961). These studies have been made in the low-fertility environments that prevail in the eucalypt biome, characterised by very weathered soils on old groundsurfaces. In these situations, the low quantities of nutrients, particularly phosphorus and calcium, may well be limiting plant growth.

In the subalpine zone, the groundsurfaces are recent, weathering of primary particles is active and a continuing source of abundant nutrients. However, sharp discontinuities in the distribution of the eucalypt commonities are the rule rather than the exception. A detailed analysis was therefore made of the relationships between nutrient pools and specific eucalypts at limits of their distribution. Analysis was restricted to the forest floor and surface soil where the great majority of the pool of "available" nutrients is concentrated, in discrete, but immediately adjacent stands of two eucalypts, E. delegatensis and E. pauciflora, differing markedly in above-ground biomass.

4.2 OBJECTIVES

The main objective of this part of the study was to discover if
the rather precise separation of *E. delegatensis* and *E. pauciflora* into discrete stands with usually contiguous boundaries was associated with some nutrient parameters which likewise might have sharp discontinuities at the point at which there is a change in the dominant eucalypt. The working hypothesis was that if the specific quality of nutrient pools was an operative factor in the sharply discontinuous distribution of the eucalypt communities, then consistent differences would be discerned by plotting a large number of ecotonal sites encompassing a wide field variation. A major component of this thesis has been to sample the same discontinuity, or ecotone, on different parent materials and at different stages of successional development. The location of all samples from one point in the "environmental space", viz. the ecotone between *E. delegatensis* and *E. pauciflora*, is advantageous to a study of secondary succession as this affords some constancy in environmental variation.

4.3 RESULTS

4.3.1 PRELIMINARY RESULTS

4.3.1.1 Field studies

During initial field-work and familiarisation with the patterns and processes of the vegetation in the Australian high country, *Eucalyptus delegatensis* was selected as the 'centre of gravity' of the study on the basis of certain field characteristics obvious to even the casual observer:

1. It is a remarkably site-sensitive species, restricted to topographically protected positions (Figure 4).

2. It occurs throughout the subalpine-upper montane zone; in much of N.E. Victoria and southern N.S.W. its distribution
is sufficiently disjunct to suggest that it was previously more widespread (Figure 5).

3. It is easily detected in the field and on aerial photographs.

4. At the local limits of its distribution it forms a narrow ecotone with the dominants of likewise exclusively eucalypt-dominated communities (Plate I).

5. In a regional sense, the upper and lower altitudinal limits of the species appear to be determined climatically, in that they are altitudinally constant for a given latitude (Figure 6). However, other factors are evidently involved locally, in the discrete separation of eucalypt dominants.

6. It forms virtually monodominant communities.

The preliminary field program served primarily to plot the distribution of the upper and lower altitudinal limits of *E. delegatensis* throughout its range on the Australian mainland (Figure 6), at the same time recording the environmental factors operative at the various ecotonal situations in determining the composition of the dominants (Table 5). Soil samples were collected from most ecotones to determine variations in nutrient concentration.

The results from the field program were combined with the reported data to construct a map of the entire distribution of *E. delegatensis*. These data, and their reliabilities, are presented in the overlays to Figure 5.
Fig. 4

Subalpine Vegetation of Cotter Catchment (ACT)

solid black (E. delegatensis), stippled (E. pauciflora), cross-hatched (E. pauciflora-E. dalrympleana). Blank areas are montane and lowland forest and woodland.
FIGURE 5 THE UPLANDS OF SOUTH-EAST AUSTRALIA

Locations of sampling sites
Overlays indicate distribution of *Eucalyptus delegatensis*

1. Delegate Mt.
2. Mt. Nugong
3. Mt. Baw Baw
4. Mt. Macedon
5. Lake Mt.
6. Mt. Buller
7. Mt. Buffalo
8. Wilson's Valley
9. Brook's Range
10. Yarrangobilly Mt.
11. Tantangara Mt.
13. Happy Jacks
14. Peppercorn Hill
15. Goodradigbee V.
17. Kings Cross
18. Geehi Valley (wildfire site)
19. Mt. Field
20. Arthur's Lake
21. Todds Corner
22. Sandbanks Tier
23. Ben Lomond

Overlays: Reliability NSW; G.H. Park (pers.obs.)
VIC; For.Comm.Vic., G.N.P.
TAS; Jackson (1965)
Overlays indicate distribution of *Eucalyptus delegatensis*.

Overlays: Reliability NSW; G.N.Park (pers.obs.)
VIC; For.Comm.Vic., G.N.P.
TAS; Jackson (1965)
Figure 5: The Uplands of South-East Australia

Locations of sampling sites
Overlays indicate distribution of *Eucalyptus delegatensis*

1. Delegate Mt.
2. Mt. Nugong
3. Mt. Baw Baw
4. Mt. Macedon
5. Lake Mt.
6. Mt. Buller
7. Mt. Buffalo
8. Wilson's Valley
9. Brook's Range
10. Yarrangobilly Mt.
11. Tantangara Mt.
13. Happy Jacks
14. Peppercorn Hills
15. Gooradigbee
16.
17.) Brindabella Ra.
18.)
19. Kings Cross
20. Geehi Valley (wildfire site)
21. Mt. Field
22. Arthur's Lake
23. Todds Corner
24. Sandbanks Tier
25. Ben Lomond

Overlays: Reliability NSU; G.H. Park (pers.obs.) VIC; For. Comm. Vic., G.N.P. TAS; Jackson (1965)
--- altitudinal limit on east slopes.
--- absolute altitudinal limit.
--- low-altitude riparian extension.
I higher altitude slopes absent.
entire sequence not examined.

FIGURE 6 The altitudinal range of Eucalyptus delegatensis in S.E. Australia (excluding Tasmania).
<table>
<thead>
<tr>
<th>Ecotone</th>
<th>Environmental factor, and direction of flux</th>
</tr>
</thead>
<tbody>
<tr>
<td>delegatensis → pauciflora</td>
<td>midslope to ridge</td>
</tr>
<tr>
<td></td>
<td>increasing altitude</td>
</tr>
<tr>
<td></td>
<td>sheltered (max. S.E.) to exposed (max. N.W.) aspect</td>
</tr>
<tr>
<td></td>
<td>gentle to steep slope</td>
</tr>
<tr>
<td></td>
<td>concave to convex slope</td>
</tr>
<tr>
<td></td>
<td>increased proximity to cold-air flow in valleys</td>
</tr>
<tr>
<td></td>
<td>decreasing soil depth</td>
</tr>
<tr>
<td></td>
<td>increasing soil stoniness</td>
</tr>
<tr>
<td>delegatensis → pauciflora + stellulata</td>
<td>midslope to valley floor</td>
</tr>
<tr>
<td></td>
<td>increased proximity to cold-air flow in valleys</td>
</tr>
<tr>
<td></td>
<td>decreasing soil aeration</td>
</tr>
<tr>
<td>delegatensis → dalrympleana*</td>
<td>midslope to ridge</td>
</tr>
<tr>
<td></td>
<td>sheltered to exposed aspect</td>
</tr>
<tr>
<td></td>
<td>gentle to steep slope</td>
</tr>
<tr>
<td></td>
<td>concave to convex slope</td>
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<td></td>
<td>increased proximity to cold-air flow in valleys</td>
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<tr>
<td></td>
<td>decreasing soil depth</td>
</tr>
<tr>
<td></td>
<td>increasing soil stoniness</td>
</tr>
<tr>
<td>delegatensis → radiata</td>
<td>midslope to ridge</td>
</tr>
<tr>
<td></td>
<td>decreasing altitude</td>
</tr>
<tr>
<td></td>
<td>sheltered to exposed aspect</td>
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<td></td>
<td>gentle to steep slope</td>
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<td>concave to convex slope</td>
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<tr>
<td></td>
<td>decreasing soil depth</td>
</tr>
<tr>
<td></td>
<td>increasing soil stoniness</td>
</tr>
<tr>
<td>delegatensis → fastigata + (viminalis)</td>
<td>decreasing altitude</td>
</tr>
</tbody>
</table>

(* restricted to lower half of maximum altitudinal range of E. delegatensis.)
4.3.1.2 Nutrient Studies

During the preliminary collection of soil samples for chemical analysis, information was maximised towards the number of sites rather than the statistical refinement of the characteristics of individual samples. The purpose of the study was to assess the nature and scale of nutritional discontinuities at the ecotones in eucalypt distribution, prior to designing a major study of the relationships of nutrients to the mosaic of upland eucalypt communities and their successional development. The preliminary set of soil samples was collected from the surface soil between 5-15 cm depth. Collection was not volumetric so a true weight/area expression is not possible. The preliminary results are illustrated in Appendix VI (Figures 82, 83, 84) where they are grouped into ecotonal types. The results can be summarised as follows:

1. In the *E. delegatensis*: *E. radiata* ecotone, all cations except Ca tend to be in greater concentration in the *E. delegatensis* sites. Mg and Mn show the least significant difference.

2. In the majority of *E. delegatensis*: *E. dalrympleana* ecotones, all cations are in greater concentration in the surface soil of the *E. delegatensis* ecosystem.

3. The *E. delegatensis*: *E. pauciflora* ecotone does not show the same clear differences in cation concentration. There is a predominance of greater concentrations in the *E. delegatensis* sites, but generally the difference is slight compared to the level of concentration.

4. In expressing the ecotonal distribution of P in the 5-15 cm soil layer, the *E. delegatensis* sites have been linked to either *E. radiata*, *E. dalrympleana* or *E. pauciflora* sites in a plot of total P concentration and the percentage of the soil sample that is
greater than 2 mm diameter particle size. The *E. delegatensis* sites are consistently of higher P concentration than any of the adjacent sites dominated by other eucalypts, and the soils of the former are less stony in terms of the 0-2 mm fraction. It should be noted that the low (< 200 ppm) concentrations of P are at the lower limits of *E. delegatensis* where it is replaced on more exposed aspects by *E. dalrympleana* or *E. radiata*. These are approaching the levels of the *E. obliqua* ecosystem studied by Attiwill (1964, 1971) where disturbance to the P cycle could be critical to eucalypt composition. The great majority of the *E. delegatensis*: *E. pauciflora* ecotones have much higher levels of soil P.

5. There are greater differences between the concentrations of P and the cations between ecosystems dominated by the same eucalypt on different sites than there are between the concentrations of different ecosystems forming an ecotone. This suggests that parent material variation is at least as important as the eucalypts themselves, and their effect on the site environment, in determining the concentrations of nutrients in the surface soil.

4.3.2 RELATIONSHIPS BETWEEN NUTRIENT POOLS AND THE ECOTONE BETWEEN *EUCALYPTUS DELEGATENSIS* AND *E. PAUCIFLORA*.

A transect across a hillock would show four eucalypt species - *aggregata*, *dalrympleana*, *delegatensis* and *pauciflora*. The transition is complete in about 30 m which is near the height of the *delegatensis* trees. Eucalypt seeds are small and in the related species *regnana*, Gilbert (1958) estimates that their terminal velocity is 11.4 ft/sec ...........

The mean distance travelled by seeds from these trees, which are over 80 m tall is 37 m. Superimposing this figure on the [Bronte] ecotone shows immediately that the interspecific cline must be the result of very high
selective coefficients. We can assume that the mean free path of a seed is about 50% of tree height, i.e. about 16 m in the Bronte ecotone. The selection agent is not known. But the height above the button-grass plain at which the ecotone takes place is scarcely affected by aspect, geology or drainage. The formation of lakes of cold-air in the frost hollows of the button-grass plains may be important. Costin (1954) has pointed out similar patterns in the Snowy Mountains, on slopes rising from the snow-grass plains. Next to nothing is known about the physiological or ecological reasons for these interspecific selection systems between closely related species."

(Barber, 1965)

4.3.2.1 Introduction

In the light of the preliminary results, the objectives of the study were narrowed to an analysis of the nutrient environment and the internal nutrient fluxes in the forest floor and surface soil of the ecotone between *E. delegatensis* and *E. pauciflora*. Although the ecotone between *E. delegatensis* and *E. dalrympleana* showed the greatest differences in nutrient concentrations, the former ecotone was selected because of a number of suitable features for a study of this nature:

1. The ecotone has a consistently contiguous form throughout the subalpine zone of S.E. Australia.

2. It occurs on a wide variety of parent materials and reflects a range of topographic discontinuities.

3. The ecotone is invariably narrow (Plate I), and usually complete in about 30 metres.

* See Figure 8.
FIGURE 7 Environmental features of the ecotone between Eucalyptus delegatensis and E. pauciflora.
4. The ecotone occurs between communities dominated exclusively by closely related species, representing either an ecological position in which a species barrier evolved, or a result of the convergence of two species that evolved in quite different environments.

5. There is always a considerable difference in above-ground biomass and production between the tall open forest of *E. delegatensis* and the open forest or woodland of *E. pauciflora* (Figures 12 and 23).

6. The ecotone can be found in areas with a wide range of fire histories, from probable pre-European ages to a history of regular burns during the period of European settlement. The sensitivity of *E. delegatensis* to a different pattern of perturbations by fire to that in which the species evolved is best examined at the limits of the species distribution.

7. The contrasting structural characteristics of the two communities results in widely different understorey and ground cover vegetation. This imparts different rates of nutrient dynamics in the forest floor and surface soil as the phasic replacement of understorey plants proceeds during succession.

8. Although the communities adjoin in the landscape mosaic, they represent a large proportion of the range of forest and woodland ecosystem types in the subalpine zone.

4.3.2.2 Field Studies

The ecotone between *E. delegatensis* and *E. pauciflora* is the vegetative response of closely related dominant species to a variety of environmental gradients. A threshold to vegetation and environmental
change occurs because of topographic discontinuity, and the ecotones can be grouped in topographic categories (Figure 7). On the mainland, the ecotone is the result of a species with narrow environmental tolerances (E. delegatensis) being replaced by one species with broader environmental tolerances (E. pauciflora, with E. dalrympleana at lower altitudes, Figures 4, 7). In the subalpine zone of Tasmania, E. delegatensis is either not replaced by eucalypts or is replaced by a number of species at its limits to distribution; E. coccifera, E. gunnii, E. archeri, E. urginera, E. johnstonii and E. rodwayi, as well as E. pauciflora. For the same kind of environmental change, the mainland mountains have a far smaller pool of potential eucalypt-dominants than in the mountains of Tasmania. For example, on the mainland, E. pauciflora replaces E. delegatensis on higher and lower slopes (Plate I; Figure 7). Nowhere in Tasmania is E. delegatensis replaced by E. pauciflora on higher slopes (M. Gilbert, pers comm), and a catenary sequence (e.g. Arthurs Lake, Central Plateau) may support E. gunnii on higher slopes, E. delegatensis on mid-slopes, and E. pauciflora on lower slopes.

The pattern of occurrence of E. delegatensis is strongly related to topography and suggests a correlation of the species subalpine limit with exposure to greater temperature extremes, soil moisture fluctuations and wind. These stresses are usually manifest where topographic and pedological fluxes are marked, and are commonly reflected as a sharply contiguous ecotone with E. pauciflora forest, or at lower altitudes a mixed community of E. pauciflora and E. dalrympleana. The features of the ecotones between these species are summarised in Figure 7, where reference is made to specific locations in the Snowy Mountains.

The ecotone was sampled at 18 localities throughout the mountains of S.E. Australia. For purposes of environmental constancy in the study of secondary succession and nutrient dynamics (Chapter 5) most of the
Ecotone between *E. pauciflora* and *E. delegatensis*, at break of slope, above Upper Tumut Valley, northern Snowy Mountains.

Ecotones between *E. pauciflora* on upper slopes, *E. delegatensis* on mid-slope, and *E. pauciflora* on lower slope. Margin of subalpine valley, Tantangara Mountain, Snowy Mountains.
sites were located in the Snowy Mountains. A few ecotones are included from Tasmania, where a number of subalpine eucalypts replace *E. delegatensis*. In all cases, the ecotone was complete in about 30 metres, and samples were collected from beneath a pure canopy of each species, but as close as possible to the point of maximum change in composition. An example of the very contiguous nature of the ecotone is illustrated in Figure 8.

![Figure 8](image)

**FIGURE 8** Transect across a hillock in the Bronte area, Central Plateau, Tasmania, showing distribution of *Eucalyptus* species (after Barber, 1965)

4.3.2.3 Nutrient Pool Studies

4.3.2.3.i Introduction

The environmental features of the ecotonal situations selected for analysis are summarised in Appendix V. The locations of the 18 ecotonal sites sampled on the mainland are indicated in Figure 5 and the physiognomic form of the ecotones and the slope of the ground surface are shown to scale in Figure 23 (Appendix I). A representative selection of individual nutrient concentrations, nutrient weights in the L and F/H layers of the forest floor and the surface mineral soil, and nutrient weight ratios between the F/H layer and the surface soil are set out in Figures 24-47 (Appendix I). A complete listing of all analyses and derived weight and ratio parameters is presented in Appendix.
(Tables III.1 to III.20) where all data for each ecotone is grouped together. Figures 24-47 are designed to be read with reference to Figure 23.

Methods of sample collection, sample treatment and chemical analysis are described in the preceding chapter. The major points of the results are summarised in the following sections.

Some indication of the inherent variation in nutrient concentration is provided in the data listed in Appendix VIII. Table 1 of this Appendix lists the results of a series of geochemical analyses of the major parent materials encountered in the study. Of the major elements studied, Ca and Mg are lowest in the granites, and highest in andesites. K is highest in the granites, and low in andesitic materials. P is low in the leucogranite and dacite. No data were available for the basalts in these areas, but comparative soil data (Figures 85-86, in Appendix VIII) show the extremely high P values, high Mg but low Ca and K. P is the only element in the soil and forest floor that approaches the concentration in the parent material.

In Appendix VIII (Figures 85 and 86), the concentrations of Ca, P, K and Mg in the 0-5 cm soil are plotted according to the concentration of Fe in the same layer, and samples are identified by parent material type. The data must be considered as a net expression of parent material variation and the effect of ecosystem processes on soil nutrient concentrations. The considerable independence of each element is apparent. The least dispersion between all data occurs for P and K, but only K shows any degree of aggregation of soil nutrient concentrations within parent material groups.

Table 2, Appendix VIII indicates the extent of the range in nutrient concentration in the L and F/H layers of the forest floor, and
the surface soil in all ecosystems examined.

4.3.2.3.ii "Organic" parameters

1. In the great majority of stands, the concentrations of total N (Figure 24) and oxidisable C are greater in the E. pauciflora ecosystem in both the F/H and surface soil, often highly significantly so.

2. There are greater quantities of total N (Figure 25) and oxid. C in the F/H and surface soil of the E. pauciflora ecosystem.

3. The ratio of the weight of N in the F/H to the surface soil is usually slightly greater in the E. pauciflora ecosystem, although the difference may be slight in the more recently burnt areas (Figure 25).

4. The C/N ratio is consistently lower in the E. pauciflora system in both the F/H and surface soil material, but rarely significantly so. The difference between the E. delegatensis and E. pauciflora ecosystems is greatest in the F/H material (Figure 27).

4.3.2.iii Cation parameters

1. The concentrations of total Ca, Mg and K in the L litter are differentiated in a very similar manner according to the ecotone, and tend to be higher, especially Ca, in the E. pauciflora system. In nearly all cases, lower-slope stands of E. pauciflora at the margins of subalpine valleys contain greater concentrations of these elements, again particularly Ca, in the L litter, than in the mid-slope stands of E. delegatensis (Figure 28).

2. Of the two selected cations, Ca++ and K+, the concentration of
Ca\(^{++}\) tends to show the greater consistent difference between ecosystems forming the ecotone. Ca\(^{++}\) is in greater concentration in the F/H in the *E. pauciflora* ecosystems, particularly in most of the lower-slope stands in subalpine valleys, but does not show the same trend or degree of difference in the surface soil (Figure 29). Often, the direction of difference in the surface soil may be the reverse of the difference in the F/H and the L litter. The concentration of K\(^{+}\) (Figure 30) tends to be higher in both the F/H and surface soil. The difference is only slight in the surface soil, and is most consistent in the more recently disturbed stands. The lack of a markedly consistent difference between the *E. pauciflora* and *E. delegatensis* ecosystems could be attributed to the redistribution of cations that occurs during succession, whereby exchangeable cations are withdrawn from the surface soil and concentrated in the forest floor during the accumulation of the F/H layer (see Chapter 5, section 5.6.3).

3. There are usually greater quantities of Ca\(^{++}\), K\(^{+}\), and Mg\(^{++}\) (kg/ha), particularly Ca\(^{++}\) in the F/H of *E. pauciflora* ecosystems than in *E. delegatensis* (Figure 31). There is a general consistence in the behaviour of the cations, although Ca\(^{++}\) tends to be independent in some cases, perhaps as a function of more rapid rates of successional redistribution. In the F/H of the more recently disturbed areas, notably the lowest row of graphs (Figure 31), there are consistently greater quantities of Ca\(^{++}\) in the *E. delegatensis*, but K\(^{+}\) and Mg\(^{++}\) tend to be the reverse of this.

4. In the majority of ecotones there are higher quantities (kg/ha) of exchangeable cations in the surface soil of *E. delegatensis* ecosystem. The difference is often highly significant. As in
the F/H layer, the behaviour of Ca\(^{++}\) is often independent of K\(^{+}\) and Mg\(^{++}\) (Figure 32). The very disturbed ecotone on sediments (bottom right graph, Figure 31) exhibits the greatest difference from the predominant trend. The weights of all three cations are highly significantly lower in the surface soil of the *E. delegatensis* ecosystem. There is no consistent tendency for cations to accumulate in the forest floor or surface soil of the lower-slope *E. pauciflora* stands in greater quantities to the midslope *E. delegatensis* stands.

5. Except for the disturbed ecosystems on sediments, the quantity of C.E.C. in the surface soil (Figure 33) tends to be higher in the *E. delegatensis* ecosystems, although in most of the subalpine valley-margin sites, C.E.C. is highest in the lower-slope *E. pauciflora* ecosystems. The quantitative differences in C.E.C. resemble the predominant pattern for the individual exchangeable cations, although clearly the considerable quantities of Ca\(^{++}\) in the soil are important in determining the C.E.C. in sites where the pattern of Ca\(^{++}\) is quantitatively different from the other cations.

6. The quantity of C.E.C. in the F/H (Figure 33) has a similar relationship to the individual exchangeable cations as in the surface soil. Except for two cases, C.E.C. is either of greater quantity in the *E. pauciflora* ecosystem or the difference is very insignificant.

7. In the main, the form of the ratios for C.E.C. (Figure 26) and the exchangeable cations, (Figures 34 and 35), of the weight in the F/H to the weight in the surface soil, are similar and correspond to the same ratio for total Nitrogen (Figure 26).
except in the more disturbed ecosystems. There is usually a greater quantity of each of these cations in the F/H relative to the surface soil, in the *E. pauciflora* ecosystem than in the *E. delegatensis* system. Ca$^{++}$ and Mg$^{++}$ tend to exhibit greater differences in this ratio across the ecotone than the monovalent cations, C.E.C. and total N. In the more disturbed ecosystems the ratio is greater in the *E. delegatensis* stands, for most cations. Ca$^{++}$ differs from all other cations in having a much higher F/H:0-5 cm ratio in the lower-slope *E. pauciflora* ecosystems.

4.3.2.3.iv Phosphorus parameters

1. The L litter, F/H and surface soil show broadly similar trends for the concentration of total P, but unlike the cations, there is less significance of difference between the stands on either side of the ecotone in L litter than in other material. The concentration of total P in the F/H and surface soil is usually greatest in the *E. pauciflora* ecosystems, but there are some important exceptions. It is notable that P differs from the cations in being in lower concentrations, in both the F/H and surface soil, in most of the lower-slope *E. pauciflora* stands than the midslope *E. delegatensis* stands. There is little difference in P concentration across the more disturbed ecotones on sediments. In these sites total P in the F/H tends to be at slightly higher concentration in the *E. delegatensis* stands.

2. The distribution of total P as a weight expression in both the F/H and the surface soil (Figure 37) in relation to the ecotones is similar to the distribution of the concentration of total P in the great majority of sites.
3. The ecotonal distribution of the concentrations of $P_{\text{NH}_4 F}$ in both the F/H and the 0-5 cm soil (Figure 38) is almost identical to the ecotonal distribution of total P in the F/H and surface soil.

4. The effect of combining $P_{\text{NH}_4 F}$ and $P_{\text{NaOH}}$ as an expression of the concentration of non-occluded inorganic P (Figure 39) is for $P_{\text{NaOH}}$ to diminish slightly the degree of difference between the $E. \text{pauciflora}$ and $E. \text{delegatensis}$ stands. However the form of the ecotonal distributions of the concentrations of $P_{\text{NH}_4 F}$, $P_{\text{NH}_4 F+NaOH}$ and total P are all very similar in both the F/H and the surface soil.

5. The kg/ha ecotonal distributions for $P_{\text{NH}_4 F}$ and $P_{\text{NH}_4 F+NaOH}$ resemble the distributions of the concentrations of these parameters, although there are slight diminuations in the degree of difference in both the F/H (Figure 40) and the surface soil (Figure 41).

6. The F/H:0-5 cm soil ratios for both total P and $P_{\text{NH}_4 F+NaOH}$ (Figure 42) resemble the ratios for total N more than the cations. The ratios of both P parameters are expectedly very similar, except for the much higher ratios for total P on basaltic materials and the differences between the two in the recently disturbed sites, (on sedimentary materials). In these sites the ratios of the quantities of non-occluded inorganic P in the F/H to the quantities in the surface soil are extremely low. The successional significance of these low ratios is discussed in Chapter 5 (section 5.6.4). It can be concluded that total and non-occluded P are usually greater in concentration and quantity in the forest floor and surface soil of $E. \text{pauciflora}$ ecosystems than they are in the same

* correlations and regressions between total P and P fractions are presented in Chapter 5 (section 5.7.4.3; Table 7).
components of *E. delegatensis* ecosystems. However there are some significant exceptions to this direction of difference.

7. The distribution of the C/total P ratios (Figure 43) suggest that there are greater concentrations of P relative to carbon in the *E. pauciflora* ecosystems, although some ecotonal situations show lower ratios in the *E. delegatensis* ecosystems, notably on rhyodacite parent materials and with the 'old' understorey at Mt. Buller, Victoria. In the lower-slope *E. pauciflora* stands at the margins of subalpine valleys, the C/total P ratio, particularly in the F/H layers, is greater than in the *E. delegatensis* stands on the adjacent slopes. The differences in the C/total P ratio between the two ecosystems are greater in the F/H material. The ratio is always greater in F/H material than the surface soil.

8. In nearly all ecosystems, the N/total P ratio decreases in the order: L litter, F/H, surface soil (Figure 44). The ecotonal distributions of the N/total P ratio is broadly similar to the C/total P ratio, except that in most of the sites that have recently been disturbed by understorey fires, the ratio is greater in the *E. pauciflora* ecosystems.

4.3.2.4.v Soil "Physical" Parameters

1. The proportion of the surface soil (0-5 cm depth) contributed by the 0-2 mm diameter particle size is important in determining the quantity of nutrients in this layer. Analyses were restricted to separates of this fraction. The percentage of the 0-2 mm fraction is usually less in the surface soil of the *E. pauciflora* ecosystem, or the difference between the two ecosystems is insignificant. A notable exception is the extremely disturbed surface soil on
sediments (Figure 45, bottom right) from which the great majority of soil fines have been removed, presumably by post-fire erosion. It should be noted that there are considerable physical differences between the entire soil profiles of *E. pauciflora* and *E. delegatensis*. *E. pauciflora* sites (see Table 5, section 4.3.1.1).

2. Bulk density of the entire surface soil (Figure 45) does not relate to the proportion of fines in general terms, and bears little relationship to the ecotones between *E. pauciflora* and *E. delegatensis*.

4.3.2.5 Understorey Vegetation Parameters

1. In almost every ecotonal situation, there is a greater amount of grass as a percentage of total ground cover, beneath *E. pauciflora* than beneath the adjacent *E. delegatensis* (Figure 46). An exception is in one of the lower-slope ecotones at the margin of a subalpine valley (Tantagara Mt.), where because of a very dense shrub layer, there is a low grass cover in the *E. pauciflora* stand.

2. The shrub percentage of total cover does not show the same consistent pattern, but is usually less in the higher-slope *E. pauciflora* stands than elsewhere (Figure 46). The difference is most consistent in the areas that have been most recently subject to fire.

3. The ecotonal distribution of the total ground cover of understorey and ground plants is similar to the shrub percentage of total cover.

4. The understorey and ground layers of the *E. pauciflora* ecosystems are more diverse in species, according to an index of species
richness,* than the E. delegatensis ecosystems. This is probably a function of the greater number of herbaceous species in the ground layer of the former. In early successional stages (bottom row, Figure 47) species diversity changes are strongly associated with ground cover changes. The relationship is discussed in the following chapter.

4.3.2.6 Nutrient Analyses in the Forest Floors of Subalpine Eucalypt Ecotones in Tasmania

During an examination of the distribution of E. delegatensis at its upper altitudinal limit in Tasmania, a series of samples of F/H forest floor material was collected from the following ecotonal situations:

1. **Seal Lake, Mt. Field National Park:** E. delegatensis on slopes above E. coccifera on gravels, and E. coccifera on sandy peat.

2. **Arthur's Lake, Central Plateau:** E. delegatensis on slopes above E. pauciflora near lake margin.

3. **Sandbanks Tiers, Central Plateau:** E. delegatensis on slopes above E. pauciflora near margin of Great Lake.

4. **Todds Corner, Central Plateau:** E. archeri on ridge crest, E. delegatensis on midslopes and E. pauciflora on lower slopes.

5. **Mt. Ben Lomond, N.E. Tasmania:** a thin discontinuous band of E. gunnii on talus, above E. delegatensis on lower slopes, at tree-line.

* described in detail in Chapter 5 (section 5.6.6.2).
Complete tables of nutrient concentrations are presented at the end of Appendix III. A range of ecotonal situations was sampled to compare nutrient levels of the *E. delegatensis*: *E. pauciflora* ecotone with the widespread equivalent in the mountains of the mainland, and to see if other ecotonal situations bore any marked discontinuities in nutrient levels. All sites were on dolerite.

The analyses can be summarised by the following points:

1. Apart from the *E. delegatensis*: *E. coccifera* ecotone at Mt. Field, which is defined by a marked pedological change, there are no marked, and/or consistent separations of communities according to nutrient concentrations in the F/H.

2. In comparison with the mainland sites, total Ca is quite high, and K low, but both are very low in the higher rainfall area at Mt. Field, especially under the *E. coccifera* communities. Mg is generally in the low part of the range of concentration in the mainland mountains.

3. Ca$^{++}$ is always very low, and K$^+$ generally so, compared to the mainland mountains, but both are extremely low in the Mt. Field sites, particularly under *E. coccifera*, where values in the "peat" site were only 195 ppm and 83 ppm respectively. The concentrations of Mg$^{++}$ and Na$^+$ are relatively high, possibly because of oceanic causes.

4. Despite the low levels of Ca$^{++}$ and K$^+$ the C.E.C. is high in most sites, and in some cases higher than any levels obtained in F/H material in the mainland sites. The *E. coccifera* site on peat, at Mt. Field, is distinctly lower than any other Tasmanian sample.

5. Except for very low values in the wetter Mt. Field area, N is equivalent to most of the mainland samples.
6. Total P is equivalent to the mainland range of values, generally about 650-850 ppm, but is only 270 ppm under *E. delegatensis* at Mt. Field, and as low as 183 and 78 ppm in the adjacent *E. coccifera* sites on gravel and "peat" respectively.

7. Whilst $P_{NaOH}$ is no different in concentration to the mainland sites, $P_{NH_4F}$ (or Al-P) is very low, as a percentage of total P.

8. The C/total P ratio and N/total P ratio are both very high in most sites, especially in the Mt. Field area, and as the range of oxidisable C% is little different than in the mainland samples of F/H material, the conclusion must be that P is at relatively lower levels relative to C and N, in the Tasmanian mountains.

9. The C/N ratio is notably high only at Mt. Field.

4.4 DISCUSSION

The results provided good evidence of ecotonal variation in the concentration and quantity of essential nutrients, in terms of differences associated with a change in the composition of the dominant eucalypts. However it is unlikely that the ecotones at the limits to growth of *E. delegatensis* represent a threshold to the nutrient supply of this "site-sensitive" species. Rather, the results indicate the considerable influence of the geochemistry of the parent material in determining the levels of nutrients that are accessible to, and mobilised by, the eucalypt biomass on these young ground-surfaces. The effect of the biomass, and site differences, that can be observed at the eucalypt ecotones is secondary to parent material in determining the absolute concentration of a nutrient in a forest floor or surface soil, but is important in determining the difference between adjacent ecosystems. The bar-diagrams of the preliminary results (Appendix VI) show that generally the ecotonal
difference in a particular nutrient is only a slight proportion of the level of concentration.

The fact that trees themselves constitute one of the important environmental differences in areas where, as in much of the eucalypt forest biome, there is a strong control by individual species over the composition of the vegetation mosaic, has been alluded to frequently (Crocker, 1952; McColl, 1969; Moore, 1959). Moore's work (1959, 1961) on *E. melliodora* and *E. rossi* communities suggests that interspecific competition for nutrients may be a factor in determining the presence of a species of *Eucalyptus* on a particular site, even though the site may be favourable for the colonisation of both species separately. This argument is certainly relevant to *E. pauciflora*, at certain limits to its distribution,* but in the case of the present study the general level of the nutrient pool, particularly P, in the subalpine ecosystem and the high site-specificity of *E. delegatensis*, apparently for reasons other than nutrient supply, does not support it.

The general difference between the preliminary results (where the evidence suggested that *E. delegatensis* sites were distinctly more "fertile" than *E. pauciflora* sites) and the main study of ecotonal differences that tended, just as distinctly, to contradict this conclusion is, at first glance, puzzling. The difference could be explained by the fact that in preliminary sampling, the 5-15 cm soil depth was collected and in the main study it was the 0-5 cm depth. It is possible that a considerable part of the zone in which the pool of available nutrients is concentrated was bypassed in the former study. It could also be that the difference between the two studies is an artefact of the sampling

* where *E. pauciflora* actually adjoins species such as *E. rossi*, in sites where Ca and P are in very low concentration.
designs. In the main study a range of understorey successional stages and different parent materials was specifically selected, whereas the preliminary sampling was done with little regard to these features. The difference between the two groups of results may itself be interpreted as meaningful as it suggests that the successional status of the two ecosystems forming an ecotone could influence the degree of difference between the nutrient pools of the two systems. Many of the differences are so slight, as a proportion of the mean weight or concentration, that the changes in the redistribution of nutrients in the forest floor and surface soil to be expected during succession (see Chapter 5: Results), including a differential in the rate of change between \textit{E. pauciflora} and \textit{E. delegatensis}, could produce a shift in the direction of difference.

Given that, in the majority of situations where the ecotone was sampled, the parent material was constant for both species, the consistent differences between the respective nutrient pools must be explained in terms of internal differences of nutrient cycling, decomposition and the modification of the site by the community. It is certainly apparent that the two species are not competing for the same environmental space at critical nutrient levels, where there is some function for a genetical differential in the efficiency of uptake and remobilization of nutrients in the biomass. Measurements of the "vegetation space" as well as the litter-fall characteristics of \textit{E. delegatensis} and \textit{E. pauciflora} communities (see Figure 12; Chapter 6) suggest that the above-ground-biomass of \textit{E. pauciflora} open forest is only about 55% of that of \textit{E. delegatensis} tall open forest. In terms of the net content of essential nutrients in the soil, forest floor and living biomass, it would be expected, whatever the standing-state of the nutrient pool in the surface soil and forest floor, that absolute "higher fertility" is a characteristic of \textit{E. delegatensis} ecosystems rather than those of \textit{E. pauciflora} when the two
are in juxtaposition, simply because of this biomass dissimilarity.

Since net nutrient movement tends to be downslope, there is usually a general impoverishment of the higher-slope and crestal sites that tends to be reflected in distinctive vegetation patterns (McColl, 1967; Reiners and Reiners, 1970). As shown in Chapter 5, post-fire erosion is likely to be a factor in depleting the nutrient capital of upland sites. In the lower-fertility soils of the south coast of N.S.W., McColl (1967, 1969) has demonstrated a topographic sequence with specific eucalypt species dominating different nutritional positions on the slope and reflecting this in the nutrient content of their tissues. Further work by Beadle (1962) and Winterhalder (1963) on the higher-slope species, *E. gummifera*, and other species in the sequence, suggests that the species of low-fertility sites are almost certainly excluded from more fertile soils by competition from those species which can germinate more quickly after fire, given ample moisture and a greater supply of available nutrients, notably P.

Observations of the distributions of *E. pauciflora* and *E. delegatensis*, at their ecotone and elsewhere, support no other conclusion than that *E. pauciflora* is more tolerant of environmental fluctuations. *E. delegatensis* appears to have a relic distribution throughout the mainland mountains, characterised by marked regional (Figure 5) and local (Figure 4) disjunction. This can be explained in palaeo-climatic terms (Costin, 1971) and is supported in detail by eco-physiological studies (Farrell and Ashton, 1973; Grose 1960). Soil surface temperature measurements made in conjunction with a study of seasonal nutrient fluxes in one ecotonal situation (Chapter 6), indicate greater extremes of both maximum and minimum temperature beneath a *E. pauciflora* canopy. It seems from the site near Emu Plain, Toolong Range, in the Snowy Mountains that even if there is a basalt flow on higher slopes immediately
adjacent to granite at the maximum upper altitudinal limit of E. delegatensis, the species will not proceed beyond a specific microclimatic limit onto soils of obviously higher fertility. It is possible that the relatively low environmental tolerance of E. delegatensis is also expressed in a lower threshold to nutrient toxicity in such sites. In the above ecotone the concentrations of total P in the surface soils were 4250 ppm in the E. pauciflora ecosystem on basalt, and 943 ppm in the E. delegatensis ecosystem on granite. In trials of the growth of two eucalypts, E. gemmifera from low-P higher slopes, and E. maculata from higher-P, lower-slopes, McColl (1967) showed that E. maculata could not tolerate high levels of P at certain N levels, whereas E. gemmifera showed much greater tolerances to higher and lower P. It is clear that in terms of the nutrient pool in the forest floor and surface soil alone, E. delegatensis sites are not necessarily "higher fertility" than adjacent E. pauciflora sites, although in absolute terms, the litter-fall data reported in Chapter 6 suggest that they may be. There is some suggestion that the characteristic "site-sensitivity" of E. delegatensis is also a feature of its nutritional tolerances compared to E. pauciflora. Study of the interaction of cations and P availability may contribute further to an explanation of the distribution and growth of these species of Eucalyptus.

Only a few studies have specifically examined the micro-climatic aspects of the ecotone between E. pauciflora and E. delegatensis. In the Bennison High Plains in N.E. Victoria, Farrell and Ashton (1973) describe a gradient from a mixed woodland of E. rubida* and E. pauciflora on the ridge crest to a mixed forest of E. delegatensis and E. rubida on mid-slopes, a mixed woodland of E. pauciflora and E. stellulata on lower

* = E. dalrympleana?
slopes, then open woodland of *E. stellulata* and grassland on the valley floor. The variation in height of the eucalypts was considered to be as important as any other competitive factor contributing to the gradient, which is similar to many gradients with sharp discontinuities between the eucalypt dominants in the Snowy Mountains (Figure 7). Temperature studies in the woodlands at the margins of subalpine valleys (Costin, 1954; Bryant, 1971; Farrell and Ashton, 1973; C. E. Harwood, *pers comm*) confirm that these valleys are severe frost hollows with markedly lower frost frequency and severity towards the wooded margins. These studies are of considerable relevance to the phenomenon of 'timberline', which can usually be defined in specific terms of temperature extremes (Wardle, 1971), but the physiological mechanisms limiting tree growth are difficult to equate in the context of the overall botanical and micro-climatic differences between the subalpine valley tree-lines and the alpine tree-line at about 2000 m altitude. Minimum grass temperatures of -10°C are common in the former, and in exceptional winters grass minima may be as low as -18°C (C. E. Harwood, *pers comm*) and severe frosts extend upslope. It is these exceptional periods that are probably the most important in explaining the distributions of eucalypts in these situations, particularly if diurnal temperature fluxes during the spring are extreme. The parallel banding of *E. delegatensis* and *E. pauciflora* along the margins of subalpine valleys (Plate 1b; Figure 7: 5a, b: 6a, b) alone suggests that temperature extremes are primary determinants of their distribution. The considerable differences in site that are so apparent are secondary factors that serve to maintain the position of the ecotone following perturbation. The ecological character of these subalpine valley margins is described by Costin (1954),

"A very interesting topographically controlled micro-climatic sequence occurs on the gneissic granite in the lower subalpine and upper montane tracts of the north-western Monaro, where broad
valleys are strongly affected by cold air drainage. Under these conditions the coldest parts of the catena are the top and bottom of the slope and the warmest part in the middle. Thus the sequence of soils as observed near Boggy Plains, Tantangara, Long Plain and Gurrangorambla within a distance of no more than 300 feet, is alpine humus soil (subalpine woodland and sod tussock grassland) on the cold top of the slope; transitional alpine humus soil (wet sclerophyll forest) on the cool upper slopes; brown podzolic [cryptopodzol] soil (wet sclerophyll forest) on the warmest middle slopes; transitional alpine humus soil (wet sclerophyll forest) on the cool lower slopes; and alpine humus soil (sod tussock grassland and subalpine woodland) on the cold valley floor. In locally wetter sites the alpine humus soils are replaced by gley podzols, silty bog soils, or fen or bog peats."

As part of the present study measurements of weekly temperature extremes throughout the year were made at the soil surface in *E. delegatensis* and *E. pauciflora* where they form ecotones, in the Brindabella Range,

(i) with *E. pauciflora* on higher slopes (see Appendix X; Table 1, Figure 13),

(ii) with *E. pauciflora* on exposed N.W. slopes and *E. delegatensis* on S.E. slopes (Appendix IX).

These show that the extremes of maximum and minimum temperature are always higher and lower respectively, at the soil surface of *E. pauciflora* sites.

The frost experiments reported by Farrell and Ashton (*loc cit*) support the work of Grose (1960) who found a clear differentiation in resistance to chilling between *E. pauciflora* and *E. delegatensis*, associated with the survival of seedlings under a prolonged cover of melting snow. Their results based on the transition of eucalypt species on the Bennison High Plains showed a clear gradient of decreasing damage to the foliage of seedlings and coppices by water infiltration
under chilling conditions (2°C) in the order, *E. delegatensis*, *E. pauciflora*, *E. stellulata* and *E. rubida*. A preliminary frost experiment on hardened seedlings at -8°C resulted in a complete kill of both of the forest species, *E. rubida* and *E. delegatensis*, and moderate to severe damage to *E. pauciflora*.

Farrell and Ashton (*loc cit*) concluded that the discontinuous distributions of species in these situations due, in part, to differential low temperature environments was a function of topographic discontinuities compounded by the physiognomy of the species themselves. Thus, due to its faster growth rate, greater potential height and denser crown, *E. delegatensis* is able to out-compete the adjacent tree species on the deeper moister midslope soils. *E. pauciflora* can occupy the adjacent higher and lower slopes because of its ability to withstand the generally more severe environment of greater dessication, lower temperatures, greater temperature fluxes as well as drier, shallower and stonier soils.

The physical differences in soil materials at the ecotone are identified in Table 5 (section 4.3.1.1). These have not been analysed in this study, but should not be disregarded in differentiating the micro-environment. Florence and Lamb (1972) have indicated the importance of differences in soil volume and physical characteristics affecting infiltration and storage of water at ecotones between upland eucalypt species.

Grose (1960) in a series of controlled germination studies of *E. delegatensis* showed that given adequate nutrients, CO₂ and light, then temperature and moisture were the main factors controlling germination whilst dormancy was controlled by hereditary, not environmental, factors. Most seeds germinate simultaneously in October-November. Therefore rapid development of roots and shoots is vital for establishment before
any drying out of the surface soil becomes critical. Extremely low percentages of seed shed survive the winter stratification, spring germination and late summer moisture stresses. The nature of the forest floor and surface soil are critical to eucalypt establishment in these ecosystems.

Considering the observations that *E. pauciflora* is a site-tolerant species whereas *E. delegatensis* is comparatively site-sensitive, the nature of the ecotone can be summarised in terms of relative change in factor intensity. Becking (1968) represents the changes in factor intensities, at the same time in space, as wave patterns along ecological gradients (see Figure 9). Where factor intensities differ significantly and sharply along the gradient, a transition approaching an *ecotone* exists like the transition from *a* to *c*. Factor intensities change more gradually from *b* to *c* creating a transition more similar to an *ecoline*. In the ecotone between *E. delegatensis* and *E. pauciflora*, the intensity in change of topographically controlled factors (Figure 7) is a predominant feature, but the fact that the ecotone is no less contiguous on slopes of constant form indicates that a high intensity of change in species tolerance is also operative.

![Diagram](image)

**FIGURE 9** Factor intensity changes along an environmental gradient (after Becking, 1968)
CHAPTER 5
SECONDARY SUCCESSIONAL FLUXES IN FOREST FLOOR AND SURFACE SOIL NUTRIENTS, AND UNDERSTOREY SPECIES COMPOSITION

5.1 INTRODUCTION

In the Introductory chapter I advanced a working hypothesis that the successional development of subalpine eucalypt ecosystems can be defined from the principles of ecosystem development theory. Development will tend to proceed directly and inevitably towards a state of inertia, or dynamic equilibrium, following a perturbation. The process will tend to proceed continuously in an environment with a high probability of random perturbation and will be truncated according to the frequency of disturbance. As elaborated in the Introduction, and later in this chapter (section 5.3), succession is an orderly and predictive process with functional capacities to resist and/or recover from perturbation.

The effect of perturbation by fire in the subalpine eucalypt ecosystems is difficult to define in absolute terms because of the alteration of community structure since European settlement. It appears that perturbation was too severe to be resisted without a change in the biotic structure of at least the understorey, forest floor and surface soil components of the ecosystem. The concentration of nutrient pools in the latter two components has been noted in the Introduction. Secondary succession may therefore be defined in functional terms, to restore rates of net nutrient accumulation and change in the structure and composition of the community to a point where relative steady-state is attained.

In this chapter, the standing-state of nutrients and understorey of some 46 ecosystems of Eucalyptus delegatensis and E. pauciflora, representing an apparent range of successional stages, are differentiated
according to change in a time-dependent ecosystem component. The trends of these analytical data are examined in conjunction with the fire history of the region, aspects of the palaeoecology of the community dominants, and observations of changes in tree population structure concurrent with the onset of European settlement. The analytical data also describe the effect of a perturbation on nutrient pools and understorey vegetation. The following chapter describes a monitoring study of flux rates of nutrients between the tree and forest floor components. In the discussion (Chapter 7) all of the studies in this thesis are integrated to form a model of long-term ecosystem development in these ecosystems.

5.2 SOME THEORETICAL CONSIDERATIONS

Essentially the present study is the construction of a *chrono-sequence* (Stevens and Walker, 1970) in that the dependent ecosystem variables are assumed to be *chronofunctions*, within the limits of environmental variation, in the sense of

\[ E = f(T_{c1}, o, r, p, ...) \]  

(after Jenny, 1961)

that is; the magnitude of any ecosystem property \(E\) is functionally related to Time if the subscripts Climate, Biota, Relief, Parent Material and other factors are ineffectively varying. The papers of Jenny (1941, 1946, 1958, and 1961), on chronosequence theory insist that the soil forming factors act independently and that the extent of ecosystem [soil] development be measured with reference to a Time Zero (Stevens, 1968). In practice, the theoretical ideal is so unique that it is practically non-existent in the long-term (Park, 1972), or confined to monogenetic situations ('ontogenetic'; Nikiforoff, 1942) in short-term ecosystem
development. The alternative to measuring at one point in space through time, is the comparative measurement of a number of successional related ecosystems at one point in time. If the environmental factors are relatively constant (Crocker and Dickson, 1957; Stevens, 1963), individual ecosystems can be linked in a direct time sequence. Environmental constancy can rarely be assumed however, so the observer must maximise the number of sampled ecosystems and refer to trends and probabilities of change rather than the specific relationships between two samples.

Since the early work on ecosystem development of Cowles (1901), Clements (1904, 1916, 1936) and others, Time, or age-from-time-zero, has been the basis for system identification in succession studies. The resultant models of different kinds of 'climax' and types of succession need careful conceptual re-examination (Bakusis, 1969; Odum, 1969; Park, 1970, 1972). Time is not a factor that can be used for systems identification within the limits of systems analysis (Ashby, 1956; Theobald, 1966). This does not affect these chronosequences as models of ecological reality but simply removes Time from a conceptually untenable position. Invariably, chronosequence models are defined by parameters which are directly and entirely time dependent, e.g. age of groundsurface, or trees (Crocker and Dickson, 1957; Stevens, 1968). The substitution of such a parameter by one in which the successionaly related ecosystems are defined by only energy and matter co-ordinates (Park, in press) removes many theoretical problems in understanding ecosystem development (Bakusis, 1969). In constructing any multi-dimensional ecosystem framework, the objective information content is maximised by identifying a series of ecosystems within these fundamental co-ordinates. Time and space are not components of the ecosystem per se but of the field in which the systems are being related. However, in
practical terms Time is such a universal concept that it is certainly beneficial to refer to it wherever this is possible, particularly if an energy or matter co-ordinate can be shown to bear a linear relation to Time. Stephens (1947) considered Time to be the only independent factor and objected to its conceptual position in the chronofunction equation of Jenny. Enlarging upon an equation by Wilde (1946)

\[ \text{soil} = \int (g, e, b) \, dt \]  
(where \( g = \) geological substrate)  
\( e = \) environment  
\( b = \) biological actions

Stephens integrated the soil forming factors

\[ \text{soil} = \int f(c, o, r, w, p) \, dt \]  
(where \( f = \) state factors (collectively)  
\( w = \) water table).

In theoretical terms, 'ecosystem' can be substituted for 'soil'.

In the present study, the mass of the fine forest floor detritus excluding that of the previous seasonal litter fall cycle is used for system identification. In the absence of sufficiently precise records of fire history in the subalpine ecosystems examined, there were no means of establishing the linearity of this parameter with Time. The original intention was to construct a chronofunction using time since the last understorey fire as the primary co-ordinate for ecosystem identification. However as field work progressed, particularly during observation of the wildfires during December 1972-January 1973 in the Upper Geehi-Grey Mare area of the Snowy Mountains, the idea was abandoned. As well as the considerable variation in immediate fire effects within one locality, ranging from crowning and incineration of the entire understorey to scorching of ground cover or even the complete absence of any effect, it
is impossible to ascertain the cumulative effect of varying fire frequency and intensity within an ecosystem from fire history records. Although it is obviously convenient to have a true time scale in a study of secondary development in these ecosystems, the net quantity and quality of the forest floor at any point in time provides an ecologically more informative scale.

5.3 THE PRINCIPLES OF SECONDARY SUCCESSION IN FOREST ECOSYSTEMS

"To deny the role of successional species in the maintenance of forest ecosystem stability is to misunderstand the real significance of stability"

(Marks, 1974)

The general theories of forest ecosystem development (Odum, 1969, 1971, 1972; Whittaker and Woodwell, 1972) can be summarised as follows:

(a) Ecological succession is an orderly process of community development that is reasonably directional and therefore predictable.

(b) It results from modification of the physical environment by the community of living organisms, i.e. succession is community controlled even though the physical environment determines the pattern and rate of change and often limits the extent of development.

(c) It culminates in a stabilised ecosystem in which maximum function between organisms is maintained per unit of available energy flow. This steady-state ecosystem is characterised by a circulation of materials with minimal quantitative difference between input and output, and a population balance of natality and mortality. Steady-state defines a temporary state of dynamic equilibrium in an open system. The concept employs 'dynamic
equilibrium' as denoting adjustment in a non-reversible sense to a state of minimal change with time. Fundamental to the meaning of a steady-state is a minimum of continuous variation within and between all parts of the ecosystem; that every variable is, and is part of, a continuum (Webster, 1968; Park, 1970). (See also Whittaker and Woodwell (1972) quoted in Prologue.) In terms of the high probability of eventual disturbance to any forest ecosystem, stability has two components; a homeostatic capacity to resist perturbation, and a capacity to recover from perturbation, once the limits of resistance have been exceeded.

The strategy of ecosystem development (Odum, 1969) is increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations. Odum (1970) in his monograph "Environment, Power and Society" showed how fundamentally the strategy of maximum protection conflicts with the homocentric goals of maximum utility and production. The recognition of this conflict is the first step in establishing an ecological base for conservation management policies. The extremes in the ecosystem development sequence can be described by the model:

<table>
<thead>
<tr>
<th>youth</th>
<th>maturity</th>
</tr>
</thead>
<tbody>
<tr>
<td>production</td>
<td>protection</td>
</tr>
<tr>
<td>growth</td>
<td>stability</td>
</tr>
<tr>
<td>quantity</td>
<td>quality</td>
</tr>
</tbody>
</table>

(Odum, 1969)

Later, in discussing the significance of the results of the studies which are the basis of this thesis, I elaborate the theme that the modern role of fire in the majority of upland eucalypt forests and woodlands ensures that successional processes, and our knowledge of them, are under the continuous impress of homocentric goals. For example, we understand and utilize eucalypt regeneration in the terms of immediate
post-fire environments because it is at an optimum in such situations (Cunningham, 1960; Grose, 1963) whilst we know little of the relationships of the eucalypt regeneration that occurs in late successional stages, to a natality/mortality balance. The question of how temperate forests reproduce and maintain themselves cannot be separated from the question of how they respond to different kinds of disturbances (Marks, 1974).

In reviewing the role of successional species, Marks (loc cit) considers a complex disturbance gradient, involving both severity and frequency of disturbance. At one extreme, when disturbances are frequent and severe, ecosystems may actually depend on the occurrence of a particular kind of disturbance, such as fire or cyclones, for their maintenance and persistence. Under such conditions, succession is cyclic and involves a phasic replacement of predominantly successional species. At the other extreme, when disturbances tend to be rare and minor, forest reproduction involves the replacement of individuals or small groups which are not necessarily successional. Most natural forest regeneration is somewhere in between these extremes.

Depending on the severity of the disturbance, a certain amount of repair is necessary to regain, or maintain stability. If a disturbance leads to a new ground surface the process of recovery is primary succession. If only the plant community, or part of it, is removed leaving the ground surface more or less intact, the process of recovery is secondary succession. In the eucalypt forest environment, secondary succession is occurring continuously, because of the high probability of perturbation by fire. The characteristics of different eucalypt ecosystems can be defined in terms of the frequency and severity of fire (Jackson, 1968; McArthur, 1965). In the subalpine environment, the whole community may be altered by fire, but the morphology and aging patterns of the dominant eucalypts suggests that the evolutionary interval between perturbations
of this intensity is in the order of 200 years (Costin, 1969). However, the kind of perturbation that altered part of the biotic structure, the understorey and the forest floor, probably occurred at shorter intervals, although as will be seen from discussion of the fire history of these ecosystems (section 5.5) the biological time-scale of this kind of secondary succession is difficult to define, because of the extent of burning by Europeans during the last century.

Where perturbations commonly alter only part of the biotic structure, as in the subalpine eucalypt ecosystems, secondary succession will be proceeding towards steady-state simultaneously on two scales: the succession dominated by the tree component, and the succession involving the phasic replacement of understorey plants and changes in the structure of the detritus on the forest floor. Because the time-scale of the former is greater, both processes will eventually become synchronous, with a minimum of disequilibrium between the tree component and the component of the ecosystem that is recovering from perturbation. As perturbations of this kind become more severe and more frequent, the disequilibrium in nutrient cycling and energy flow between ecosystem components becomes greater, and the role of successional species in the maintenance of stability becomes increasingly important (Marks, 1974; Marks and Bormann, 1972). Successional plant species, typically unable to maintain themselves continuously on a given site (Egunjobi, 1969; Stevens, 1964; Major, 1955; Cröker and Dickson, 1957) are not usually conspicuous components of the stable ecosystem. However, a disturbance will inevitably create conditions that favour their germination, establishment and growth. Perhaps the most important factor limiting the ability of such species to colonise a disturbed site is the availability of seed, which must come either from a successional stand in close proximity or from storage in the soil following prior colonization of the
same site (or a combination of the two). Accordingly, successional
species have evolved at least two different dissemination strategies
(Marks, 1974). One relies exclusively on the continuous input of seed
from outside the site; the other, for example, the shrub Leguminosae
species in eucalypt and other sclerophyll vegetation, relies largely on
storage in the soil of dormant seed. Analysis of the seed buried in the
soil beneath woodland of *Eucalyptus pauciflora* (Howard and Ashton,
1967) showed evidence of seeds of legumes. *Acacia dealbata*, a
common understorey shrub in upland forests, has a longevity in excess
of 100 years (W. D. Jackson, *pers comm*).

In general, species of the Leguminosae contain root nodules in
which the bacterium *Rhizobium* is linked to somatic plant cells. These
bacteria convert atmospheric nitrogen into nitrogenous organic forms
enabling uptake for higher plant metabolism (Black, 1968). Although the
total nitrogen accession from such sources may not be large it is of
possible significance in many Australian forest soils where nitrogen is
relatively low and subject to frequent losses as a result of fire and the
harvesting of the biomass.

From the extensive work on *Alnus*, a nitrogen fixing genus commonly
occurring in early seral stages of northern boreal ecosystems, it is
clear that an important effect of nitrogen fixing species is the
influence of their litter on the decomposition nature and rate of the
litter of other species. Increases in soil nitrogen appear to result
more from the decomposition of enriched litter than from direct excretion
by nodulated roots. Research in both primary succession (Crocker and
Dickson, 1953; Crocker and Major, 1955; Stevens, 1968; Ritchie, 1966)
and secondary succession following fire (Egunjobi, 1969) involving
numerous species of the Leguminosae concludes that following the creation
of a new soil surface or alteration of an existing surface there is
usually a predominance of N-fixing higher plants whose presence has a profound effect upon the accretion of organic matter and N. The N-fixing species are eliminated later by other plants which occupy the site for a variable but lengthy period of time utilising the N accumulated by the N-fixing species. A large number of shrubs that are members of the Leguminosae, and probably N-fixing, are common understorey plants in the understorey vegetation of eucalypt forests in the subalpine zone. Where the interval between severe fires has been shorter than the minimum period from establishment to reproduction for the eucalypts, members of the Leguminosae tend to dominate the entire vegetation. Many of these genera, *Acacia*, *Bosssiea*, *Daviesia*, *Oxylobium* and *Pultanaea*, are associated with early successional stages and are particularly abundant in sites with a high fire frequency. Their relationship to the attainment of stability and N-accumulation are discussed in the results (section 5.6.6).

5.4 THE RELATIONSHIPS OF THE DEVELOPMENT OF SUBALPINE FORESTS AND WOODLANDS TO FIRE

"... their first job was to burn and keep on burning the woody shrubs and snow gums"

"In only one place did I see a snow gum stand in the almost natural state, with old trees 30-40 feet high and girths around 12 feet; in this case there were practically no dead trees, but all the trees were badly burnt at the butt. Under the stand was a light growth of snow grass."

"That fires of a severity sufficient to kill ash trees 150 feet high and 14 feet girth have increased tremendously in the last 100 years, is shown by the abnormally small number of fully grown or even half grown trees ..... the net result is that the ground is covered with a very heavy layer of inflammable scrub, the wind travelling up the narrow valleys reaches a very high velocity so that the fire, when burning up the slope takes everything in its path."
"I am quite safe in saying that 99% of the fires in the mountains are lit by human agency. People living in the mountains may talk about lightning glass bottles and spontaneous combustion, but anyone getting to know them well soon realizes what the mountain folk do not admit except among themselves, viz. that nearly all the fires are deliberately lit by stockmen for one reason or another; when a fire has broken out the locals know very well who lit it and if it happens to burn one of their own paddocks they feel justly annoyed, but having no definite proof, their only satisfaction lies in the hope that they will be able to get even with the man who lit it the following summer."

"Most of the fires are lit in the snow grass country or in the kangaroo grass foothill country, in both cases the fires spread into the steep slope [alpine ash] country which is not used for grazing and the man who lit it cares not where the fire stops. The fires in the foothill country generally come back into the fences of the cleared country, the owners of the cleared country then turn out and 'trail' the fire along their fences, sending it off into the hill country where, in their opinion, it will do no harm."


5.4.1 INTRODUCTION

For the purposes of this reconstruction of a fire history of the subalpine zone, the literature on fire is considered only as fire is a mechanism of disturbance, particularly to nutrient cycling, the composition and structure of understorey and ground vegetation, and long-term successional development. The immediate effects of fire on upland forest ecosystems have been extensively reviewed (e.g. Ahlgren and Ahlgren, 1960; N.S.W. Forestry Commission, 1966; Costin, 1969; Watson, 1972; Slaughter, Barney and Hansen, 1971; U.S.D.A. Forest Service, 1972) and will not be elaborated on, except where specifically cited in the discussion of the results of this study.
5.4.2 THE HISTORY OF PRE-EUROPEAN FIRES

Although today it is impossible to assess objectively the area of wildfires caused solely by lightning, the fact that it was a cause in the past is obvious. During the period, 1950-1965 lightning caused 16% of all forest fires in Victoria (Victorian Forests Commission, 1950-1965). It can be assumed (Heinselman, 1971) that in landscapes with a fire history, because of recreational, forest management and pastoral use, the location and frequency of most modern fires is 'unnatural'.

The most recent palaeoclimatic evidence (Costin, 1971, and pers comm) suggests that the major climatic changes of the Late Pleistocene in S.E. Australia (commencing about 32,000 years BP and continuing with gradual amelioration until about 10,000 years BP), either occurred before Aboriginal man reached the region, or effectively halted his movement into the high country. The alpine summits of the Snowy Mountains and the Victorian Alps probably became hospitable to man about 10,000 years BP. Determination of a more exact date is limited by scant information on the nature and scale of perturbations in the post-glacial environment (Costin, 1971). The recent evidence of Aboriginal man in the Monaro region (Flood, 1973) would suggest that his presence in the subalpine was confined to the last 8,000 years, that it was seasonal, localised and determined by the location of the important food source of Bogong moths (Agrostis infusa) on high rocky peaks, and to a lesser extent, the native 'yam' the daisy (Microseris scapigera aggr.) common in subalpine and alpine grasslands. The prehistoric cultural sequence for the Monaro region (Flood, 1973) spans only the last 4,000 years, from rock shelter evidence.

That man was earlier established at lower altitudes in the region is demonstrated by Flood's (loc cit) data from the Upper Buchan Valley,
in sites affording a more temperate climate immediately adjacent to the
main axis of the Snowy Mountains and the N.E. Highlands of Victoria.
Hancock (1972) has liberally estimated a maximum period of occupation
of 15,000 years, or 600 generations of Aboriginals. In terms of sub-
alpine ecosystem development, considerably fewer eucalypt generations are
involved, maybe 200-300 generations for 50-75 year secondary succession
cycles,* 80-100 generations for 100-150 year cycles, and as few as 60
generations for 250 year cycles, a scale for which there is ample
evidence from even the current vegetation of Eucalyptus delegatensis and
E. pauciflora aggr. (S. Barker, A. B. Costin, pers comm 1973; G.N.P.,
pers obs). There is little support in such an argument for the protagon-
ists of the viewpoint that these ecosystems have evolved under the impress
of regular aboriginal burning, although it is not uncommon for such a
viewpoint to equate the arrival of the European man in the early nine-
teenth century with less intensive burning of relatively low frequency,
if not exclusion of fire (King, 1963; Moriarty, 1974; Mount, 1969;
McArthur, 1962, 1970; Reischel, 1974). We have such little relevant
information on the probability of pre-European fire in the wetter
montane and subalpine eucalypt vegetation that the fire frequencies
estimated by advocates of a 'control-burning' policy in these ecosystems
has a range greater than 10-fold; from once every 30 years to once every
350 years (Gilbert, 1959; McArthur, 1970).

In a survey of mountain country now in Kosciusko National Park
during the snow-lease period of grazing, Byles (1932) was highly critical
of the extent of disturbance to the subalpine and alpine vegetation.
Byles had to consider the previous aboriginal inhabitants and concluded,
much in the manner of A. B. Costin some 40 years later,

* refers to replacement of trees by wildfire, not just forest and
woodland understoreys.
"... this climax [alpine ash] type is possible only if fires are absent or occur at long intervals, since, as we have seen, alpine ash is a species very readily killed by fire. Before the advent of white man in Australia, fires did undoubtedly occur, they were lit by the blacks on the grass country of the plains and no doubt some of them reached the mountains but the interval between successive fires was great and this fire-sensitive species was able to develop."

The modern notion that land management should endeavour to emulate the Aboriginal patterns of fire lighting, even assuming that they were of significance, was countered by Costin (1960) who has pointed out that our requirements from land and our attitudes to fire should be somewhat more varied and exacting than those of the Aboriginal who 'only burnt as an aid to hunting, probably for fun, and perhaps to intimidate early white explorers and settlers'. Costin (loc cit) and Floyd (1966) conclude that the vegetational response to fire in the high altitude communities reflects long-term development in an environment with only rare fire, otherwise these communities could not have produced mature, yet particularly fire sensitive, trees of 200 years age or more. Open floors are characteristic of such situations (Floyd, 1966; Jarrett and Petrie, 1929).

Even the dramatic accounts by Townsend (1860) of the incendiary behaviour of the Aboriginals of the Monaro region, restricts the burning to lower slopes, below the alpine and subalpine, during their summer incursions into the high country.

The use of fire for access and the immediate nutrition of game animals is well documented for the Aboriginals of Tasmania (Jones, 1968) and for peoples, generally, with hunting-gathering economies (Rappaport, 1972). The arrival of Aboriginals in Tasmania is also recent (Jones, 1969); however, both that author and Jackson (1965, 1968, pers comm: 1974), describe subalpine and montane Poa grassland and open woodlands
of *Eucalyptus delegatensis*, *E. obliqua* and *E. pauciflora*, maintained by Aboriginal burning, but reverting to forest in the last 130 years. There is nothing to suggest a scale of burning of this nature in the subalpine zone of the mainland, and on present evidence one can only assume a far greater utilisation of the same-eucalypt-dominated ecosystems by the Tasmanians.

There is some confusion of the inter-relationships of aborigines, early settlers and fire in the alpine-subalpine zone, with the more often recorded effects in the lower tablelands of N.S.W. Hancock (1972) discusses in detail the return of trees and scrub to this lower open country, and the closing of woodland systems to form forests following the disappearance of the Aborigine from the southern tablelands. In explanation, Hancock contrasts the light, regular burning practices of the Aborigines intended to keep hunting grounds open, with the exclusion of fire by Europeans intended to protect property, or burning of open woodlands and grassland to improve grass quality.

The anthropological evidence certainly supports the argument that where the Australian aboriginal went, he burnt. Observations of Arnhem Land aboriginals still practising a pre-European hunting-gathering economy (Rhys Jones, *pera comm* 1973) are that indiscriminate burning is a corollary to any movement of the people occupied with hunting. A given area could be burnt more than once annually to reduce grass in the eucalypt woodlands, if required for easy access. However, whilst we may accept Jones’ principle in the subalpine forests and woodlands, it is to be realised that his observations relate to flat to rolling topography with few, if any problems of access. In the higher areas of the Monaro, Flood (1973) concludes that aboriginal access was very limited, for specific food sources, and highly seasonal. It is most improbable therefore that the vast majority of subalpine eucalypt systems were
subject to fires from aboriginal sources.

5.4.3 FIRE AND HIGH COUNTRY GRAZING FOLLOWING EUROPEAN SETTLEMENT

"To the early settlers, grass was the most sought after vegetation, and so those areas providing a maximum of grass with a minimum of clearing were the first to be claimed. Later, extensive areas of forest and woodland were cleared to improve the grazing. It was learned that burning the forest floor induced a fresh growth of grass, which was more palatable to stock than the unburned grass, and so the forests were burned periodically. The burning however, also encouraged shrub species [Leguminosae] with mechanisms such as propagation from hard seeds, which enabled them to survive the fires and regenerate promptly. These shrubs are now so abundant, that vast areas of previously good forest grazing country are practically useless for that purpose. The fires also caused much damage to the trees. Those that were not killed suffered fire scars which provided ready access for wood-destroying fungi and insects."

(R. K. Rowe, 1967)

It is now doubtful whether any part of any alpine, subalpine or montane ecosystem, except in a few inaccessible areas, has escaped the effects of the land-use practices of European man (Bryant, 1969, 1971; Costin, 1951, 1954, 1958, 1967), particularly burning and summer grazing. Sequences of progressively altered ecosystems can be observed, depending on the frequency and intensity of use. The historical burning pattern is indicated by the higher fire-scar frequencies since European settlement in the forests of the Monaro region, near the periphery of tree stumps, than towards the centre (Costin, 1954). The effects of burning on the plant communities were considerable and are described in the following section.

The subalpine woodland of *E. pauciflora* has suffered considerable damage by fire, and in most areas in the N.E. Highlands of Victoria and in the Snowy Mountains has been converted to low forest or dense mallee-
form trees, dense scrub or grassland (Ashton, 1969; Bryant, 1969, 1971; Costin, 1967). Fire, either wild or controlled, destroyed saplings of at least 3 m in height. Subsequent grazing effectively suppressed regrowth of survivors (Bryant, 1971). The conversion of *E. pauciflora* woodlands to mallee scrub has been shown to have an adverse hydrological effect on the accumulation and melting of snow (Costin et al.). It appears that the repeated fires during the grazing era have been the cause of the development and extent of dense scrub in the montane and subalpine forests dominated by *E. delegatensis*, *E. dalrympleana*, *E. radiata*, *E. obliqua*, *E. fastigata* and associated species.

This in turn, has led to a greater probability of severe damage to the ecosystems from wildfire, in providing greater quantities of living and dead fuel. Wild fire in forests of *E. delegatensis* may kill the trees as this species is fire sensitive. Most other forest eucalypts have considerable vegetative capacities to withstand fire and for regrowth (McArthur, 1968; Cochrane, 1968). However the fire usually induces abundant seedling regeneration of the trees (Grose, 1963; Rowe, 1967). Even a light ground fire in the *E. delegatensis* forests, although not killing the trees may form fire scars providing access to decomposers (Rowe, 1967).

There are very few data on the early patterns of burning, associated with burning in the subalpine areas of Victoria and New South Wales, particularly the periodicity of burning in the more mountainous areas. Costin (1954), states that until the Kosciusko State Park Act (N.S.W. Government, 1944), burning in this region was practised annually in the montane, subalpine and alpine areas, and in places was still continuing at that time. Grazing by cattle probably dates from about 1835 (Bryant, 1971) in the Snowy Mountains. Use of the area was promoted by the Kiandra gold rush (1859-61) and the protracted drought in the adjacent
lowlands between 1885 and 1905. The Snow Lease Act, under which grazing was permitted, remained in force until grazing was progressively terminated up until the summer of 1957-58 when those areas above 1370 m (4500 feet) within the then Kosciusko State Park were excluded from further grazing. A few years later some of the grasslands and woodlands and forests within cold-air-drainage valleys were reopened to summer grazing under snow lease conditions (Bryant, 1971). This situation is still occurring in drought years, for example the 1972-73 summer. However, there is considerable opposition to the practice amongst conservation groups.

In the N.E. Highlands of Victoria, very few fires were lit by graziers until about 1890 (Fawcett, 1940), but miners were responsible for many fires in the 1850-60's. The open understorey of the old forests and their conversion to dense scrub by the cattlemen's fires was described by Andrew (1921) and later Rowe (1967) concluded that it may take many years of protection from fire, and perhaps grazing also, to allow the natural processes of succession to re-establish the open grassy nature of these forests. Grazing is still continuing in much of the Crown land in the Victorian mountains and on freehold land, but burning is under the control of Forests Commission. Investigation of forest assessment records (Forests Commission of Victoria) by the present author showed repeated reference to regular burning in the last 60-70 years.

Byles (1932), a critical observer of grazing and burning practices in the high altitude alpine ash and snow gum ecosystems, drew attention to the ecological importance of the ballotted lease system of grazing rights under the Snow Lease Act, the indiscriminant use of fire for the 'improvement' of the grass ground cover (and later the reduction of a shrub cover), and access up the steep forested slopes as cattle were
driven from the lowland plains. The spread of fire into areas not of interest to the grazier was not prevented. At the time of Byles' study virtually all the forest land in the upper catchment of the Murray (i.e. the Gibbo-Pilot-Pinnabar areas in Victoria, and the majority of the western Snowy Mountains) was under some kind of short term grazing tenure. Practically all the subalpine and alpine country, within the rolling plateaux above 1200 m was held under 5-7 year leases, at an annual cost of 2.5-6.0 pence/acre. Blocks varied in size from 3,000-10,000 acres (1200-4000 ha). The snow gum and alpine ash communities of steeper slopes between 950 m and 1450 m were held under tenancies that varied from year to year, the rental from 0.1-2.3 pence/acre/year in 1,000-60,000 acre (400-24,000 ha) units depending on the "quality" (my italics) of the land.

Under the impress of such a system of land-use, which prevailed in some districts for 100 years, it is not irrelevant to describe the absence of any protection, concomitant with ownership, as an ecological stress. The history of the period of high country grazing underlies the current dilemma of future conservation of these ecosystems, the magnitude of probable wildfire damage, and the ecological problems of renewed grazing rights (cf. Moriarty, 1974) which is still a political issue.

5.4.4 THE RECENT ROLE OF FIRE IN MANAGING UPLAND FOREST VEGETATION

"Ironically, it is our traditional approach to protection that is being questioned today with regard to management of national parks and wildernesses. Rather than just protecting these wildlands from fire, insects, and disease, we are beginning to discuss strategies to protect these areas from ourselves and man-centred goals."

(Aldrich and Mutch, 1972)
of growth and production (Hendee and Stankey, 1973) which are characteristics of instability and youth in ecosystems (Odum, 1969, 1972). The role of fire in modern resource management and protection in the eucalypt forests of Australia is homocentric to the extent that it has become almost irrelevant to rationalise the changing role of fire in a historical context because of the enormity of the modern fire risk. Whilst the legacy of the grazier in altering forest succession may be recognised, it is accepted that a policy of regular 'fuel reduction' is economically more realistic than waiting for understorey succession to proceed through a prolonged state of high fire risk.

In ecological terms, there is a continuum from the grazing period until the present day. Studies in the Snowy Mountains have shown the disastrous effects of frequent light fires combined with grazing on both the catchment and the biological quality of the alpine and subalpine zones (Wimbush, 1974). The published evidence indicates that since European settlement, there has been increase in the frequency of severe wildfires (Pryor, 1939), and consequently large tracts of even-aged young forests, and an increase in the frequency of ground fires causing the development of 'fire scrub'. Being highly inflammable, these shrubs increase fire frequency, perpetuating the shrub understoreys. Because vegetation in this state predominates in the landscape, it increases the fire risk in a district, and tends to perpetuate even-aged immature forests. In forests with this structure, secondary succession will be characterised by continuing 'fuel' accumulation on the forest floor, as fine fuel weights are considerably below the point of equilibrium between litter production and decomposition. Since wildfires

* see section 5.6, on results of this study.
† approximately equivalent to the F/H layer of the forest floor.
seem inevitable in this situation, the use of prescribed burning to reduce fuel accumulation, usually to below about 13 tonnes/ha (Blake, 1973), is often recommended and hence the concept of 'fire hazard' has strong appeal.

This study does not attempt to formulate a conservation management strategy that will accommodate both the modern homocentric demands on these ecosystems and their biocentric time-scale of development. In the subalpine forests and woodlands that ideal is impossible at the one place and time (cf. Odum, 1969). Instead my aim has been to construct a model of long-term successional development in order to describe the trend towards the steady-state, whether or not such a state has itself any 'reality' in the subalpine eucalypt ecosystems.

5.4.5 RESPONSES OF THE UNDERSTOREY VEGETATION TO FIRE

An important objective in this part of the study has been the amalgamation of all data on understorey vegetation from different sites, representing the range of response to different kinds of perturbation, differing net response to a long-term history of perturbation, and the changing response in time since a perturbation.

The most abundant species of shrub in the understories of forests and woodlands throughout the subalpine zone are members of the Leguminosae, notably Daviesia latifolia, D. ulicina, D. corymbosa, Acacia dealbata, A. obliquinervia, A. polymorpha, Platyllobium formosum, Bossiaea foliosa, Oxylobium alpestre, Hovea longifolia. As well as subterranean renewal buds, like some of the eucalypts, the legumes have hard seeds with extreme longevity under forest floor conditions. W. D. Jackson (pers. comm., 1974) has noted seeds of Acacia spp.* in the forest floor of

* taxonomically similar to understorey species in the subalpine forests of the mainland.
Tasmanian *Nothofagus* forests. This forest type replaces *Eucalyptus* forest in long-term succession, and *Acacia* is associated with only the latter. After 100 years the seed is still viable. In the drier forests of the mainland, the combination of post-European burning and the increasing density of leguminous understoreys would suggest a vast store of seeds in the forest floor with this kind of longevity. The elimination of Leguminosae as shrubs can be shown to occur over about 30-40 years depending on the site. The elimination of Leguminosae seeds is not as simple. It bears enormous implications for the determination of conservation and wilderness policies in a wildfire environment.

In a study of the subalpine forests of the A.C.T. at the northern limit of the subalpine zone, Pryor (1939) concluded that continued periodic burning of the understorey resulted in an increasing accumulation of undecomposed litter and an increasing density of xeric understorey shrubs over a given period. Pryor drew attention to the diminishing areas of high altitude *E. delegatensis* forest with pre-European characteristics which he summarised as:

1. maximum uneveness of dominants
2. maximum height of dominants
3. minimum density of understorey shrubs
4. maximum density of vascular plant cover of forest floor
5. maximum species richness of plant cover of forest floor
6. maximum constancy in mass of litter on forest floor.

Thirty-five years later, following the 1939 fire, continuation of high country grazing until 1958 and the development of fuel-reduction burning the area of subalpine vegetation with pre-European features has been further reduced. The features noted by Pryor, which were a useful guide in the early field-work for this study, can now be only rarely observed. "Maximum height of dominants" is a characteristic more of
mature forests that regenerated in large even-aged pure stands, than of strictly pre-European systems. Most of the trees in the forests and woodlands of the entire subalpine zone, certainly in the stands measured in this study, are less than 75 years old.

Pryor (1939a) considered that, despite variation because of site and the intensity and frequency of previous fires, there are clear trends in the secondary succession of the understorey vegetation of high altitude E. delegatensis forest. His observations were for the northern part of the Snowy Mountains. Immediately following fire, the forest floor is usually colonised by Parahebe derwentia, Poa spp., Stylidium graminifolium, Ranunculus hirtus, Viola hederacea, and at lower altitudes, also Pteridium aquilinum.

After about a year, the shrub legumes, Acacia dealbata, A. obliquinervia, A. falciformis and Daviesia mimosoides and Cassinia aculeata form an increasingly closed upper understorey over the lower stature shrubs, Daviesia ulicifolia, Bossiaea foliosa and a sparse ground cover dominated by Poa spp., Brachycome scapiformis, Ranunculus hirtus, Tetraheoa ericifolia, Viola hederacea and Parahebe derwentiana. Any regenerating eucalypts tend to assume dominance.

If the dominant eucalypt trees are undisturbed by fire, there is no further growth of eucalypt saplings. The only change in the understorey is a gradual replacement of shrub Leguminosae by shrubs typical of the more mature forest, Coprosma hirtella, Lomatia longifolia, and Drimys xerophila. Pryor's observations (loc cit) were that the shrub cover becomes more open and the ground cover more dense, and richer in species, with time. Rowe (1967) describes a similar succession in N.E. Victoria. Except for the higher rainfall areas in southern Victoria and Tasmania, observations in forest assessment survey records (Forests Commission of
Victoria) suggest that succession of understorey species is more or less equivalent throughout the subalpine zone, in terms of both composition and structure.

Whilst successional patterns in the understorey beneath a 'forest' (Specht et al., 1974) canopy are the immediate object of the vegetation study in the present work, it is important to consider change involving the whole community. As a result of excessive alteration of some sites, it appears that deflections in the development of the entire community are occurring. The frequent burning by graziers, in cases until the late 1950's, in the Snowy Mountains converted much of the fire-sensitive *E. delegatensis* forest to *E. dalrympleana* and *E. pauciflora* (Byles, 1932; Costin, 1954; Newman, 1955; Pryor, 1939). A similar shift in the composition of the dominants, *E. regnans* and *E. delegatensis* to *E. obliqua*, has been described by Gilbert (1959) in Tasmania, and also occurs in Victoria. The same species can be replaced by scrub species if the intervals between successive severe fires are less than the minimum period for reproduction (Jackson, 1968, and pers. comm; Ashton, 1970). Costin (1966) estimated that roughly 10% of all the high mountain catchments of the Australian mainland have actually been deforested by European fires and grazing. Numerous authors (Ashton, 1970; Bryant, 1971; Costin, 1954, 1967; Rowe, 1967, 1970) relate the widespread communities of coppiced *E. pauciflora* with a 'mallee' habit, to the same factor. Repeated burning of these communities may also result in even-aged scrub of Leguminosae and Epacridaceae species which mature in 20-30 years and later develop into a shrub-grassland, for example, the slopes between Perisher Creek and Guthega in the Snowy Mountains.

In the wetter upland eucalypt forests of southern Victoria and Tasmania, burning for regeneration increases the area covered by sclerophyll understorey at the expense of rainforest understoreys.
(Cremer, 1963; Cunningham, 1960; Cunningham and Cremer, 1965). Mount (1964) observed that at the start of each 'rotation' following fire, the sclerophyll species appeared to control the site, and at the end the rainforest did. Ashton (1970) showed that on certain sites, such as steep slopes and poor soils in high rainfall areas, losses of nutrients would be likely following repeated burning. This would permit the dominance of sclerophyll species.

5.5 SOME ASPECTS OF THE PALAEOECOLOGY OF THE SUBALPINE FORESTS AND WOODLANDS

5.5.1 DISTRIBUTION

From the disjunct present-day distribution of *E. delegatensis* (overlays, Figure 5) and *Notofagus cunninghamii* (Howard, 1974), and the scant palaeoecological evidence from the northern mountains of S.E. Australia (e.g. Costin, 1971; Jennings and Caine, 1968) there is a valid case that the high altitude ecosystems of *E. delegatensis* evolved in the geographic presence of, and in seral relationship to, *Notofagus*. In Tasmania and the southern highlands of Victoria one can observe clear seral relationships between the two genera of the form; immature eucalypt forest of 1000-250 trees/ha where the successional cycle induced by wildfire was 25-80 years; mixed eucalypt/rainforest with 250-40 eucalypts/ha where the cycle is 80-100 years; and *Notofagus* forest with rare eucalypts where the cycle is longer (Jackson, 1965, 1968).

The increasing mesicity of the seral gradient to *Notofagus* is duplicated latitudinally from the northern Snowy Mountains to southern

*E. pauciflora* is not associated with *Notofagus* in Tasmania, but restricted to drier subalpine areas. However mixed communities do occur in the southern highlands of Victoria, e.g. Baw Baw Plateau and Lake Mountain.
Victoria and Tasmania. This, together with the presence of subfossil evidence such as the 35,000 years old *Notothfagus* affin. *cunninghamii* stump under the block stream on the Toolong Range (Jennings and Caine, 1968) is important in any speculation of the evolutionary status of the present-day subalpine eucalypt ecosystems. Even today, *Notothfagus cunninghamii* is not far removed from the main subalpine areas of N.E. Victoria and the Snowy Mountains (Howard, 1974). An extensive search of early survey records of forest composition, held on file in the Forests Commission of Victoria, by the present author revealed reference to isolated trees of *Notothfagus* in gullies adjacent to the Nunniong Plateau, N.E. Victoria. The species does not appear as a major forest component until the valleys of southern Victoria.

Studies of the rates of lateral colonisation of *Notothfagus* in New Zealand (Holloway, 1954; Wardle, 1964) and Patagonia (Auer, 1966; D. R. McQueen, *pers comm*) suggest extremely slow centripetal migration, relative to extinction, since the late Pleistocene. In reconstruction of the palaeoecological relationships of *Notothfagus* and the subalpine species of *Eucalyptus*, the considerable differences in rates of seedling success, reproductive maturation and biogeographic 'rebound', following perturbation to forest type distributions, must be considered.

Other 'rainforest' elements in the uplands of S.E. Australia exhibit very disjunct distributions, that suggest a more widespread mesic climate than the present-day. In these mesothermal situations, for example, the lower Geehi Valley in the Snowy Mountains, the Nunniong Plateau, and the Errinundra Plateau in the coastal ranges of southern N.S.W., species such as *Atherosperma moschatum*, *Hedycarya*, *Elaeocarpus*, *Bedfordia salicina*, *Dicksonia antarctica* and numerous ground ferns, all common at greater latitudes, form multilayered understoreys associated with the lower altitudinal limits of *E. delegatensis*. Costin (1954)
commented on the absence of *Nothofagus cunninghamii* from the coastal ranges in southern N.S.W., and considered that this species was a dominant in valleys during the mild, and more humid conditions during much of the Pleistocene.*

5.5.2 COMMUNITY STRUCTURE

Examination of the structure of older *E. delegatensis* communities, or remnant old trees within predominantly younger forest (Plates IIIa, VII, VIII and IX) and old *E. pauciflora* communities (Plate IIb), as part of this study suggested a successional trend to woodland from the widespread younger forest communities (Plates IIa and IIIb) if the interval between severe perturbations is long enough. Their relative distribution in the landscape suggests that the probability of *E. pauciflora* proceeding to a woodland from forest is greater than *E. delegatensis*, for a given period of time. In ecotonal stands of common age, the rates of thinning and mortality are greater for *E. pauciflora*. Evolutionarily, the interval between severe fires, i.e. ecosystem age, would expectedly be greater with increasing altitude. Ashton (1969) has reported a decline in the development of lignotubers, an anatomical adaption for fire resistance (McArthur, 1970), from 300-1200 m altitude in populations of *E. pauciflora*. Green (1967) related other morphological clines, not necessarily related to fire, to altitude in populations of *E. pauciflora*. Today, low, open woodlands of *E. pauciflora* are more common at higher altitudes, † than where the species adjoins *E. delegatensis*.

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* There is no *Nothofagus* pollen in a peat section (max. age 11,000 years BP) on the Errinundra Plateau (P. L. Ladd, *pers comm*, November, 1974).

† often referred to as *E. niphophila*, 'a small, crooked alpine tree or mallee, with several whip-stick-like stems springing from a large woody rootstock' (Maiden and Blakely, 1933). Green (1967) considered that this form was simply fire regrowth; mature, undamaged trees appear to be always single stemmed at the highest altitudes.
A. B. Costin (pers comm) and S. Barker (pers comm) have obtained dates in excess of 200 years from the oldest and predominant age class in woodlands of *E. pauciflora* in the northern Snowy Mountains (Plate IIb). Widely spaced trees, often greater than 2 m dbh are common; more accurate ages are difficult to obtain because of the extent of decay in the older rings. There is little information on the long-term population dynamics of the subalpine eucalypts, and in this study a number of assumptions have been made about regeneration (see Chapter 7; section 7.4) in deriving a general model of succession. Nevertheless, it is clear that in sites where the tree population structure has been initiated by a severe fire, both *E. delegatensis* (Plates IIIb, Xb) and *E. pauciflora* (Plates IIa, Xa) regenerate in even-aged stands. *E. delegatensis* is killed by fire and regenerates only from seed, whilst *E. pauciflora*, also killed by fire, will regenerate from both seed and lignotuber. In the trees of large even-aged stands, the bole height to the first branch will be greater than in a tree that grows alone or quickly dominates a small group of saplings. Pryor (1939a) noted that most of the trees in the few remaining old communities (>150 years age) of both species have very low bole heights, considerably less than in nearby even-aged stands, up to 100 years old. This suggests that the old trees did not arise from large even-aged groups (formation of which commenced about 1850 AD) and that the post-European fire cycles did not occur 200 years previously, when the oldest trees established.

It is not uncommon to note in forest survey records, a considerable frequency of severe fires following European settlement. Costin (1954) and in later papers refers to a marked increase in large fire scars during the period. Pryor (1939b) noted an interval of only about six years between 11 major fires from 1876 to 1939. In N.E. Victoria records show major fires in 1851, 1898, 1917, 1932, 1939 and 1944 (Forests
Commission of Victoria). In the pre-European condition, reproduction of eucalypts and shrub Leguminosae would have been rare in the highly endorganic soil beneath virtually a total cover of grass and herbs (Plate VIb). Maintenance regeneration would require disturbance of the dense ground cover and mineral soil (cf. Grose, 1963) as provided by branch and stem windfall and marsupial burrowing.

Barker (pers comm, 1973) has noted massive regrowth of seedlings in 250 year old *E. pauciflora* open woodland (Plate IIb) following the sudden removal of the grazing stress in 1957-58, and considered that the structure of the communities would have been maintained if grazing had been gradually phased out. By 1958, the effective cover of the soil surface had been markedly reduced, and the composition of the understoreys sufficiently altered as to change the whole effect of light burning and grazing (Bryant, 1971). The resultant seedling and sapling growth is now so dense in many areas that a wild fire could destroy many old open woodland communities, and lead to dense stands of multi-stemmed individuals (c. 1000 stems/ha) characteristic of much of the snow gum country throughout the subalpine zone (Plate IIa).

The seral replacement of eucalypts by rainforest species in the southern upland forests has been well documented (Gilbert, 1959; Ashton, 1955; Jackson, 1968) although the evolutionary ecology of the ecosystems dominated by the same eucalypts in the geographic absence of *Nothofagus*, and other rain forest species has received little critical examination. Florence (1968) reviewed the concept of succession towards rainforest in the sclerophyll forests of eastern Australia and concluded, with support from his own earlier work (Florence, 1964), that the complete expression of development in these forests is rainforest. The complete succession is usually restricted by the joint influences of eucalypt forests on
their sites, and periodic fire. For Tasmania as a whole, Jackson (1968) has gone as far as saying, "there would appear to be no aspect, soil type, or edaphic situation which cannot be occupied by cold temperate rainforest".

The preceding hypothesis of the development of the same eucalypt ecosystems in the absence of rainforest elements, suggests that as the open eucalypt forest matures the population shifts towards a natality/mortality balance, that the steady-state community becomes a woodland with an open grass-herb understorey. Certainly, the long-term successional trends would be different from where these eucalypts have a seral status in proximity to the present areas of cold temperate rainforest, or had so, in a more extensive palaeo-distribution of rainforest.

The alternative, long-term cyclic succession (Watt, 1947), postulated by Florence (1968) to explain purely eucalypt forest succession, cannot be considered in isolation from the succession to rainforest, or to open woodland. Probably both kinds of succession occur simultaneously in the subalpine landscape. If the seral development of the subalpine forests is examined in the context of general theory of forest ecosystem development, in which fire is considered as "a superimposed factor affecting the relative occurrence of species adapted to specific habitats, rather than as a major determinant of broader species patterns" (Florence, 1965), it is probable that seral eucalypt communities could perpetually maintain themselves in the absence of dominance-competition stresses, between species, that would be features of the majority of long-term successions in temperate forests. Instead, the primary stress on seral stages is because the inherent seral features, instability and imbalance, of ecosystem processes and components, render the immature forest liable to perturbations that can set succession back to initial seedling establishment.
PLATE II

A young dense thicket stand of *E. pauciflora* (c. 1000 stems/ha)
Mt Skene, Victoria

An old open woodland stand of *E. pauciflora* (c. 50 stems/ha)
Kings Cross area, northern Snowy Mts
Old open woodland stand of *E. delegatensis*, on dolerite boulder-field
Sandbanks Tiers, Central Plateau, Tasmania

Tall open forest of *E. delegatensis*, Mt Pinnabar, NE Victoria

PLATE III
Open forest of *E. delegatensis*, its upper altitudinal limit, near Emu Plain, Toolong Range, northern Snowy Mts
- 42.5 tonnes F/H per ha, only a few leguminous shrubs in understorey, and dense grass-herb ground cover

PLATE IV
Open forest of *E. delegatensis*, at its upper altitudinal limit, Tantangara Mt, northern Snowy Mts. Trees are c. 100 years old, but young forest floor - 16 tonnes F/H per ha understorey dominated by leguminous shrub spp.

PLATE V
A dense understorey of leguminous shrubs in a low open forest of *E. pauciflora*, regenerated since 1939, Wilson's Valley, Snowy Mts.

A dense ground cover of grass, ferns and herbs, from which shrubs have been eliminated during succession, at upper altitudinal limit of *E. delegatensis*, Mt Buller, NE Victoria.

PLATE VI
PLATE VII.

Tall woodland of senile tall-boled trees of *E. delegatensis* that regenerated in an even-aged regrowth forest, Toolong Range, Snowy Mts. Regeneration is occurring in patches in disturbed mineral soil.
A remnant old tree of *E. delegatensis*, whose low bole and deep crown suggests establishment in an uneven-aged woodland vegetation rather than the younger open forest now occupying the site, Mt Buller, NE Victoria
Old short-boled, deep-crowned trees of *E. delegatensis* surrounded by younger tall-boled shallow-crowned trees, and understorey of leguminous shrubs, Lake Mt, E. Victoria
5.6 PRESENTATION AND DISCUSSION OF ANALYTICAL RESULTS

5.6.1 INTRODUCTION

The analytical results reported in this section are divided for convenience into four loosely-named and arbitrary groups:

5.6.2 "Organic" parameters. (Oxidisable carbon, loss on ignition, nitrogen, C/N ratio)

5.6.3 Cation parameters (total calcium, iron, potassium, magnesium, manganese, sodium and zinc for soils; total calcium, potassium and magnesium for the L and F/H components of the forest floor; exchangeable calcium, potassium, magnesium and sodium and cation exchange capacity and ratios between the exchangeable and total fractions of each element)

5.6.4 Phosphorus parameters (total and organic phosphorus, non-occluded inorganic phosphorus, phosphate sorption; ratios of both nitrogen and oxidisable carbon to total phosphorus and the non-occluded inorganic fractions)

5.6.5 "Physical" parameters (reaction, weights of L, F/H and components of the 0-5 cm soil depth, soil bulk density)

5.6.6 Vegetation understorey parameters. Growth forms as % of ground biomass cover, % of total cover, % of total number of species, species diversity.

5.6.7 Fluxes in nutrients and vegetation immediately following wildfire in Kosciusko National Park. Discusses changes in organic matter and nutrients, forest floor/surface soil, and in the composition of the understorey in the first 10 months after a fire.
5.6.1.1 Presentation of Analytical Results

The problems of constructing a method of presenting and interpreting results within the limits of a true time-function have been described in Section 5.2. Environmental variation, particularly between and within parent material types is considerable in the study area. In order to encompass a maximum of variation in understorey vegetation and the rate of accumulation of organic matter on the forest floor during succession, 46 ecosystems were sampled, and included in the plotting of results.

In the absence of a strictly time dependent scale on which to measure successional change, the variation in nutrient, organic matter and understorey parameters is related to the mass of the F/H component of the forest floor.

In the following descriptions, and in the Tables and Figures in Volume II that accompany this section, all results have been converted to an oven-dry basis. Complete results appear in the tabular matter (Appendix III), where they are arranged so all analytical results from individual ecotones between adjacent stands of *E. delegatensis* and *E. pauciflora* are grouped together in one table. This serves the purposes of both Chapters 4 and 5.

It proved impossible, in practical terms, to present all forest floor and surface soil data in tables where the variables from all 46 ecosystems were tabulated according to the mass of the F/H.

For the graphical illustration of results, 62 selected parameters, utilizing all 46 stands, are related to the mass of the F/H and a quadratic function derived for the relationship. These paramenters comprise Figures 48-81 in Appendix II. The figures were drawn in the following way:
1. A least squares non-linear regression of the form, \( y = a_0 + a_1x + \frac{1}{2}a_2x^2 \), was derived for each pair of co-ordinates, the \( x \) axis in all cases being the mass of the F/H component of the forest floor, and the \( y \) axis denoting some aspect of nutrient composition, organic matter, or the understorey vegetation. Stand positions were located and a curve [for \( y = f(x) \)] fitted using a Hewlett-Packard plotter.

2. Stand positions were defined according to the identity of the dominant eucalypts: \( E. \) delegatensis (■) and \( E. \) pauciflora (▲).

3. It is assumed, for the purposes of this study, that the successional accumulation of organic matter above the mineral soil increases until there is a marked and continued opening in the mature forest canopy with the onset of senility in the canopy trees. The net accumulation of organic matter is, however, a function of changing conditions in the forest floor environment and cannot be assumed to be linear in time. The mass of the F/H component is a valid index of progressive change with time, only up to its own quantitative peak (position B in Figure 10).

![FIGURE 10](image-url)

(a) arrangement of stand data as quadratic functions in this study.

(b) arrangement of stand data, according to mass of F/H, but showing the limitations of this criterion as a 'true time scale'.
An open woodland stand of *E. pauciflora* (A, in Figure 10a) (see also Plate IIb) has been included in the graphs of results. It is denoted separately (⊙) in all figures. Whilst the mass of the F/H in this stand is only 10.3 tonnes/ha, it is a feature of ecosystems with a protracted 'fire-free' understorey rather than recent perturbation. If a 'true time scale' were possible for the X axis, the position of this stand would shift from A₁ to A₂ (Figure 10b). The relative distribution of nutrients (weight/area) defined by the Y axis between the origin and point B is representative of all nutrient parameters examined. The distribution of nutrients between B and A₂ is inferred. Some of the F/H layers beneath a grass-herb ground cover, for example, the sites at Emu Plain, Toolong Range, Snowy Mountains (Plate IV) and at Mt. Buller (Plate Vlb) are of lower weight than the estimated maximum. They are plotted as C₁ (Figure 10b) but may be more accurately positioned at C₂ on a true time scale (see also section 7.3 (Chapter 7)).

Only brief descriptions will be made of the results, which are sufficiently described as graphs in Appendix II. The scale of environmental variation, particularly parent material, is such that many of the results can only be interpreted as trends or probabilities of change. However, it is evident that the scale of dispersion between the 46 ecosystem-points can be narrowed by expressions of relative accumulation of nutrients in the forest floor, for example the ratio,

\[
\frac{\text{weight of nutrient } x \text{ in F/H}}{\text{weight of nutrient } x \text{ in 0-5 cm soil}}
\]

Some ecosystem-points are described in detail, for example the relative position of the open *E. pauciflora* woodland discussed above, the very disturbed soils beneath stands of both *E. delegatensis* and *E. pauciflora* on Ordovician sediments in the Brindabella Ranges, A.C.T., and the samples collected from the Upper Geehi Valley immediately after
the wildfires during the 1972-73 summer. In the latter case the F/H data must be considered, as the ashed material above the mineral soil represented incinerated understorey plants as well as the forest floor.

In the selection of the 62 parameters, some concentrations of nutrients (ppm) are plotted, but greater consideration is given to nutrient weights (kg/ha) as these are more meaningful in a dynamic ecological sense (Walker, 1965). In some cases, one or two cations are used to demonstrate the dynamics of cations in general.

5.6.2 "ORGANIC" PARAMETERS

Analytical data illustrating the accumulation of organic matter in the F/H layer relative to the weight of the 0-2 mm fraction of the surface soil, the accumulation of N in the F/H relative to the surface soil, and the actual accumulation of N and oxid. C in the F/H and surface soil are graphed in Figures 48, 49 and 51a. As both a F/H:0-5 cm ratio and the actual weight expression, N tends to accumulate (up to 1300 kg/ha at a greater rate than either oxid. C or total weight of the F/H layer). In successional studies, there is often a stated relationship between the accumulation of N and the botanical succession of macro-N-fixing plants. In this study, although Leguminosae spp., which dominate the shrub understorey layers, have virtually disappeared from the understorey by the stage represented by 60 tonnes/ha of F/H, (Figure 78), the accumulation of N and oxid. C continues at a rate greater than that of the F/H. However, the position of the open woodland stand (10.3 tonnes/ha; F/H) suggests that once there is a change in the litter input:decomposition balance, there is a rapid decline in the rate of accumulation of N in the F/H, to the extent that there is a continuing net loss in weight to about 300 kg/ha. There is no significant trend in the accumulation of N in the 0-5 cm soil (Figure 51a). However,
immediately after fire in the Geehi sites, the weight of N was as high as 6 tonnes/ha, but these levels appear to wane during the early stages of succession, and in the exceptional disturbed surface soils from sediments in the A.C.T. mountains, there may be as little as 500 kg/ha in the upper 5 cm of mineral soil. Generally there is about 2-3 tonnes/ha of N in these early stages. It is interesting to note the extremely high levels of soil N (> 7 tonnes/ha) beneath the open E. pauciflora woodland (Plate IIb). If the Geehi post-fire sites and the open woodland site are removed from consideration, the distribution of points defining the accumulation of N (tonnes/ha) in the 0-5 cm soil suggest increasing accumulation between 0-20 tonnes F/H per ha, maximum accumulation between 20-40 tonnes/ha, and then a decline. The trend is not significant but could be explained in terms of the concomitant maximum development of macro-N-fixing shrubs, and their subsequent diminution (Figures 78-80). Analyses were not made of the N concentration of understorey shrubs, but there is no trend in the concentration of N in the eucalypt L litter (Figure 52a) to suggest that the trend of N accumulation in the surface soil is attributable to the eucalypt canopy.

The amount of N in the F/H (Figure 49a) tends to be relatively high immediately after fire, at which stage there was only 2-3 tonnes/ha of ashed forest floor and understorey material above the mineral soil. Following a considerable decline, this quantity of N in the F/H is not re-attained until there is a F/H weight of 35-40 tonnes/ha above the mineral soil. In the older sites (> 50 tonnes/ha) as much as 50% of the total N in the F/H and upper mineral soil is held in the F/H, whilst only about 30% of the combined weight of primary fines and organic matter is within the F/H.

Oxid. C in the F/H accumulates steadily, and in a manner similar to the accumulation of the F/H layer as a whole. There is a lack of any
apparent steady-state in any curve representing the accumulation of organic matter. Although there is some curvilinearity in the relationships of accumulation of oxid. C and N to the accumulation of the F/H layer, simple regressions showed very highly significant correlations ($p < 0.001$) of $r = 0.898$ and 0.903 respectively.

Figure 50 shows a tendency for C/N ratios to narrow progressively in the F/H from maxima greater than 60, and rise in the surface soil to equilibrate in the later stages of the succession beneath a grass and herb ground cover at about 15, perhaps maintaining this level as the canopy opens, litter fall declines and decomposition becomes more efficient with the development of an open woodland (Plate IIb). In both the F/H and the surface soil beneath *E. delegatensis* and *E. pauciflora* there was a markedly narrow C/N ratio immediately after the wildfires in the Upper Geehi sites (January, 1973) compared to other recently disturbed sites examined in this study. However, the narrow C/N ratio probably represents a large temporary store of 'surplus' N (Figure 49a) rather than a decomposition balance. The dispersion of ecosystem-points in the C/N distributions is probably a function of the local variation in decomposition conditions.

5.6.3 CATION PARAMETERS

The successional dynamics of selected cationic elements and their ions, expressed mainly in terms of nutrient-weights (kg/ha) in the F/H and surface soil, are illustrated in Figures 53-62. Details of all nutrient concentrations and weights are tabled for each ecosystem in Appendix III.

The comparative dynamics of nutrients in general, in the F/H and surface soil are illustrated for C.E.C., expressed on a weight basis, in
Figures 53 and 54a. The C.E.C. accumulates in the F/H at a slightly reduced rate than the F/H itself, but in a closely linear manner, particularly in the earlier stages. During the same period, i.e. from zero to about 80 tonnes/ha of total F/H, there is a net but scarcely significant decline in C.E.C. in the surface soil. If expressed as a F/H:0-5 cm soil ratio, it is apparent that C.E.C. is accumulating on the forest floor at progressively greater rates as long as the forest floor itself is accumulating, to the extent that at the stage of 70 tonnes of F/H per ha, the ratio is about 0.6. It is only 0.05 at the stage of 10 tonnes of F/H per ha. It is obvious that there are similarities between changes in C.E.C. and the accumulation of oxidisable C, in the F/H (see Figure 49a). Linear regression utilizing the mean values of 46 ecosystems showed a significant (p < 0.05) relationship, whereby, C.E.C. (ppm) = 8790 +136.6 oxid. C % (r = 0.296; r² = 0.087). Linear regression of the dynamics of C.E.C. and oxid. C in the surface soil shows a positive, but non-significant, relationship of the same form. Stevens (1968) in a study of primary succession and soil development showed highly significant relationships between C.E.C. and oxid. C %. In fact, oxid. C % was an overwhelming determinant of C.E.C. compared with other factors, as shown by multiple regression. The net change in C.E.C. in the F/H relative to the surface soil (Figure 54a) is greater than the comparative rates of accumulation of the individual exchangeable cations examined, Ca²⁺, K⁺, Mg²⁺, and Na⁺ (Figures 61 and 62). There is consistence in the distributions of each cation for this same ratio, but at different scales. In the older forest floor situations, the ratio of F/H Ca²⁺ or Mg²⁺ to the surface soil Ca²⁺, Mg²⁺ may be as great as 2.0 compared with a maximum ratio of 0.6 for C.E.C., 0.75 for K⁺, and only 0.45 for Na⁺. The dispersion of ecosystem-points about the determined function for the F/H:0-5 cm soil ratios of the weights of exchangeable cations is least for K⁺. This may be attributable to the fact that in
the only upland eucalypt ecosystems studied in terms of nutrient cycling, K has a cycle in rainwater more than in plant litter (Attiwill, 1971) which could place it in a position relatively independent of the geochemical variation in parent material.

There is a marked difference in the accumulations of monovalent and bivalent cations in the F/H. The weights (kg/ha) of Na⁺ and K⁺ (Figures 54b, 56a) are closely linear to the weight of the F/H layer, and have a similar distribution to the accumulation of C.E.C. and oxid. C. The bivalent cations, Ca⁰⁺ and Mg⁰⁺ (Figures 55a, 57a) show quite a different distribution, rising sharply to about 70 and 9 kg/ha respectively, at 50-60 tonnes of F/H per ha, but declining as the F/H continues to accumulate.

Ca⁰⁺ is clearly the dominant exchangeable cation (in most cases, more than four times the weight of the next most abundant cation, K⁺). The markedly non-linear distribution of Ca⁰⁺ and Mg⁰⁺ is probably a function of their very rapid accumulation during the early stages of succession. There is comparatively little significance in the dispersion of ecosystem-points in the later stages. Between zero and 20 tonnes of F/H per ha, Mg⁰⁺ is accumulating at more than twice the rate of the F/H mass. In montane forests of E. obliqua, Attiwill (1964) found that these cations began to accumulate in the forest floor at quite early stages in a succession that commenced with the even-aged regeneration of the canopy trees. The rates of accumulation of Na⁺ and K⁺ are, respectively, slightly less and slightly greater than the rate of accumulation of F/H.

It can be assumed that the great majority of cations accumulating in the F/H have either been cycled through the biomass or are input from atmospheric sources. However the same assumptions cannot be made about the
cations in the surface soil. The majority of the soils sampled contain much weathered primary material, which continues to supply ions available to plants to the nutrient pool. The wide range in the total cation and phosphorus composition of the soils has been described earlier (Figures 85 and 86; Appendix VIII).

Despite these limitations, there are marked trends in the weight distribution of individual exchangeable cations in the surface soil. In some cases, the degree of dispersion of ecosystem-points about the quadratic function is not much greater than in the weight distributions of the cations in the F/H. This would support the earlier observation that the concentration of a particular nutrient in the L and F/H layers, to an extent, reflects the concentration of the nutrient in the mineral soil. This applies particularly to Ca$$^{++}$$, and to a lesser extent to Mg$$^{++}$$, which have cycles almost completely in plant litter in these forests (cf. Attiwill, 1964, 1971).

There is a consistent grouping to the weight distributions of monovalent (Na$$^+$$ and K$$^+$$) and bivalent (Ca$$^{++}$$ and Mg$$^{++}$$) ions in the surface soil (Figures 58, 59) as well as in the F/H. Ca$$^{++}$$ and Mg$$^{++}$$ have very similar declining distributions during the succession and appear to maintain low levels if the succession proceeds to open woodland (Plate 11b). Both cations show considerable dispersion in the early stages of F/H accumulation, with very low values for the group of heavily disturbed soils from sediments and high values in the soils from acid igneous rocks, which generally do not have such disturbed surfaces. Clearly, if the group of disturbed surface soils from sediments were removed from the regression there would be very steep declines in the weights of these cation fractions in the surface soil as the F/H accumulates, from about 500 kg/ha Ca$$^{++}$$ and 50 kg/ha Mg$$^{++}$$ to less than 100 and 10 kg/ha respectively (the least squares function falls to zero by 75 tonnes of F/H per ha).
Although there is little apparent meaning in the trends of $K^+$ and $Na^+$, it is obvious that as a group, the disturbed surface soils from sediments contribute to the degree of dispersion of points about the function. Without these points there would also be a distinct net decline of these cations in the surface soil. However the very low levels under deep forest floors, observed for $Ca^{++}$ and $Mg^{++}$, are not apparent. By the stage of successional development represented by open woodland (Plate IIb), it would be expected that much of the exchangeable cation pool stored in the F/H under conditions of accumulation of organic matter, becomes incorporated in the upper mineral soil. The results suggest that the monovalent ions regain high levels in the soil similar to the earliest undisturbed successional stages. However the bivalent cations, particularly $Ca^{++}$, remain at low levels. This may be an artefact due to including only the one open woodland ecosystem.

Total $Ca$, $K$, $Mg$ and $Na$ were determined by wet digestion so that the nutrient supply characteristics of the various parent materials as well as the nutrient cycling and accumulating characteristics of the $E. delegatensis$ and $E. pauciflora$ ecosystems could be estimated. Total $Fe$, $Mn$ and $Zn$ were determined simultaneously, but are not plotted as quadratic functions because of the relatively large intra-site variation. The conclusion is inescapable that the inherent variation of these elements particularly $Fe$, in the subalpine soils is not adequately encompassed by the sample size used in this study. Data of all cationic elements are presented in Appendix III.

The dispersion of points in the distributions of total cationic elements relative to the accumulation of F/H did not suggest a trend of any nature, not even a disjunct grouping of the disturbed soils from sediments. Apart from the effect of parent geochemical variation (see Figures 85 and 86, Appendix VIII), this dispersion is, to a great extent,
TABLE 6  Regression formulae and correlation coefficients (r) for significant linear relationships in the concentrations (ppm) of exchangeable and total cations from 46 ecosystems.

(A)  total cation in F/H and total cation in surface soil\(^{+}\)  

<table>
<thead>
<tr>
<th>Cation</th>
<th>Regression Formula</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca (F/H)</td>
<td>(2944 + 1.500 \text{ Ca (0-5 cm)})</td>
<td>0.750 ***</td>
</tr>
<tr>
<td>K</td>
<td>(611 + 0.556 \text{ K}^{\text{+}})</td>
<td>0.869 ***</td>
</tr>
<tr>
<td>Mg</td>
<td>(682 + 0.592 \text{ Mg}^{\text{+}})</td>
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(B)  exchangeable cation in F/H and exchangeable cation in surface soil  

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</thead>
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<td>Ca(^{++}) (F/H)</td>
<td>(1480 + 1.134 \text{ Ca}^{++}(0-5 \text{ cm}))</td>
<td>0.505 ***</td>
</tr>
<tr>
<td>K(^{+})</td>
<td>(284 + 0.947 \text{ K}^{\text{+}})</td>
<td>0.311 *</td>
</tr>
<tr>
<td>Mg(^{+})</td>
<td>(205 + 1.479 \text{ Mg}^{\text{+}})</td>
<td>0.637 ***</td>
</tr>
<tr>
<td>Na(^{+})</td>
<td>(18.04 + 1.054 \text{ Na}^{\text{+}})</td>
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(C)  exchangeable cation in F/H and total cation in surface soil  

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<td>Ca(^{++}) (F/H)</td>
<td>(1480 + 0.241 \text{ Ca (0-5 cm)})</td>
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<td>K(^{+})</td>
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<tr>
<td>Mg(^{+})</td>
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</tr>
<tr>
<td>Na(^{+})</td>
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(D)  total cation in F/H and exchangeable cation in surface soil  

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<td>Ca (F/H)</td>
<td>(3492 + 5.89 \text{ Ca}^{++}(0-5 \text{ cm}))</td>
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<td>Mg</td>
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(E)  exchangeable cation in F/H and total cation in F/H  

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<td>Ca(^{++}) (F/H)</td>
<td>(1929 + 0.012 \text{ Ca}^{++})</td>
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<tr>
<td>Mg(^{+})</td>
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</tr>
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(F)  exchangeable cation in surface soil and total cation in surface soil  

<table>
<thead>
<tr>
<th>Cation</th>
<th>Regression Formula</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca(^{+}) (0-5 cm)</td>
<td>(42.22 + 0.171 \text{ Ca (0-5 cm)})</td>
<td>0.793 ***</td>
</tr>
<tr>
<td>K(^{+})</td>
<td>non-significant</td>
<td>-0.183</td>
</tr>
<tr>
<td>Mg(^{+})</td>
<td>non-significant</td>
<td>0.095</td>
</tr>
<tr>
<td>Na(^{+})</td>
<td>non-significant</td>
<td>0.187</td>
</tr>
</tbody>
</table>

\(^{+}\) = 0-5 cm depth.
a function of the youth of the soils, their considerable lithic content, and the continuing deflation of fines in the upper parts of the profile. Thus there is little continuing deflation of fines in the upper parts of the profile. Thus there is little correspondence between this study and chronosequence studies of the fate of cationic elements in soil profile development (e.g. Franzmeier et al., 1963; Stevens, 1968). The time scale of soil profile development proceeds at pedo-geochemical weathering rates, for example in a warm superhumid climate the average percentage loss of K from aggregated soil and weathering rock is approximately only 0.1%/1000 years (Hensel and White, 1960; Stevens, 1968). In this study, I am concerned with the net change in the cationic elements during a single secondary succession cycle of the vegetation, which is unlikely to exceed even 250 years. A large component of the total cations in the forest floor and surface soil has either been cycled several times in similar fashion, or is input from atmospheric sources. This would suggest that exchangeable cations are a more valid parameter of cycling rates than total elements. However the comparative distributions of the two fractions, as F/H weight is increasing during the succession, indicates complex dynamics of cation accumulation, immobilization and mobilization rather than a simple recycling of a distinct 'exchangeable' fraction.
$K(F/H) = 611 + 0.556K(0-5\text{cm soil}) \quad r = 0.869$

$K(L) = 1096 + 0.042K(0-5\text{cm soil}) \quad r = 0.339$

$P(F/H) = 312 + 0.61P(0-5\text{cm soil}) \quad r = 0.907$

$P(L) = 405 + 0.09P(0-5\text{cm soil}) \quad r = 0.472$

FIGURE II Simple linear regressions of the relationships between total K and total P in the forest floor layers and the surface soil. Data from 46 ecosystems.
Simple regression analysis for 46 ecosystems of the concentrations of cationic elements in the L litter, F/H and surface soil (Table 6) suggest that the levels of total cations in the soil have a stronger influence on the concentrations of nutrients recycled from the biomass, i.e. their concentrations in the L litter, and the concentration of nutrients in the accumulating F/H layer, than the levels of exchangeable cations in the surface soil. To an extent this is an artefact of the sampling method, as nutrient supply characteristics are being assessed only at the time of sampling. In Attiwill’s (1964) opinion, the critical period of nutrient supply (in forest of E. obliqua) is from the commencement of the new forest succession to the ‘pole’ stage (cf. Plate 11a). Beyond this stage, there is a net accumulation of nutrients in the forest floor that have been returned from the living biomass.

Ca\(^{++}\) is the only ion, in the F/H and the surface soil, to bear a significant relationship (in fact, as high as \(p < 0.001\)) to the concentration of the parent element in the soil and in the F/H. This could be explained in terms of the relatively high concentrations of Ca\(^{++}\) relative to total Ca. The other ions investigated have extremely low exchangeability relative to the total concentration, in the F/H as well as the surface soil. The concentration of K\(^+\), for example, in the F/H is usually about 10\(^\%\) of the total K in the F/H, whereas Ca\(^{++}\) is about 35-50\(^\%\) of the total Ca. Similarly, the concentration of K\(^+\) in the 0-5 cm soil is only about 4\(^\%\) of the total soil K, whilst Ca\(^{++}\) is about 25-30\(^\%\) of the total soil Ca. Even in soils where the concentration of total K in the surface depth is as high as 13,000 ppm, the concentration of K\(^+\) is only about 350 ppm. Ca is quite distinctive from the other cationic elements in that it exhibits significant correlations between its total and exchangeable concentrations, within and between the F/H and the 0-5 cm soil.

\* these percentages are approximate averages from very wide ranges.
Ca++, Mg++, Na+ and C.E.C. show very highly significant relationships between their concentrations in the F/H and the 0-5 cm soil. K+ shows a significant relationship. Total K shows at least significant concentration for the L, F/H and surface soil. The nature of the accumulation of total cations is different from the accumulation of exchangeable cations, relative to that of the F/H. The accumulation of Ca, K, Mg and Na is more rapid initially (up to about 25 tonnes of F/H per ha) and at far greater quantities (2X for Ca, 6X for K, and 10X for Mg), but later occurs at a progressively slower rate (Figures 55b, 56b, 57b). These data, more than any other, define the forest floor of the subalpine eucalypt forest as a zone of immobilization as well as accumulation. There appears to be a point at which there is a decline from the considerable peak quantities of all total cations (> 200 kg/ha Ca, 120 kg/ha K, and 140 kg/ha Mg), although the F/H layer is still accumulating. It would seem that there is a threshold to the immobilization of cationic elements prior to the threshold of net organic matter accumulation, late in the 'forest' productivity succession. Tentatively, the differential could be explained in terms of increasing decomposition efficiency, and increased incorporation of organic matter within the mineral soil as a result of long-term microbiological efficiency with the development of a grass and herb ground cover (cf. Wood, 1971) (Plates IIb, IV, VIb).

The independence of the concentrations of individual cationic elements in the biomass is indicated by the distributions of total Ca and K (Figure 62) in the L litter. The relatively distinct trend in total K appears to be related to the successional process and suggests that accumulation and immobilization of K in the forest floor and surface soil (Figure 55, 57b) could be sufficient to reduce the uptake of the element by the biomass. There are similar rates of accumulation of Ca, at greater scale than K, but with no apparent effect on uptake.
Relatively tight cycling of K is also suggested by the linear regressions (Table 6) showing K as the only cationic element to bear very highly significant correlations between the concentrations in the L, F/H and 0-5 cm soil.

5.6.4 PHOSPHORUS ANALYSES

Analytical data describing the concentrations, weights and F/H:0-5 cm soil weight ratios of total P, organic P, and the fractions of non-occluded inorganic P (NH₄Cl-P, NH₄F-P, and NaOH-P) in the L litter, F/H and surface soil are tabulated in Appendix III, in conjunction with other nutrient analyses. Some 28 parameters, selected to illustrate the dynamics of phosphorus, are plotted against the accumulating weight of the entire F/H layer. These plotted data and the derived quadratic functions (Figures 63-77) are the basis of this description of results.

5.6.4.1 Total Phosphorus

No marked trends with successional age in the concentration of total P (ppm) in the L litter, F/H, or surface soil are evident (Figures 63, 64a) except for the very low concentrations in the very disturbed groundsurface from sedimentary rocks in the A.C.T., (F/H, 3 tonnes/ha) and an old site on muscovite granite on Mt. Buffalo, Victoria (F/H, 54 tonnes/ha). (Concentrations are generally about 200 ppm in L litter, 400 ppm in F/H, 200 ppm in surface soil.) The wide dispersion of ecosystem-points is more noticeably a feature of the total P distribution than of organic P or the non-occluded inorganic fractions and resembles the variation in the concentration of the total cations, in that it is a function of the lithic nature of a range of soils from different parent materials. The extent of the control of geochemical variation in the parent materials on the accumulation of soil P is indicated by the
very similar dispersion of points in both the concentration (ppm) and weight distribution of P (Figure 64). The soils with less than 7 tonnes of F/H per ha are, as a group, very low in P concentration (< 700 ppm) and more noticeably so in the weight of P (about 200 kg/ha). In this respect, the P concentration of the subalpine soils distinguishes them from the eucalypt forest soils at lower altitudes, where the concentration of P is characteristically, perhaps notoriously, low, generally in the order of 200-400 ppm (Attiwill, 1964; Beadle, 1962, 1966). At these levels, the concentration of total P in the biomass is higher in the foliage and forest floor than in the soil. As P is recycled in the foliage, removal of large portions of an immature biomass, on soils of this order of P concentration may lead to P deficiency in the early stages of secondary succession (Attiwill, 1964).

Except for the ecosystems on basaltic materials, where the P concentration of surface soil may be greater than 2000 ppm, there is a general equivalence in the concentrations of total P in the L litter, F/H and the surface soil. In the soils of apparently low P, from Ordovician sediments and rhyodacite, the concentration of total P in the soil is often less than in the F/H and L litter. The concentration of non-occluded inorganic P fractions combined in the surface soil is only about 25-30% of the total P. The discrepancy suggests that considerable amounts of the total P pool are bound either as organic P or occluded inorganic forms, in the living biomass and the forest floor detritus. To a very significant degree, total P uptake and accumulation tend to be at concentrations that correspond to the relatively high concentrations of total P in the surface soil (Figure 30b). The data suggest that the uptake of P in the subalpine ecosystems is in the order of luxury consumption, compared to the *E. obliqua* ecosystem studied by Attiwill (1964).
Simple linear regression of the relationships between total P in the 0-5 cm soil, and in the L litter and F/H were significant at the 1% level:

\[ P_{\text{total}}(L) = 404.9 + 0.090 P_{\text{total}}(\text{surface soil}) \quad r = .472 \quad *** \]

\[ P_{\text{total}}(F/H) = 314.9 + 0.614 P_{\text{total}}(\text{surface soil}) \quad r = .907 \quad *** \]

Only in the high-P ecosystems on basaltic materials is the concentration of total P in the L and F/H appreciably less than in the 0-5 cm soil.

The slightly higher concentrations of total P in the F/H compared to the L litter in most ecosystems (Figure 63), suggests some immobilization of P in the forest floor. The slight decline in the quadratic function (Figure 63b) may indicate some re-mineralization of this P during the later stages of the succession beneath a grass and herb ground cover and a 'forest' canopy (Plates IV, VIb).

It is probable that because the absolute amounts of total P in the fines (0-2 mm dia. fraction) are in such high supply in the vast majority of the young surface soils in the subalpine zone, the apparent net loss of total P from the surface soil is countered by the formation of organic and non-occluded and occluded P. It may be noted that the non-occluded fractions of soil P do not exhibit the decline characteristics of the exchangeable cations and C.E.C.

Stevens (1968) noting that the amount of any element in the fine fraction is the result of the balance between loss to the vegetation and leaching processes and gain from the weathering of coarser fractions, observed a similar lack of any marked decline, or trend, of total P in the fines in early successional stages in a low-P environment, although the total P of the whole solum was declining considerably.
There do not appear to be any problems of availability in the later stages of the long-term succession from forest to woodland in these ecosystems. The highest levels of total P in the L litter of any ecosystem measured, were about 1000 ppm in the open woodland of *E. pauciflora* (Plate Iib). Total P is also at high levels in the F/H of this ecosystem, although the surface soil data do not suggest markedly high concentrations or weights of total P.

Quadratic functions of the weight-distributions of total P (kg/ha) in the surface soil (Figure 64b) and the F/H (Figure 65b) broadly resemble the equivalent functions for the exchangeable cations. However, the accumulation of total P in the surface soil appears to be more a function of the geochemical variation between the different parent materials (cf. Figure 64a) than a result of the successional redistribution in the ecosystems, that is a feature of the quantitative distribution of the exchangeable cations.

The accumulation of total P in the F/H bears a very highly significant relationship to the accumulation of the F/H layer as a whole, remarkably so in the early stages of secondary succession (Figure 66b). The linearity of the relationship is expressed as:

$$ P_{\text{total, kg/ha (F/H)}} = 1.502 + 0.783 \ F/H \ \text{tonnes/ha} \quad r = 0.764 \quad *** $$

Thus the scale of total P accumulation to some extent overcomes the inherent geochemical variation in total P concentration.

The results support the thesis of Attiwill (1964) that the commencement of net return of total P to the forest floor, following re-establishment of a eucalypt community, occurs at later stages of succession than of the cations. However, the fact that total P in the F/H is accumulating at almost exactly the same rate as the weight of the entire
F/H further confirms the hypothesis that P uptake and return by the biomass is at luxury levels, in contrast to the montane *E. obliqua* ecosystem studied by Attiwill. Clearly, if P is recycled within the biomass, as it is in the low-phosphorus *E. obliqua* ecosystem, there appears to be little nutritional requirement for it to do so.

The initial accumulation of total P is in extremely low quantities, and at lower rates compared to the accumulation of the exchangeable cations over the same period (up to 10 tonnes F/H per ha), to the extent that the least-squares function has a slightly negative origin (Figure 66b). Likewise the small amount of F/H material in the open woodland ecosystem (▲) contains very low quantities of P compared to the cations. Accumulation of total P in the F/H relative to the surface soil during succession (Figure 74b) is at lower levels but overall a greater rate than the exchangeable cations (Figures 61, 62). In terms of the same ratio, the accumulation of total P is closely equivalent to both the level and rate of accumulation of the entire F/H relative to the weight of fines in the surface soil (Figure 48a). The relative position of the open woodland ecosystem is identical in both graphs.

5.6.4.2 Organic Phosphorus

The probability that P in the soil fines is simultaneously immobilized as well as released from the primary state by weathering during secondary succession is supported by the linear increase in the concentration of organic P (hereafter $P_0$) as the F/H is accumulating, particularly up to about 20 tonnes/ha. Although the Upper Geehi sites, sampled immediately after the fires in January 1973, contain more than 100 ppm of $P_0$ in the surface soil (and 400 ppm and 610 ppm of $P_0$ in the F/H of *E. pauciflora* and *E. delegatensis* ecosystems respectively), the $P_0$ concentration during the first 20 tonnes/ha of F/H accumulation is
less than 75 ppm. In some of these sites the concentration of $P_0$ is negligible. $P_0$ rises to be about 30-40% of the total P concentration in the later stages of succession beneath a forest canopy, and maintains this level if the succession proceeds to open woodland.

At the time of sampling of the post-fire sites in the Upper Geehi, the incinerated understorey and forest floor had not become incorporated in the surface soil and were removed, and sampled, separately from the mineral soil. The high concentration of $P_0$ in the 0-5 cm soils immediately after the fire is therefore likely to be a reflection of the pre-fire concentration of $P_0$, and would appear to be a very temporary feature. Incineration, at temperatures that consumed the understorey and forest floor and defoliated and killed *E. pauciflora* and *E. delegatensis* respectively, does not appear to mineralise organically-bound P in the surface soil.

In view of the clear successional trend of the concentration of $P_0$ in the soil, it is interesting to speculate on the relative lack of any trend in the concentration of $P_0$ in the F/H. Whilst it is obvious that P is being immobilized during the succession, in the absence of a fractionation of occluded inorganic P it is not possible to attribute the immobilization to any particular fraction.

The ecosystems on basaltic materials show the highest concentrations of $P_0$ in both the F/H (> 600 ppm) and the 0-5 cm soil (> 350 ppm). There is no diminution in the high $P_0$ concentration and no significant change in the weight of $P_0$ proportionate to total P if succession proceeds to the open woodland stage (Plate IIb), which in this case is on Tertiary basaltic tuff. The relative dispersion of ecosystem points according to $P_0$ concentration in the F/H (Figure 65a) results in a quadratic function of accumulation that is of the same general form.
as the accumulation of total P in the F/H (Figure 66b), but of slightly less significance. There is marked significance, however, in the very low amounts of \( P_0 \) in the early stages of F/H accumulation. Comparing the quadratic functions of the accumulation of \( P_0 \) and total P with the accumulation of oxidisable C (Figure 49b) it is evident that the P accumulations are at lower rates than the input of carbon. The negative origins (least squares) of \( P_0 \) and total P may suggest a greater retention of 'mobile' forms of P in the biomass in the early stages of recovery from perturbation. The late decline in the accumulation of F/H P relative to total P is not significant (Figure 66) but could suggest, as do the accumulations of cations, an increase in the rate of mineralization of \( P_0 \) under a grass and herb ground cover.

5.6.4.3 Inorganic Phosphorus Analyses

The analytical procedure of Williams et al. (1967) has, in modified form (see Methods), been the guide for fractionation of inorganic phosphorus in this study. On the basis of solubility in a range of extractant solutions, these authors and Stevens (1968) group the inorganic P fractions thus:

- \( P_{\text{NH}_4\text{Cl}}; P_{\text{NH}_4\text{F}}; P_{\text{1st NaOH}} \) = non-occluded inorganic P
- \( P_{\text{reductant-sol}}; P_{\text{2nd NaOH}} \) = occluded inorganic P
- \( P_{\text{HCl}} \) = acid-extractable Ca-P
- \( P_{\text{residual inorganic}} \)

For the purposes of this ecological study, consideration of P fractionation has been restricted to non-occluded inorganic forms likely to be accessible to the ecosystem, in acid soils with a tendency for organic matter to accumulate at the surface. This can only be an
arbitrary restriction. It has been already suggested in discussing the accumulation of organic and total P, that large amounts of P are returned to the forest floor, or later bound, in organic or occluded inorganic forms, such as Ca-P. Russell (1961) says that there is evidence in some soils that Ca-phosphates are more available than surface sesquioxide forms. Ca-P forms generally change very readily to available forms in acid soils. P weathered from gravels in the surface soil may even go almost directly to occluded forms, or be leached, if not changed to P₀ (P. R. Stevens, *pers comm*).

The majority of studies of P availability (e.g. Suzuki *et al.*, 1963; Dos Santos, *et al.*, 1960; Pratt and Garber, 1964) indicate that in acid, organic soils the opposite is true. In these soils non-occluded inorganic P is usually present, adsorbed onto the surface of the hydrated oxides of Al and Fe, exchangeable Al+++ ions and exposed Al on the clay particles themselves. Some Ca++ may combine with these forms of P, but the Al and Fe combinations predominate (Humphreys, 1966). The 'dispersed phosphate' theory of Williams and Walker (1969) regards Al- and Fe-bound P in soils as consisting of phosphate-retaining soil components such as gibbsite, goethite, amorphous alumino-silicates, etc.. Stevens (1968) regressed the weights of 'active' Al and Fe against weights of the non-occluded fractions of inorganic P and found highly significant correlations for \( P_{NH_4F} \) and 'active' Al, and \( P_{1st NaOH} \) and 'active' Fe.

Many studies have been made of the relationships between 'available P' as defined in a various ways, and the various fractions of soil P. The evidence is difficult to analyse because of the many definitions of 'available P', the different types of soils analysed, and quantitative differences in the phosphorus pool. No one form of P or method of analysis, will account for inherent differences in P mobility in a group of soils such as encompassed in this study, although it will provide
information in absolute terms. With increasing soil P availability, however, the relationship between P uptake (which must be assumed to vary during succession in the ecosystems of this study) and the chemical nature of soil P availability becomes curvilinear (Dos Santos et al., 1960), and values of individual soils can be expected to deviate further from the 'average' relationship, because growth, response to stress etc., are controlled less and less by P and more and more by other factors.

As is apparent from the preceding results of the concentration and accumulation of total P and P₀ within the range where soil P availability does not limit plant growth, measurements of P uptake no longer will represent an index of true P 'availability', but will be independent of it. Previous studies of P nutrition in eucalypt forest ecosystems (Attiwill, 1964, 1971; Beadle, 1962, 1966) suggested that P availability certainly did limit plant growth. Only at a late stage in the present study was the comparative youth and the relative abundance of available P apparent for the subalpine soils as a whole, at least in forest floor and surface soil material. Nevertheless, a study of the available forms of P should provide insight into the successional dynamics of the nutrients in the acid forest floors and surface soils under investigation.

Concentrations and weights of the $P_{NH_4Cl}$, $P_{NH_4F}$, and $P_{1st NaOH}$ (hereafter, $P_{NaOH}$) fractions of non-occluded inorganic P, and their percentage contribution to total P, in the F/H and 0-5 cm soil, are tabulated in Appendix III and plotted against the accumulating weight of the F/H layer in Figures 67-74a (Appendix II).

Simple linear regression (Table 7) shows very highly significant correlations, at the 1% level, in both the F/H and surface soil, between total P and all fractions analysed except $P_{NH_4Cl}$ (only measured in F/H material) and the $P_{NaOH}$ in the soil.
TABLE 7  Regression formulae and correlation coefficients \((r)\) for significant linear relationships in the concentration of phosphorus fractions and total phosphorus from 46 ecosystems.

(A)  \(P\)-fractions in \(F/H\) and total \(P\) in \(F/H\)

\[
\begin{align*}
P_{NH_4F} &= -68.52 + 0.139 P_{total} & r = 0.801 \quad *** \\
P_{NaOH} &= 37.40 + 0.028 P_{total} & r = 0.546 \quad *** \\
P_{NH_4F+NaOH} &= -30.46 + 0.168 P_{total} & r = 0.907 \quad *** \\
P_{NH_4Cl} &= \text{non-significant} & r = 0.125 \\
P_0 &= 16.15 + 0.274 P_{total} & r = 0.692 \quad *** \\
\end{align*}
\]

(B)  \(P\)-fractions in surface soil and total \(P\) in surface soil

\[
\begin{align*}
P_{NH_4F} &= -10.25 + 0.089 P_{total} & r = 0.881 \quad *** \\
P_{NaOH} &= \text{non-significant} & r = 0.051 \\
P_{NH_4F+NaOH} &= 10.42 + 0.165 P_{total} & r = 0.844 \quad *** \\
P_0 &= -35.53 + 0.171 P_{total} & r = 0.773 \quad *** \\
\end{align*}
\]

(C)  \(P\)-fractions in \(F/H\) and \(P\)-fractions in surface soil

\[
\begin{align*}
P_{total}(F/H) &= 314.9 + 0.614 P_{total}(0-5 \text{ cm}) & r = 0.907 \quad *** \\
P_{NH_4F}(F/H) &= -8.43 + 0.918 P_{NH_4F}(0-5 \text{ cm}) & r = 0.808 \quad *** \\
P_{NaOH}(F/H) &= \text{non-significant} P_{NaOH}(0-5 \text{ cm}) & r = 0.045 \\
P_{NH_4F+NaOH}(F/H) &= 42.34 + 0.494 P_{NH_4F+NaOH}(0-5 \text{ cm}) & r = 0.776 \quad *** \\
P_0(F/H) &= 175.0 + 0.781 P_0(0-5 \text{ cm}) & r = 0.670 \quad *** \\
\end{align*}
\]

\(P_{NaOH}\) also bears comparatively little relationship to total \(P\) in the \(F/H\).

In the correlation of like-fractions between the \(F/H\) and surface soil, \(P_{NaOH}\) is the only fraction displaying little inter-relationship. All other correlations are very highly significant.

The high levels of correlation between 'available' \(P^*\) and total \(P\)

\*(here assumed to be non-occluded inorganic \(P\)*)
supports earlier observations that the subalpine soils are youthful, well supplied with a source of P from the weathering of primary parent material. The high correlations suggest that 'available' P is being released at similar rates, particularly the P surface-bound to Al, \( P_{\text{NH}_4\text{F}} \), and that immobilization in the biomass, forest floor and surface soil does not change the relationship. There is little to suggest that the supply of P is made inadequate because of immobilization in organic matter and detritus during succession. Considering the general biological similarity of all ecosystems, the high correlations between \( P_0 \) and total P, and between \( P_0 \) in the F/H and surface soil suggest a similar level of pedogenesis in all soils, in terms of the mobilization of P in organic matter. The chronosequence data of Stevens (1968) demonstrated progressive changes in the relationships of non-occluded inorganic P and \( P_0 \) to total P, during pedogenesis spanning 22,000 years during which total P of the entire soil profile declined to extremely low levels. Individual fractions of P tended to change relatively independently.

A feature of the P-fractionation analyses is the consistently very high degree of correlation between the 'available' fractions and total P, in comparison with the low significance of the comparable relations between the exchangeable cations and the parent element. Only \( \text{Ca}^{++} \) showed any significance and then at lower levels than the correlations for P. From this evidence, and the comparatively very high significance of the correlations between total P in the L and F/H components of the forest floor and in the surface soil (Figure 11) it is safe to assume that P is usually being mobilised in the biomass at levels not limiting to growth in the subalpine ecosystems.

Although it may be expected from the regressions that non-occluded inorganic P will accumulate in a similar manner to total P, a linear regression equation provides little information about their relationship
in the very disturbed soil surfaces where there are low concentrations and weights of both $P_0$ and total $P$. It is in these sites that the level of 'available' $P$ could be critical to the future of the present ecosystems.

Analysis of $P_{\text{NH}_4 \text{Cl}}$ (easily-soluble $P$) was confined to F/H material after preliminary analysis of both F/H and surface soil samples, because the latter, except in a few cases, had negligible $P$ in this form. However all samples were agitated in 1N NH$_4$Cl for 30 minutes to ensure constancy in the analysis of other P-fractions. Williams (1965) found very large amounts of $P_{\text{NH}_4 \text{Cl}}$ were removed by repeated extraction of F/H materials. Although in this study the fraction is determined by only one 30 minute extraction, it is apparent that organic matter characteristically will yield large amounts of $P_{\text{NH}_4 \text{Cl}}$ in repeated extraction. The distribution of $P_{\text{NH}_4 \text{Cl}}$ according to the accumulation of F/H is anomalous to all other nutrients examined (Figures 51, 52a). The easily-soluble form of $P$ is the only parameter, perhaps with the exception of $P_0$ in the surface soil, that shows a strong relationship between concentration and the successional process. It is also the only parameter to exhibit a clear decline in concentration, and proportion of the total element, as the F/H accumulates, from 6 ppm to less than 1 ppm, and 0.8% to less than 0.1% respectively. The quadratic function of the proportion of total $P$ becomes negative, attributable to the marked decline between 20 and 30 tonnes of F/H per ha. It appears that considerable quantities of $P_{\text{NH}_4 \text{Cl}}$ occur in the litter-fall in these ecosystems, but that the fate of the fraction is very short-term (Table 8) and it is virtually absent from the mineral soil. The concentration of $P_{\text{NH}_4 \text{Cl}}$ at the time of litter-fall in this stand (see Chapter 6) is almost ten times as great as any F/H sample (F/H does not include any litter-fall of the preceding year).

* sampling of forest floors and surface soils, and the litter-fall for analysis of decomposition rates, was in late summer.
TABLE 8 Mean changes in concentration of $P_{NH_4Cl}$ in decomposing foliage of *E. delegatensis* in mesh bags on the forest floor between April and December, 1973 (values represent pooling of 4 sample means x 2 fortnight collections)

<table>
<thead>
<tr>
<th>conc. (ppm)</th>
<th>Apr</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
<th>Dec</th>
</tr>
</thead>
<tbody>
<tr>
<td>56</td>
<td>34</td>
<td>32</td>
<td>30</td>
<td>26</td>
<td>28</td>
<td>25</td>
<td>25</td>
<td>23</td>
<td></td>
</tr>
</tbody>
</table>

In 8 months in the forest floor, the concentration of $P_{NH_4Cl}$ in the litter has decreased to only 40% of the concentration at the time of litter-fall.

It is interesting to speculate on the fate of this easily-soluble P fraction during initial decomposition. Most of the loss occurs during the first month on the forest floor suggesting that in this form P is either rapidly recycled or is very susceptible to immobilization on the surface of organic complexes, becomes bound to sesquioxides and $Ca^{++}$ that are concentrated in the F/H layer, or is eluviated in solution. The relatively high values for $P_{NH_4Cl}$ concentration, and as a percentage of total P, in the shallow F/H layers of the more recently disturbed ecosystems and in the open woodland stand suggest a negative relationship between the half-life of $P_{NH_4Cl}$ and the absorptive surface area of partially decomposed organic detritus. The weight-distribution of $P_{NH_4Cl}$ (Figure 68a) could suggest that the level of decomposition activity is important in determining the actual quantity of this fraction. The marked peak in the distribution of plotted points suggests a threshold to the accumulation of $P_{NH_4Cl}$ at only about 20 tonnes of F/H per ha, although numerous other stands in this vicinity have low accumulations, for a given weight of F/H material, at
about this point (Figure 50a) suggesting that although $P_{\text{NH}_4\text{Cl}}$ declines in concentration throughout the succession, particularly after 20 tonnes F/H per ha (Figure 67), it will accumulate in the relative absence of decomposers capable of immobilising it. The $P_{\text{NH}_4\text{Cl}}$ fraction is a large component of the total non-occluded inorganic P in the F/H of the most disturbed ecosystems, with regard to the nature of the soil surface (cf. the points nearest the origin in Figures 67b, 69, 70). If the differential between $P_{\text{NH}_4\text{Cl}}$ in the litter-fall and the litter after a few months of decomposition in these stands is similar to the stand in Table 8, it is likely that considerable quantities of easily soluble P are being lost in solution from a forest floor and surface soil not capable of retaining it. Thus, in the early stages of F/H accumulation (up to 10 tonnes/ha) there is low net accumulation of $P_{\text{NH}_4\text{Cl}}$ (Figure 68a).

The concentrations of $P_{\text{NH}_4\text{F}}$ and $P_{\text{NaOH}}$ in the F/H tend to increase during the succession (Figure 69), from very low levels in the case of $P_{\text{NaOH}}$. In both fractions, the lowest concentrations occur in the forest floors overlying the very disturbed surfaces of soils from sediments, although very low concentrations do occur in the more disturbed granodiorite, rhyodacite and quartzite sites. The dispersion of ecosystem-points about the quadratic function is less for $P_{\text{NaOH}}$, but both fractions reflect the inherent geochemical variation described earlier for total P. The effect of combining the two fractions is to steepen the gradient of increasing concentration and reduce the dispersion (Figure 71a). The asymptotic distributions appear to result from low concentrations occurring only in the early stages of F/H accumulation (up to 15-20 tonnes/ha). This conclusion is supported by the graphs expressing $P_{\text{NH}_4\text{F}}$ and $P_{\text{NH}_4\text{F+NaOH}}$ as percentages of total P concentration. There is a grouping of low values where the weight of F/H is less than
20 tonnes/ha. Although these fractions have been shown to bear very highly significant relationships to total P (Table 7), it is apparent (Figures 68b, 70b) that this relationship varies throughout the succession. Generally, less of the total P in the F/H is 'available' in the early stages of secondary succession than in later stages. This could support my interpretation of the accumulation of $P_{NH_4Cl}$, that less of the P mobilized in the biomass and returned to the forest floor is accumulating there, because of lower amounts of organic matter capable of absorbing non-occluded inorganic P than in the deeper F/H layers. The alternative is that P is being returned to the forest floor in lower concentrations because of increased recycling of P within the biomass on disturbed sites. The graph of P concentration in the L litter (Figure 63a) does not support this, as only one very disturbed site shows a distinctly lower concentration.

This interpretation is further strengthened by the successional trends of accumulation (kg/ha) of $P_{NH_4F}$ and $P_{NH_4F+NaOH}$ (Figure 71). There is negligible accumulation of either fraction until a minimum of 5 tonnes/ha of F/H has accumulated on the forest floor, giving the quadratic function a temporary negative value, of greater magnitude than for the accumulation of any other nutrient examined in this study. Considering the less negative origin for the quadratic function defining the accumulation of $P_0$ and total P in the F/H (Figure 66) it can be concluded that whereas there is initially a net loss of P relative to accumulation of the F/H layer, a high component of this loss is in the form of non-occluded inorganic P. The same effect is apparent if the ratios of accumulation, in the F/H relative to the surface soil, are compared for $P_{NH_4F+NaOH}$ and total P (Figure 74). It is to be noted that the initial absence of non-occluded inorganic P in the F/H (Figure 71) is not accompanied by any significant build-up of this fraction in the
surface soil at the outset of the succession (Figures 72, 73). The extremely low values of the ratio for $P_{\text{NH}_4\text{F}+\text{NaOH}}$ (Figure 74a) up until the stage of 5 tonnes F/H per ha, reflect the dynamics of the fraction in the F/H, rather than changes in the surface soil. Initially at least, accumulation of non-occluded inorganic P, in the F/H relative to the surface soil, is at lower levels than the equivalent accumulation of total P (Figure 74b) and at much lower levels than the exchangeable cations (Figures 60, 61). The early rate of relative accumulation is initially less, then greater, than either total P or the cations. The 'exponential' distribution of the quadratic function of $P_{\text{NH}_4\text{F}+\text{NaOH}}$ (Figure 74a) is probably a result of the extremely low ratios near the origin.

It has been emphasised, in discussing the total P economy in the subalpine eucalypt ecosystem, that whilst successional redistribution of P can be demonstrated, it is only in the few most intensively disturbed ecosystems, where there is evidence of permanent damage to soil structure and, at present, an unusually severe incidence of recent fires, that the disturbance to the phosphorus pool is now critical to continuation of $E. \text{delegatensis}$, in these sites. However, the majority of fuel-reduction fires observed during this study in $E. \text{delegatensis}$ and $E. \text{pauciflora}$ forests, as well as wildfires, have burnt the F/H to weights less than 5 tonnes/ha. Bearing in mind the level at which the forests and woodlands of these species mobilize P (Figure 63a), it is pertinent to consider the dynamics of non-occluded inorganic P in the forest floor, in the light of regular perturbations whereby forest floors approaching weights in excess of 20 tonnes/ha are deliberately reduced to these low levels. At the same time the addition of mineralised P to the forest

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* see also P data in Chapter 6, for concentrations at time of litter-fall.
floor and surface soil occurs (see section 5.6.7.3.iii), due to the incineration of the understorey and much of the forest floor, effecting some saturation of the existing sites for chemical bonding of P. It is known from Australian evidence that non-occluded inorganic P increases as a proportion of total P, and is the major 'active' fraction, between 100°C and 500°C when a 'forest' soil is heated (Humphreys, 1966, 1969). At 500°C this fraction had increased to more than three times its original concentration. Humphreys' research studies used soils where the total P was only 250 ppm. It can be assumed that in the subalpine ecosystems where total P is usually 600-1200 ppm in the F/H and surface soil, the scale of mineralization of P is at least of this order if not greater, considering the importance of organic matter in concentrating P at or above the soil surface. However, the net effect, in the time-scale of F/H accumulation, is a depression in the accumulation of non-occluded inorganic P in the F/H (Figure 71) and in the F/H:0-5 cm soil ratio (Figure 74a) in the early stages of secondary succession following fire, rather than a build-up. In terms of the F/H:0-5 cm ratio of accumulation, the initial depression in the quantities of P_{NH_4F+NaOH} during this period is much greater than the individual exchangeable cations or C.E.C.. My conclusion is that 'available' P is unduly affected by alteration of the forest floor mass by fire, and that as non-occluded inorganic P comprises some 20-25% of total P, (much of which in the surface soil is within primary soil particles), it will be increasingly difficult to conserve the 'available' pool of phosphorus and maintain ecosystems that are restricted to high-phosphorus environments if regular burning of the understorey is pursued.

5.6.4.4 Organic Matter:Phosphorus ratios

There are very highly significant linear relationships between the
accumulation of oxidisable C and total N in the F/H and the accumulation of the entire F/H layer in the 46 ecosystems (at the levels of \( r = 0.898 \) and 0.903 respectively). At the same time, the relationship between the accumulation of total P and the F/H, whilst still very highly significant, is perhaps less so \( (r = 0.764) \). A probable reason is the very slow rate of P accumulation, particularly of the non-occluded inorganic fraction, in the early stages of F/H accumulation. Therefore, a more precise definition of the successional dynamics of P as it relates to the accumulation of organic matter would be according to the changes in organic matter:phosphorus concentration ratios.

The quadratic functions defining the probability distributions of the organic matter:phosphorus ratios (Figures 75, 76, 77), in all cases except oxid. \( C/P_{\text{NH}_4F+\text{NaOH}} \) show wide values in the early stages of F/H accumulation. The conclusion is that during this period, the accumulation of P is at disproportionately low concentrations. At the same time, the \( C/P_{\text{NH}_4F+\text{NaOH}} \) ratios of the F/H of the more disturbed stands (Figure 76a) are at a relatively higher position than for the \( C/\text{total P} \) ratio of the same stands (Figure 75a), confirming the previous observation that whilst the concentration of total P is lowest in the F/H of these stands, the relative depression in the concentration of non-occluded inorganic P is much greater. Some recently disturbed forest floors, notably in the Geehi sites sampled immediately after the severe wildfires, show the narrowest \( C/\text{total P} \) and \( C/P_{\text{NH}_4F+\text{NaOH}} \) ratios. The relatively greater susceptibility of the non-occluded inorganic P fraction to disturbance of the forest floor, compared to total P, is indicated by the steeper slope of the quadratic function defining the narrowing ratio of the former (Figure 75a). The non-significant dispersion of points, in the later stages of F/H accumulation, in the distribution of the organic matter:phosphorus ratios suggests that the
general form of the quadratic function is dictated by the predominantly wide ratios in the early stages of secondary succession. The anomalous distribution in Figure 76b could be interpreted as suggesting a slight increase in the concentration of non-occluded inorganic P relative to carbon accumulation, and at a greater initial rate than total P, in the surface soil. This could represent only some of the non-occluded inorganic P lost from the F/H in sites where the weight of the F/H is less than 5 tonnes/ha, according to the initial slopes of the respective quadratic functions (Figure 76). At the same time, total P declines slightly in the surface soil, relative to carbon accumulation, immediately after fire, equilibrating after about 5 tonnes F/H per ha have accumulated.

The lack of any trend in the N/total P ratio of the L litter (Figure 52b) compared to the organic matter:phosphorus ratios in the F/H and surface soil suggests that the clear trends in the latter two components result from disturbance to the phosphorus pool on the forest floor rather than a disturbance to the mobility of P in the biomass.

5.6.5 "PHYSICAL" PARAMETERS

Trends in soil reaction are shown in Figure 51b. There is a general decrease in the pH of the surface soil during the succession with values between 6.3 and 4.0.

The youth of the solum, the recent deflation in most sites, and the different physical structure of the various parent materials result in a scale of physical variation in the soils that cannot per se be related to the accumulation of organic matter on the forest floor during secondary succession. Although physical fractionation of the soils was necessary to obtain weights of the 0-2 mm particle size, and derive accurate nutrient-weight coefficients, they have not been graphed in
this successional study because of this variation. The parameters of bulk density, the percentage > 15.0 mm, the percentage from 2.0-15.0 mm, and the percentage < 2.0 mm fractions, were correlated with the % oxidisable C in the 0-5 cm soil. Only bulk density showed any significant relationship,

$$BD(0-5\,\text{cm}) = 1.117 - 0.023\%\,\text{oxid. C}$$

\[r = 0.419\,\text{**}\]

5.6.6 VEGETATION UNDERSTOREY PARAMETERS

5.6.6.1 Introduction

Changes in the structure and composition of the understorey layers are illustrated in Figures 78-81 (Appendix II). These graphs are selected from a wealth of vegetation parameters that could have been derived from the field data of 200 point samples, and presence data for all species encountered. The percentage cover and presence data for all species are tabulated for each stand in Appendix II, together with numerous whole-stand parameters, expressing total shrubs, shrub Leguminosae, herbs and grasses as % of the total ground cover, % of the ground biomass cover, and % of the total number of species, in the understorey in each case. Total cover and species diversity indices are also tabulated. Reference should be made to these tables for details of species composition. Only the trends of change are described here. The dispersion of ecosystem-points for all parameters is immediately apparent, and in fact the understoreys show greater variation about the quadratic function than do the nutrient parameters. The general impression at the conclusion of field sampling was of a succession from sparse grasses and herbs immediately after a fire, then a long stage dominated by shrubs, mainly legumes, with a grass and herb ground cover and a gradual diminution in shrubs after about 30-40 years, depending on the site, to
a 100% grass and herb ground cover. However, because of variation in site, particularly parent material and aspect, in the previous history of fire at any one site, and the enormously complex variation in revegetation after the fire (cf. Marks, 1974), there is little quantitative constancy in the successional patterns as related specifically to accumulation of the F/H component of the forest floor. The quadratic functions do confirm the general impression, but would require a very large number of sites to do so significantly. It is difficult, for example, to measure the change in the contribution of grasses throughout the succession because of the effects of site, soil depth, quantity of coarse litter, density of shrubs, openness of tree canopy etc., on their abundance.

The only concession to this scale of variation was to derive separate quadratic functions for *E. delegatensis* and *E. pauciflora*, instead of amalgamating all 46 stands. Field observations suggested that the more open canopy and smaller crown space (Figure 12; see also Park, 1973) of the *E. pauciflora* stands was reflected in a different rate of successional development. The major difference in the understorey structure of the *E. pauciflora* and *E. delegatensis* communities are illustrated by Plate 10 in Chapter 6.

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* the variation in the intensity, frequency, seasonality and regularity of previous fires, as well as the variation in the local effect of any one fire ranging from crown-kill, incineration of the understorey to a scorching of plants and even completely undisturbed patches.

† Availability of seed; direct seeding from pre-fire relics, or buried seed; a good seed year; varying migration, dormancy, germination and establishment rates for different species, as well as variable resistance to variable heat of fire; timing of fire with seed arrival and/or germination; microclimate favourable for germination and establishment. Degree of shoot regrowth and its competitive advantage over seeding. Variation in available biota, and degree to which the previous succession had proceeded.
5.6.6.2 Description and Discussion of Results

The quadratic functions of the quantitative distribution of shrubs, expressed as % of total ground cover (Figure 80b) define a successional trend that is apparent from the amalgam of my field observations. It supports the few descriptive studies reported in the literature, particularly of the diminution in shrub cover in late stages. The marked scatter of points is considerable but does indicate the very dense shrub cover (75% in some stands) at the stage of about 15-25 tonnes F/H per ha on the forest floor (Plate VIa). Some of the more recently disturbed sites contain very few shrubs, but within a few years there is a rapid increase in their, and the total, cover. Grasses (Figure 80a) are always major components of the total ground cover, at initial stages of revegetation (see section 5.6.7.3.iv), beneath the shrub understory, and later. Whilst grasses tend to increase as the F/H accumulates, they share the ground cover in late stages with herbaceous species (Figures 79, 80a), particularly beneath *E. pauciflora*. Total ground cover by living plants is greatest in the very late successional stages where it may be 90% or more, for example the open forest stand in Plate IV, (see Appendix IV, Table 12), and the open woodland stand in Plate IIb (see Appendix IV, Table 19). Loose eucalypt litter is the other main category of total ground cover. Bare ground is rarely encountered except for the first 3-4 years after fire in these ecosystems.

In comparing shrubs as % of total ground cover with their % of ground biomass cover (Figure 78b), it is clear that the low shrub cover in some recently disturbed sites (i.e. low F/H weight) is because of a low total ground cover. Whilst shrubs are important early in the succession, they generally do not reach a peak of dominance until later (ca. 40% of total cover at 1-20 tonnes F/H per ha under *E. delegatensis*; ca. 30% at 30-40 tonnes F/H per ha under *E. pauciflora*), as defined by
the quadratic. In some stands, shrubs may occupy more than 75% of the living ground cover.

The successional distributions of shrubs and shrub-Leguminosae, as percentages of the ground biomass cover, have been graphed on one page to illustrate the very marked dominance by the Leguminosae in the earlier stages of secondary succession. Even from the scatter of ecosystem-points (Figure 78) the diminution in shrubs, particularly Leguminosae, as succession proceeds, is obvious. The Leguminosae comprise a greater proportion of the shrubs in the early stages, on new ground surfaces and in recovery from disturbance. The association usually stimulates vegetative growth because of the ability of the Leguminosae to fix nitrogen (see section 5.3). Because of the quantitative importance of legumes in the early stages of the succession, it is tempting to assume that they have a profound effect on the accumulation of N. However whilst N-accumulation can be demonstrated (Figures 48b, 49a) it is at a slower rate early in the succession than later, when it has almost an exponential component as the understorey becomes a dense grass and herb cover. Correlations of N concentration with the relative amounts of shrubs and legumes in the understoreys showed, in fact, negative relationships (Table 9). The C/N ratio of the F/H showed a highly significantly linear negative correlation with grasses, expressed as % of the ground biomass cover, suggesting that decomposition is more efficient under a predominantly grass cover (cf. Figures 32a and 63a). N-enrichment seems to depend far more on the efficiency of decomposition. The highest concentrations of total N (> 20,000 ppm) occur in both the F/H and surface soil of stands where F/H accumulation is near the point of equilibrium between litter-fall and decomposition (Plate IVb), and later, when litter-fall has declined but decomposition has increased to reduce the F/H to a thin layer in open woodland (Plate IIb). In the
latter ecosystem the concentration of total N in the F/H (27,500 ppm) and surface soil (21,500 ppm) is four times the concentration of N in the respective components of the more recently disturbed ecosystems.

TABLE 9 Relationships of Nitrogen to understorey parameters in 46 stands, for forest floor and surface soil material

<table>
<thead>
<tr>
<th>Nitrogen</th>
<th>understorey parameter</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (ppm) in F/H</td>
<td>shrubs, % of total ground cover</td>
<td>-0.158 n.s.</td>
</tr>
<tr>
<td>N (ppm) in F/H</td>
<td>shrub-legumes, % of total ground cover</td>
<td>-0.166 n.s.</td>
</tr>
<tr>
<td>N (ppm) in F/H</td>
<td>shrubs, % of biomass ground cover</td>
<td>-0.315 *</td>
</tr>
<tr>
<td>N (ppm) in F/H</td>
<td>shrub-legumes, % of biomass ground cover</td>
<td>-0.320 *</td>
</tr>
<tr>
<td>N (ppm), 0-5 cm</td>
<td>shrub-legumes, % of biomass ground cover</td>
<td>-0.228 n.s.</td>
</tr>
<tr>
<td>N (kg/ha) 0-5 cm</td>
<td>shrub-legumes, % of biomass ground cover</td>
<td>-0.159 n.s.</td>
</tr>
<tr>
<td>C/N ratio, F/H</td>
<td>grasses, % of biomass ground cover</td>
<td>-0.365 **</td>
</tr>
</tbody>
</table>

Woodwell (1974) has described the N succession in a secondary sere comprising agricultural field, old field, pine forest and oak forest. There is no particular phase of macro-N-fixing plants, and total N concentrations in the shallow water table were 0.017, 0.042, 0.928 and 4.480 mg/l respectively. In a similar sequence, Rice and Pancholy (1972) found a decrease in nitrate ions and nitrifying bacteria, but a parallel increase in NH$_4^+$ ions. They concluded that mature systems inhibit nitrification, which is associated with disturbance and the mobilization of cations, whilst plants of mature systems absorb nitrogen as ammonia.

During the early stages of successions described in the present study, shrub species occupy as much as 40% of the total number of species in _E. delegatensis_ forest. During the period when shrubs dominate the succession, they comprise considerably fewer of the total number of species, but this tends to increase later. Dominance is actually by very few shrub-legume species. The kind of shrub-legume varies regionally
throughout the subalpine zone and from site to site, the major dominants being *Acacia obliquinervia*, *Daviesia latifolia*, *Bossiaea foliosa*, *Daviesia ulicina* and *D. mimosoides* with the first two tending to be on wetter sites than the others. Shrub species are designated separately in the tables in Appendix III. The *E. pauciflora* ecosystems show little trend for shrubs, as a percentage of total number of species. The relative proportions of herb and grass species are detailed in the tables in Appendix II. Species variety was also measured by a type of species diversity index expressing equitability, or the variation in the proportions amongst species. The index used, proposed by McIntosh (1967), is a sum of squares measure of statistical variability, viz.

$$D_y = \sqrt{\frac{\sum n_i^2}{n}}$$

where $s$ equals the number of species, and $n$ equals the number of individuals in each species

All 46 stands were included in the analysis, which was restricted to understorey species. For both ecosystem types (Figure 65a), understorey species diversity ($D_y$) increased very rapidly after the perturbation to peaks during the domination by shrub-Leguminosae. The subsequent decline in diversity is greatest under *E. delegatensis*. Under *E. pauciflora* the index declines marginally, but is still quite high in the open woodland stand (4). Concentration of dominance, a diversity index proposed by Pielou (1966) was investigated because of the nature of the understoreys. A plot of the data showed declining concentration of dominance, but at a non-significant rate.

Diversity has been shown to increase in many successions (Odum, 1960, 1969; Richards, 1952; Tagawa, 1964; Margalef, 1963; Monk, 1967; Reiners *et al.*, 1970). In some successions however, diversity decreases from a late successional stage towards a state of community stability (Margalef, 1969; Loucks, 1970; Auclair and Goff, 1971). Whittaker
(1972) considers that such a decrease may be the result of strong dominance late in the succession suppressing subordinate species that occurred earlier. Reiners et al. (1970) followed changes in diversity in cool-superhumid forests in Alaska on glacial moraines of known age, in which there was an early phasic dominance by macro-N-fixing plants. Diversity increased rapidly during the first century and then more slowly to an apparently stable maximum in a final muskeg stage. Diversity increased with a series of wave-like invasions by plants of the different strata. Diversity generally declined and dominance-concentration increased in a particular stratum after the early period of its wave, while the stratum dominated the community. Auclair and Goff (1971) suggested that competitive exclusion of species in the most stable communities was the main reason for the decrease in diversity, between late successional and 'equilibrium' forests throughout the upland forests of N.E. North America. They used an index of equitability which they stated was very similar in function to the index of McIntosh (1967). Disturbance in 'equilibrium' forests maintains diversity, as mentioned specifically in the boreal transition forests (Maycock and Curtis, 1960), but competitive exclusion of species in low-stress environments, such as a dense grass and herb ground cover in the subalpine eucalypt forests, reduces diversity in time.

Finally, it should be emphasised that in these ecosystems vegetation response to a perturbation is highly specific and very dependent on post-fire conditions (see footnote, p. 174). The phasic replacement of species and growth forms can really only be measured if one stand is observed over a period of time. This is being attempted in a number of ecosystems in the Snowy Mountains (D. J. Wimbush pers comm) and the A.C.T. (Florence, 1973).
In late December, 1972 a wildfire started in wet sclerophyll forest near Geehi Dam in Kosciusko National Park and swept up the slopes of the Grey Mare Range and the west-facing slopes of the Main Range of the Snowy Mountains through young forests of *E. delegatensis* and *E. pauciflora*, woodlands of *E. pauciflora* and other species, and through alpine heathland. It just encroached onto tall alpine herbfield, where it died out (D. J. Wimbush, *pers comm*). The fire continued into early January, 1973. I was able to visit the area near Dicky Cooper Creek, where I had made descriptive notes on the vegetation during the previous summer, on 5 January immediately after the fire had passed through and prior to any rainfall. It was not possible to sample prior to the wildfire, but comparable ecosystems on similar parent material could be observed elsewhere, for example, the ecotonal site at Wilsons Valley in Kosciusko National Park (Appendix I, Table 8). However nutrient and organic matter losses resulting from incineration could still not be measured. The sites were visited again in late summer after a series of convection storms, and finally, early in the following summer. At each visit, the vegetation was sampled by point analysis.* On the first visit, all organic matter (the great majority being incinerated, including the reduced understorey) was carefully removed, by brush, from the mineral soil. ** The uppermost 5 cm of mineral soil was excavated.*** On the subsequent visits, the organic matter had been redistributed to the extent that it was no longer a distinct layer, and only the 0-5 cm soil was sampled. Thus, although a considerable quantity of nutrients may have been lost to the atmosphere during the fire, this

* all methods are identical to those described in Chapter 3.
study attempts to measure only the fluxes in nutrients attributable to surface transportation or deep leaching of the ash into the soil.

The sites selected for analysis were in young forest of *E. delegatensis* and young low forest of *E. pauciflora*, where the trees had been killed and the dense shrub understorey completely consumed to ground level by the fire. In both communities the trees were even-aged, regenerated by a fire earlier this century (probably 1939), during the period of extensive lease of these areas for grazing. The soils are in deep, permeable, weathered granite. Both sites were near the road between Schlink Pass and the Geehi Dam. The site in *E. delegatensis* forest at a lower slope position was at an altitude of 1480 m, at the upper limit of this species in the area. The higher slope *E. pauciflora* low forest site was at 1500 m.

5.6.7.2 The ecosystem prior to the Wildfire

From previous field notes on the sample sites and from analysis of comparative ecosystems at Wilson's Valley, it is apparent that the shrub understoreys covered about 50% and 65% of the entire ground cover in the *E. pauciflora* low forest and the *E. delegatensis* forest respectively. In the *E. pauciflora* low forest, shrub-Leguminosae comprised 65% of the shrub cover, which was about 44% of the living ground cover. In the *E. delegatensis* forest, the shrub legumes comprised 90% of the shrub cover, which was about 35% of the living ground cover. In both sites the major shrub legume was *Bossiaea foliosa*, which was almost the sole dominant of the understorey in the low forest (Plate VIa). In the *E. delegatensis* forest, *Acacia obliquinervia* was also important. The broad-leaved grass, *Poa anceps* aff., as well as the more common *Poa ensiformis*, was important in the ground layer. A few shrub species characteristic of young understoreys, notably *Drimys xerophila*, *Lomatia myricoides* and
the herb *Dianella tasmanica*, were present. The weight of the F/H component of the forest floor, shown to be a reliable index of the stage of succession, particularly during the period of dominance by shrub-legumes, was 21 and 26 tonnes/ha in the low forest of *E. pauciflora* and the forest of *E. delegatensis* respectively, in the comparable ecosystems at Wilson's Valley. The conclusion is inescapable that the ecosystems were at an early successional stage, when the rate of accumulation of fuel and the inflammability of the understorey is greater than later stages, where although fine fuel accumulation may be greater, the rate of accumulation is less and shrubs are in diminution.

**5.6.7.3 The Ecosystems After the Wildfire**

The results of analyses of exchangeable and total elements, expressed as weights per area (kg/ha) are presented in Table 10., to illustrate the fluxes in nutrients near the soil surface during the first 10 months after the fire. Data for the consumed understorey and forest floor (termed "litter") remaining on the ground immediately after the fire are tabled separately, and then summed with the surface soil data. The ratios of the concentrations of oxidisable C and total N, and to total P and non-occluded inorganic P in the surface soil are listed in Table 11. The results of point analysis of the ground cover are listed in Table 12.

**5.6.7.3.i "Organic" parameters**

The mean % oxidisable C of the consumed understorey and forest floor remaining on the ground immediately after the fire was only 13.6% and 12.9% for the *E. pauciflora* and *E. delegatensis* sites respectively. That this was only 40% of the concentration of oxid. C% in the similar F/H layers at Wilson's Valley, and quite the lowest extreme concentration
of oxid. C% in any "organic matter" sampled in this study, points to the large amount of carbon lost from the ecosystem during combustion. The concentration of N in the material remaining above the mineral soil (8400 ppm in each site) was relatively higher, and can be estimated at about 65% and 85% of the N concentration in the F/H of the *E. pauciflora* and *E. delegatensis* sites respectively, at Wilson's Valley. The C/N ratios of this material were 15 and 16 which is remarkably low for undecomposed organic matter in these eucalypt forests. There are also extremely low C/N ratios in the surface soil, relative to other sites examined, suggesting that here too, there was considerable oxidation of carbon during the fire. For this reason, C/N ratios are characteristically low in some recently burnt stands (see section 5.6.2), whilst low ratios in the older forest floors and surface soils (in stands like those in Plates VIb and IIb) are because of very high concentrations of N (i.e. > 20,000 ppm). Following fire, there is a continuous loss in the total weight of oxid. C in the surface soils of both sites, significant over 10 months under *E. pauciflora* (Table 11). There is also significant loss of N in the *E. pauciflora* site, whilst the *E. delegatensis* site appeared to gain N from upslope during this period.

5.6.7.3.ii Cation parameters

Because Ca, K, Mg and Na do not occur in gaseous form, it can be assumed that any divergence of the concentrations of these elements in the "organic matter" remaining on the soil surface after the fire, from their general concentration in the F/H layers of the subalpine eucalypt ecosystems, is a function of their concentration in the biomass consumed in the fire. The concentration of K⁺ (560 and 615 ppm, in *E. pauciflora* and *E. delegatensis* sites respectively) in the consumed organic matter was higher than any F/H material analysed, and the concentration of K
(4219 and 3133 ppm) higher than in most. Similarly, both $\text{Ca}^{++}$ (2740 and 3100 ppm) and total Ca (10520 and 11960 ppm) are higher than in the majority of F/H layers. The concentration of total Mg is higher in the consumed organic matter, but $\text{Mg}^{++}$ is no different than in most F/H layers. However, whilst no analyses were made of total Na, the concentration of $\text{Na}^{+}$ (21 and 16 ppm) is remarkably low, relative to all F/H materials, and to $\text{Na}^{+}$ in the surface soil (Table 10). It would appear that combustion, probably at temperatures in excess of 500°C, reduced the exchangeability of Na, and to some extent Mg. Combustion could have affected the concentration of $\text{Ca}^{++}$ and $\text{K}^{+}$, although it would seem that the considerable quantity of these essential ions concentrated in the understorey biomass is responsible for the high quantities of Ca and K temporarily on the ground after a fire of this kind.

For most cation parameters (except total K, total Mg and $\text{Na}^{+}$) the weight of the ion or element in the consumed organic matter remaining on the soil surface is 30% or more of its weight in the 0-5 cm soil (Table 10) immediately after the fire. The additive effect of the former can be measured in the 0-5 cm samples collected 7 weeks after the fire. In most cases, however, at least all of this "added" nutrient pool has been removed by surface transport and/or leaching in the ensuing 8 months. Comparable results have been obtained for cations by Rowe and Hagel (1974) in experimental leaching of a forest floor and surface soil following a 'fuel reduction' burn, and a control, in montane wet sclerophyll forest in N.E. Victoria. It is apparent that greater quantities of cations are entering the surface soil in the $E.\ delegatensis$ site during the first 2 months than in the $E.\ pauciflora$ site (Table 10) because of the lower-slope position of the former.

C.E.C. behaves similarly to the individual cations, but it would appear that C.E.C. is reduced by combustion, as it is in lower quantities
in the consumed "organic matter" relative to the 0-5 cm soil immediately after the fire, than in other ecosystems sampled.

5.6.7.3.iii Phosphorus parameters

Phosphorus, particularly the non-occluded inorganic fraction, like N and S but unlike the cations, is susceptible to atmospheric loss in gaseous form following oxidation in a forest fire. It also occurs in low concentrations in the biomass and F/H relative to the surface soil, compared to the cations (section 5.6.4). There is a significant loss of total P from the combined consumed "organic matter" and the surface soil in only two months, but only in the higher-slope _E. pauciflora_ site. Some of this is apparently attributable to the $P_{\text{NH}_4}$ fraction (Table 10), but in quantitative terms it would seem that much of the lost P is bound to Ca, which is a common form of soil P. This is not improbable considering the very large amounts of Ca$^{++}$ present in the consumed organic matter immediately following fire (50% of the Ca$^{++}$ in the surface soil) and the significant rapid loss of Ca$^{++}$ from the surface soil. $P_{\text{NaOH}}$ actually accumulates in the surface soil. It was surprising that $P_0$ remained in a high concentration in the consumed organic matter, considering the probable high temperature of the fire. $P_0$ has by far the lowest "litter":0-5 cm soil ratio of any P fraction, including total P, (Table 10). The ratios of oxid. C and N to total P show a relative net loss of total P from the surface soil, considering the added effect of consumed organic matter. But because of the increase in $P_{\text{NaOH}}$ (Table 10) there is a net accumulation of non-occluded P relative to C and N (Table 11).

Soil reaction

There were significant increases in pH in both sites throughout the 10 months (Table 10).
5.6.7.3.iv Vegetation understorey parameters

Prior to the fire the understorey in both stands was a dense shrub cover, dominated by legumes. All of this was consumed by the fire to ground level. The most immediate vegetative response was the appearance of lignotubers, and basal epicormic growth on *E. pauciflora* and on the few trees of *E. dalrympleana* in the *E. delegatensis* site. *E. delegatensis* itself was killed by entire cambial scorching in all trees. Only herbs made any significant appearance in the *E. pauciflora* stand during the remainder of the summer, whilst in the *E. delegatensis* stand the broadleaved grass, *Poa anceps* aff. and the fern *Polystichum proliferum* were most common. In each site, ground plants had only revegetated 1% of the soil surface by this stage, and most of the "ash" had been either washed into the soil or downslope. By the time the sites were re-sampled early the following summer, 32% of the ground surface in the *E. pauciflora* site and 66% in the *E. delegatensis* site was covered by vegetation. Most of this cover was by grasses, *Poa ensiformis* and *P. anceps* aff., a few herbs, shrubs, and the epicormic growth of the eucalypts. At this stage, only a few plants of one shrub legume, *Acacia obliquinervia*, had entered the succession. The site was not revisited again, so the degree of shrub-legume succession could not be observed. Although many of these shrubs can regenerate by shoot regrowth, they tend to appear after the initial flush of grasses and herbs, and dominate succession in the subalpine eucalypt forests (Pryor, 1939; D. J. Wimbush, pers comm). The fire was undoubtedly very hot in both sites, but as germination and regrowth of herbs and grasses was immediate, and numerous patches of unburnt understorey scrub were in close proximity, a high degree of legume regrowth, and germination from buried and cast seed would be most likely to follow. However, substantial revegetation of the ground surface, particularly in the *E.*
pauciflora stand following this mid-summer fire was out-of-phase with the net loss of most nutrients that occurred in the first 10 months.

5.6.7.4 Discussion

The wildfire occurred at a time when it was becoming apparent from laboratory analyses that some nutrients, particularly phosphorus, reflected the marked discontinuities in the composition of eucalypt dominants in the subalpine-montane zone. It was also clear that understory burning, as well as severe wildfires, produced perturbations in the forest floor and surface soil sufficient to contribute to net loss, in the long-term, of essential nutrients. The fire thus provided an opportunity to assess the fate of nutrients immediately after a perturbation, albeit an extreme one, within the sampling and analytical design used in the study of long-term secondary succession.

In terms of the very highly significant relationships between the accumulation of oxidisable C and the entire F/H layer during succession, the most interesting point of the monitoring of immediate post-fire processes was the large amount of carbon lost from the ecosystem during combustion, and later from the soil surface, particularly under the upslope E. pauciflora low forest. The initial % loss of carbon is much greater than any other nutrient examined, notably Ca++, K+, and Mg++. The loss of carbon also represents a de-structuring of colloid surfaces that provide sites for the exchange and bonding of cations and P. In this sense, the relatively large loss of carbon during a fire explains, at least in part, the extremely low levels of

* organic matter, N, P and exchangeable cations accumulate in the forest floor and surface soil in the upland forest soils (see Introduction; section 2.2.4; and profile analyses in Appendix VII).
some nutrients in very disturbed stands during the early stages of F/H accumulation. It can be concluded that the extent, frequency, seasonality and regularity of any loss of carbon will determine the redistribution of essential nutrients, which must occur in any forest fire.

In terms of the relative distribution of *E. pauciflora* and *E. delegatensis* it should be noted that whilst there was a net loss of most nutrients from the surface soil of both ecosystems, the lower-slope *E. delegatensis* site often accumulated the same element that was lost from the *E. pauciflora* site on higher slopes. The ecological importance of the difference is clear:

1. It demonstrates that slope-position is an important factor in nutrient distribution.

2. It reflects the relative local-distribution pattern whereby *E. delegatensis* occurs on the higher-fertility, lower, concave slopes and *E. pauciflora* on higher convex slopes.

3. It suggests that surface-flow and leaching, in suspension and solution, is an important process immediately after fire, even on deep granitic soils.

It is difficult to agree, in this case, with the conclusions of Hodgson and Heislers (1972) that in the eucalypt forests of S.E. Australia, "Ca, Mg, Na and K are more available [presumably to the plant] following burning, providing that the ash is not blown away by strong winds". In their comparison of the leaching of nutrients from burnt and unburnt forest floors in montane eucalypt forest, Rowe and Hagel (1974)

\* see Chapter 4.
demonstrated that a "fuel reduction" burn will significantly increase the susceptibility to leaching of \( \text{Ca}^{++} \), \( \text{K}^{+} \), \( \text{Na}^{+} \) and \( \text{SO}_4^{2-} \) and that leaching to depths greater than 5 cm may be expected with heavy rain after the fire. If heavy rain fell soon after the fire uptake of leached ions would depend on those species which did not suffer loss of photosynthetic tissue. In the present study, the increase in nutrients was generally very short lived after the fire, and was out-of-phase with any significant vegetation regrowth. The literature (section 5.5) suggests that frequency of severe wildfires, as well as understorey fires, has increased during the last 100 years in the subalpine forests. The nutrient analyses reported in this study, suggest in general, and in detail, that subalpine soils are significantly more fertile than soils under eucalypt forest at lower altitudes, where the groundsurfaces are not only older, but also affected by a greater natural frequency of fire. The analyses also suggest that the eucalypts on these subalpine soils mobilise nutrients at concentrations proportionate to their concentration in the primary materials. \( E. \text{delegatensis} \) appears to be restricted to high fertility sites, and at the same time is one of the very few absolutely fire-sensitive eucalypts (Jacobs, 1955).

In considering these factors in conjunction with the rapid net loss of nutrients in these physically stable granitic soils immediately after a wildfire, it seems obvious that a great deal more needs to be known about its effect on native vegetation before fire can be used with any degree of "success" as a management tool, that is, if the conservation of nutrient pools and ecosystem distribution are real objectives.

\(^*\) there was insufficient leachate solution in Rowe and Hagel's (1974) study to analyse for P.

\(^+\) see also analyses in Costin (1954) and Rowe (1967) where comparison can be made of an altitudinal range of soils.
## TABLE 10
Changes in the weight of cations and cationic elements at 3 dates in the first 10 months following a wildfire, Geehi Valley, Kosciusko National Park

<table>
<thead>
<tr>
<th>Date</th>
<th>5.1.73</th>
<th>25.2.73</th>
<th>15.11.73</th>
<th>5.1.73</th>
<th>25.2.73</th>
<th>15.11.73</th>
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<td>790</td>
<td>773</td>
<td>107</td>
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<td>790</td>
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<td>Oxidisable Carbon (kg/ha)</td>
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<td>------</td>
<td>--------</td>
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TABLE 10 continued

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<th>NH₄F+NaOH-Phosphorus (kg/ha)</th>
<th>Organic Phosphorus (kg/ha)</th>
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<td>total</td>
<td>33.3</td>
<td>48.9</td>
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* denotes a significant difference at p < 0.05, for 2 lab. analyses x 3 field samples.

TABLE 11 Some ratios of the concentrations of oxid. Carbon and total Nitrogen to Phosphorus, in the 0-5 cm soil during the first 10 months following a wildfire, Geehi Valley.

<table>
<thead>
<tr>
<th>Date</th>
<th>5.1.73</th>
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<th>16.11.73</th>
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<td>C/N ratio</td>
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<td>5.40</td>
<td>5.67</td>
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<tr>
<td>C/N ratio</td>
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</tr>
<tr>
<td>C/P₁ ratio</td>
<td>159.9</td>
<td>157.6</td>
<td>161.4</td>
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<tr>
<td><strong>E. delegatensis</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>C/P₁ ratio</td>
<td>206.6</td>
<td>185.6</td>
<td>210.4</td>
</tr>
<tr>
<td><strong>E. pauciflora</strong></td>
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<td></td>
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<td>N/P₁ ratio</td>
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<td>28.61</td>
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<td><strong>E. delegatensis</strong></td>
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<tr>
<td>N/P₁ ratio</td>
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<td>28.35</td>
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<tr>
<td>C/PNH₄F+NaOH ratio</td>
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<td>964</td>
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<td>C/PNH₄F+NaOH ratio</td>
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TABLE 11 continued

<table>
<thead>
<tr>
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<th>N/P_{\text{NH}_4F+\text{NaOH}} ratio</th>
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<td>E. pauciflora</td>
<td>E. delegatensis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>149.7</td>
<td>179.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>175.8</td>
<td>163.4</td>
</tr>
<tr>
<td>pH</td>
<td></td>
<td>E. pauciflora</td>
<td>5.54 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>E. delegatensis</td>
<td>5.10 *</td>
</tr>
</tbody>
</table>

TABLE 12 Changes in the % ground cover (200 point samples) during the first 10 months following a wildfire, Geehi Valley

<table>
<thead>
<tr>
<th>Date</th>
<th>5.1.73</th>
<th>25.2.73</th>
<th>15.11.73</th>
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<tbody>
<tr>
<td>Eucalyptus pauciflora low forest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. pauciflora (lignotubers)</td>
<td>x</td>
<td></td>
<td>3.0</td>
</tr>
<tr>
<td>Geranium solandrii</td>
<td>0.5</td>
<td></td>
<td>5.0</td>
</tr>
<tr>
<td>Gnaphalium collinimum</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Helipterum anthemoides</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Olearia erubescens</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Poa aniceps aff.</td>
<td></td>
<td></td>
<td>9.0</td>
</tr>
<tr>
<td>P. ensiformis</td>
<td>x</td>
<td></td>
<td>13.0</td>
</tr>
<tr>
<td>Ranunculus hirtus</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Stellaria media</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Stylidium graminifolium</td>
<td>0.5</td>
<td></td>
<td>2.0</td>
</tr>
<tr>
<td>Viola hederacea</td>
<td></td>
<td></td>
<td>x</td>
</tr>
</tbody>
</table>

TOTAL % COVER

1,0 32.0
<table>
<thead>
<tr>
<th>Species</th>
<th>TOTAL % COVER</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia obliquinervia</td>
<td>x</td>
</tr>
<tr>
<td>Asperula gunnii</td>
<td>x</td>
</tr>
<tr>
<td>Coprosma hirtella</td>
<td>x</td>
</tr>
<tr>
<td>Dianella tasmanica</td>
<td>2.0</td>
</tr>
<tr>
<td>E. dalrympleana (lignotuber)</td>
<td>1.0</td>
</tr>
<tr>
<td>Geranium solandrii</td>
<td>x</td>
</tr>
<tr>
<td>Gnaphalium collinimum</td>
<td>x</td>
</tr>
<tr>
<td>Haloragis micrantha</td>
<td>x</td>
</tr>
<tr>
<td>Lomatia myricoides</td>
<td>x</td>
</tr>
<tr>
<td>Olearia lirata</td>
<td>5.0</td>
</tr>
<tr>
<td>Poa anceps aff.</td>
<td>0.5 57.0</td>
</tr>
<tr>
<td>Polystichum proliferum</td>
<td>0.5 x</td>
</tr>
<tr>
<td>Ranunculus hirtus</td>
<td>x</td>
</tr>
<tr>
<td>Rubus trilobus</td>
<td>x</td>
</tr>
<tr>
<td>Stellaria media</td>
<td>1.0</td>
</tr>
<tr>
<td>Viola hederacea</td>
<td>x</td>
</tr>
</tbody>
</table>

**TOTAL % COVER**

|                        | 1.0 66.0 |

x denotes a species presence, but not as intercepted in the point analysis.

---

### 5.7 A SUMMARY OF RESULTS

The dynamics of nutrients and understorey vegetation during secondary succession have been examined in the context of the general theory of ecosystem development; that succession following a perturbation tends toward an eventual steady-state. A review has been made of the evidence for pertinent palaeoecological and historical change in the distributional and successional patterns of the vegetation. This has drawn upon publications and official records as well as recent observations...
of myself and others.

Summarising the palaeoecological evidence and the present distributions of two eucalypts, *E. delegatensis* and *E. pauciflora*, and *Nothofagus cunninghamii*, the following general points emerge:

1. The present-day distributions of these species are relic. That *E. pauciflora* was probably widely distributed in the humid periods, prior to aridity in the Late Pleistocene, is shown by its present sporadic occurrence in non-mountainous areas. It may be that fragmentation of the populations has led to the various forms of the species. The relic nature of *E. delegatensis* is manifested by a highly disjunct distribution, particularly in the northern part of its range. The distribution of *Nothofagus cunninghamii*, and other rainforest species, is likewise most disjunct in the northern, and perhaps more xeric, mountain areas, but there is evidence that it was previously less so.

2. The subalpine eucalypts appear to have evolved in a more mesic climate than that of the present day in the N.E. Highlands of Victoria and the Snowy Mountains, when the steady-stage vegetation was rainforest, as in present-day Tasmania. The eucalypts were seral, although commonly replacing themselves if perturbations were frequent.

3. The present absence of *Nothofagus* from most of the mainland subalpine zone could be explained by failure of biogeographic rebound, relative to the eucalypts, following the Pleistocene fluctuations in coldness and aridity.

4. In the absence of a rainforest biota, the long-term succession in the subalpine eucalypt ecosystems tends toward a steady-state characterised by an open woodland structure and a dense grass-herb
ground cover, in which there is a natality/mortality balance of
the dominants. Successional development towards inertia, whilst
proceeding continuously in an environment with a high probability
of disturbance, will be truncated according to the frequency of
disturbance.

The prehistorical and historical evidence may be summarised by
the following points:

1. In the subalpine zone, aboriginal access was very limited, for
specific food sources, and highly seasonal. It is most improbable
that much of the vegetation at these altitudes was subject to
aboriginal fires.

2. Recent evidence suggests that 8000 years BP was the earliest date
at which Aborigines were living close to the subalpine zone. Even
the most liberal estimate of 15,000 years BP allows for only about
60 generations of eucalypts with 250 year successional cycles,
an estimate for which there is ample evidence in these ecosystems.

3. If the proposition of rarity of Aboriginal fires is correct then
major changes have occurred in the incidence and severity of
wildfires since white settlement which have altered the tree
population structure throughout the subalpine zone. It is
doubtful whether any alpine, subalpine or montane ecosystem has
escaped the land-use practices of European man. Repeated fires
associated with grazing, and recently for fire protection, have
increased the cover and extent of dense understorey scrub and
altered the probabilities of long-term succession to a low-fire-
risk steady-state.

In the absence of a strictly time-dependent scale on which to
measure successional change, the variation in nutrient, organic matter and understorey parameters have been related to the mass of the F/H component of the forest floor. Amalgamation of data from 46 stands at different stages of recovery from a fire of some kind permitted the construction of probability distributions showing patterns of change in understorey and ground layer species composition, and the nutrient and organic matter content of the forest floor and the surface 5 cm of mineral soil. These distributions indicate that:

1. Whilst the canopy remains 'closed' there is a net accumulation of decomposing organic matter above the surface of the mineral soil, as long as severe disruption in the form of wildfire or 'fuel reduction' burn is absent. Accumulation continues to a point at which there is equilibrium between litter-fall and decomposition, at which stage the mass of the F/H is about 75 tonnes/hectare. During later stages, the tree canopy becomes more open, slowing the rate of litter accession. At the same time decomposition efficiency is increasing. The net result is the contraction of the F/H to a thin layer under open woodland.

2. During the same period of change the understorey, in general, passes through initial stages of either grass or shrub dominance, depending on the immediate post-fire conditions, followed by continued shrub dominance in which Leguminosae predominate, usually exclusively. Species diversity is at a peak in the later stages of shrub dominance, which is followed by a gradual shift to a dense ground cover almost exclusively of grasses and herbs. Diversity increases rapidly in the early stages as the amelioration of environmental conditions and structural changes in the forest permit the successful establishment of invading species.

3. In terms of general theory of secondary ecosystem development,
the most dramatic feature of the probability distributions of nutrients was the relative lack of any steady-state function as long as the forest floor is accumulating, except the slowed rates of net accumulation and apparent immobilization of total cations late in the succession. In certain cases, for example the concentration of N, this trend continues into the open woodland stage. During the forest-open forest succession, N, total P, non-occluded inorganic P, organic P and the cations all accumulate in the F/H, often exponentially, because of the tendency for nutrients to be lost for short periods after disturbance. There is a progressive decline in soil exchangeable cations as they are withdrawn by the biomass and immobilized in the forest floor. These distributions, together with the shift in the relative weight-distributions of nutrients from the forest floor to the soil by the stage of the open woodland ecosystem, suggest a period of instability in nutrient cycles and ecosystem processes during succession beneath a forest canopy, and shrub understorey. During this period there is progressive enrichment of the potential nutrient pool, once the initial losses have been overcome. As long as the succession is within these limits, considerable quantities of nutrients will be held above the mineral soil and largely unaffected by decomposition. It is in the advanced stages of this succession that the potential effect of a perturbation (such as a ground fire) will be greatest on the nutrient pool.

4. The dispersion of data from both *E. delegatensis* and *E. pauciflora* ecosystems indicate the essential similarity in their quantitative nutrient distributions according to the accumulation of F/H. The same process may occur at different rates because of the variation in biomass between the two, but it occurs with the same form in time.
5. The study shows the considerable variation in nutrient pools on different materials and under different community structures. Nevertheless the amalgamation of all stand nutrient data shows significant changes in time, particularly for forest floor:surface soil (kg/ha) ratios. There would be enormous difficulties in constructing similar long-term distributions in which parent material, soil morphology and the weathering status were constant, or in which there was a true-time-scale, i.e. a quantitative knowledge of all aspects of fire history. Instead, I have used a parameter such as the weight of the F/H component of the forest floor, which has an approximate rectilinear relationship to time, at least up until the opening of the forest canopy. The only alternative is to measure one site over a long period (Stevens and Walker, 1970).

6. The different nutrients accumulate not only in different quantities but at very different rates, and independently of the accumulation of the F/H layer itself.

7. Accumulation of nutrients above the soil surface under a forest canopy is at the expense of the plant available nutrients within the surface soil. Ratios show that as much as twice the weight of Ca^{++} and Mg^{++} in the surface soil, is in the F/H at the later stages of forest floor accumulation. Other ratios are 0.75 for K^{+}, 0.45 for Na^{+}, 0.6 for C.E.C., and 0.3 for total P and non-occluded inorganic P.

8. There is a marked difference in the accumulation of monovalent and bivalent cations in the F/H. Na^{+} and K^{+} broadly resemble the rates of accumulation of C.E.C., oxidisable C and the F/H itself. Ca^{++} and Mg^{++} differ in that they accumulate rapidly at first and then decline as the F/H continues to accumulate beyond about 50-60
tonnes/ha.

9. Point 8. above, and the different rates and levels of accumulation of total exchangeable cations, suggest that there is a threshold to the immobilisation of exchangeable cations prior to the equilibrium point for net organic matter accumulation. This could suggest that during the later stages of the 'forest' succession there is a change in the decomposition regime, so that whilst there is still net accumulation of organic matter on the forest floor, some of the accumulated cations bound to organic complexes are being mobilized.

10. The C/N ratios indicate increased decomposition in the later successional stages.

11. The weight distributions of total P, organic P and non-occluded inorganic P broadly resemble the cations, but with apparent net losses early in the secondary succession. There are slower rates of accumulation in the late stages. Organic P, as a weight and percentage of the total P, accumulates in both the F/H and the surface soil. Easily soluble P in the F/H decreases in concentration as succession proceeds, but has a weight peak early in the stage of shrub dominance. It appears that considerable quantities of this fraction occur in the litter-fall of these ecosystems but that its fate is very short lived, because of immobilization in organic complexes. Easily soluble P is virtually absent from the mineral soil.

12. The results support the thesis of Attiwill (1964) that the commencement of net return of P to the forest floor, after a disturbance, occurs later than for the cations. However in all except the most disturbed sites, uptake and immobilization of P
are at luxury levels, and P accumulates at almost the same rate as F/H and carbon. There is little to suggest that the supply of P becomes inadequate because of immobilization in organic matter and detritus during succession.

13. Analysis of forest floors and surface soils of ecosystems subjected to an intensive history of 'fuel reduction' burning, showed that there is not only minimal quantities of organic matter, and minimal concentration and quantities of available nutrients in these sites, but also a minimal amount of soil fines. Although the quantities and concentrations of 'available' nutrients are stimulated by fires of this nature, the effect of successive small-fire-events during the early stages of F/H accumulation is to truncate the recovery process, particularly the consolidation of the soil surface cover. The degree of perturbation may be such that on some parent materials, there is already a debility-trend in soil physical structure and levels of available nutrients as a fraction of less disturbed systems.

14. "Available" P is disproportionately affected by alteration of the forest floor mass by fire. As non-occluded inorganic P comprises some 20-25% of total P, much of which is in the 0-5 cm primary soil-particles, there is an increasing problem in conserving the "available" pool of P and maintaining the ecosystems that are restricted to high-P environments, if regular burning of the understorey is to be pursued in some of these ecosystems.

15. Monitoring of the quantities and concentrations of nutrients immediately after a wildfire and during the following 10 months indicates that compared to any other nutrient, large amounts of carbon are lost from the ecosystem during fire. The degree of loss of C is critical in determining the flux of nutrients,
particularly if the topographic position of a stand tends to increase its susceptibility to leaching and surface flow of nutrients in suspension and solution. The concentration of most cations, particularly Ca$^{++}$ and K$^+$, in the consumed organic matter on the ground immediately after the fire was greater than in any F/H material sampled in this study. All of this added nutrient pool has been lost from the surface soil in the space of 10 months. Combustion seems to retard exchangeability of some elements, notably Na. Likewise C/N ratios, and C/total P and C/non-occluded inorganic P ratios in the soil during this first 10 months after fire, are lower than in any other site. It is clear that whilst considerable C is lost from the surface soil during combustion, insufficient is added later to absorb exchangeable nutrients.

The increase in nutrients was very short-lived and out-of-phase with any significant regrowth in the understorey vegetation cover.

In general, it is apparent that the subalpine tall open forests, open forests and low open forests (Specht, 1970) of *Eucalyptus* spp. are unstable systems, in terms of the fluxes of nutrients between ecosystem compartments, and the rate of phasic replacement of the understorey vegetation. The rate of production of organic matter and its accretion to the forest floor exceeds the rate of biodegradation. The concept of these systems tending towards a steady-state, in terms of ecosystem processes, is fundamental to an understanding of their evolutionary development, despite the fact that the present-day ecosystems in the entire subalpine eucalypt biome are so altered that they are in a highly unstable state.
The quantities of nutrients and energy in the older forest floors represent a considerable proportion of their total quantities in the ecosystem. Until there is a marked diminution in the weight of the forest floor, these quantities of nutrients and energy will be temporarily inaccessible to ecosystem processes. If succession proceeds beyond the point of maximum biomass production, nutrient cycling and energy flow become increasingly closed systems as respiration and decomposition become more efficient in balancing the reduced input of materials to the forest floor and their uptake by the biomass. If succession is truncated at this point the loss of carbon will be considerable, and will be followed by a general equivalent loss of cations and phosphorus, because of the de-structuring of organic complexes and exchange-surfaces.
CHAPTER 6
NUTRIENT CYCLING FLUXES IN ADJACENT ECOSYSTEMS OF
E. DELEGATENSIS AND E. PAUCIFLORA

6.1 INTRODUCTION

The preceding chapters have indicated differences in the nutrient pools, within the forest floor and surface soil, between adjacent ecosystems of *E. delegatensis* and *E. pauciflora*, and fluxes in the same nutrient pools during secondary succession following disturbance. It is apparent that whilst the rate of flux in nutrients during succession is similar for both ecosystem types, there are considerable differences in the quantity and quality of the nutrient pools. Because of the constancy in parent materials and topography across most ecotones, it would appear that the differences are attributable to differences in ecosystem processes, and site factors dependent on the structure of the vegetation.

In order to understand the origin of these differences in the nutrient pools, a study was designed to measure the differences in above-ground biomass, and the differences in the internal fluxes in nutrients that are dependent on the different structure of the vegetation. These are represented by the inputs from litter to the forest floor, and decomposition on the forest floor.

The objectives of the study were to ascertain any marked differences in the fluxes of particular nutrients between the two ecosystems in an ecotonal situation. This would enable greater interpretation of the behaviour of these nutrients described in the previous studies in this thesis. Therefore, sample-sizes were smaller than would be necessary to measure the absolute quantities of nutrients in litter-fall and
decomposition sequences. The monitoring study was carried out for 12 months at an ecotone between *E. delegatensis* and *E. pauciflora* in the Brindabella Ranges, New South Wales near the upper altitudinal limit of the former species at 1520 m (see Plate X). Measurements were made of the following parameters:

1. **Weekly maximum and minimum temperature at the forest floor** (2 thermometers per stand).

2. **Weekly throughfall precipitation** (2 gauges per stand, located adjacent to the decomposition samples).

3. **Tree basal area** (point-centre-quarter analysis (Cottam and Curtis, 1956), 100 trees per stand; quadrat analysis (Greig-Smith, 1952)).

4. **Vegetation space** (Point-height-intercept analysis (Park, 1973); 100 points per stand).

5. **The concentration and mass of the standing-state nutrient pool on the forest floor** (10, 1.102 m² samples of the L and F/H layers of each stand). All samples analysed for total cations and nitrogen and phosphorus, as well as total weight.

6. **Seasonal variation in the mass and nutrient content of litter-fall** (fortnightly collections from 15 sieves, 0.258 m² per stand). Samples weighed separately and pooled for analysis of total cations, nitrogen and phosphorus for each date.

7. **Seasonal variation on dry weight and the release of nutrients in decomposing litter on the forest floor** (4 mesh bags of leaves, collected during period of maximum leaf-fall, sampled fortnightly). Samples weighed separately and analysed separately for total and exchangeable cations, nitrogen and phosphorus.

The monitoring studies were made between March 1973 and April...
1974. Methods of sampling, sample treatment and chemical analysis are described in Chapter 3 (section 3.3).

6.2 THE ENVIRONMENT OF THE STUDY AREA

The study area was located on a south-west facing slope of Bendoura Hill in the Brindabella Range, an interfluve between the Goodradigbee and Cotter Rivers, at the western boundary of the Australian Capital Territory about 40 kilometres south-west of Canberra. The range rises toward the south, from about 1200 m near Picadilly Circus to just over 1850 m at Mt. Gingera, over a distance of about 20 kilometres. The descent into the river valleys on either side is steep, particularly to the west where the mean gradient is about 1 in 3. Vegetation patterns reflect the dissected topography. The study area is exposed to prevailing westerly winds across a broad valley about 12 kilometres wide.

The ecotonal site was selected where stands of *E. pauciflora* and *E. delegatensis* occupy similar topographical positions. *E. pauciflora* occurs higher up the slope than *E. delegatensis*, with which it forms a contiguous boundary. However, the nature of the surrounding slopes defines the *E. delegatensis* site as occupying a more sheltered position.

The general climate of the area is continental, with summer temperatures reaching 40° occasionally each summer and winter temperatures frequently below freezing. Snowfalls occur almost every winter and snow may lie for a few weeks. Weekly maximum and minimum temperatures and throughfall precipitation data, collected as part of this study, are presented in Figure 13. Detailed climatic data, in part summarizing observations from the official Bureau of Meteorology at Bulls Head Station, in a very similar environment about 10 kilometres distant, are presented
(a) Open forest of *Eucalyptus pauciflora*

(b) Tall open forest of *Eucalyptus delegatensis*

The stands at Bendoura Hill in which measurements were made of vegetation structure and nutrient cycling fluxes.

PLATE X
The soils at the study site are formed from a granodiorite pluton of the Bendora batholith (M. Owens, pers. comm). The stand of *E. delegatensis* has developed on a slope deposit (Costin and Polach, 1971) of variable depth formed, in part, by deflation under periglacial conditions of the ground surface of higher slopes now occupied by *E. pauciflora*. The soils beneath both species exhibit disturbance such as concentrations of stones at the surface and a lack of a highly organic upper soil. In the *E. pauciflora* site, an alpine humus soil is developing (Appendix VII) whilst the soil in the *E. delegatensis* site is more typical of the transitional alpine humus soils (Appendix VII), and shows some features of an acid brown earth such as a compact upper soil with very little organic matter. This is a feature of youth in soils at this altitude, resulting from recent disturbance by fire.

The understorey vegetation shows considerable differences in composition and structure (Plate X, and Figure 12), which are important factors in the flux of nutrients to, and on, the forest floor. Point analysis (200 points at two-pace intervals) gave the following percentages for leaf and litter cover in the two ecosystems:

<table>
<thead>
<tr>
<th></th>
<th><em>E. pauciflora</em></th>
<th><em>E. delegatensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrubs</td>
<td>6</td>
<td>13</td>
</tr>
<tr>
<td>Grasses (mainly <em>Poa ensiformis</em>)</td>
<td>63</td>
<td>34</td>
</tr>
<tr>
<td>Other plants (mainly herbs)</td>
<td>15</td>
<td>3</td>
</tr>
<tr>
<td>Litter</td>
<td>13</td>
<td>50</td>
</tr>
<tr>
<td>Bare ground</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

The shrub understories are mainly of Leguminosae; (*Acacia polymorpha*, *Daviesia mimosoides* and *D. ulicifolia*, as well as *A. dealbata* in the *E. delegatensis* stand). *Coprosma hirtella* is an important shrub in the *E. delegatensis* stand.
The study area was included in the analysis of the nutritional relationships of the forest floors and surface soils of the ecotone between *E. delegatensis* and *E. pauciflora* (Chapter 4). In this case, the site was sampled during the previous summer, so the data must be considered separately. They are presented in Appendix III (Table 16).

6.3 RESULTS

6.3.1 INTRODUCTION

The results of the study are shown in Figures 12-18. The data presented in these figures are tabulated in Appendix X. Some data which are not graphed are tabulated in the text. An important aspect of the interpretation of the results is the relative distribution of specific nutrients, total weights and estimations of above-ground biomass in the *E. pauciflora* and *E. delegatensis* ecosystems. In Figure 18 these parameters are expressed as ratios in the form,

\[
E.p/E.d. = \frac{\text{quantity in } E. \ pauciflora \ \text{ecosystem}}{\text{quantity in } E. \ delegatensis \ \text{ecosystem}}
\]

6.3.2 ESTIMATION OF ABOVE-GROUND BIOMASS

The results are presented in Figure 12 and Table 13. Destructive sampling of above-ground biomass was not practical, but a meaningful basis from which to assess the relative fluxes of nutrients could be derived by the customary comparison of the cross-sectional area (basal area) of the vegetation, and by comparing the space occupied by the two different communities. *Vegetation space* is one of numerous structural parameters that can be calculated from a plot of point-height-intercept information (Park, 1973). It is defined as the "space" enclosed by the
canopy of the vegetation in a height frequency distribution (Figure 12). Specific vegetation space relates the space enclosed by the canopy to the space enclosed by the maximum canopy height. In closed forests where the canopy height is even, with few gaps, the ratio will be greater than about 0.70 (Park, 1973). In the open eucalypt forests of the study site, the ratios are less than 0.50.

Major structural differences are apparent between the two communities; the *E. delegatensis* forest clearly has the greater above-ground biomass. The vegetation data also demonstrate the monodominant nature of both communities and the lack of any understorey layer as a significant component of the total biomass and input of nutrients to the forest floor.

By comparison with the biomass of *E. obliqua* forest in the montane zone of Victoria (Attiwill, 1964) total biomass can be approximately determined from the assumption that annual production of litter correlates highly with total biomass in forests of similar physiognomy (Whittaker and Woodwell, 1968). The similar Ep/Ed ratios for vegetation space and annual litter production supports this assumption.

**TABLE 13  Structural features of the vegetation**

<table>
<thead>
<tr>
<th></th>
<th><em>E. delegatensis</em></th>
<th><em>E. pauciflora</em></th>
<th>Ep/Ed ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal area (P.C.Q.) m²/ha</td>
<td>64.98</td>
<td>26.97</td>
<td>0.384</td>
</tr>
<tr>
<td>&quot;  &quot; (Quadrat) &quot;</td>
<td>68.86</td>
<td>29.78</td>
<td>0.432</td>
</tr>
<tr>
<td>Vegetation space (units)</td>
<td>1545</td>
<td>822</td>
<td>0.532</td>
</tr>
<tr>
<td>Specific vege. space (ratio)</td>
<td>0.495</td>
<td>0.444</td>
<td></td>
</tr>
<tr>
<td>Annual litter-fall (tonnes/ha)</td>
<td>6.25</td>
<td>3.56</td>
<td>0.548</td>
</tr>
<tr>
<td>Total biomass (est.) (tonnes/ha)</td>
<td>620</td>
<td>330</td>
<td>0.532</td>
</tr>
</tbody>
</table>
FIGURE 12 Simplified P.H.I. diagrams (Park, 1973) outlining the vegetation structural relationships between adjacent stands of *E. pauciflora* and *E. delegatensis*.
6.3.3 THE CONCENTRATION AND MASS OF THE STANDING-STATE NUTRIENT POOL ON THE FOREST FLOOR

The total and relative contributions of the L and F/H layers to detritus pools in terms of total dry-weights, and concentrations and weights of nutrients, are given in Table 14. In making comparisons between these forest floors and with the literature, several points must be remembered. Litter (L) and fermentation and humus layers (F/H) have been defined, and were sampled in the customary way (see Chapter 3, section 3.3). The Bendoura Hill ecosystems are therefore comparable with examples in the literature.

Generally the results (Table 14) support the conclusion of the ecotonal study (Chapter 4) that whilst the mass of the forest floor may be greater under a stand of *E. delegatensis* than under a stand of *E. pauciflora*, there are greater quantities and concentrations of most nutrients beneath *E. pauciflora*. However, as a proportion of the total quantity or concentration, the difference is usually slight; a result of internal fluxes rather than primary differences in site.

The scale of difference between the forest floor layers of the two ecosystems, and the independent behaviour of individual elements, is best described by the Ep/Ed ratios of concentrations and weights (Figure 18). Relative to dry weight, the quantity of elements in the L layer is greater in the *E. pauciflora* ecosystem, especially for Ca, Mn and Na. There is a shift in this relationship for individual elements in the F/H layer; for example, Ca accumulates considerably in the *E. pauciflora* ecosystem, whilst Na and K appear to be lost from the forest floor of *E. pauciflora* during decomposition to the extent that there are greater quantities in the F/H of the *E. delegatensis* ecosystem. N, P and Mg occur in slightly greater quantities in both the L and F/H layers of *E. pauciflora*, whilst Fe and Zn resemble the differences in total dry weight
TABLE 14

CONCENTRATION AND MASS OF DRY MATTER AND NUTRIENT ELEMENTS IN THE FOREST FLOOR OF ADJACENT ECOSYSTEMS OF *E. DELEGATENSIS* AND *E. PAUCIFLORA*.

(a) CONCENTRATION (ppm)

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>P</th>
<th>Ca</th>
<th>Fe</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>Na</th>
<th>Zn</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. pauciflora</em> (L layer)</td>
<td>7520</td>
<td>14620</td>
<td>730</td>
<td>870</td>
<td>950</td>
<td>960</td>
<td>34</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>S.E.</td>
<td>604</td>
<td>1200</td>
<td>41</td>
<td>42</td>
<td>59</td>
<td>121</td>
<td>8</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>E. delegatensis</em> (L layer)</td>
<td>6560</td>
<td>11720</td>
<td>680</td>
<td>830</td>
<td>920</td>
<td>500</td>
<td>23</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>S.E.</td>
<td>541</td>
<td>1090</td>
<td>44</td>
<td>67</td>
<td>78</td>
<td>49</td>
<td>5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Ep/Ed ratio (L layer)</td>
<td>1.14</td>
<td>1.04</td>
<td>1.25</td>
<td>1.07</td>
<td>1.04</td>
<td>1.93</td>
<td>1.48</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td><em>E. pauciflora</em> (F/H)</td>
<td>9970</td>
<td>15630</td>
<td>13180</td>
<td>4590</td>
<td>3640</td>
<td>1840</td>
<td>93</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>S.E.</td>
<td>590</td>
<td>1190</td>
<td>1010</td>
<td>309</td>
<td>161</td>
<td>142</td>
<td>18</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Ep/Ed ratio (F/H)</td>
<td>7.14</td>
<td>1.22</td>
<td>1.86</td>
<td>1.00</td>
<td>0.95</td>
<td>1.15</td>
<td>0.97</td>
<td>1.14</td>
<td></td>
</tr>
</tbody>
</table>

(b) NUTRIENT-WEIGHT (kg/ha); TOTAL DRY WEIGHT (tonnes/ha)

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>P</th>
<th>Ca</th>
<th>Fe</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>Na</th>
<th>Zn</th>
<th>dry matter</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. pauciflora</em> (L)</td>
<td>122.2</td>
<td>6.75</td>
<td>237.5</td>
<td>11.60</td>
<td>14.14</td>
<td>14.27</td>
<td>15.72</td>
<td>0.56</td>
<td>0.23</td>
<td>16.23</td>
</tr>
<tr>
<td>S.E.</td>
<td>8.1</td>
<td>29.5</td>
<td>1.0</td>
<td>1.16</td>
<td>1.27</td>
<td>1.32</td>
<td>0.10</td>
<td>0.01</td>
<td>1.64</td>
<td></td>
</tr>
<tr>
<td><em>E. delegatensis</em> (L)</td>
<td>100.5</td>
<td>5.62</td>
<td>205.5</td>
<td>13.13</td>
<td>13.87</td>
<td>13.83</td>
<td>9.57</td>
<td>0.29</td>
<td>0.25</td>
<td>16.90</td>
</tr>
<tr>
<td>S.E.</td>
<td>7.5</td>
<td>19.4</td>
<td>1.92</td>
<td>1.37</td>
<td>1.50</td>
<td>1.17</td>
<td>0.04</td>
<td>0.03</td>
<td>1.61</td>
<td></td>
</tr>
<tr>
<td>Ep/Ed ratio</td>
<td>1.21</td>
<td>1.16</td>
<td>0.88</td>
<td>1.02</td>
<td>1.03</td>
<td>1.64</td>
<td>1.94</td>
<td>0.93</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td><em>E. pauciflora</em> (F/H)</td>
<td>201.1</td>
<td>12.87</td>
<td>259.4</td>
<td>246.9</td>
<td>78.3</td>
<td>65.6</td>
<td>35.0</td>
<td>1.70</td>
<td>0.58</td>
<td>17.96</td>
</tr>
<tr>
<td>S.E.</td>
<td>25.7</td>
<td>20.7</td>
<td>21.5</td>
<td>8.1</td>
<td>4.5</td>
<td>4.9</td>
<td>0.24</td>
<td>0.04</td>
<td>1.42</td>
<td></td>
</tr>
<tr>
<td><em>E. delegatensis</em> (F/H)</td>
<td>156.9</td>
<td>10.98</td>
<td>162.0</td>
<td>264.5</td>
<td>97.3</td>
<td>64.0</td>
<td>19.6</td>
<td>1.97</td>
<td>0.61</td>
<td>20.24</td>
</tr>
<tr>
<td>S.E.</td>
<td>16.1</td>
<td>14.1</td>
<td>21.6</td>
<td>8.3</td>
<td>5.2</td>
<td>1.8</td>
<td>0.28</td>
<td>0.04</td>
<td>1.71</td>
<td></td>
</tr>
<tr>
<td>Ep/Ed ratio</td>
<td>1.25</td>
<td>1.18</td>
<td>1.35</td>
<td>0.92</td>
<td>0.82</td>
<td>1.02</td>
<td>1.73</td>
<td>1.00</td>
<td>0.93</td>
<td>0.92</td>
</tr>
<tr>
<td><em>E. pauciflora</em> (L+F/H)</td>
<td>323.3</td>
<td>19.62</td>
<td>496.9</td>
<td>257.4</td>
<td>92.4</td>
<td>79.8</td>
<td>50.7</td>
<td>2.26</td>
<td>0.81</td>
<td>34.19</td>
</tr>
<tr>
<td><em>E. delegatensis</em> (L+F/H)</td>
<td>257.4</td>
<td>16.59</td>
<td>367.5</td>
<td>277.6</td>
<td>111.2</td>
<td>77.8</td>
<td>29.2</td>
<td>2.25</td>
<td>0.86</td>
<td>37.17</td>
</tr>
<tr>
<td>Ep/Ed ratio</td>
<td>1.25</td>
<td>1.18</td>
<td>1.35</td>
<td>0.92</td>
<td>0.82</td>
<td>1.02</td>
<td>1.73</td>
<td>1.00</td>
<td>0.93</td>
<td>0.92</td>
</tr>
</tbody>
</table>
and are slightly greater in the *E. delegatensis* layers. In most cases the differences are non-significant. All *Ep/Ed* ratios are within the 0.75-1.25 range except for those of Ca and Mn, and Na in the L litter, which show markedly preferred accumulation beneath *E. pauciflora*.

6.3.4 SEASONAL FLUXES IN THE MICROCLIMATE OF THE FOREST FLOOR

Results are presented in Figure 13 and Appendix X (Table 1). Both stands show close correspondence to the same weather patterns and the differences between stands, particularly for the temperature parameters, are strikingly consistent. Because of the differences in stand structure, the consistent pattern of greater maximum and lower minimum temperature in the forest floor of the *E. pauciflora* stand cannot be interpreted as limiting the establishment of the component eucalypts, notably *E. delegatensis*. However, such a difference could suggest a threshold to frost resistance of seedlings in periods of extremely low temperature which may only occur once every several years (see Chapter 4; section 4.4.2.7). The difference is mainly a function of the more open structure of the *E. pauciflora* community. It may be interpreted as an important direct factor in the efficiency of decomposition on the forest floor, and as an indirect factor through an accumulated effect on the nature of the ground vegetation and the forest floor/surface soil interface. During brief periods of high rainfall, there is usually greater through-fall in the *E. pauciflora* stand. The thermometers and raingauges were located near the series of litter decompositions samples so that the effect of specific weather events could be monitored.
FIGURE 13 Seasonal fluxes in micro-climate at the forest floor in adjacent stands of *E. delegatensis* and *E. pauciflora*.
FIGURE 14 Seasonal fluxes in the physical components of litter-fall in adjacent stands of *E. delegatensis* and *E. pauciflora*.
FIGURE 15.1 Seasonal fluxes in the concentration of total nutrients in litter-fall in adjacent stands of *E. delegatensis* and *E. pauciflora*. 
FIGURE 15.2 Seasonal fluxes in the weight of total nutrients in litter-fall in adjacent stands of *E. delegatensis* and *E. pauciflora*.
6.3.5 SEASONAL FLUXES IN LITTER-FALL

6.3.5.1 Physical components of litter-fall

The results are presented in Figure 14 and Appendix X (Table 2). Using the t-test (Sokal and Sneath, 1969), a significant value of t was obtained (p < 0.01) for differences between stands in total annual litter-fall, and for weekly collections during the summer and autumn. Significance at this level has been taken as acceptable by many workers, e.g. Miller and Hurst (1957). In this study 15 collections per stand, each 0.258 m² in area were made every two weeks. The significantly greater total annual litter-fall of the *E. delegatensis* community (6.25 tonnes/ha compared to 3.56 of the *E. pauciflora* community) is largely a function of the considerable differences in litter-fall during summer and autumn.

Litter-fall was not continuous throughout the year, but reached a well-defined peak in late summer. In the *E. pauciflora* sites, the weight of material (mainly branches and bark) deposited during winter storms was almost as great as the late summer peak. There are two seasonal forms of litter-fall; in late spring to autumn, fall is almost exclusively dominated by leaf material, from early winter to early spring there is a much lower quantity of litter-fall and it is dominated by bark and branch material detached by storms.

6.3.5.2 The concentration of nutrients in the litter-fall

Results are presented in Figure 15.1 and Appendix X (Table 3). Three major generalisations can be drawn from these data,

(i) there is a trend (non-significant) for the concentrations of all elements, except Ca, to be greater during the
period of maximum litter-fall, in both ecosystems.

(ii) During the period of maximum litter-fall there is a tendency (non-significant) for the litter of *E. pauciflora* to contain greater concentrations of elements than the litter of *E. delegatensis*. The concentration of Ca is always greater, usually significantly, in the litter of *E. pauciflora*, particularly in midwinter when the accession of bark on the forest floor is greatest. Only in winter does the concentration of Mg differ between the two ecosystems, when it is greater, often significantly, in the litter of *E. pauciflora*.

(iii) Each element shows considerable fluctuations in concentration, often over short periods. The concentration and quantity of nutrient elements at the time of sampling are the net result of physiological transfers prior to litter-fall, leaching on the tree, leaching and decomposition on the forest floor prior to sampling, and atmospheric inputs.

Because the objective of this specific study of litter-fall was to ascertain marked differences in the seasonal fluxes of nutrients, in order to aid the interpretation of ecotonal and successional studies, no attempt was made to obtain a statistical sample by analysing the nutrients in each of the 15 sub-samples at each two-weekly collection.

6.3.5.3 The quantity of nutrients in the litter-fall

Results are presented in Figures 15.2 and 18, Tables 15 and 16, and Appendix X (Table 4).
TABLE 15 Annual contribution of nutrient elements in litter-fall (kg/ha)

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>P</th>
<th>Ca</th>
<th>Fe</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>Na</th>
<th>Zn</th>
<th>total dry matter tonnes/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>E. pauciflora</strong></td>
<td>24.9</td>
<td>1.83</td>
<td>44.9</td>
<td>0.6</td>
<td>9.5</td>
<td>5.0</td>
<td>3.0</td>
<td>0.2</td>
<td>1.2</td>
<td>3.55</td>
</tr>
<tr>
<td><strong>E. delegatensis</strong></td>
<td>35.8</td>
<td>2.9</td>
<td>52.0</td>
<td>0.9</td>
<td>1.3</td>
<td>8.2</td>
<td>4.0</td>
<td>0.4</td>
<td>1.5</td>
<td>6.23</td>
</tr>
<tr>
<td><strong>Ep/Ed ratio</strong></td>
<td>0.69</td>
<td>0.61</td>
<td>0.86</td>
<td>0.68</td>
<td>0.70</td>
<td>0.60</td>
<td>0.74</td>
<td>0.51</td>
<td>0.82</td>
<td>0.56</td>
</tr>
</tbody>
</table>

TABLE 16 Grouped seasonal contributions of nutrient elements in litter-fall (kg/ha)

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>P</th>
<th>Ca</th>
<th>Fe</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>Na</th>
<th>Zn</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>AUTUMN</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>E. pauciflora</strong></td>
<td>4.64</td>
<td>0.31</td>
<td>8.74</td>
<td>0.19</td>
<td>1.66</td>
<td>0.91</td>
<td>0.51</td>
<td>0.085</td>
<td>0.36</td>
</tr>
<tr>
<td><strong>E. delegatensis</strong></td>
<td>7.45</td>
<td>0.64</td>
<td>11.56</td>
<td>0.34</td>
<td>3.61</td>
<td>1.65</td>
<td>0.86</td>
<td>0.12</td>
<td>0.28</td>
</tr>
<tr>
<td><strong>WINTER</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>E. pauciflora</strong></td>
<td>1.93</td>
<td>0.12</td>
<td>5.09</td>
<td>0.08</td>
<td>0.59</td>
<td>0.49</td>
<td>0.17</td>
<td>0.019</td>
<td>0.10</td>
</tr>
<tr>
<td><strong>E. delegatensis</strong></td>
<td>1.91</td>
<td>0.09</td>
<td>2.76</td>
<td>0.08</td>
<td>0.47</td>
<td>0.38</td>
<td>0.16</td>
<td>0.017</td>
<td>0.09</td>
</tr>
<tr>
<td><strong>SPRING</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>E. pauciflora</strong></td>
<td>2.82</td>
<td>0.16</td>
<td>6.00</td>
<td>0.11</td>
<td>0.62</td>
<td>0.51</td>
<td>0.28</td>
<td>0.021</td>
<td>0.19</td>
</tr>
<tr>
<td><strong>E. delegatensis</strong></td>
<td>2.79</td>
<td>0.21</td>
<td>3.45</td>
<td>0.11</td>
<td>0.78</td>
<td>0.47</td>
<td>0.22</td>
<td>0.039</td>
<td>0.22</td>
</tr>
<tr>
<td><strong>SUMMER</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>E. pauciflora</strong></td>
<td>15.51</td>
<td>1.24</td>
<td>25.13</td>
<td>0.28</td>
<td>6.68</td>
<td>3.14</td>
<td>2.07</td>
<td>0.102</td>
<td>0.58</td>
</tr>
<tr>
<td><strong>E. delegatensis</strong></td>
<td>23.65</td>
<td>1.98</td>
<td>34.29</td>
<td>0.42</td>
<td>8.63</td>
<td>5.78</td>
<td>2.85</td>
<td>0.308</td>
<td>0.90</td>
</tr>
</tbody>
</table>

For each element, the total annual weight is considerably greater in the litter-fall of *E. delegatensis* than in *E. pauciflora*. However, for all elements except Na the Ep/Ed ratio is greater than for the total dry weight (Figure 18, Table 15). This relationship is borne out in the
grouped seasonal data (Table 16), for the autumn and summer periods when about 80% of the total litter-fall occurs. In winter, the weight of every nutrient is marginally greater in the litter of the *E. pauciflora* ecosystem, except Ca which is twice as abundant in *E. pauciflora* litter than it is in that of *E. delegatensis*. In spring, the difference is also marginal with N, Ca Mg and Mn in greater quantities in the litter of *E. pauciflora*. Ca is almost twice as abundant in the *E. pauciflora* litter during the spring. The high quantities of Ca are most likely due to the input of considerable quantities of bark and branch tissue in the *E. pauciflora* ecosystem during two storms in July and October (Figures 14; 15.2).

The dominant influence on the quantities of the individual element during the year is undoubtedly the total weight of litter-fall. In both ecosystems the rate of flux of all element-weights parallels litter-fall, peaking in mid-summer and autumn, the period of maximum leaf-fall; the fluxes in concentration (Figure 15.1) produce relatively small divergences from an essentially similar trend. However the fluxes in concentration during the year do result in some degree of individuality in the fluxes in element-weights. The greatest divergence of the distributions of element-weights from the distribution of total litter-fall during the year occurs during early summer. In winter and spring, Ca and Mg show considerable peaks during storms. P and K are least affected by the different kind of litter-fall during these storms.

6.3.6 SEASONAL FLUXES IN THE DECOMPOSITION OF LEAF LITTER

6.3.6.1 Introduction

The flux rates of nutrients were monitored for 12 months, at two-weekly intervals in leaves placed in contact with the fermentation-humus (F/H)
layer of the forest floor. The experiment started immediately after the period of maximum litter-fall in late summer and early autumn. The study was restricted to examining the flux rates of nutrients in *E. delegatensis* and *E. pauciflora* foliage in the respective communities of these species. Alternatives would have been to have compared the flux rates of nutrients in foliage of both species in both stands, or in a common intermediate forest floor environment. To avoid problems of interpretation of initial changes in nutrient concentrations subsequent to litter-fall, samples were collected from the oldest series of canopy leaves and combined with recently fallen litter. It is known that there are considerable changes in the concentrations of individual nutrients in foliage immediately prior to leaf-fall (Attiwill, 1968; Miller, 1963) as well as leaching on the trees and immediately after the leaf comes in contact with the forest floor. Generally, the concentration is greater in the foliage collected for the study of decomposition than in litter-fall.

6.3.6.2 The concentrations of nutrients in decomposing leaf litter

Results are plotted in Figures 16 and 18. Data are tabulated, according to Figure 16, in Appendix X (Table 5). In view of the nature of the original leaf litter, it is important to note that in all elements, except N in *E. delegatensis* litter, the major flux in concentration is a marked decline during the first few weeks on the forest floor (Figure 16). Fe, Mn, Na and Zn were analysed but have not been plotted in this way because of the relatively high degree of variation between the four samples at each collection. The five elements plotted show quite independent fluxes in concentration. All except N in the *E. delegatensis* litter show rapid initial declines. The concentration of Mg continues to decline throughout winter and spring. The concentration
FIGURE 16 Seasonal fluxes in the concentration of nutrients in decomposing leaf litter in adjacent stands of *E. delegatensis* and *E. pauciflora*
FIGURE 17 Seasonal fluxes in the weight of total dry matter and nutrients in decomposing leaf litter.
of most other elements, except K, increase at the end of winter and
maintain generally higher levels until the end of the 12 month experiment,
There is a marked increase in Ca during the summer months in the *E.
pauciflora* ecosystem, and a lesser increase in Ca and Mg in the *E.
delegatensis* ecosystem. Apart from distinctly lower concentrations of
N and P during the first 5 months (April-August) of decomposition, the
concentration of all elements in the *E. pauciflora* litter is either
higher than, or similar to that of *E. delegatensis*. The concentrations
of Ca and Mg are consistently higher in the *E. pauciflora* litter, the
difference becoming progressively greater for Ca, but less for Mg until
it is in fact less than in the *E. delegatensis* litter during the last
few weeks of the year. Only Mg and N show marked fluctuations in
concentration between the two-weekly collections, although most of the
nutrients respond to perturbations in temperature, rainfall and litter
falling on the samples during the year.

The flux in easily soluble P ($P_{NH_4Cl}$) in the first eight months
on the forest floor is described in Chapter 5 (5.6.4.3). Considerable
quantities of this fraction occur in the litter-fall but it appears to
be rapidly fixed in, or leached from, the forest floor.

6.3.6.3 The quantity of dry matter and nutrients in decomposing leaf
litter

Results are plotted in Figures 17 and 18. Data are tabulated,
according to Figure 16, in Appendix X (Table 6). Element-weights
are calculated as a percentage of the original weight of total dry matter
(approximately 15 g) of leaves placed on the forest floor, in mesh bags,
in early autumn. The data are plotted in this manner so that the
different rates of flux for the *E. pauciflora* and *E. delegatensis*
ecosystems are distinguished in relation to the distinct overall trends
in decomposition.

The loss of dry matter in both ecosystems is of approximate rectilinear relationship to time. Although the plotted data are means of only four samples, the loss of dry weight is consistent and even, despite the high frequency of sampling. Loss is most rapid in the first few weeks and from mid-summer to autumn in the latter stages of the study. The decomposition of *E. pauciflora* litter was progressively less than *E. delegatensis* litter; 47.5% and 69.5% of original dry weight respectively (a difference of 32%) at the end of 12 months. Individually, the elements have quite independent weight-distributions, following a common, rapid decline in the first few weeks. Except for K and Mg, the weight of a particular element remaining in the litter becomes increasingly greater in the *E. pauciflora* ecosystem than in the *E. delegatensis* ecosystem. Whilst all nutrient-weights exhibit continuous decline in *E. delegatensis* litter, most nutrients in *E. pauciflora* litter recover from low weights following the initial decline, to maintain higher levels for the rest of the year despite progressive loss in dry weight. N, P and Ca show very distinct increases in weight, but only in *E. pauciflora* litter, after mid-winter. The weight of K is usually slightly higher in *E. pauciflora* apart from the initial period of rapid losses. The weight of Mg is always higher in *E. pauciflora*, and for both ecosystems the weight-time distribution of Mg is the most similar to total dry weight.

6.3.7 THE RELATIVE MOBILITY OF ELEMENTS IN THE FOREST FLOOR

In this study the relative mobility of nutrients has been defined in three ways,

(i) by plotting the $Ep/Ed$ ratios of estimated above-ground biomass, and the dry weights and concentrations and weights
of nutrients in the litter-fall, L and F/H layers of the forest floor, and the fluxes in leaf-litter after one year on the forest floor (Figure 18),

(ii) by calculating turnover times of the dry weight and nutrient-weights of litter-fall, in terms of the respective weight on the forest floor, using the annual decomposition constant, \( k \), defined by Jenny et al. (1949) as

\[
k = \frac{L}{L + A}
\]

where \( L \) = dry weight or element weight of the annual litter-fall, and \( A \) = dry weight or element weight of the combined litter layers (Table 17).

(iii) by calculating the half-life and time of total loss of the dry-weights and element-weights in decomposing leaf litter (Tables 18 and 19).

### TABLE 17

Values of \( k \), and turnover times derived from \( k \) for dry matter and certain nutrients in the forest floor

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>( k (%) )</th>
<th>Turnover time (years)</th>
<th>Turnover time (nutrient total) ratio</th>
<th>E.p.</th>
<th>E.d.</th>
</tr>
</thead>
<tbody>
<tr>
<td>dry matter</td>
<td>9.4</td>
<td>14.4</td>
<td>10.6</td>
<td>6.9</td>
<td>1.00</td>
</tr>
<tr>
<td>nitrogen</td>
<td>7.6</td>
<td>13.7</td>
<td>13.1</td>
<td>7.3</td>
<td>1.23</td>
</tr>
<tr>
<td>phosphorus</td>
<td>9.1</td>
<td>17.3</td>
<td>11.0</td>
<td>5.8</td>
<td>1.03</td>
</tr>
<tr>
<td>calcium</td>
<td>8.9</td>
<td>13.9</td>
<td>11.1</td>
<td>7.1</td>
<td>1.05</td>
</tr>
<tr>
<td>iron</td>
<td>0.2</td>
<td>0.3</td>
<td>400.0</td>
<td>294.0</td>
<td>37.73</td>
</tr>
<tr>
<td>potassium</td>
<td>10.3</td>
<td>12.0</td>
<td>9.7</td>
<td>8.3</td>
<td>0.92</td>
</tr>
<tr>
<td>magnesium</td>
<td>6.3</td>
<td>10.5</td>
<td>15.9</td>
<td>9.5</td>
<td>1.50</td>
</tr>
<tr>
<td>manganese</td>
<td>6.0</td>
<td>13.8</td>
<td>16.7</td>
<td>7.2</td>
<td>1.57</td>
</tr>
<tr>
<td>sodium</td>
<td>10.0</td>
<td>19.6</td>
<td>9.9</td>
<td>5.1</td>
<td>0.93</td>
</tr>
<tr>
<td>zinc</td>
<td>133.0</td>
<td>148.0</td>
<td>0.75</td>
<td>0.6</td>
<td>0.07</td>
</tr>
</tbody>
</table>

**ORDER OF MOBILITY:**

E.p. Zn > K > Na > dm > P > Ca > N > Mg > Mn > Fe

E.d. Zn > Na > P > dm > Ca > Mn > N > K > Mg > Fe
## TABLE 18  Loss in first 12 months, and derived time of total loss of dry matter and certain elements in decomposing leaf litter

<table>
<thead>
<tr>
<th>% loss in first 12 months</th>
<th>time for total loss (years)</th>
<th>turnover times (nutrient) ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>dry matter</td>
<td>47.5</td>
<td>69.4</td>
</tr>
<tr>
<td>nitrogen</td>
<td>36.9</td>
<td>67.5</td>
</tr>
<tr>
<td>phosphorus</td>
<td>69.2</td>
<td>83.0</td>
</tr>
<tr>
<td>calcium</td>
<td>43.1</td>
<td>67.8</td>
</tr>
<tr>
<td>iron</td>
<td>34.7</td>
<td>36.6</td>
</tr>
<tr>
<td>potassium</td>
<td>90.8</td>
<td>93.9</td>
</tr>
<tr>
<td>magnesium</td>
<td>74.5</td>
<td>78.8</td>
</tr>
<tr>
<td>manganese</td>
<td>48.6</td>
<td>84.0</td>
</tr>
<tr>
<td>sodium</td>
<td>60.0</td>
<td>40.0</td>
</tr>
<tr>
<td>zinc</td>
<td>56.1</td>
<td>53.5</td>
</tr>
</tbody>
</table>

ORDER OF MOBILITY  
E.p.  K > Mg > P > Na > Zn > Mn > dm > Ca > N > Fe  
E.d.  Mn > K > P > Mg > Zn > dm > Ca > N > Na > Fe

## TABLE 19  Half-lives of dry matter and certain elements in decomposing leaf litter

<table>
<thead>
<tr>
<th>half-life (weeks)</th>
<th>half life (nutrient) total ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>dry matter</td>
<td>54</td>
</tr>
<tr>
<td>nitrogen</td>
<td>60+</td>
</tr>
<tr>
<td>phosphorus</td>
<td>0.75</td>
</tr>
<tr>
<td>calcium</td>
<td>55</td>
</tr>
<tr>
<td>potassium</td>
<td>0.25</td>
</tr>
<tr>
<td>magnesium</td>
<td>29</td>
</tr>
</tbody>
</table>

ORDER OF MOBILITY  
E.p.  K > P > Mg > dm > Ca > N  
E.d.  K > P > Mg > Ca > dm > N
The results plotted as E.p./E.d. ratios in Figure 18 indicate that the basic pattern of fluxes in nutrients commences with greater quantities of all elements in the litter-fall of E. deleguineae than E. papuanae, reflecting the greater biomass of the former. Compared to the forest floor, the elements are in generally similar quantitative relationships between the two ecosystems. However, the rate of flux weights of major elements out of the litter in the first 12 months seems to be far greater in the E. papuanae ecosystem, despite a slower rate of physical decomposition of the litter than in E. deleguineae. Individual elements exhibit very independent flux rates, i.e., a wide dispersion of E.p./E.d. ratios, compared to the litter-fall (Figure 18). These trends of the latter lead to a greater contribution of Mg and Mn to the overall nutrient cycling and quantities of elements in the forest floor layers of the two ecosystems. Some elements, notably Co and Cu, continue to accumulate in the E. papuanae ecosystem. The accumulation rates in the E. papuanae ecosystem are much smaller than in the E. deleguineae ecosystem. Fe and Mg show preferential accumulation in the forest floor layers of the two ecosystems, with Fe continuing to accumulate more in the E. papuanae ecosystem than in the E. deleguineae ecosystem. The differences in the relative mobilities of the elements result in more mobile elements in the forest floor of the latter ecosystem. The results, however, are not a complete reflection of the relative mobilities of the elements in the two ecosystems, as the total turnover flux of certain elements may be more mobile in the forest floor of the former ecosystem.
The results plotted as Ep/Ed ratios in Figure 18 indicate that the basic pattern of fluxes in nutrients commences with greater quantities of all elements in the litter-fall of *E. delegatensis* than *E. pauciflora*, reflecting the greater biomass of the former. Compared to the forest floor, the elements are in generally similar quantitative relationship between the two ecosystems. However the rate of flux weights of these elements out of the litter in the first 12 months tends to be far greater in the *E. pauciflora* ecosystem, despite a slower rate of physical decomposition of the litter than in *E. delegatensis*. Individual elements exhibit very independent flux rates, i.e. a wide dispersion of Ep/Ed ratios, compared to the litter-fall (Figure 18). These rates of flux lead to a predominance of higher concentrations and quantities of elements in the L layer of the forest floor in the *E. pauciflora* ecosystem. Some elements, notably Ca and Mn, but also N and Fe, continue to accumulate in the F/H layer of *E. pauciflora* more than in *E. delegatensis*, whilst Na and K, show preferred accumulation in the F/H of *E. delegatensis*. P accumulates more in the F/H of *E. pauciflora*, but the difference is less than in the L layer. Zn and Mg do not show any change in relative accumulation from L to F/H.

All elements (Table 18) have much longer turnover times in the *E. pauciflora* ecosystem where decomposition itself is much slower, as calculated in terms of the annual decomposition constant k for dry matter turnover. There are differences in the relative mobility of most elements between the *E. delegatensis* and *E. pauciflora* ecosystems on the basis of nutrient:total turnover-time ratios. All elements except K, Fe and Zn are more mobile in the forest floor of the *E. pauciflora* ecosystem. The greatest difference between the ecosystems in the ranked order of mobility is the relative position of K (Table 17). P and Mn are the only elements that are more mobile in the *E. pauciflora* system,
relative to *E. delegatensis*. Despite these differences, the net loss in weight of all elements is greater in the litter of *E. delegatensis*.

The same distinctions are not necessarily borne out for the fluxes of nutrients in decomposing leaf litter alone. On the basis of nutrient:total ratios for the decay of leaf litter, all elements except P, K, Na and Zn are more mobile in *E. delegatensis* litter. There are some important differences between the relative mobilities of elements in total litter turnover and in leaf litter alone. K is far more mobile in the decomposing leaf litter than in the turnover of total litter in *E. pauciflora*, confirming the observation of Attiwill (1968), in an *E. obliqua* ecosystem, that K is leached readily from the L layer but is held within the F/H layer, perhaps by microorganisms or as lignin complexes. The mobility of Mg and Ca is also reduced in the F/H layers but to a lesser extent than for K. On the other hand, P is more mobile in the decomposing leaf-litter of *E. delegatensis* than in the total turnover of litter.

The half-lives of nutrients in leaf litter (Table 19) show similar patterns of flux to the total times of loss of nutrients in leaf litter. The data indicate the extremely rapid loss of the more mobile elements, K and P, compared to the relatively immobile Ca, Mg and N. Whilst the order of relative mobility is the same for each ecosystem, the rate of flux of K and P, relative to the half-life of dry matter decay, from *E. pauciflora* litter is respectively three and four times that from *E. delegatensis* litter. The half-lives of Ca and Mg, however suggest that their rate of flux is more than twice as slow from *E. pauciflora* litter.

Clearly, it is important to distinguish the fluxes of individual nutrients in terms of the turnover of total litter which falls throughout the year and the decay of leaves commencing at a specific time of the
year. There are considerable problems in defining the different rates at which elements concentrate in the F/H layers of the forest floor and become involved in organic complexes and reversible transfers between organic matter and the mineral soil. Fe, for example, is mobilised in very low concentrations in eucalypt litter, yet attains extremely high concentrations in the F/H layer (Table 17). The concentration of Zn, on the other hand, is even lower in the F/H than its low level in the L layer. All elements, except K, Na and Zn in *E. pauciflora* litter and P, Na and Zn in *E. delegatensis* litter, exhibit some degree of accumulation in the F/H relative to the decay and accumulation of dry matter (Table 17). Given that leaves contribute about 60% of the total litter-fall of both ecosystems (Figure 14), it is interesting to note the marked difference in the times of total leaf decay (Table 18) and total litter turnover (Table 17). It is apparent that leaves decay in only 20% of the time taken for total litter decomposition. Apart from Zn, where the relationship is distorted due to only slight accumulation in the F/H, the loss of all elements from leaves takes only a small fraction of the time of loss from total litter-fall.

6.4 DISCUSSION

6.4.1 INTRODUCTION

Gross differences were evident between the adjacent mono-dominant forests of *E. delegatensis* and *E. pauciflora*, in structural parameters such as microclimate of the forest floor, the growth form of the trees, and the physiognomy and above-ground biomass of the communities. Given the scale of these differences, and the restriction of *E. delegatensis* to sites where one would expect "higher fertility", one might ask whether differences in functions such as the flux of nutrients in the fall,
decomposition and standing-state of litter on the forest floor are proportional to various structural differences. However if the ratios of individual nutrients and dry matter, between *E. pauciflora* and *E. delegatensis*, in litter fall and the detritus pathways are compared with those for the basal area and vegetation space of the two communities (Figure 18), they show a marked convergence of function in litter-fall, and a reversal of the gross difference in rates of decomposition. This results in greater quantities of most nutrients in the forest floor of the *E. pauciflora* ecosystem. The differences in decomposition during only the first few months were sufficient to overcome the greater concentration and quantities of nutrients in the litter-fall of *E. delegatensis*. In Chapter 4 it was shown that the L and F/H layers of the forest floor and the surface soil of *E. pauciflora* ecosystems contain consistently greater concentrations and quantities of nutrients than the equivalent layers in adjacent ecosystems of *E. delegatensis*. This difference is maintained through a range of successional stages, in which a major variable is the changing mass of the forest floor. The arrangement of data in Chapter 5 does not indicate any long-term difference in the form of nutrient flux distributions, although there may be difference in rate of flux. Data from a preliminary study of the 5-15 cm soil layer suggests that the "soil fertility" of *E. delegatensis* ecosystems exceeds that of *E. pauciflora* ecosystems, and it is most probable, given the nature of the differences in biomass (Figures 12; 14) and concentrations and quantities of nutrients in the litter fall during the year (Figures 15.1; 15.2), that, in absolute terms, the *E. delegatensis* ecosystem contains a greater pool of nutrients than does the *E. pauciflora* ecosystem, with which it forms a sharply contiguous boundary. The data indicate faster rates of decomposition, humification and mineralisation in the moist and more equable (Figure 13) environment of the forest floor of *E. delegatensis* forest.
6.4.2 INPUT

Basal area is usually assumed to be a convenient index of litter production (Ovington, 1962; Reiners and Reiners, 1970; Whittaker and Woodwell, 1968). In this study, the comparison of stand structure and litter production in separate ecosystems of *E. delegatensis* and *E. pauciflora* suggests that vegetation space (Park, 1973) is much more closely related to litter production (*E*/*E* ratios of 0.532 and 0.548), and that leaf productivity (leaves comprise 60% of total litter-fall) is not proportional to basal area (*E*/*E* ratio = 0.384) when comparing physiognomically different communities (see Plate X). Reiners and Reiners (1968) show, in a series of structurally different forest communities adjoining in a vegetation mosaic, that total biomass shows intermediate convergence between basal area and litter-fall. Vegetation space bears an equivalent relationship in this study, and on this basis could be interpreted as an accurate estimate of comparative biomass. Whatever the real functional relationship between total biomass and annual litter production in these ecosystems, there is certainly a convergence, between the two ecosystems, in terms of the quantity of nutrients in the litter-fall, particularly for Ca (Figure 18). Apart from the period of maximum litter-fall, where the input of nutrients and dry matter by the *E. delegatensis* biomass is twice that of the *E. pauciflora* biomass, few differences between the quantitative fluxes of nutrients were statistically significant. This could be caused by inadequate replication of samples, but it is more likely (Figure 15.2) that for the rest of the year there is no real difference between input in the two ecosystems. Input concentrations of all elements except Ca show few marked differences between ecosystems, although the concentration of most elements is greater in *E. delegatensis* litter during the period of maximum litter-fall.
The data are comparable with those from other temperate zone forests in the southern hemisphere. Miller and Hurst (1959) recorded 5.6 tonnes/ha of total litter-fall in a hard beech (*Nothofagus truncata*) forest in New Zealand. Ashton, according to Bray and Gorham (1964) recorded values ranging between 6.9-8.1 tonnes/ha for *Eucalyptus regnans* forests of various ages in Victoria. Attiwill (1964) records a total annual litter-fall of 3.56 tonnes/ha for mature *E. obliqua* forest in montane forests of Victoria. McColl (1966) recorded mean annual values of 3.6 and 6.8 tonnes/ha respectively for a young stand and mature virgin forest of spotted gum (*E. maculata*) in southern N.S.W.. McCauley (pers comm) has recorded 2.0 tonnes/ha litter-fall in the eight snow-free months of the year from woodland of *E. pauciflora* (cf. Plate IIb).

6.4.3 DETRITUS POOLS OF THE FOREST FLOOR

As a result of predominantly biological reactions, the forest floors contrast qualitatively as well as quantitatively, thus enhancing some structural and functional differences between ecosystems. Whilst the total litter-fall of *E. pauciflora* per annum is only about 56% of *E. delegatensis*, the time taken for total loss of a given amount of leaf litter in the *E. delegatensis* ecosystem is only 58% of that in the *E. pauciflora* system. The time for total turnover of the litter-fall in the *E. delegatensis* ecosystem is 65% of that in the *E. pauciflora* system. The forest floors are the net product of different inputs, different leaf structure, different understorey vegetation (Plate X) and different surface soils. Data from the samples collected for the study of the nutritional relationships of the ecotones (Chapter 4; see also Appendix III, Table 16) show lower C/N ratios in both the F/H and surface soil (where the difference is significant) of the *E. pauciflora* ecosystem. This suggests greater microbial activity, but may reflect the
much greater grass cover beneath the canopy of *E. pauciflora*. The actual difference in decomposition of a given amount of litter-fall of constant physical and chemical characteristics is not known, but it seems certain that the decomposition of litter that does occur results in greater quantities of nutrients being mobilized from the litter-fall of *E. delegatensis*. The relative distributions of nutrients conform to the typical pattern of greater concentrations and quantities in the L and F/H layers of *E. pauciflora* (see Chapter 4), despite lower quantities in the annual litter-fall, and lower weights of total dry matter in both layers than the *E. delegatensis* ecosystem (Figure 18). It is a common feature of most ecotones that whilst the F/H layer of *E. pauciflora* stands may contain greater quantities of total cations, there may be lower quantities of exchangeable cations than in the F/H of *E. delegatensis* (see Appendix III, Table 16). It would seem that in the Bendoura Hill site we are observing a feature of this specific ecotone whereby the forest floors of *E. pauciflora* contain greater quantities of nutrients, but rather than defining these sites as more "fertile" than those supporting *E. delegatensis*, it simply means that nutrients are immobilised in the organic matter of the forest floor and surface soil of *E. pauciflora*, whereas the nature of the forest floor environment of *E. delegatensis* ecosystems allow a greater degree of humification and mineralisation. This is borne out by the environmental features of the two ecosystems that would be expected to have the greatest influence on the cycling of nutrients, such as the greater grass cover. There is also a greater susceptibility to drought in the soils beneath *E. pauciflora* than the deeper and less stony soils, from slope deposits, beneath *E. delegatensis*, allowing greater storage of moisture. There is usually a greater rate of immobilisation of nutrients in grassland soils than forest soils, and a grass cover is likely to slow the rate of leaching of nutrients from litter during periods of rainfall.
6.4.4 Decomposition of Leaf Litter and Turnover of Total Litter

There are very few data on the fluxes of nutrients in eucalypt ecosystems. A few studies have been made on the fate of nutrients in litter-fall in eucalypt ecosystems; Hatch (1955) in *E. marginata* forest, Attiwill (1968) in *E. obliqua* forest, and the recent unpublished work of McCauley (*pers comm*) in higher-altitude *E. pauciflora* woodland. In all of these studies, selected quantities and types of litter have been placed in various containers on the soil surface for given periods, and the losses in dry weight and nutrients calculated from the original weights in each sample. In cases where the weights of the litter layers and the annual litter-fall are known, annual decomposition constant may be calculated (e.g. Attiwill, 1968; Jenny *et al.*, 1949; Olsen, 1963). The time required for total turnover of litter may be derived from this information. However, the calculation of turnover times and annual decomposition constants assume that the total accumulation of energy and nutrients in forest floors represent more-or-less stable pools maintained in equilibrium with input (litter-fall) and output (decomposition) (Reiners and Reiners, 1970). Whilst steady-state energy and nutrient pools can be demonstrated and predicted (Olsen, 1963) the assumption is not tenable in eucalypt forests. However if stability is considered in the sense of Loucks (1970), the decomposition constant, \( k \), can be used in these ecosystems. In the subalpine eucalypt forests, which are predominantly at an early stage of secondary succession, the forest floor is a very dynamic component of the youthful and unstable character of these ecosystems. During succession (see Chapter 5) the accumulation of detritus in the F/H layer proceeds to an equilibrium-point at about 70-80 tonnes/hectare, following which decomposition becomes more efficient relative to litter-fall, resulting in a net decrease in the mass of the forest floor. The community composition of the stands at
Bendoura Hill shows characteristics of the early stages of succession, with a large component of shrub *Leguminosae* predominating in a shrub understorey (Chapter 5; section 5.6.6). The mass of the F/H layer is only 15-20 tonnes/hectare. Therefore, the total accumulation of nutrients may not be assumed to represent a state of relative stability in terms of the successional development of these forest ecosystems, but the forest floors do represent the standing-state of nutrient pools at a particular stage of succession. The relative stability of the nutrient pools, and the cycling of individual nutrients, may be defined by measuring the rates of decomposition of recently fallen litter, relative to the rates of accession. The forest floors at Bendoura Hill were therefore measured in the context of the separate study of the standing-states of nutrient pools in the forest floors and surface soils of a range of successional situations at the ecotone between *E. delegatensis* and *E. pauciflora* (Chapter 4) and the fluxes of nutrients in litter-fall and decomposition.

One object of this study of nutrient-cycling fluxes has been to derive some basis for the calculation of the time-scale of secondary succession, whereby organic detritus appears to accumulate on the surface of the mineral soil to a point of maximum storage and subsequently decreases in mass towards an apparent steady-state between input (litter-fall) and output (decomposition). The decomposition constant, $k$, can, in general, be derived from the equations of Jenny *et al.*, (1949) and Greenland and Nye (1959) as a ratio of annual litter production to the amount of organic detritus accumulated on top of the mineral soil. Olsen (1963) has developed a general differential equation for the rates of change in energy storage, and illustrated it by models for build-up and decomposition of organic matter in environments where there is steady production and decay of litter. Whilst in the short-term
duration of one year's decomposition of eucalypt leaf litter, the relationship between loss of dry matter and time is approximately rectilinear (Figure 17), the estimates of $k$ for the Bendoura Hill ecosystems fit the general position for cool-temperate (subalpine) ecosystems in Olsen's model. Attiwill (1968) also assumed rectilinearity for a similar relationship, and considered that this kind of data was too restrictive to allow the calculation of a relationship of the form described by Olsen (1963) which is negative exponential. If the accumulation of detritus above the mineral soil is considered as tending toward a steady-state (see Chapter 5) in a manner that is predictive, stability can be defined as a characteristic series of transient phenomena which collectively make up the stable system, capable of repeating itself everywhere a perturbation restarts the sequence (Loucks, 1970). In the sense that Olsen's general exponential model describes the rate of decomposition and accumulation of organic matter towards a steady-state, $k$, as derived from a stand at a particular successional stage, can be used in estimating the time required to attain maximum storage of organic matter. In fact, Olsen (1958) has used the relationship to measure rates of accumulation in sand-dune soils. In the subalpine forests an exponential function for $k = 0.092$ (E. pauciflora) and $k = 0.144$ (E. delegatensis) would show an apparent rectilinear form, because annual decomposition is such a small proportion of total detritus.

A convenient virtue of the simple exponential model is that half-lives for decomposition of the accumulated organic matter may be calculated, and Olsen (1963) provides a constant, $3/k$, for the period of time required to attain 95% of the steady-state level of accumulation if the exponential model is valid, while $5/k$ should approximate the time required to reach 99% of the steady-state level. These constants indicate that the forest floors of E. pauciflora and E. delegatensis
would take about 55 and 35 years respectively, to reach 99\% of the "steady-state" level. Considering the total long-term development of these ecosystems postulated in the preceding chapter, the point of maximum storage is not equivalent with the steady-state; zero net community storage of matter or energy may not be attained until long after composition and biomass have become nearly constant. Some biological developments may be delayed until litter and soil humus have approached near their steady-state values.

In comparing turnover rates and relative mobility of nutrients in the two ecosystems, it should be pointed out that whilst the calculation of decomposition constants from one year's data may be somewhat tenuous, the comparison of seasonal fluxes is quite valid from the same data because of the immediate proximity of the two stands and the identical sampling methods. Thus atmospheric input is constant, although because of differences in recreation of nutrients, throughfall input of nutrients may not be. Apart from the topographic pattern of slope deposits producing differences in soil-form, any site differences, like the differences in nutrient fluxes themselves, are a function of the different community structure of *E. pauciflora* and *E. delegatensis*.

Three major facts emerge from the comparison of leaf-litter decomposition in the two ecosystems. Firstly, after initially lower levels, the concentrations of all nutrients tend to be higher in the decomposing foliage of *E. pauciflora*. Secondly, the decomposition of *E. delegatensis* foliage is progressively greater than that of *E. pauciflora*. Thirdly, the net effect is that the fluxes of nutrients in the two ecosystems become progressively more divergent. The differences confirm studies by Wood (1971), where the decomposition of leaves of *E. pauciflora*, *E. delegatensis* and snow-grass (*Foa caespitosa aggr. = P. ensiformis?*) was compared in each of the sites which they
respectively dominated. Wood concluded that the nature of the litter obviously affects the rate of decomposition for all three sites, including alpine herbfield, the relative losses in weight were $E. \text{delegatensis} > E. \text{pauciflora} > \text{Poa caespitosa}$. The greatest loss in weight of all litters was greatest in the alpine site, with the notable exception of $E. \text{delegatensis}$ which decomposed most rapidly at its own site. No physiological studies were made in the present study, but it was very apparent that relative to $E. \text{delegatensis}$, physical comminution of $E. \text{pauciflora}$ foliage was restricted by a stronger leaf structure, and a thicker and waxier cuticle.

A review of angiosperm tree leaf litter (Jensen, 1974) concludes that the decomposition of cellulose occurs mainly after microbial activity has led to the mechanical disintegration of the litter, and is probably carried out mainly by fungi in forests. Lignin, which appears to be a greater component of the leaf margin of $E. \text{pauciflora}$ than of $E. \text{delegatensis}$ is the most resistant of the compounds occurring in appreciable quantities in litter. Decomposition of lignin is by Basidiomycetes, and these do not develop in the L layer, but in the F and H layers and the mineral soil.

A considerable proportion of the weight of inorganic elements in the litter of both species was rapidly lost by initial leaching, particularly K and P, the half-lives of which were only a few days. There is considerable independence in the mobility of nutrients within the same litter, and between litters. There is a marked divergence from the results of a similar study by Attiwill (1968) who monitored the loss of elements from decomposing litter $E. \text{obliqua}$. Despite a generally very high mobility and low concentrations of P in the ecosystem, P was the least mobile of the elements examined; the order of mobility was $\text{Na} > \text{K} > \text{Ca} > \text{Mg} > \text{P}$ over two years. In the present study P was one of
the most mobile elements. The only constancy between mobility in the ecosystems of *E. pauciflora* and *E. delegatensis* was \( K > P > Mg > Ca > N \) in the half-lives of leaf decomposition.

Preliminary studies of decomposition of *E. pauciflora* foliage, during the first few months (B. J. McCauley, *pers comm*) showed similar changes in the concentrations of \( N \) and \( P \) to those observed in this study. Isolation of decomposer organisms suggested that fungi tend to immobilize \( N \) but mineralize \( P \). Invertebrates tend to counter the effects of fungi so that in the natural situation there is a steady release of \( N \) and \( P \) from the litter. From the few studies of the fluxes of nutrients in decomposing litter of *Eucalyptus*, it would seem that the rate of litter decomposition eventually determines the nature of the equilibrium between accession, leaching and uptake of nutrients and hence the long-term process that defines the nature of the forest floor and the upper soil layers. These components of the ecosystem accumulate nutrients selectively, due to the slow breakdown of the forest floor itself and because of the relative independence in the release of nutrient elements. The rate of flux of any element will vary between different eucalypt ecosystems, even when adjacent in the landscape. The flux in the quantity or concentration of an element from litter-fall through decomposition, and eventually to a state of relative equilibrium between the compartments of the ecosystem (Jordan *et al.*, 1972) must be defined individually, and little can be assumed about the elemental content of an ecosystem from an analysis of the elemental composition of one or a few compartments.

6.5 SUMMARY

Biomass, total litter production, forest floors and litter
decomposition were measured in contiguous forests of *E. delegatensis* and *E. pauciflora*, and the seasonal fluxes of nutrients compared. The structure of the two forests varied widely in terms of vegetational components - species composition, growth-form, density, vegetation space and basal area - and in terms of the understorey vegetation, and micro-climate and nature of the forest floors. In terms of successional status, the stands were young with a large number of shrub-*Leguminosae* in the understorey and light forest floors, indicating recent disturbance.

Levels of nutrients tended to converge in the litter-fall of the two forests in spite of much greater quantities of biomass and total litter production in the *E. delegatensis* forest. This convergence was dramatically continued in the flux of nutrients, partly because of greater decomposition rates in *E. delegatensis* litter, but also because of greater net accumulation of nutrients in the decomposing litter of *E. pauciflora*. Consequently, the quality of the forest floors and the long-term net flux of nutrients varied greatly between the two forests. Individual nutrient elements also showed marked variation in the rate of flux, and there was considerable divergence in the relative mobility of nutrients from studies of other eucalypt forest ecosystems. This could be a function of the relatively high levels of all nutrients in the ecosystems of *E. pauciflora* and *E. delegatensis*.

The results provided some insight into the different standing-states of nutrient pools in the forest floors and surface soils of *E. delegatensis* and *E. pauciflora* ecosystems in ecotonal situations, described in the preceding chapter. The results also provided data from which a time-scale of net accumulation of detritus could be derived from the majority study of this thesis, that is, the long-term successional development of subalpine eucalypt ecosystems.
CHAPTER 7

GENERAL DISCUSSION

7.1 INTRODUCTION

In this discussion I attempt to integrate these studies of nutrient dynamics in relation to the long-term successional development of subalpine eucalypt forest and woodland ecosystems. The discussion also serves to evaluate and reconcile the empirical results in this thesis with the recent anthropomorphic history of the subalpine zone, with the palaeo-ecology of the biota, and with certain concepts of ecosystem development. From this information I have developed some general models of long-term ecosystem development. Finally I discuss, in the form of a coda, the problems of the present-day state of the ecosystems in terms of the conservation of diversity of 'natural' patterns and processes.

This thesis has been an evaluation of the hypothesis that the successional development of subalpine eucalypt ecosystems will TEND to proceed directly and inevitably towards a state of dynamic equilibrium, following a perturbation. The process, whilst proceeding continuously in an environment with a high probability of disturbance, will be truncated according to the frequency of disturbance. In particular, it was suggested that the processes of succession in the understorey vegetation, the litter layers of the forest floor, and the surface layer of the soil would provide the best readily-available information for a model of ecosystem development. In Chapter 5 some of the net effects of successional fluxes in litter accumulation and decomposition on the quantities and concentrations of nutrients in the forest floor and surface soil of Eucalyptus pauciflora and E. delegatensis ecosystems are examined. The successional changes in the composition and diversity of
understorey vegetation are related to the same long-term fluxes in litter accumulation and decomposition. The same data are examined separately in Chapter 4 to evaluate the differences in rates of organic matter and nutrient cycling between adjacent stands of *E. pauciflora* and *E. delegatensis*.

In both of these studies, the data from some 46 stands are integrated to form general models. The working hypothesis has been that if there are strong relationships between the compositional dynamics of the understorey vegetation, the quantitative and qualitative dynamics of the nutrient pools of the forest floor and surface soil layers and the secondary succession, (as represented by the net accumulation of organic matter detritus) then consistent trends would be discerned by plotting data from both ecosystem types, at different successional stages whilst encompassing a range of environmental variation.

Although there are clear successional trends in the general models of most of the nutrients and understorey-vegetation parameters the quadratic functions defining the trends are often non-significant derivations from a field of considerable variation. Similarly, there is no absolute pattern of differences between the nutrient pools of the forest floor and surface soil layers of *E. pauciflora* and *E. delegatensis* ecosystems.

In order to determine more accurately the functional relationships between disturbance of the ecosystem, nutrient cycling, the long-term fluxes in the net accumulation of detritus, and the ecotone between *E. delegatensis* and *E. pauciflora*, two specific studies were undertaken.

(a) The short-term successional fluxes in the nutrient pool of the forest floor and surface soil, as well as the composition of developing understorey vegetation were
monitored in nearby ecosystems of *E. delegatensis* and *E. pauciflora* for 12 months following a wildfire, to ascertain the response of these ecosystem components to this kind of perturbation (Chapter 5; section 5.6.7).

(b) Within adjacent stands of *E. delegatensis* and *E. pauciflora* a 12 month study was carried out to examine some aspects of nutrient cycling within the perspective of the total ecosystem processes, involving aboveground biomass, annual litter production, detrital nutrient pools of the forest floor, and internal translocation of nutrients (Chapter 6).

These separate studies have enabled conclusions to be drawn as to the factors bearing on the perturbation to different nutrient cycling systems the response to perturbation and the differences. To an extent, the interpretation of the general models of long-term dynamics of nutrients relies on a true time scale. This is not possible from tree-dating or historical sources because of the variable post-fire characteristics of forest floors. However, one method of deriving the time-scale of the successional process is by calculating the decomposition constant, $k$, from the ratio of litter-fall and the total forest floor, which estimates the time-period required to attain maximum net accumulation of detritus on the forest floor. Apart from absolute ages of trees (the oldest size class in stands such as Plate 11b), there are a few criteria for a time-scale beyond the point of maximum accumulation of detritus.

The cautionary statement of McIntosh (1972) is to be heeded -

"As the possibility of reconstructing a primeval "climax" from undisturbed remnants recedes and vanishes we must depend on analyses of current vegetation as it is, not as what it may become".
7.2 ECOTONAL DIFFERENCES IN THE STANDING-STATE OF NUTRIENTS IN EUCALYPT FOREST ECOSYSTEMS

My field studies of the distribution limits of species of *Eucalyptus* in the montane and subalpine zones suggest that the primary factor in distribution is topography, (see Figures 4 and 7), largely because of topographic control of micro-climatic extremes, Quaternary landscape processes, pedogenesis, and the frequency of fires. All of these variables could be expected to effect discontinuities in the rate and quality of nutrient supply from the physical environment to the biomass, and in the rate of flux of nutrients within the ecosystem. Many contiguous boundaries between eucalypt dominated communities represent discontinuities in community structure - growth-form, density, vegetation-space, basal area, biomass - and in terms of the understorey vegetation, and microclimate and nature of the forest floor. In these situations one may expect considerable discontinuities in the total nutrient pool of the contiguous ecosystems.

The preliminary results reported in this thesis suggest that the soils supporting *E. delegatensis* contained greater concentrations of cations and P than the soils supporting the eucalypt species forming adjacent communities. The geomorphic and pedological differences between the respective sites accentuates this pattern in terms of the potential nutrient content of the solum. Later studies of about 23 ecotones between ecosystems dominated by *E. delegatensis* and *E. pauciflora* indicate greater concentrations and greater net accumulation of nutrients in the forest floor and the uppermost 5 cm of the mineral soil of *E. pauciflora* ecosystems. In most cases the difference is slight, as a proportion of the mean weight or concentration, and can be altered by a change in the successional status of the forest floor. Given the considerably greater quantities of nutrients transferred annually to the forest floor from
the above-ground biomass of *E. delegatensis*, it is interesting to note
the greater nutrient pools of the forest floor of ecosystems dominated
by *E. pauciflora*, in ecotonal situations where the accumulation of
detritus has originated from the same perturbation, usually fire. Some
insight into this relationship was provided by monitoring the seasonal
fluxes of nutrients between the biomass and the fermentation-humus (F/H)
layers of the forest floor. By relating litter fall to the standing-
state of the forest floor layers it was also possible to evaluate the
long-term effect of short-term differences in decomposition, mobilisation
and accumulation of litter and nutrients.

The results suggest that differences in the morphology of
decomposing leaves and the nature of the forest floors in the respective
ecosystems are more important determinants of the long-term processes
of decomposition, mobilisation and net accumulation of nutrients in
detrital layers, than are quantitative differences in community structure.
The time-period required to attain 99% of maximum accumulation of organic
matter above the mineral soil (derived from the constant, \( k \); Olsen, 1963)
is estimated to be 35 years in *E. delegatensis* ecosystems and 55 years
in *E. pauciflora* ecosystems. Individual nutrient-elements show marked
variation in the rate of flux, both short-term (seasonal) and long-term
(successional), and independence from the fluxes of organic matter. This
is borne out in Table 20 where the time-period required to attain 99% of
the maximum accumulation in the detrital layers is presented for certain
elements.
TABLE 20 Values of $5/k$ for certain elements (see Olsen, 1963) in long-term ecosystem development, based on the short-term mobility of the nutrients in the ecosystems of *E. delegatensis* and *E. pauciflora* at Bendoura Hill.

<table>
<thead>
<tr>
<th>Element</th>
<th><em>E. pauciflora</em></th>
<th><em>E. delegatensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>dry matter</td>
<td>55 years</td>
<td>35 years</td>
</tr>
<tr>
<td>nitrogen</td>
<td>65 &quot;</td>
<td>36 &quot;</td>
</tr>
<tr>
<td>phosphorus</td>
<td>55 &quot;</td>
<td>29 &quot;</td>
</tr>
<tr>
<td>calcium</td>
<td>56 &quot;</td>
<td>36 &quot;</td>
</tr>
<tr>
<td>potassium</td>
<td>49 &quot;</td>
<td>42 &quot;</td>
</tr>
<tr>
<td>magnesium</td>
<td>80 &quot;</td>
<td>48 &quot;</td>
</tr>
<tr>
<td>sodium</td>
<td>50 &quot;</td>
<td>26 &quot;</td>
</tr>
<tr>
<td>manganese</td>
<td>84 &quot;</td>
<td>36 &quot;</td>
</tr>
</tbody>
</table>

Whilst there are clear differences in the rate of long-term flux between the two ecosystems, the integration of the nutrient data as differential functions of the net accumulation of the forest floor (Chapter 5), indicates that the process of flux is similar.

The monitoring of seasonal fluxes of nutrients in the two ecosystems indicated that the quantities of all nutrients tended to converge in the litter-fall of the two forests, compared to the differences in biomass and total litter-fall. This convergence was increased in the decomposing litter to the extent that within a few months there were greater quantities of nutrients in the *E. pauciflora* leaf litter. This difference prevails in the standing-state of nutrients in the forest floor layers. A comparison of turnover rates showed that there is preferential accumulation of all elements, except perhaps Na and K, in the forest floor layers of *E. pauciflora*. It is notable that the two ecosystems, despite the constancy of the physical environment, showed considerable divergence in the rates of nutrient mobility.

An important feature of the ecotonal analysis of nutrient pools was the high levels of fertility in the subalpine ecosystems compared to ecosystems that have been examined in other parts of the eucalypt biome. However, a few of the more disturbed systems appeared to have degraded
to concentration levels, for example of phosphorus, that have been
considered critical in lower-altitude ecosystems that appear to have
Monitoring of the rate of loss of nutrients in the forest floor and
soil surface following the wildfire in the Grey Mare-Geehi area (Chapter
5; section 5.6.7) indicates a more rapid impoverishment of the nutrient
pool in the higher slopes occupied by *E. pauciflora*.

There is general support for the hypothesis, advanced in the
Introduction, that the geomorphic surfaces are predominantly recent and
support comparatively young, fertile soils. The data suggest that the
eucalypts on these subalpine soils mobilise nutrients at higher
concentrations than their counterparts on older groundsurfaces at lower
altitudes, and in approximate proportion to the concentration of elements
in the mineral soil and parent material. The differences between the
concentrations of nutrients in the forest floors of the same species
on different parent materials (e.g. 200-4000 ppm of P in *E. pauciflora*)
appear to be greater than between the forest floors of different species
on the same material. The lowest concentrations of P obtained from the
forest floor of all except exceptionally disturbed systems was 270 ppm
in a high-leaching environment at Mt. Field in Tasmania. Soil data
showed a similar 'threshold', with the lowest levels associated with the
lower altitudinal limits of *E. delegatensis* where it is replaced by *E.
dalrympleana*, *E. radiata* and a few other species. *E. delegatensis* is
known to be a 'site-sensitive species' and there is some support for an
hypothesis that the species evolved in a relatively high-fertility
environment. It is doubtful, however, whether the ecotone between this
species and *E. pauciflora* has evolutionary origins in competition for
nutrients. There is little in these studies to support such a conclusion.
Quantitative differences in the patterns and processes of nutrient
mobilisation are certainly apparent, but collectively are insignificant when viewed in the context of the quality and degree of variation in the nutrient content of subalpine soils and parent materials. If the ecotone between \textit{E. delegatensis} and \textit{E. pauciflora} does in fact represent a point of evolutionary divergence from a common genetic pool rather than a point of convergence following the development of the species in discrete parts of the landscape, it is more probable that the predominant environmental factors were microclimatic.

My conclusion is that the ecotone represents the common border between two species that, despite a genetic affinity that permits introgression (Pryor, 1951), have evolved in fundamentally different parts of the landscape, and is the result of a contraction in climatic conditions that truncated both the genetic pools and distributional range of each species. \textit{E. delegatensis} exhibits a marked response to altitudinal and latitudinal gradients (Figure 6, Chapter 4) and appears to have a relic distribution, characterised by regional and local disjunctions, over the part of its range where there is a tendency towards warmer and dryer summers (see overlays to Figure 5). Green (1967) has suggested that \textit{E. pauciflora} was probably more widespread during the humid periods preceding aridity, as indicated by its present sporadic occurrence in non-mountainous areas. Fragmentation of the species led to isolation and consequent ecotypic divergence of the relic populations. The subsequent release of this climatic pressure led to recolonisation, the genetic mixing of forms of \textit{E. pauciflora} and the contiguous boundaries between upland eucalypt species. The idea of convergence is also supported by the marked difference in the scale of anatomical adaption to fire and the far greater tolerance of \textit{E. pauciflora} to environmental

* Perhaps this conclusion alone, is sufficient reason to examine ecological phenomena on a broad field scale rather than in a few situations.
fluctuations, including possible nutrient toxicity on soils from basalts. Lack (1969) from a study of closely related bird species has suggested that where two such species meet along a common border, they will gradually evolve tolerances for the physical environment occupied by the other and for the presence of the other species. This will allow for overlap and opportunity for further overlap. The little overlap beyond the influence of the trees that form the ecotone between E. delegatensis and E. pauciflora would suggest that it is recent.

7.3 DEVELOPING A MODEL OF SECONDARY ECOSYSTEM DEVELOPMENT FROM THE ORDINATION OF EMPIRICAL, DESCRIPTIVE AND HISTORICAL INFORMATION

As a form of inductive argument, integration of like-data as a chronofunction (Jenny, 1961) can only indicate probable, or probably true, relationships. However, there are criteria for establishing the degree to which the conclusions reached by integration of data are more or less probable. Firstly, a model for comparative analysis integrates measured variables of environmently-related ecosystems according to a common time-dependent parameter such as the flux of a forest floor between a perturbation and the point of maximum accumulation. Secondly, a direct historical model is based on a demonstrable continuity according to a true scale of time. A historical model may be based on recent field-work where a time-plane can be determined from dated groundsurfaces, trees, varves etc., and where re-study is possible. However, in complexly disturbed fire-environments, such as the subalpine areas of the eucalypt biome, the ecosystems are so modern that a workable time scale does not extend beyond one, or a few, tree generations. As it is not possible from contemporary evidence to determine the natural time-scale of ecosystem development, in systems where the natural fire-cycle may have been in the order of 200-300 years, the only alternatives are models
based on historical records and descriptions, and comparative analysis of current vegetation as it is. For studies of long-term ecosystem development, the argument of Pryor and Moore (1954) becomes increasingly idealist:

"If the vegetation that now exists is to be understood, the communities of pre-settlement days must be studied .... The arrangement of species combinations in virgin [upland eucalypt] communities and their patterns of distribution were relatively stable and precise and therefore it is comparatively easy to interpret the irregularity and diversity that are now so widespread and to see how the vegetation sample in the field has been degraded and from what it has been derived."

In the sense that these chronofunctions can only express probable relationships they are all 'limiting models'. Chronofunctions of comparative analysis, such as this study of secondary fluxes in nutrient pools and understorey vegetation, cannot define a long-term flux in terms of a specific ecosystem, but can only define trends derived from the dispersion of environmentally related ecosystems in a vector field in dimensional space, one dimension of which is a priori time-related. Although comparative analysis invariably involves a degree of variation that would be unacceptable to the experimental biologist, it does facilitate a generalised model of ecosystem development at the scale of the landscape. In doing so it avoids the danger of constructing a general model of ecosystem development from specific ecosystems, and precludes much sampling bias.

On the other hand, the historical model may be defined within very narrow limits of variation, but may be based only on a limited number of observations determined by dates, ages, etc., and restricted to a small vector field of environmental variation with no record of contrary examples. Because of the limited number of observations,
individual points assume a relative importance that determines the form of the chronofunction. Although such data give high probability to the function, there can be no statement of reality.

Studies of long-term natural succession in the subalpine zone are awkward and unsatisfactory because the biological features of the landscape are dominated by modern forests. Although the evolutionary role of fire in subalpine eucalypt forests can be generally inferred, objective quantitative examinations of the time scale of successional processes in modern forests are hampered because of the extent of disturbance since European settlement. There are few descriptions of the specific nature of pre-European eucalypt communities in the subalpine zone (Costin, 1951, 1954; Pryor, 1939a). Today, the extent to which ecological patterns and processes are "natural", or a response to the recent stresses of Man, cannot be stated categorically. For most of the subalpine zone, the historical record of fire is not adequate for quantitative evaluations of its changing importance. More than anything else in this thesis, I am concerned with the development of certain concepts of secondary ecosystem development within the framework of the subalpine landscape, rather than the absolute definition of a particular pattern or process limited to a few stands within an apparently constant environment.

The development of a landscape model of secondary succession that is relevant to conservation management requires a tenable historical base. It is not sufficient to ask "Was fire a natural factor before the white man came?" The relevant questions to establish an ecological base for the conservation of the component ecosystems are, "How much and what

* a seemingly impossible ideal, in the subalpine eucalypt biome (see Chapter 5; Section 5.2).
kinds of fire were natural, and were there changes associated with the 
build-up of human populations with the arrival of the white man, and 
with interglacial and post-glacial climatic fluctuations" (Heinselman, 
1971). In his papers describing the natural role of fire in the 
northern conifer forests of North America, Heinselman (loc. cit; 1973) 
concludes that the interaction of vegetation types, stand age, successional 
age, and their different fuel factors with climatic oscillations 
regulated the pattern of burns in primeval times. Charcoal fragments 
and fossil evidence found in lake sediments, peat bogs and glacial 
deposits indicate that fire was a major factor in these forest ecosystems 
long before the arrival of European man. In the high country of S.E. 
Australia, there is no such historical record, and given the paucity of 
sites for the preservation of fossil pollen, as well as the low potential 
for identification of eucalypt pollen types, it is unlikely whether this 
kind of record will ever be found. The historical model must be derived 
from scant macro-fossil evidence, such as the Nothofagus trunk in the 
northern Snowy Mountains (Jennings and Caine, 1968), vegetation dis­ 
junctions (Costin, 1971), the dynamic relationship between fire­ 
sensitivity and distribution of specific eucalypts and the interval 
between severe fires (Figure 20), observations of changes in tree-form, 
and population structure (Pryor, 1939), the changes in the frequency of 
fire scars in cross-sections of old trees (Costin, 1951, 1954) and the 
changes in the succession of understorey vegetation.

By deduction and inference, a general model can be formulated 
from this kind of evidence, for example:

"... whilst there have undoubtedly been fires in 
most types of vegetation, the frequency, intensity 
and seasonal incidence of these fires varied widely,

* primeval, in the sense that there was no direct alteration by man 
through logging, land clearing, burning, grazing, or similar activities. 
Essentially all areas have burned in the past 100 years, and 
virtually all the forest still contain first-generation postfire 
elements.
both between and within the various types of vegetation. For example, some particularly fire-sensitive communities such as snowgums, alpine ash, mountain ash and some types of rainforest must have been burned on only rare occasions otherwise these communities could not have produced mature trees of 200 years or more. 

(Costin, 1969)

Sources of data for a basic model (Figure 19a)

In tending towards the steady-state, it is natural for the net accumulation of detritus, as well as net production and biomass, to proceed towards a peak, but this peak occurs earlier than a state of maximum relative stability. At this point relative stability will be a feature of gross ecosystem processes and specific characteristics of the detrital layers. The analytical data in this thesis are integrated in time according to a parameter that defines secondary ecosystem development only to the point of maximum accumulation of the forest floor.

![Graph showing basic models of long-term ecosystem development in subalpine eucalypt forests and woodlands](image.png)

**FIGURE 19** Basic models of long-term ecosystem development in subalpine eucalypt forests and woodlands

(A) Total mass of forest floor  (B) Stand structural parameters

* It is important to note that because of the complex nature of fire in the eucalypt communities, fire can affect the understory vegetation, forest floor and surface soil without affecting community structure (basal area, density etc.). Therefore Figure 19a and Figure 19b are not necessarily coincident.

† Sources of data: stand measurements by G.N.P., and S. Barker (pers comm).
From studies of litter-fall in relation to the mass of the forest floor it has been possible to calculate the time period required to attain 99% of the maximum accumulation of organic matter, and nutrients, above the mineral soil, using the constant, \( k \) (Olsen, 1963). In the general model (Figure 19a), the value for \( E. pauciflora \) (55 years) has been used, because of the inclusion of a woodland stand of \( E. pauciflora \) to indicate a state of apparent stability in the nature of the forest floor. From litter-fall data of similar woodland stands in the Northern Snowy Mountains (B. J. McCauley, pers. comm.) the derived value of \( 5/k \) (43 years) indicates little absolute increase in decomposition, but that the more rapid turnover of litter is a function of reduced litter-fall as stand structure shifts from open forest (Plates I la, Xa) to a woodland (Plate I lb).

A few stands characterised by open canopy structure and open understorey layers (Plates IV and VI) are considered to occupy positions slightly beyond the point of maximum accumulation of the forest floor. The open woodland stand of \( E. pauciflora \) (Plate I lb) contains little accumulated organic matter above the mineral soil, but a very organic mineral soil, few shrubs in the understorey layers and an estimated age of 250 years for the oldest class of trees. For these reasons, although the woodland stand is integrated with the rest of the stands in the differential analysis of nutrient dynamics (Chapter 5.6) it is distinguished as denoting maximum relative stability in the derivation of a strict time scale. There is support for the separation of these two groups of stands to positions beyond the point of maximum accumulation, in the gradient of change in stand structure (Figure 19b).

It is not possible to construct a model of long-term ecosystem development from data of this form alone. A basic model (Figure 19a) therefore also draws upon:
(i) historical records and descriptions, and

(ii) comparative analysis of current vegetation.

These can be summarised in relation to the probability of long-term ecosystem development.

1. Historical records and descriptions

(i) Fire was certainly a major factor in pre-settlement times, but at a considerably reduced frequency to that promoted by the activities of European man. A good case can be made for the proposition that aboriginal fires were rare in the subalpine zone. Wildfires were inevitable, but were random perturbations promoted by lightning and extreme weather patterns.

(ii) There are sufficient direct observations of marked increase in severe wildfires following changes in fire-risk brought about by European man.

(iii) There is vegetational evidence from tree-ring and fire-scar records. The increased frequency of fires has altered the long-term dynamics of stand structure, as shown by early observations that forests of few low-boled, deep-crowned trees were replaced by forests of many tall-boled, shallow-crowned trees (Plate IIib) over most of the landscape (Plate IX). There is evidence that the understorey in these forests was open, and that the predominance of shrubby, leguminous understoreys (Plates, V, VIa) in the present-day landscape is a result of altered fire patterns. A period of about 40 years is required to eliminate a shrub understorey in snow-gum vegetation.

(iv) There is evidence that Nothofaginea rainforest has occurred throughout the subalpine zone in the Late Pleistocene, whilst at present it
is restricted to Tasmania and southern Victoria. Whilst eucalypt vegetation is seral in the presence of Nothofagus, the long-term tendency, in the absence of this competitive element, would be toward open forests and woodlands of low-boled deep-crowned trees. This supported by remnants (Plates IIIa; VIII) and relics (Plate IX) in the present-day landscape. A few dates are known (S. Barker, A. B. Costin, *pere. comm.*) that enable a construction of the trends in the dynamics of stand structure (Figure 19b).

2. Comparative analysis of current vegetation

The upland vegetation of S.E. Australia contains an unusually large number of taxonomically related dominants, most of which exhibit marked site-specificity. The ecotonal relationships between some of these species have been examined in part of this study. Although the evidence is complex, it can be said that, in any region, there are clear distributional relationships between topographical position, altitude, nutrient status and fire (Figure 20a and b). Jackson (1965) has constructed a similar ordination of species and vegetation types as an ecological base for the determination of the frequency between severe fires that would evolutionarily have controlled the patterns and the processes in the vegetation. In both cases there is a strong relationship between species distribution and environments differentiated according to a range of fire frequency. Superimposed on this relationship are gradients of anatomical and physiological adaptions and sensitivity to fire (cf. Blake, 1972; Blake and Lacey, 1973; Gill and Ashton, 1968; Jacobs, 1955; McArthur and Cheney, 1972).
The general model of Costin cited above, is relevant in this context because it indicates the fundamental relationship between fire, adaption to fire, and distribution. Even within eucalypt species there are morphological clines of adaption to fire frequency, for example the decline, with altitude, in the development of lignotubers in *E. pauciflora* (Ashton, 1969), and between provenances of species. There is abundant support from studies in lower-altitude eucalypt communities that the highly flammable characteristics of the sclerophyll species might be detrimental to the functioning of ecosystems under programs of attempted fire exclusion (Hodgson and Heislers, 1974) because the accumulation of flammable fuels over a long period of time on some sites may lead to fires of 'unnatural' intensity. Because of adaptive features, such as epicormy, these communities can compensate for frequent perturbation by fire. Of equal concern is the introduction of fire at shorter intervals than the ecosystem experienced naturally, and for which there is little or no compensatory adaption. Slobodkin *et al.* (1967) defined the balance of
nature as the persistence of ecological systems to compensate for perturbations. Odum (1969) emphasised that pulse stability occurs only if there is a complete community adapted to the particular intensity and frequency of perturbation and that adaptation - operation of the selection process - requires time measurable on the evolutionary scale.

In the absence of a true time-scale of the frequency of perturbations, from fossil and historical sources, considerable deduction must be made from the communities resulting from the selection process in upland eucalypt ecosystems.

3. Defining a natural fire-cycle

The primeval upland eucalypt forests and woodlands were fire-dependent ecosystems. Fire was the key environmental factor that initiated new successions, controlled the diversity of species and age structure of the communities and produced the vegetation patterns upon which the animal components of the ecosystems were dependent. In this, as Heinselman (1971; 1973), Loucks (1970) and Mutch (1970) have concluded in studies of the conifer forests of North America, the evolutionary success of these ecosystems, and the component species, is ultimately dependent on the random rejuvenation of the system. In Louck's opinion, an understanding of the interruption by man of natural processes of ecosystem development is critical to ecosystem conservation. The conclusions of the many recent reviews of the ecological role of periodic perturbations, mainly by fire, in natural conifer forest in western and northern America (Habeck and Mutch, 1973; Heinselman, 1973; Loucks, 1970; Mutch, 1970; Wright, 1974) is that any modifications of the system that preclude periodic, random perturbation and recycling would be detrimental to the system in the long term. All of these authors recognise the principle that the species composition of any
ecosystem must be the product of adaption, not only to heterogenous
environments, but also to a repeating pattern of changing environments.
This is a stationary process that represents a composite of time
intervals over which replacement of species is repeated over and over
again during the evolution of species and ecosystems (Loucks, 1970).
It is clear from the North American literature that the mosaic of
vegetation types in the landscape reflects a mosaic of fire-cycles of
differing intervals. Thus white pine seems to have evolved in an
environment where the predominant interval between severe fires was
300-400 years, whilst deciduous forests reflect shorter intervals.

Because of the large number of tree species involved in any
forest succession in North America (Goff, 1969; McIntosh, 1968;
Whittaker, 1953), there is little difficulty in defining the successional
interval of each tree species, and therefore the natural intervals
between perturbations. In the eucalypt biome, apart from the replace-
ment by rainforest, for example in western Tasmania, there is no
phasic seral replacement of tree species. However, there are gradients
of fire-sensitivity, and fire-adaption (McArthur, 1962), and a response
to topographic position, all of which are the evolutionary products of
a range in the length of the interval between perturbations.

Whilst conservation research in the high-country of Australia
has much to learn from the North American experience, particularly in
the application of ecosystem-ecology to the conservation of natural
processes, there is an important difference in the historical origins
of the problems of the natural role of fire. In both regions we have
the traditional view that forest and property are destroyed by fire; in
North America, fire was long ago rejected as a management tool with the
result that fire exclusion has deflected the process of ecosystem
development. The regional biological landscape reflects intervals
between severe fires that are too wide to be in phase with the dominant species (Figure 21a). For the last 100 years in the high-country of Australia, fire has been used regularly in conjunction with grazing. Again, the processes of ecosystem development have been deflected; the biological landscape reflects intervals between severe fires (undoubtedly stimulated by the response of shrub understories to regular light fires) that are too narrow to be in phase with the dominant species (Figure 21b).

![Graphs showing response of seedling layer diversity and ecosystem properties to random perturbations (fires)](image)

**FIGURE 21** Two models showing the pattern of response in transient phenomena across an extended period of time. The whole series of transient response phenomena making up the stable system is restarted by each perturbation. The differing impress of European man is evident.

(A) Forests of southern Wisconsin (after Loucks, 1970)

(B) Forests and woodlands of the subalpine zone of S.E. Australia.

It should be noted that whilst the North American model is based on the availability of long-term historical and fossil evidence (Heinselman, 1973), the model for the subalpine eucalypt ecosystems is postulatory, and derived from extrapolation of the basic model described.
earlier (Figure 19).

7.4 THE DYNAMICS OF ORGANIC MATTER, NUTRIENTS AND UNDERSTOREY VEGETATION IN SUCCESSION

While recognising that it is difficult or impossible to control the considerable variation in environmental influences affecting the quality of nutrient pools, some cognisance of the more apparent trends must be made, and some idea of their functional interactions determined. I have described the rationale for construction of a basic model (Figure 19a) from the analytical data, supported by the derivation of decomposition rates as well as historical information and comparative analysis of stand structure (Figure 19b) and the relationships between eucalypt distribution and morphological adaptations (Figure 20). By integrating the ecosystems in Chapter 5 that were differentiated according to the accumulation of the F/H layer of the forest floor in this manner, the long-term dynamics of organic matter, nutrients and understorey vegetation can be compared.

The changes in some of these parameters throughout the postulated "chronosequence" are depicted in Figure 22. While this is in no way comprehensive, it may serve to illustrate changes in the forest floor and surface soil layers. No quantitative relationship is intended between parameters; it is merely an attempt to scale long-term processes of ecosystem development against the most viable time-scale that can, at present, be deduced from the available information, and to relate ecosystem development to the overview (Figure 21b) that whatever the postulated state of relative stability, perturbation is inevitable. The relative magnitudes of the various parameters and their regressed interrelationships have been discussed in conjunction with the presentation of
results (Chapter 5; sections 5.6.2-5.6.6). The main points are summarised in Section 5.7. It should be noted that the models (Figure 22) estimate the long-term successional response of ecosystem properties following the initial short-term shift in nutrient levels in the forest floor and surface soil that accompanies a perturbation of the magnitude of a severe wildfire (see section 5.6.7). The shift is too brief to be plotted at the scale of Figure 22.

From the point of view of the monitored fluxes in nutrients and understorey vegetation immediately after a fire of this kind, this short-term factor is important. If the magnitude and net direction of flux is viewed in terms of the maintenance of high quality nutrient pools, and the hypothesis advanced in this thesis that high fertility and geomorphic youth are integral ecological features of the subalpine zone, the interaction between the frequency and intensity of random perturbations in the model of ecosystem development in extended time (Figure 21b) is critical. The concentration of most nutrients, particularly Ca++, K+ and P, was greater in the organic matter consumed by the wildfire, and temporarily lying upon the soil surface, than in any tissues, forest floor or soil material sampled in this entire study. All of this added nutrient pool plus some of the existing nutrient pool was lost from the surface soil within 10 months. In some cases, such as non-occluded inorganic P, Ca++ and K+, combustion enhanced potential availability, whilst in other cases, such as Na+, availability was retarded. While the study of seasonal nutrient fluxes has shown that the mobility of most nutrient-elements is somewhat independent of fluxes in organic matter, in the long-term overview (Figure 22) the weight-distributions of nutrients (kg/ha) and the F/H:0-5 cm soil weight-ratios of nutrients show marked correspondence to the equivalent distributions for total organic matter.
FIGURE 22 Suggested models of the long-term successional fluxes in organic matter and nutrients, of the forest floor and surface soil layers, and understory vegetation in subalpine eucalypt ecosystems.
Monitoring of quantities and flux rates immediately after the Geehi-Grey Mare wildfire and for the following 10 months, indicated that vast amounts of carbon are lost from the ecosystem during and after a perturbation of this nature. The loss of carbon, and the concomitant de-structuring of organic-nutrient ion complexes, is critical in determining the flux of nutrients out of the forest floor and surface soil layers. Because growth of understorey vegetation is slow and out-of-phase with the brief period of enrichment of its rooting zone, and because *E. delegatensis* and *E. pauciflora* trees themselves are often killed, nutrients are lost from the ecosystem in suspension and solution. Expectedly, C/N ratios, C/P fractions etc., are temporarily lower than in any other sites examined in this thesis. Whilst considerable carbon is lost from the system during combustion, insufficient is added later to absorb the large pool of readily available nutrients. Some nutrients, notably the non-occluded fractions of P, may take a long time to attain net accumulation in the forest floor following perturbation.

'Recovery' of ecosystem properties following perturbation is a fundamental and well understood property of succession (Marks, 1974; Odum, 1969). In the subalpine eucalypt ecosystems, recovery proceeds initially to a point of maximum storage of nutrients and energy in the forest floor following homeostatic adjustment of the immediate effect of the perturbation. This process is estimated to take about 55 years in *E. pauciflora* (Figures 19 and 22) and about 35 years in *E. delegatensis* ecosystems for organic matter, and proportionately different periods for nutrients (Table 20). Beyond this point, it appears that declining litter production, related to structural changes in the community (Figure 19b), is concomitant with increasing decomposition, so that the mass of the forest floor is reduced and the organic matter becomes endorganic (Wilde, 1966), in marked contrast to an earlier sharply
differentiated ectorganic distribution. The phasic replacement of understorey shrub vegetation in the subalpine ecosystems is also a readily observable feature of 'recovery' in the earlier stages of the succession, whilst later stages showed apparent stability in composition (Figure 22). From long-term observations, Costin (1966) and Costin et al. (1959) have estimated that considerable thinning and diminution of shrubs will occur if the community is protected from fire for about 40 years. A similar time period is evident from the general models of vegetation succession from a shrub to grass+herb understorey (Figure 22), including a very distinct trend in understorey species diversity during the most intensive period of recovery from perturbation.

One reason why it was decided to use the net accumulation of the forest floor for a dimension of differential analysis of nutrient dynamics, and thereby forgo an absolute time-scale, was the considerable additional work that would be required to analyse stand structure, and even then the unknown fire history of the understorey vegetation and forest floor layers remained as an insuperable obstacle. Increment cores were collected from many individuals in numerous stands, but time did not allow development of these investigations. This study has therefore made a number of assumptions that, in fact, require evaluation:

(i) That if the interval between severe random perturbations was greater than about 150 years, gap-phase replacement was possible, given the probability of marsupial burrowing as well as reduced forest floor mass allowing access of seeds to the mineral soil.

(ii) Fire-sensitive species, such as *E. delegatensis* and *E. pauciflora*, are readily killed by fire. Their evolutionary development, as distinct from that of eucalypt species with fire-adaptive features, was possible only if fires were absent or occurred at long intervals.
(iii) Because we can observe relic trees (Plate IX) or uneven-aged stands (Plates IIb; VIII) of relatively few low-boled, deep-crowned trees of both *E. delegatensis* and *E. pauciflora*, senile, even-aged stands of the same species in the landscape today we can assume that they represent valid stages in successional development of the pre-European ecosystems. The literature provides evidence of the progressive disappearance of open stands of low-boled, deep-crowned trees in the last 100 years.

(iv) It is therefore valid to integrate the forest floor and understorey vegetation parameters of stands that are assumed to represent 'maturity', with the same parameters of stands that are known to represent 'youth'.

It should be noted however, that it is possible a low density of *E. delegatensis* may result from a mild wildfire in conditions unfavourable to massive seedling production and seedling establishment, and therefore lead to low-boled, deep-crowned trees of even age. Likewise, a light fire could drastically thin a regenerating stand and produce the same condition from the survivors. There is very little known of the population structure of the older forests and woodlands, and the effects of an irregular frequency, intensity and seasonality of fires on young and old stands are poorly understood. Any re-attainment of what I have concluded to be the primeval condition, of uneven-aged stands of trees with short boles and deep crowns, over a large component of the subalpine landscape will require the present-day young, even-aged forests that almost exclusively dominate the landscape, to thin as succession proceeds, to densities in the order of 50 senile, tall-boled trees per hectare (Plate VII). This would be accompanied by uneven regeneration of short-boled, deep crowed trees. The two-generation process would require a minimum of 200 years free of severe fire, and would produce
the massive amounts of detritus concomitant with the phasic decay of an even-aged forest.

Wilderness fire management means the restoration of a natural incidence of fire in an ecosystem. In the high country of Australia, wilderness fire management requires much more than an ecological understanding of fire cycles, fire frequencies and ecosystem development in the various communities.
A CODA
ECOSYSTEM DEVELOPMENT, FOREST FIRES AND
CONSERVATION MANAGEMENT

The ecosystem approach to the conservation of nature is the study of processes such as the cycling of nutrients, the flow of energy and the tendency toward a state of relative stability, so that the natures and effects of the stresses concomitant with the desired and undesired activities of modern *Homo sapiens* can be evaluated. In the eucalypt biome, it is new, as a conscious approach, and has not yet developed a methodology nor established its values and limitations. It is evident from the present work that in studying ecosystem processes at the landscape level, where it is most relevant to conservation management, very little long-term evidence may be deduced from situations with strict time control. The eucalypt ecologist has to derive *trends*, formulate *concepts* and develop theories based to a large extent on comparative analysis of the current vegetation. But wherever those responsible for the conservation of 'natural' ecological patterns and processes are seeking explanations of biological differences and similarities in more than strictly limited terms, ecosystem theory has an important role, for an understanding of the *probability* of processes lies behind all descriptive analysis of present-day, pre-European and palaeo-ecological patterns in the landscape.

The classification of ecosystems, usually as vegetation, geology and soils, has historically been the basis of forestry, wildlife and watershed management. Classification has produced inventories of vegetation, soil and landform types but little information on the complex, contiguous nature of ecosystem processes essential for the formulation of a dynamic policy of management and conservation. There is much useful information in a classification system, but it is
invariably confined within static, monothetic units which are, by definition, ecological abstractions. The effect is well recognised in the application of soil classification studies to forestry and other environmental studies (Webster, 1968). An ecological survey should not only use a framework of wide interest, but should be designed so that the results express ecological reality in time and space. Environmental and ecosystem components form continua in both dimensions (Whittaker, 1967), forming a continuously changing mosaic of polythetic systems.

FIRE AND ECOSYSTEM DEVELOPMENT

There is little argument that all eucalypt ecosystems are subject, inevitably, to random perturbations by fire, severe enough to set ecosystem development back to zero. But from comparative analyses of eucalypt distribution and adaptive morphology, it is apparent that different scales of intensity and frequency of fire are associated with different eucalypt ecosystems. It becomes important, then, that our approach to the analysis of these ecosystems is able to explain the dynamic status of individual species, and the long-term development of the ecosystems which they dominate.

Because of a paucity of long-term chronological criteria in the Australian high-country, much of our approach has to be by deduction and inference. It is therefore important that we examine the origins of a particular point-of-view or policy that leads to an interaction between man-centred goals, fire and ecosystem processes. In this thesis I have discussed the dynamics of the oldest ecosystems in the subalpine zone as an essential prerequisite for any understanding of the theoretical tendency of ecosystems to develop towards a state of relative stability. In the probable absence of truly primeval ecosystems (Costin, 1954, 1967),

* see page 246.
any concept of the natural interaction of fire and ecosystem development is derived from the relative effects of human activity.

I offer the argument that the homocentric role of fire in modern eucalypt ecosystems ensures that successional processes, as well as our knowledge of them, is under the continuous impress of man-centred goals. Succession, an orderly process leading to a state of relative stability (Odum, 1969, 1971, 1972; Whittaker, 1972), has two principal components, viz:

- a homeostatic capacity to resist perturbation,
- a capacity to recover from perturbation, once the limits of resistance to perturbation have been exceeded.

The strategy of 'maximum and continuing utility and production' (Odum, 1969), more than anything else, has understood and successfully used the second component, but our human 'time-scale of concern' (Frankel, 1974) does not allow for an understanding of the first component in ecosystems where the evolutionary interval between severe random perturbations may have been in the order of 100-300 years.

The homocentric bias inherent in this strategy is often very apparent. Mount (1969a, b) for example, has dismissed the relevance of general ecosystem development theory (Whittaker and Woodwell, 1972; Odum, 1969; Slobodkin et al., 1967) in the context of eucalypt forests, as is evident in the following statements:

(i) "nutrient recycling, patently not achieved by biological agencies in [eucalypt] forests where fuels accumulate, is more efficiently carried out by the combination of storage in durable debris and periodic processing by fire ....."

(ii) "A frame of reference that makes 'progress' (my italics)
difficult ..... is the tacit assumption that plants [ecosystems] do not produce waste materials ....."

(iii) "... waste disposal ... is a possible function of fire in the environment".

(iv) "... the unavailability of certain elements in the soil ..... is a product of growth, an organic compound that has been discarded by the living organism [ecosystem].

My conclusion, after reflection on ecological evidence and theory, as well as public and management attitudes to fire, is that any conservation of ecological patterns and processes in fire-sensitive ecosystems, such as snowgum woodlands and open forests of alpine ash, is compromised by these kinds of biases, entrenched as they are in a tradition of 150 years of modification of the eucalypt biome for man-centred goals. There is considerable evidence that the snow-gum and alpine ash ecosystems evolved in environments with a frequency of random perturbations such that succession could recommence once every 150-300 years. This evidence is difficult to reconcile with the currently predominant point-of-view of forest and national park management, and a large component of the interested public that,

"... the eucalypts have evolved in a fire-environment and are adapted to resist fire in the early stages of their development, while being the major source of fuel for fire at a later stage."

(Mount, 1969a)

One reason for this attitude appears clear. Although wildfires have been fundamental evolutionary stresses in the development of upland eucalypts, it is the profound effect of the extensive wildfires during the period of European settlement on the strategy of 'maximum utility and production' (Odum, 1969) that have molded professional and public opinion. Consider, for example the following:
"To have experienced a day such as the 7th February, 1967 in southern Tasmania, is to realise that conflagration in Australian ecosystems cannot conceivably be controlled by anything but preventive measure ..... On that day, one half million acres were burnt, 1300 city and country homes were destroyed, and 62 people died."

(Crane, 1972)

"In the course of this tragic day [January 13th 1939] the death toll increased to over 70 as townships, mills and buildings were razed to the ground and hundreds of square miles of forest and farming land laid waste."

(Forests Commission of Victoria, 1939)

Having recently observed first-hand the scale and ferocity of wildfire in the high altitude forests and woodlands (Brindabella Ranges, Snowy Mountains and Mt. Buffalo Plateau, 1972-73), I am aware of the dilemma of the national park manager confronted with the immediacy of fire-control and the legacy of the exploitative snow-lease grazing for short-term gain, and the criticisms and recommendations by the ecologist who is concerned with the conservation of diversity, and maintenance of nutrient pools in relation to their homeostatic response to perturbations. At the same time, the manager realises the absolute inevitability of wildfire.

The steady-state in forest ecosystems, a state of low net-productivity relative to the optimum, and a population structure with a high potential for maintenance (Odum, 1969), has doubtful credibility to those with the onerous tasks of resource and national park management within the conflicting value-systems of sectional groups in contemporary Australian society. However, if ecosystem development theory is valid, then it is the scientific responsibility of the ecologist to ascertain...
the nature and probability of the state of developmental inertia of ecosystems such as snow-gum woodlands and alpine ash forests, as well as the process of attainment of this state.

This study has described the considerable difficulty, largely due to environmental variation, in evaluating the successional dynamics of nutrients and understorey vegetation. Nevertheless, many trends can be defined, at least qualitatively from the data, and are supported by analysis of decomposition rates, historical information and comparative analysis of the relationships between eucalypt distribution and morphological adaptations. It certainly cannot be said, at present, that we understand the processes of ecological succession in even the major subalpine ecosystems to the extent that the stages desired by management, conservation and preservation interests can be maintained and/or re-established. Nor do we know enough about the same processes to reverse, deflect or accelerate succession to suit specified management purposes (Costin, 1969). Noting the desire of those with responsibilities of fire control to characterise different vegetation types in the high country, in terms of flammability indices, Costin has concluded that an understanding of the successional processes with respect to fire will really only be achieved by long-term studies, restricted to specific ecosystems whereby varying fire histories (intensity, frequency, seasonality and so on) can be modelled. In this sense the 'landscape' model derived from the present study is limited. Although different ecosystem types have been observed separately, data from sites of different parent materials and largely unknown fire histories have been pooled, and integrated according to the net accumulation of the forest floor following perturbation.

Anyone knowing something of successional patterns in eucalypt forests can readily observe many stages of successional development in
each forest type. I have postulated that, given the obvious agents of
ground disturbance in the subalpine eucalypt ecosystems in late
successional stages (burrowing marsupials, windfalls etc.) as well as
the decline in litter production and the forest floor, self-maintenance
of the eucalypts is possible, without an ash-bed in the manner suggested
critical to cyclic regeneration of these eucalypts (Grose, 1960). It is
probable that both self-maintenance and cyclic-succession occurred
simultaneously in the primeval subalpine landscape, and that the one
eucalypt species regenerated in short fire-cycles on some sites, and
long cycles, including self-maintenance, on other sites. This pattern
can be observed in *E. delegatensis* and *E. pauciflora* communities in the
present landscape.

Interpretation of the meaning of cyclic succession in these
ecosystems will vary according to one's interest in, or demands on, them.
The production-conservation-wilderness management dilemma is
essentially interpretive and more likely to reflect management skills
than an ideal of the 'primeval' ecosystem. A wet sclerophyll forest can
be managed to an 'optimum' of health and production, and then regenerated
to this point. Alternatively, as is the trend in natural forest
succession (Odum, 1969; Whittaker, 1972), forest development can exceed
the production and biomass optima and proceed towards maintenance and
relative stability. In the latter process the eucalypts *may* be only
seral, for example to *Nothofagus* rainforest (Howard, 1971; Jackson, 1968).

**MULTIPLE USE AND ECOSYSTEM DEVELOPMENT**

One conclusion from this study is that if conservation management
is to identify with the maintenance of diversity of ecological patterns
and processes, we will have to develop a deliberately diverse management
strategy. In some areas we will have to keep fire out at all costs so
that long-term succession can be monitored in a fixed series of ecosystems, to take enormous risks involving a let-burn policy (Aldrich and Mutch, 1972) in other areas, as well as maintaining other conservation values. Similarly, Cooper (1971) in a specific critique of the historical preoccupation of fuel reduction burning with homocentrically determined optimal land-use policies in North America, emphasised the long-term advantages of promoting ecosystem diversity in a landscape, through alternative policies enabling a mosaic of ecosystems differing in age and composition. The alternatives would include some in which prescribed or fuel-reduction burning was precluded. In the high-country of Australia we need biological models that present alternatives to past and continuing land practices to show the consequences of the management options on the full spectrum of biological and management factors. If we are to create a 'wilderness' within our national parks we must be prepared to re-create what we determine to be a 'primeval' state in parts of the landscape.

If, as this study suggests, there are simultaneous long-term successional trends from inflammable shrub understories to a ground layer of grasses and herbs, and a decline in the mass of the forest floor after progressively attaining maximum storage of organic matter and nutrients, we are faced with waiting the appropriate time-periods for these trends to proceed. In the meantime, on the evidence of the vegetative response to light burning during the snow-lease grazing period and following prescribed burning in related communities, the modern changes in the understories magnify the risk exponentially.

* The majority of shrubs have been eliminated by phasic replacement in about 40 years following fire; the time-period for maximum accumulation of the forest floor is about 35 years in *E. delegatensis* and 55 years in *E. pauciflora* ecosystems.
Such management policy is radical, in that it is independent of the assumption that conservation reserves are basically economic units. Almost without exception, an increase in the economic yield of ecosystems is accompanied by a decrease in richness and diversity of species (Cooper, 1970). The 'fuel-reduction' burning technique, for example, has made a considerable impact on the natural interaction between fire and ecosystem development. Despite an apparent biocentric rationale (McArthur, 1962, 1968, 1970; Hodgson and Heislers, 1974), it is basically a history of efforts to create simple systems in which preferred species are kept free of others which interfere with man-centred goals through one process or another.

Odum (1969) has criticised the prevailing trends of an economic base to ecosystem management, particularly the usual assumptions of the 'multiple use' concept, as being fundamentally aecological. His model emphasises the relevance of ecosystem development theory to landscape planning,

\[
\begin{align*}
\text{young} & : & \text{mature} \\
\text{production} & : & \text{protection} \\
\text{growth} & : & \text{stability} \\
\text{quantity} & : & \text{quality}
\end{align*}
\]

It is mathematically impossible to obtain a maximum for more than one of these elements at a time, so one cannot have both extremes at the same time and place. Since all six elements are desirable in the aggregate, two possible solutions to the dilemma are immediately apparent. Society can compromise so as to provide moderate quality and moderate yield on all the landscape, or deliberately compartmentalise so as to simultaneously maintain for example, highly productive and predominantly protective types as separate units subject to different management strategies (allowing for the scale of management to include nil management).
The restoration of fire to a natural role in the eucalypt ecosystem provides society with an enormous dilemma of values. If we intend to conserve 'natural' ecological patterns and processes in parts of the landscape it is essential that we develop an empirical understanding of eucalypt distribution, ecosystem development, particularly the dynamics of eucalypt populations, and understorey and forest floor succession from the current vegetation that is independent of research of fire control, fire prevention and wood production. The ecological objectives (cf. Aldrich and Mutch, 1973) should be synchronous with those of management policy, viz:

1. To determine the trends, limits and probabilities of long-term ecosystem development.

2. To determine the relationships between subalpine eucalypt ecosystems and fire.

3. To determine strategies that optimise the natural incidence of fire in these ecosystems, particularly proportions of the landscape that are to be occupied by various successional stages.

Fundamentally, there must be clear, specific and biologically-tenable policies of management that enunciate the philosophy of conservation of ecological patterns and processes, and the biological nature of the ecosystem to be maintained, restored or disturbed.

"The implications of natural history for wilderness and national park preservation programs are far-reaching. For if we are serious about maintaining the natural ecosystems of these areas, then clearly the elemental forces of the past must still prevail."

M. L. Heinselman (1970)
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