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SECONDARY SUCCESSION IN THE LOWLAND FORESTS  
OF THE MARLBOROUGH SOUNDS MARITIME PARK

by  
Margaret Wassilieff

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## ABSTRACT

This study documents aspects of the forest recovery process in secondary communities of the Marlborough Sounds Maritime Park. Some 38 types of seral vegetation were recognised as being common in the lowland zone of the Marlborough Sounds.

Data on vegetation structure and composition, forest floor biomass and nutrient status and soil nutrient status were collected from 39 seral communities ranging in age from 2 to 84 years and were compared with data collected from 6 adjacent undisturbed lowland forest communities.

Three seral pathways were represented at the study sites, the vegetation was developing toward either:

- Weinmannia racemosa dominated forests
- mixed broadleaved species forests
- or Dysoxylum spectabile coastal forests.

A number of vegetation structural parameters (crown cover, specific vegetation space, basal area and stem density) showed rapid recovery to levels similar to those of undisturbed forests. However, other structural parameters (mean canopy height, total stand volume, total stand foliage) had not recovered to levels typical of adjacent undisturbed forests some 70 to 80 years after disturbance.

The pattern of vertical development of the forest foliage during succession was from short concentrated foliage distributions in young stands to tall, relatively evenly spread distributions throughout the height profile in older stands. Foliage in stands older than 25 years tended to be concentrated in the height class near, or just below, the mean canopy height of the stand. Shrub understorey development commenced some 45 years after disturbance.

Few trends in species diversity were evident during succession. Species richness ( $d$ ) was very high and at a maximum in the youngest study stand. Species richness was relatively constant after two years and changes in species diversity during succession were due mainly to decreases in species evenness ( $J'$ ).

Duration of seral vegetation in the Marlborough Sounds Maritime Park was related to the life spans of the dominant pioneering species at a particular site. Gahnia pauciflora dominates a site for only 1 year, Cassinia leptophylla can dominate for 20 years, Leptospermum scoparium for some 45-55 years and L. ericoides can dominate the vegetation for between 70 and 85 years.

Linear relationships were derived between age and d.b.h. measurements for three seral tree species (Weinmannia racemosa, Leptospermum scoparium and L. ericoides). Leptospermum scoparium and L. ericoides have similar average diameter growth rates of 0.6 cm/yr for most of their growing period. The average diameter growth rate of Weinmannia racemosa was 0.29 cm/yr.

The variation in weight of the forest floor at any one study site was very high and the sample size employed in this study was inadequate for estimating the weight of the forest floor within reasonable limits. However broad trends in the recovery of the forest floor during succession were noted. There were two main patterns of forest floor accumulation. Sites dominated by Pteridium esculentum showed rapid recovery of forest floor biomass to very high levels. Sites dominated by Leptospermum and Cassinia species showed much slower rates of forest floor recovery and never approached the weights attained by Pteridium-dominated stands. Two types of forest floor (laminated mors and moroid-mulls) developed under seral vegetation but were not present under undisturbed forests.

There was a trend toward a decline of the forest floor under Leptospermum-dominated stands after 40 years and this was coincident with a decrease in the contribution of L. scoparium to a stand's basal area and crown cover and an increase in dominance in a stand by L. ericoides and Pseudopanax arboreus. Seral stands located on slopes and ridges never attained forest floor weights similar to those under virgin forests on comparable sites.

Rates of nitrogen, organic carbon, total cation and total phosphorus accumulation in the forest floor layers were directly related to the rate of forest floor biomass accumulation. No large accumulation of nitrogen was noted in the forest floors during the early stages of succession. A high proportion of the available nutrient capital of many of the seral stands and the undisturbed forests was located in the forest

floor and the top 1 cm of mineral soil. Nitrogen was the one element that appeared to be in ample supply in the mineral soil to a depth of 30 cm.

No relationships between rates of regeneration and measured soil parameters were evident in this study. It did appear, however, that the broad seral patterns of vegetation recovery were related to the soil and topographical pattern of the Marlborough Sounds. Soils of valley floors and terraces and steep colluvial slopes support seral communities that are developing toward a mixed broadleaved species forest or to a Dysoxylum coastal forest. The pioneering shrub Leptospermum scoparium was not important in seral vegetation at such sites. Soils of the gentler slopes and ridges support communities that are tending toward either a Weinmannia racemosa-dominated forest or a mixed broadleaved species forest. Leptospermum scoparium is usually an important component of the seral vegetation at these sites. All sites that supported vegetation which was developing toward a Weinmannia racemosa forest possessed low or very low exchangeable calcium levels in the A horizon soils.

Seasonal fluxes of nutrients in litterfall were monitored in two adjacent young seral stands. One stand was dominated by a Leptospermum ericoides - L. scoparium low forest and the other stand by a Coriaria arborea - Aristotelia serrata low forest. Quantities of litter returned to the forest floor under both stands were higher than those reported from undisturbed forests in New Zealand. The annual litterfall under the Leptospermum-dominated stand was 7.80 tonne/ha and under the Coriaria-Aristotelia stand it was 10.07 tonne/ha. High quantities of nutrients were returned to the forest floor under both stands.

Leaf-litter decomposition in the Coriaria-Aristotelia stand was rapid. After 6 months on the forest floor the leaf litter reached such a degree of disintegration that it could not be separated from the mineral soil. In contrast the decomposition of Leptospermum leaf litter was slower. Approximately 40% of the litter weight of the Leptospermum material was lost after 13 months on the forest floor. The nutrient flux behaviour of the litter differed at the two seral stands and this reinforced the soil nutrient differences of the two sites.

The value of young regenerating vegetation to the integrity of the Marlborough Sounds lowland forest ecosystem has not been appreciated by authors of recent land use studies of the Marlborough Sounds.

A critique of some of the recommendations made in the land use studies has been undertaken. Guidelines to assist with the management of scenic reserves in the Marlborough Sounds Maritime Park have been drawn up and are discussed within the context of modern ideas of successional theory.

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A Study of Lowland Forest Succession in the Marlborough Sounds  
Maritime Park

1.1 Introduction

The lowland forest ecosystems of New Zealand have proved to be a resource well suited to exploitation following the colonization of the islands by Europeans. It is estimated that less than 20 percent of the area that carried lowland forest at the time of arrival of European man now supports mature indigenous forest (Wards 1973, Edmonds 1979). Much of the lowland area in New Zealand cleared of forest since 1850 has been sown to pasture, planted in horticultural crops or replanted in exotic tree species.

There are tracts of cleared lowland where agriculture has proved to be unprofitable and the area has started to regenerate back to a forest condition. The process of forest regeneration is colloquially referred to as "land reverting to scrub" by many New Zealanders. Ecologists recognize the process as secondary succession.

Secondary succession occurs after a severe disturbance has disrupted an ecological community. It is the process whereby different species and groups of species come to occupy the same area over a time period; it terminates in a species combination or community that persists in a dynamic equilibrium with the habitat (McNaughton and Wolf 1973, McCormick 1968, Horn 1974).

The Marlborough Sounds region of the South Island of New Zealand is an area where much of the lowland forest was cleared during the period 1860 to 1940 (Bowie 1963, Matthews 1980). At present the Marlborough Sounds is covered in a mosaic of vegetation types; many of which owe their origins to the land clearance activities of the settlers.

Approximately one third of the land area of the Marlborough Sounds is in Reserves administered by the Marlborough Sounds Maritime Park Board (area of the Maritime Park as at 31 March 1980 was 43,457.9 ha). In many of the Reserves the forests are regenerating after clearance and unsuccessful attempts at pastoral farming.

Those seeking to manage the Maritime Park must realise that the Reserves contain dynamic vegetation communities. The vegetation present twenty years hence on any area will not necessarily be composed of the same plant species or life forms and may not possess the same functional attributes as the present day vegetation cover.

The major portion of this thesis (Chapters 4, 5 and 6) is devoted to a study of aspects of change in the structure, composition and function of secondary communities in the Reserves of the Marlborough Sounds.

The study has been undertaken in the hope that the information gained will be of assistance to the managers of the Maritime Park. It is the author's belief that the wise management of the Reserves must be based upon ecological principles integrated with a sound knowledge of the structure and function of the communities in the Reserves. A secondary theme of the thesis has been to assess the relevance of ideas held on secondary succession and ecosystem development to the present study. Ideas on succession have been central to ecological thought but over recent years there has been much debate about the validity or applicability of different successional theories. In order to integrate the findings of the present study within the framework of ecological studies it has been necessary to examine the arguments advanced by the proponents of different successional theories.

### 1.2.1 Modern Ideas On Succession

"It almost seems that the moment one formulates a concept and provides it with a name and a terminology the spirit of it flies away and only the dead body remains".

- from Cooper 1926.

"Time has dealt unkindly with generalizations about succession, whether the organismic-like monoclinal theory of Clements, the successional trends of Whittaker (1953, 1975b), the ideas relating to diversity and maturity of Margalef (1963), or the structural and functional characterizations of succession by Odum (1969)".

- from Whittaker and Levin 1977.

The introductory sentence to Whittaker and Levin's 1977 paper, quoted above, is a succinct summary of the state of the classical and contemporary models of succession.\*

Objections to the classical model of succession were raised initially by Gleason (1917, 1926, 1927) but his arguments were largely ignored until recent times. It would now be fair to say that Gleason's views on the individualistic concept of the plant association and succession have withstood the attacks to which his contemporaries' models (Clements 1916, 1936, Phillips 1934, 1935a, b) have succumbed.

It is only over the last ten years that it has become apparent that no model of succession exists which can adequately explain the trends associated with succession on all sites.

---

\* Nomenclature follows Drury and Nisbet (1973)

The Classical view of succession is that outlined by F.E. Clements (1916) where succession is seen as an universal, orderly process of change. The development of the community proceeds from diverse pioneer stages to a single stable stage (climax) that is determined by the regional climate. In the development from the pioneer to the climax stage the community is thought to pass through the same stages of development (birth, maturation, senility, death) passed through by individual organisms.

The Contemporary theory of succession (also called the Developmental theory - Horn 1974) is concerned with the development of the community and the change in community characteristics such as biomass, production, diversity, efficiency, stability and homeostasis through time.

McCormick (1968) presented a review and reappraisal of successional theory as it was accepted by most ecologists around that time. His attack was directed toward the concepts that had been popularised by Clements and later workers. These concepts were:

- succession is repetitive,
- succession is predictable,
- succession is terminative,
- succession is progressive; it tends toward greater complexity of community structure, greater diversity of species present and life forms present, greater stability of the vegetation to perturbation, greater productivity and biomass, and is accompanied by modification of site parameters,
- succession is caused by the reaction of vegetation upon the habitat in such a manner to produce conditions unfavourable to its permanence, but advantageous to invaders of the next stage (the reaction mechanism).

In his review McCormick presented evidence from his observations and from species removal experiments to challenge the notion of the reaction mechanism being a causative mechanism of succession. McCormick also referred to the paper by Egler (Egler 1954) which provided an alternative to classical successional theory. Egler provided evidence to show that the initial flora of a site was important in determining the successional pathway and also presented examples of the persistence of species at a site through a number of defined seral stages.

McCormick concluded that "the sequence of vegetation types (or of conspicuous plant populations) and the duration of occupancy by each type (or population configuration) may not be as predictable as many ecologists have implied". His view that succession is best regarded as a species population phenomenon was to be echoed in a number of reviews presented in the following years.

In 1969 E.P. Odum presented a paper in which were outlined his ideas on the development of ecosystems (Odum 1969). In the paper Odum presented a number of hypotheses about the expected direction and magnitude of change in ecosystem parameters during succession. These hypotheses (reproduced in Table 1:1) quickly became accepted as the contemporary model of ecosystem succession (Drury and Nisbet 1973). The model of succession presented by Odum owes much to the ideas advanced and developed by Margalef (1963, 1968, 1969).



Table 1:1. Model of ecological succession: expected trends in the development of ecosystems.

- From Odum 1969

Ecosystem Attributes	Developmental Stages	Mature Stages
<u>COMMUNITY ENERGETICS</u>		
1. Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1
2. Gross production/standing crop biomass (P/B ratio)	High	Low
3. Biomass supported unit energy flow (B/E ratio)	Low	High
4. Net community production (yield)	High	Low
5. Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
<u>COMMUNITY STRUCTURE</u>		
6. Total organic matter	Small	Large
7. Inorganic nutrients	Extrabiogenic	Intrabiogenic
8. Species diversity - variety component	Low	High
9. Species diversity - equitability component	Low	High
10. Biochemical diversity	Low	High
11. Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well organized
<u>LIFE HISTORY</u>		
12. Niche specialization	Broad	Narrow
13. Size of organism	Small	Large
14. Life cycles	Short, simple	Long, complex
<u>NUTRIENT CYCLING</u>		
15. Mineral cycles	Open	Closed
16. Nutrient exchange rate, between organisms and environment	Rapid	Slow
17. Role of detritus in nutrient regeneration	Unimportant	Important

Table 1:1 Continued

Ecosystem Attributes	Developmental Stages	Mature Stages
<u>SELECTION PRESSURE</u>		
18. Growth form	For rapid growth ("r-selection")	For feedback control ("K-selection")
19. Production	Quantity	Quality
<u>OVERALL HOMEOSTASIS</u>		
20. Internal symbiosis	Undeveloped	Developed
21. Nutrient conservation	Poor	Good
22. Stability (resistance to external perturbations)	Poor	Good
23. Entropy	High	Low
24. Information	Low	High

Odum's paper is important in at least two respects. Firstly, attention is directed toward structural and functional aspects of developing communities and the hypotheses are framed within terms of the 'strategy of ecosystem development'. The strategy was for the ecosystem to gain control over the physical environment by achieving maximum protection from disturbance which was realised by community controlled changes during succession. Hence, the emphasis in the contemporary model of succession is directed toward an understanding of the changes in the biological and physical components of the ecosystem and is not solely concerned with the species composition of each seral stage.

The second important aspect of Odum's paper is that his list of hypotheses provided the impetus for further field studies and reviews that have provided the information which has been used to challenge the validity of the contemporary and classical models of succession.

Drury and Nisbet (1973) presented a critical review that challenged both the classical and contemporary views of succession. They discussed a number of studies of succession in forests and concluded that most do not conform to contemporary or traditional generalizations. Other reviews have followed that challenge one or a section of the hypotheses forwarded by Odum. Most criticisms have been concerned with structural aspects of ecosystem development (Horn 1974, Pickett 1976).

Bormann and Likens (1979) in their Hubbard Brook ecosystem study have shown that a number of Odum's hypotheses are not substantiated by their detailed case history study of secondary succession in a northern hardwood forest.

The following discussion concerns examples that pose a challenge to the classical and contemporary views of succession and is limited to those examples from secondary forest ecosystems for the most part. It is apparent that exceptions and contradictions to the classical and contemporary views of succession are found in other ecosystems (e.g. van der Valk 1981, Matthews 1979 and examples in Drury and Nisbet 1973).

Both community production and species diversity are described as increasing during succession and reaching a maximum just before the climax in the contemporary model of succession (Margalef 1968, Odum 1969). A model has been developed, describing secondary development of the northern hardwood forests after clearcutting, from the data accumulated by the Hubbard Brook

workers (Bormann and Likens 1979a). This model indicates that the ratios of gross primary production to total ecosystem respiration (P/R ratio) do not follow the simple curve from greater than 1 to 1 as the ecosystem develops from early to mature stages. The curve is of a more complex form and there are at least two stages of ecosystem development when the P/R ratios are less than 1.

Drury and Nisbet (1973) reason that community production and species diversity should be correlated during succession if the contemporary model is valid. They present evidence from field studies of Odum (1960) and Whittaker (1965) to show that the correlation between production and diversity does not exist in the two studies.

The problem of species diversity trends to be expected during succession is a complex one and the literature on this topic is quite extensive. Part of the problem concerns the different measures of species diversity that are employed in research. Whittaker (1972, 1977) summarised the uses and limits of the most frequently encountered diversity indices. Hulbert (1971) has gone so far as to suggest that species diversity has become a meaningless concept.

Nicholson and Monk (1974) undertook a study of trends in species diversity in 51 seral communities on the Georgia Piedmont in order to record seral changes in diversity in different plant strata as well as the total plant component and to interpret variations in diversity trends within the strata and amongst the different diversity indices employed. Their study is one of the most comprehensive attempts to record species diversity parameters. Their results show that there is an increase in species richness\* among the strata until a plateau stage (reached at different times with different strata) is reached. Seral changes in equitability\* were mostly limited to early succession. They conclude that divergent seral trends in richness and equitability reflect differing influences of regulatory mechanisms on these two diversity attributes. They also suggest that since their results differ from results obtained from other floristic zones, but are in agreement with trends detected in floristically similar areas, that diversity succession trends may differ in different vegetation zones but there may be generalized regional trends along with similar diversity regulating mechanisms in similar areas.

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\* species richness is the number of species in a sample.

\* species equitability is a measure of the distribution of numbers of different species in a sample.

The Hubbard Brook ecosystem study is currently the most detailed study that presents data on the biotic control of the biogeochemistry of successional forest ecosystems. Species richness is lowest during middle stages of ecosystem development when an even-aged aggrading forest is present and control of biogeochemical exports is maximal and highly predictable. Species richness is highest during the earliest stage of development and biotic control over nutrients in the ecosystem is low at this time (Bormann and Likens 1979).

Diversity has been linked to ecosystem stability in the contemporary successional model. The diversity-stability hypothesis is that species diversity stabilises ecosystem functional properties (McNaughton 1977). The problem with this hypothesis is in part a semantic one. Stability may be defined in a number of different ways. With regard to succession ecosystem stability is expected to increase with time. Drury and Nisbet dismiss this hypothesis rather lightly by stating that no generally accepted definition of stability in ecological systems is available. In light of the fact that it is a commonly expressed belief that mature ecosystems are more stable than immature seral stages it is important to review the hypothesis in depth, and appreciate the constraints on this concept dependant upon the type of stability that is being discussed.

Horn (1974) has reviewed some of the problems connected with stability of ecosystems during succession and the diversity-stability hypothesis. He clearly distinguishes between different meanings that stability can have in his discussion. If stability is defined as absence of change then stability increases during succession as longer lived species become more dominant in the succession. If stability is defined as resistance to perturbation, and is measured by the speed with which a community returns to its original state after disturbance, then stability decreases through succession since early successional stages return to early successional stages and mature climax stages, if severely perturbed, become early successional stages that take a long time to return to a mature state.

May (1973) provided a challenge to the diversity-stability hypothesis when he showed by the use of mathematical models that diverse, complex ecosystems may be unstable. This approach led further workers to challenge the diversity-stability hypothesis. At the 1st International Congress of Ecology (Proceedings 1st Int. Congr. Ecology 1974) it was evident that the views held by some ecologists had changed quite dramatically during the 5 years since the Brookhaven conference on diversity and stability where many

authors had accepted the diversity-stability hypothesis (Woodwell and Smith 1969).

Some of the participants from the 1969 Symposium were present at the 1st International Congress at the Hague. Odum (1974) presented data to show that quite stable systems, in terms either of persistence in time or in terms of his earlier definition (1969) as resistance to perturbation, can have either a low or high diversity. He relates the optimum diversity of an ecosystem to the quality and quantity of energy flow moving through the system.

Although mathematical modelling presented the main challenge to the diversity-stability hypothesis it did not refute its validity in real ecosystems. S.J. McNaughton and others (Hurd *et al.* 1971, Mellinger and McNaughton 1975, McNaughton 1977) have provided empirical evidence in support of the diversity-stability hypothesis for the producer level of ecosystems (but not for other trophic levels). Perturbation experiments (nutrient perturbation by addition of fertilizer to the soil and addition of a herbivore to grassland enclosures) have shown that less diverse plant communities show a greater response in functional properties to a perturbation than do more diverse plant ecosystems. McNaughton concludes that diversity stabilises ecosystem function through compensating interactions to environmental disturbances among co-occurring species.

Finally with regard to stability of ecosystems, the destruction of the tropical forests is surely the key example to stress the need for clear definition of the term stability. These mature, diverse ecosystems are extremely fragile entities when subjected to the development plans of modern man (Horn 1974, Farnworth and Golley 1973, Odum 1970).

Another hypothesis that has been challenged concerns the conservation of nutrients by developing ecosystems. The contemporary model of succession holds that as succession proceeds an ecosystem conserves nutrients more efficiently. Vitousek and Reiners (1975) state that this is an oversimplification of ecosystem behaviour. They suggest another hypothesis derived from their own work and from an examination of published data that the output of elements from an ecosystem will be proportional to the rate at which that element is incorporated into the nett biomass increment for the ecosystem. In this model nutrient incorporation into biomass will be rapid in early succession, will reach a maximum and then will slowly decline to

zero as a steady state is approached and the nutrient loss rate from the ecosystem will be the complement of the rate of incorporation of an element into the biomass. From watershed studies they show that  $K^+$ ,  $Mg^{++}$ ,  $Ca^{++}$  and  $NO_3^-$  concentrations are higher in streams draining mature ecosystems than in streams from successional ecosystems.  $Na^+$  which is not accumulated above trace levels in plant biomass in this ecosystem had virtually identical levels in the streams draining mature and successional ecosystems. Their studies indicate "that intermediate aged successional ecosystems will have lower nutrient losses than either very young or very old ecosystems".

Bormann and Likens (1979) present a more detailed model of nutrient export from the Hubbard Brook ecosystem. Whilst they are in agreement with Vitousek and Reiners's hypothesis that total biomass storage is an important factor in the regulation of nutrient export from an ecosystem they also recognise that other factors are involved. At Hubbard Brook a net loss of nutrients from the ecosystem was recorded during the initial stage of ecosystem development following clearcutting of the forest. The following stage of ecosystem recovery was one in which the ecosystem accumulated nutrients and the export of dissolved nutrients in stream waters was at a minimum. Nutrient losses then increased at the end of this development stage. Nutrient losses beyond this stage are unknown although computer simulation models of the Hubbard Brook ecosystem led Bormann and Likens to suggest that nutrient losses will be greater in the final stages of succession than those that occurred in the previous intermediate stage.

It is clear that considerable work in a range of forest ecosystems is required before we have a good understanding of the successional relationships of nutrient budgets. In a recent review of the regulation of chemical budgets over the course of terrestrial succession it was concluded that the input and output levels of nutrients to an ecosystem could not be predicted from contemporary ecosystem generalizations about nutrient conservation (Odum 1969) but were dependent upon the nutrient under ~~the~~ consideration, the nature of the parent material and the interrelations among the many ecosystem processes that undergo change during the course of succession (Gorham, Vitousek and Reiners 1979).

There is no universal theory of ecosystem development and succession at present. Whittaker and Levin (1977) suggest in a paper, that deals with succession in relation to patch phenomena and microstructure, that their reasoning on the evolution of communities leads them to believe that no "master plan" will be found.

There remain however, a number of observations that are used to recognize succession and Drury and Nisbet (1973) hold that these observations do need an explanation. The emphasis in papers that have offered alternative explanations to the contemporary model of succession has been toward the understanding of life histories of the species involved in succession and the species distributional patterns along environmental gradients. The essential elements of the alternative approach to successional theory are:

- succession provides a complex gradient of physical and biotic environments to which species populations are adjusted by selection pressures (Pickett 1976, Whittaker and Levin 1977, Drury and Nisbet 1973, Bormann and Likens 1979).
- most of the phenomena associated with succession can be understood in terms of differential growth, differential colonising ability and differential survival on environmental gradients of the species involved (Drury and Nisbet 1973, Horn 1974, Colinviaux 1973, Connell and Slatyer 1977, McCormick 1968, Bormann and Likens 1979).
- the driving forces of succession are due to a number of factors including
  - (a) competition for resources between species
  - (b) intermeshing of life cycles
  - (c) allelopathic responses
  - (d) disturbance factors
 (Pickett 1976, Bormann and Likens 1979).

The basic philosophies behind the contemporary theory of succession and the alternative modern approach are quite different. The deterministic view of ecosystem development put forward by Odum and Margalef is not accepted by modern critics who seek an understanding of succession solely in terms of individual species differential growth and survival in an environment that is changing in space and time.

Modern successional adherents have emphasised the importance of life history strategies in understanding the pattern and course of any succession. The following life history strategy characteristics have been associated with species that occupy the two extremes of the successional continuum from pioneer to steady-state (climax) communities (Horn 1974, Bazzaz 1979, Wells 1976, Grime 1979, Ewel 1980).



## Pioneer Characteristics

### Reproduction factors:

Regular, copious production of vagile offspring (Wells 1976).  
 Seldom reproduce locally (Wells 1976).  
 Seeds relatively small and light (Budowski 1965, Wells 1976).  
 Dioecious sex structure common for trees (Wells 1976, Falinski 1980).  
 Self fertilising in herbs (Lloyd 1980).  
 Wind borne seeds (Wells 1976).  
 Early reproductive maturity (Wells 1976, Bazzaz and Pickett 1980).

### Germination factors:

Epigeal germination (Bazzaz 1979, Bazzaz and Pickett 1980, Ng 1978).  
 Some species seeds can survive for years in the soil (Bazzaz 1979, Bazzaz and Pickett 1980).  
 Seeds sensitive to light; germination strongly inhibited by vegetation filtered (high far red: red) light (Bazzaz 1979, Bazzaz and Pickett 1980).  
 Seed germination may be linked to disturbance, (light openings, fluctuating soil temperatures, flush of nitrates) (Bazzaz 1979, Bazzaz and Pickett 1980).

### Growth and maintenance factors:

Seedlings intolerant of shade; low photosynthetic efficiency at low light intensities, low energy reserves in seed correlative with light seed (Wells 1976).  
 Rapid excurrent growth (strong apical dominance) (Wells 1976, Ashton 1978).  
 Low wood density, reduced lignification, large vessels in xylem, weak wood, subject to infestation by insects and fungi (Wells 1976, Bazzaz and Pickett 1980, Ewel 1980).  
 Rapid diameter growth rates (Bazzaz and Pickett 1980).  
 Longevity less than 100 years (Wells 1976).  
 Microphyllous leaves (Wells 1976)  
 Marked phenotypic plasticity (Baker 1975).  
 Short leaf longevity (Mattson 1980).  
 High concentration of nutrients in actively growing tissues (Golley and Medina 1975).  
 Leaves scattered lossely through the volume of plant (multi-layered to maximise light interception (Horn 1971).  
 Low order of branching and reiteration (Wells 1976, Oldeman 1978).

## Steady-state (Climax) Characteristics

### Reproduction factors:

- Lavish provisioning of few offspring (large energy and nutrient reserves in cotyledons or endosperm of seeds) (Wells 1976).
- Large, heavy seeds (Wells 1976).
- Short range dispersal capacity (Wells 1976).
- Monoecious or hermaphrodite flowers on trees (Wells 1976).
- Cross fertilization for herbs (Lloyd 1980).
- Delayed reproductive maturity (age at first fruiting often > 30 years) (Wells 1976, Bazzaz and Pickett 1980).
- Mast years of seeds common (Wells 1976).
- Bird, mammal or gravity distributed seeds (Wells 1976).

### Germination factors:

- Hypogeal germination of forest trees with large seeds, epigeal germination of small seeds (Bazzaz 1979, Bazzaz and Pickett 1980).
- Seeds lose viability quickly (Bazzaz 1979, Bazzaz and Pickett 1980).
- Some species seeds do not require light for germination or only require less light than early successional species (Bazzaz and Pickett 1980).

### Growth and maintenance factors:

- Seedlings tolerant of shade (Wells 1976).
- Suppressed seedlings can exist near ground level for years awaiting release by a break in dense canopy (Wells 1976).
- Slow growth rates (Bazzaz and Pickett 1980, Mattson 1980).
- Hard, heavy, mechanically strong wood; thick walled xylem cells, heavily lignified, often impregnated with antibiotic substances, resistant to decay (Wells 1976, Bazzaz and Pickett 1980).
- Long lived, often > 250 years (Wells 1976).
- Long leaf longevity (Mattson 1980).
- Broad leaved (Wells 1976).
- Weak apical dominance, resulting in broad spreading crowns with numerous branching orders (Wells 1976).
- Leaves arranged in a single continuous layer around the perimeter of the tree (mono-layer) (Horn 1971).

Species possess any number of combinations of the pioneer and climax attributes and most species would be expected to have a combination intermediate between the two extremes (Miles 1980). Wells (1976) has provided evidence that in reality most tree species of a major forest association possess ecomorphological characters that adapt them to occupy an intermediate or mid-seral position in the forest succession. Wells considered that, of the 75 principal species of broadleaf trees that are characteristic of the eastern deciduous forest of the United States of America, 61 fell into the intermediate range of his successional scale, 9 in the pioneer interval and 5 into the climax interval. Wells presented a multivariate successional model for the 75 tree species that was derived from information about each of 26 life history characters (light absorption factors, reproduction factors and maintenance and longevity factors). His model is consistent with the successional sequence observed in the eastern deciduous forest.

Some authors have interpreted the pioneer and climax roles of plants in terms of r- and K-selection strategies\* (Wells 1976, Harper 1977, Opler, Baker and Frankie 1980). Pioneer plants are considered to exhibit an r-selection strategy where population growth is not limited by resources and the plants produce large annual crops of easily dispersed light seeds. Climax plants are considered to exhibit a K-selection strategy where the population is in equilibrium with the resources of the site and the plants produce few seeds with large energy and nutrient reserves which help to buffer the seedling during establishment under a close canopy.

Grime (1977, 1979) has expanded the r-K selection strategy hypothesis into a model of succession that not only acknowledges the importance of established and regenerative strategies and life forms of a population but also recognizes that a major factor that determines the role of strategies in succession is the potential productivity of the habitat. Grime differentiates between competition, disturbance and stress tolerance as factors that determine the course of succession.

Grime classifies the life strategies of higher plants on the basis of the intensity of disturbance they can tolerate and the intensity of stress they can endure. He recognizes three strategy types:

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\* See Appendix III for definition.

the competitive strategy - associated with low stress and low disturbance environments,  
 the stress tolerant strategy - associated with high stress and low disturbance environments, and  
 the ruderal strategy - associated with low stress and high disturbance environments.

No viable strategy exists for high stress, high disturbance environments. Ruderals are equated with r-selected strategies and stress tolerant plants with K-selected strategies. Competitors occupy intermediate positions.

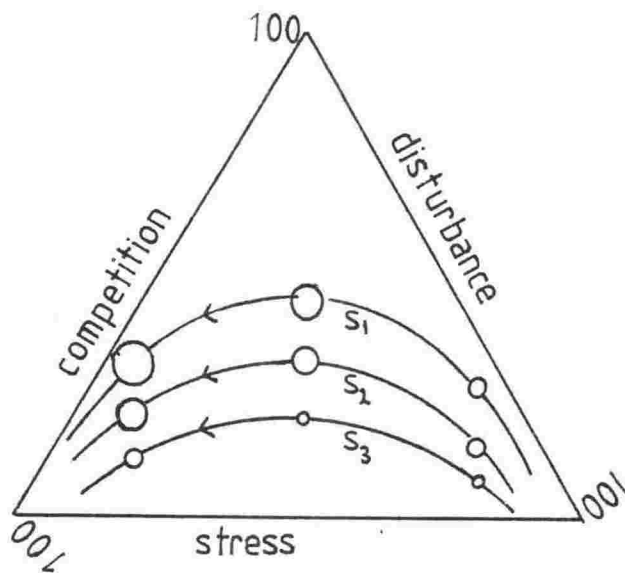
Whereas Horn views secondary succession in terms of competitive interaction, "Secondary succession is usually a result of interspecific competition, with pioneer species often beating later species to openings and perhaps outcompeting them in openings as well but themselves producing an environment in which later species are competitively superior" (Horn 1974). Grime believes that climax and late successional species are not so much involved in competition with other species but are the species that are adapted to a stressed environment; they are stress tolerant species.

The model of vegetation succession is presented with the three life strategies occupying the axes of an equilateral triangle. The paths of succession are depicted as vectors across the triangle. The size of plant biomass at each stage of succession is dependent upon the site productivity (Figure 1:1). The pathway of succession is from vegetation dominated by plants with a ruderal strategy through to stages dominated by competitors and ending with plants possessing stress tolerant life strategies.

To date there does not appear to have been any critical experimental tests of Grime's model of succession although MacMahon (1980) has presented data from a subalpine succession (developing toward an Engelmann spruce forest) in Northern Utah that suggests that the species represented in early successional stages show a range of adaptive strategies and as succession proceeds there is a contraction of the strategies present.

Figure 1:1. Paths of Vegetation Succession Under High ( $S_1$ ) to Low ( $S_3$ ) Potential Productivity.

- (Grime 1977)



(Size of plant biomass at each stage of succession is indicated by the size of the circles).

A number of alternative models and approaches have been proposed by other workers who, like Grime, have recognized that the classical and contemporary theories of succession are inadequate in furnishing models that offer explanations for the vegetation successions they have studied. There has been no attempt to apply any of these models as a universal explanation for vegetation development and in fact most workers would acknowledge that they could all apply in varying degrees to any one successional sequence (Connell and Slatyer 1977, Peet and Christensen 1980).

Egler presented a model of succession that emphasised the importance of the initial floristic composition of a site in the development of the successional pattern (Egler 1954). He contrasted this phenomenon of initial floristic composition (I.F.C.) with the concept of classical succession theory that groups of species successively appear on a site, prepare the way for another group of species and then disappear from the site when conditions become unsuitable for their continued survival, that is groups of species invade the site at certain stages of vegetation and site development. Egler called this pattern of vegetation development relay floristics.

Egler presented evidence from old field successions that, up until the time of abandonment, a site receives many species as seeds and vegetative propagules. After abandonment vegetation development unfolds from the initial flora without additional species entering by further invasion. Annual weeds quickly dominate the vegetation with other species occurring only as seeds or seedlings. The annuals die out and perennial herbs and grasses come to dominate for a time, then shrubs and trees manage to grow through the perennials and come to dominate. Eventually the shrubs are overtopped by the trees which are the ultimate dominants on the site. As each group drops out a new group of species, there form the start of the succession, predominates.

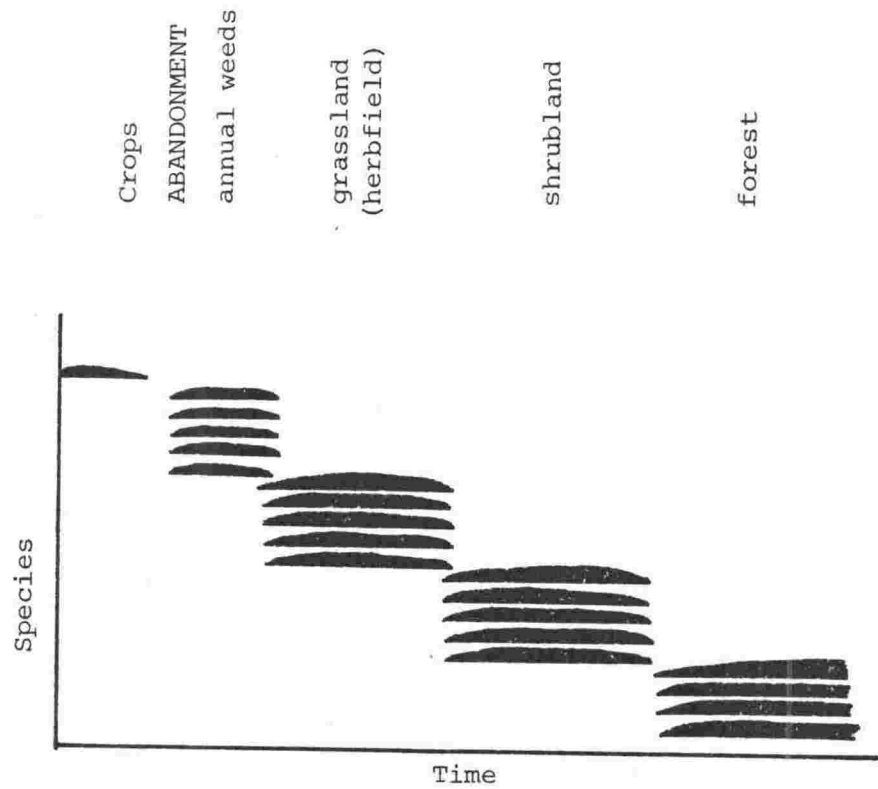
The two contrasting models are presented in Figure 1:2.

The model is presented in its extreme form with each species reaching peak abundance and then disappearing abruptly. In reality few species, once they enter an oldfield become extinct from it for many years (McCormick 1968). Egler recognized that on any particular oldfield both relay floristics and initial floristic composition pathways could operate together (Egler 1954).

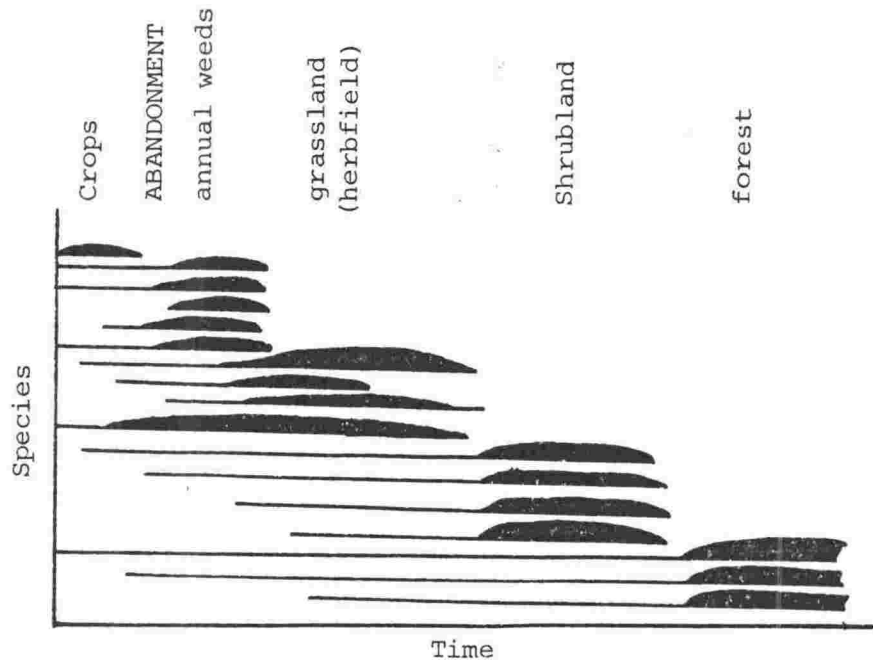
Figure 1:2. Models of Succession.

- (Egler 1954)

1:2a. RELAY  
FLORISTICS  
MODEL



1:2b. INITIAL  
FLORISTICS  
MODEL



A broader approach to succession has been proposed which incorporates the possibility of relay floristics and initial floristic composition pathways operating either independently or in combination (Connell and Slatyer 1977). Connell and Slatyer also propose a third pathway in which succession is truncated short of the expected climax vegetation. This phenomenon of truncated succession has often been observed but had not been sufficiently incorporated into successional theory before Connell and Slatyer presented their models of succession.

The three models proposed by Connell and Slatyer are presented as Figure 1:3.

Model 1: the facilitation model is essentially the classical succession or relay floristics model whereby only certain species are able to colonize a site and they modify the environment so that it becomes suitable for the entry of later successional species which grow to maturity whilst the colonizing species die out.

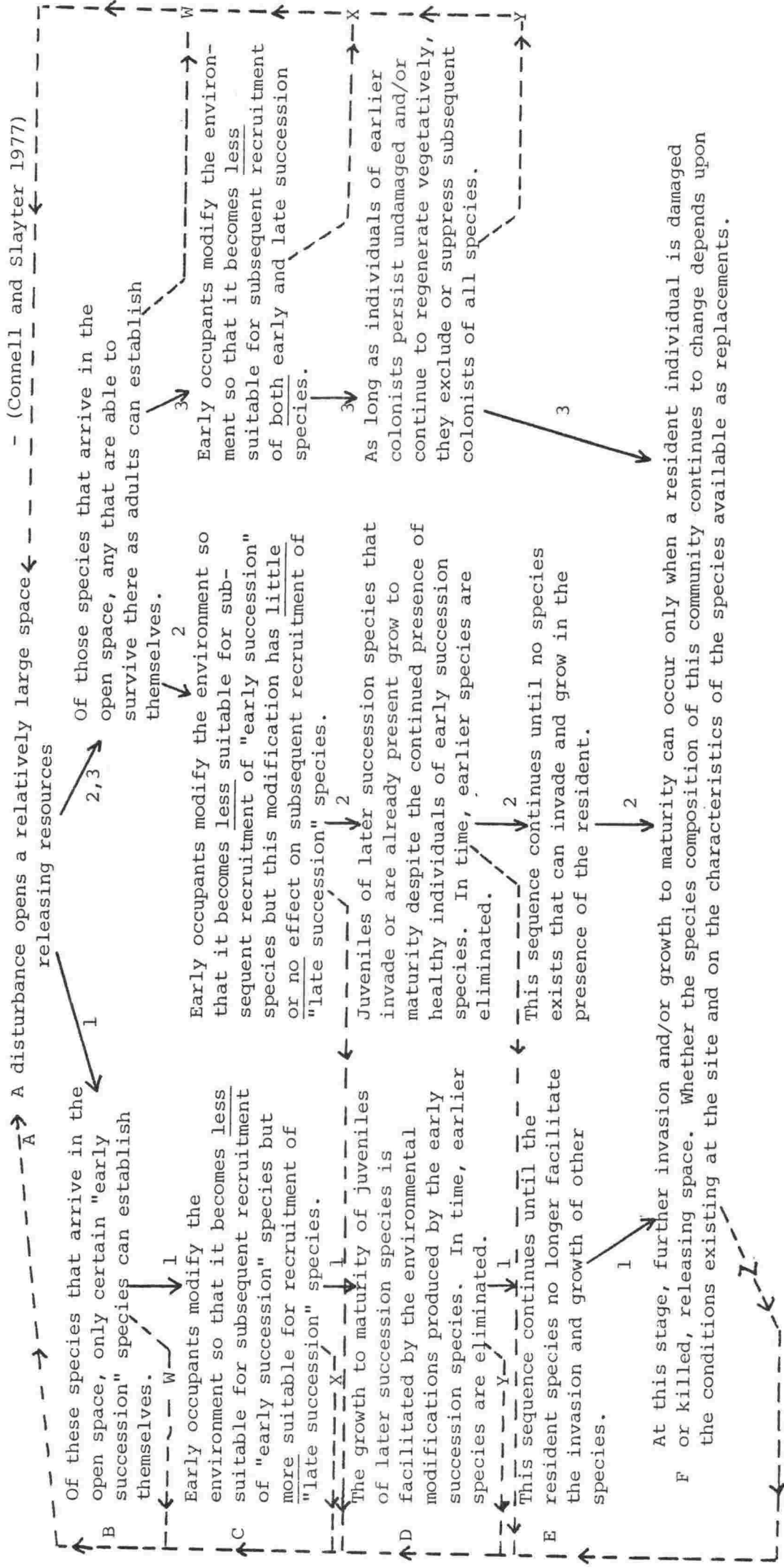
Model 2: the tolerance model allows for any species with colonizing abilities to initially dominate the site. The colonizing species modify the environment in such a manner that the regeneration of the colonizers is prevented but the appearance and dominance of later successional species are neither enhanced or decreased by the modifying effects of the colonizers.

Model 3: the inhibition model is essentially one of "site pre-emption" by species which have long lived individuals or other life strategy characteristics that lead to persistence at the site. Once early colonists have established on the site they inhibit the invasion of subsequent species and prevent the growth of other species already present on the site. Other species can only invade or grow when the dominant inhibiting species are damaged or destroyed.

Connell and Slatyer consider that the facilitation model operates in certain situations especially in the early stages of succession where site modification may be necessary before other species can successfully establish. They do not believe that there is much evidence to support the tolerance model and feel that most successions involve the inhibition model to some extent whereby the established plants exclude or inhibit later species from establishing until a disturbance occurs and resources are made available to late successional plants (Connell and Slatyer 1977).



Figure 1:3. Three Models of the Mechanisms of Succession



- 1 - facilitation model
- 2 - tolerance model
- 3 - inhibition model

The models of Connell and Slatyer are based on the premise that the occurrence of a species in a succession is dependent upon the probability of a propagule being available at the site and the probability of the propagule being able to become established at the site and reach reproductive maturity (in Slatyer ed. 1977).

A scheme for deriving successional models which incorporates the above premise of Connell and Slatyer has been recently developed by Noble and Slatyer (1978, 1980). Noble and Slatyer identify a small number of life history characteristics which they term "vital attributes" and which they believe are the key to understanding the role of a species in a successional sequence. Three main groups of vital attributes are recognized, those that pertain to:

- the method of arrival and persistence of a species at the site during and after disturbance,
- the ability of a species to establish and grow to maturity in the developing vegetation,
- the time taken for a species to reach critical life stages.

In applying the scheme to any succession the major species involved are categorized into a "species type" determined by the characteristics each species possesses in the first two vital attribute groups. The vegetation replacement sequence following disturbances is then derived by considering the possibilities of interactions between various species based on their species type and life stage attributes.

The scheme has been applied to successions in the Tasmanian wet sclerophyll rainforests and to a mixed coniferous forest community in north-western U.S.A. Models were derived which were consistent with observed patterns of vegetation replacement in these ecosystems. The models also provided more detailed replacement sequences than those offered by classical succession theory (Noble and Slatyer 1980).

A number of mathematical techniques have been employed by recent workers to derive models of succession for particular vegetation types. The best known of these are the use of Markov chains which have been popularised by Horn (1975b, 1976). With this technique a matrix is derived that is based on the tree-by-tree replacement probabilities or state transition probabilities of a stand of vegetation. Future states of the vegetation are calculated from the matrix.

Successional models based on Markov chains have been criticized by some workers who point out that ecological systems do not exhibit Markovian properties; that is, transition rates from one state to another (or tree-by-tree replacement probabilities) are not constant over a time period and the future state of an ecosystem is not independent of the immediate past history of the system (Horn 1976, Slatyer 1977, van Hulst 1980).

Ordination techniques have been employed which are based on the analysis of data from a site over different time periods (van der Maarel 1969, 1980, Austin 1977, Persson 1980). The use of these and other mathematical techniques are similar in the respect that the workers rely upon either a detailed documentation of stand composition over extended periods of time or a knowledge of the life histories (birth, growth and death rates) of the major successional species in the stand (Slatyer 1977, Peet and Christensen 1980) and hence recognize that it is the individual properties of species that are vital to an understanding of the vegetation dynamics of a site.

#### 1:2:2 Nutrient Cycles and Secondary Succession

The functional aspects of ecosystem recovery have received attention over the last decade. The information that has been derived from studies of the functional recovery of ecosystems during secondary succession has proved to be of value to land managers when faced with the task of assessing the effect of some management technique upon the long term health of an ecosystem. A number of studies have investigated the effect of management practices (for example; prescribed burning, conversion of forest to agricultural land, different methods of timber harvesting, fertilization etc.) upon nutrient cycles in forests. Although some general trends about the response of nutrient cycles to disturbance have become evident from recent studies it seems apparent that each forest ecosystem responds in an individual manner to disruption of its nutrient cycles.

When the structure and function of a forest ecosystem is disturbed or destroyed there is a consequent disruption of the nutrient cycles of the forest. Severe disturbance to the forest can lead to loss of nutrients from the ecosystem by the physical removal of forest floor surface horizons and erosion of top soil or by the volatilization of elements. Less severe disturbance to a forest ecosystem can also lead to nutrient loss from the system by the leaching of inorganic ions or to a redistribution of nutrients in the soil profile (Miller, Stout and Lee 1955, Miller 1962, Nye and

Greenland 1960, Jackson 1968, Likens *et al.* 1977, Grier 1975, Park 1975, Stark 1977, Bormann and Likens 1979).

There have been a few studies that attempt to look at the role of successional species in the restoration and recovery of nutrient cycles in forest ecosystems. The basic hypothesis that has developed is that regrowth of successional species retards nutrient loss after destruction of the vegetation cover (Marks and Bormann 1972, MacLean and Wein 1977, Vitousek *et al.* 1979, Aweto 1971a, b).

The forced devegetation experiment at Hubbard Brook showed quite clearly that nutrient losses from a catchment that was allowed to naturally revegetate after clear felling were much less than from a catchment that was experimentally prevented from revegetating (Likens *et al.* 1977). The nutrient losses decreased from the experimentally manipulated catchment when it was permitted to revegetate (Likens *et al.* 1978).

Clear cut ecosystems that were allowed to revegetate immediately after forest clearance showed some leakage of nutrients from the ecosystem for the first few years of forest recovery (Bormann and Likens 1979). The rapid germination and growth of successional species did not result in total nutrient capture but the strategy was effective since it acted to prevent even greater nutrient losses by erosion and in solution.

Marks and Bormann (1972) suggest that the rapid revegetation of disturbed ground by successional species acts to minimise nutrient losses from the ecosystem. This regulation of nutrient cycling is achieved by a complex interaction involving; (1) the reduction of erosion and nutrient loss by the channeling of water from runoff to evapotranspiration; (2) the reduction in the supply of soluble ions in drainage waters due to decreasing rates of organic matter decomposition that occurs with the amelioration of the microclimate when vegetation growth commences; and (3) the incorporation of nutrients, that do become available, into the rapidly growing biomass, thus preventing their loss from the ecosystem.

Marks (1974) further suggested that the amount of nutrients retained in the ecosystem is determined by the speed at which regeneration occurs. The rapidity of regeneration is a function of the rate of colonisation of the disturbed ground and rate of vegetation growth. His study of the pioneering tree species *Prunus pennsylvanica* led him to conclude that certain life cycle characteristics of this species (wide seed dispersal, rapid germination

after the creation of light gaps in the forest, rapid growth and early sexual maturity) made it important in the conservation of nutrients after forest removal in the northern hardwood forests of North America. Most tree and shrub species involved in the initial stages of secondary succession share these life cycle characteristics (see section 1:2:1, page 13) and thus could also be important in the conservation of nutrients from disturbed forest ecosystems.

Harcombe (1977a, b), in an interesting experiment, decided to test the hypothesis that the rate of ecosystem recovery was dependent upon the ability of the pioneering vegetation to retain nutrients after forest removal. His experiment involved the clear felling of tropical forest plots and the fertilization of some of these plots after clear felling. Comparison of nutrient losses from plots kept bare for 12 months with plots that were naturally revegetated showed significant losses in the bare plot soil of N, Ca and Mg. Thus the presence of vegetation resulted in the retardation of loss of nutrients. The second part of the experiment involving the fertilization of some of the revegetating plots showed, however, that ecosystem recovery (measured by rate of biomass increase, rate of increase in vegetation nutrient content and rate of attainment of specific successional stages) was not related to nutrient retention. In fact, at least for the first year after disturbance, the successional tree species appearing on the plots were not particularly successful at enhancing recovery by immobilization of nutrients. Recovery was not necessarily accelerated where soil fertility was high. On some plots fertilization actually retarded succession by favouring the development of a complete cover of forbs which suppressed the trees and shrubs. At least for this particular tropical site, where soil nutrients were not in short supply, succession was not delayed by rapid nutrient loss following forest disturbance.

Another study of secondary succession in a tropical forest ecosystem that failed to establish any relationship between types and rates of vegetation recovery and soil nutrients was that undertaken by Kellman (1970) in a tropical montane forest ecosystem at Mindanao, Phillipines.

Harcombe rejects the hypothesis that the rate of forest recovery is dependent upon the nutrient status of the disturbed site. He favours an explanation of rate of ecosystem recovery in terms of species competition:

'The characteristics of a successional species are molded by competition for a time slot in the sequence and hence the rate of succession or ecosystem recovery and the role of a particular species in recovery is dictated by that. Appropriate strategies for early colonizers may or may not include adaptation for rapid responses to high levels of soil fertility'.

P.A. Harcombe 1977b

In a recent reply to Harcombe's challenge (Harcombe 1980) to the idea that secondary succession is unaffected by nutrient losses following tropical forest removal Jordan and Herrera (1981) argue that there is no reason to suppose that all tropical forests cycle nutrients in a similar manner. They postulate different types of cycling strategies on nutrient poor soils and on nutrient rich soils. There are a number of mechanisms that exist in nutrient poor tropical forest ecosystems that permit the ecosystem to conserve nutrients. The forest floor (in this context; the root mat and humus) plays an especially important role in nutrient cycles in some tropical forests. Most of the small feeder roots of the forest trees are distributed in the organic layer above the mineral soil and in labelling experiments it has been shown that there is direct physical adsorption of nutrients by the roots into the plants (Herrera *et al.* 1978) and there is very little leakage of nutrients through the root mat into the mineral soil. The nutrient conserving mechanisms associated with the forest floor of nutrient poor tropical ecosystems are destroyed or severely disrupted when the forest is cleared for agricultural purposes and there is quite a body of evidence that the growth of crops is uneconomic on such land (Nye and Greenland 1960).

Gorham, Vitousek and Reiners (1979) have produced a review of a number of processes affecting the chemical budgets of an ecosystem during the course of secondary succession. Their review shows that the interaction of these processes is complex and little understood for most ecosystems. They conclude that an analysis of component parts of the processes in ecosystem studies will assist in the better understanding of chemical cycles during succession.

The workers at Hubbard Brook have shown that detritus-based processes are vital in controlling the extent of nutrient loss from a disturbed ecosystem. The process of litter accumulation on the forest floor was identified as a key element in controlling the long term productivity of the soil at Hubbard Brook (Bormann and Likens 1979).



During secondary succession there are changes in the quantity and quality of the forest floor that are associated with the different stages of vegetation development. The forest floor represents a key component of the ecosystem from which one can study the effects of disturbances to the nutrient reservoir and nutrient cycles of the forest ecosystem (Charley and Richards 1974).

The forest floor (defined in this present study as being all organic matter lying above the mineral soil and less than 0.2 cm diameter) is an important reservoir of ecosystem nutrients (Gosz *et al.* 1974, Kittredge 1948, Bormann and Likens 1979). The forest floor is also a vital component of the ecosystem from other functional points of view as the following examples illustrate; the forest floor has a role in the control of nutrient cycling due to the mineralization of its organic matter; the forest floor is important in the chemical buffering of drainage waters; the forest floor is important in the control of the hydrologic properties of the ecosystem by virtue of its moisture holding capacity; the forest floor is important in the control of soil erosion; the forest floor is the major site for decomposition processes which release nutrients immobilized in litterfall for re-use by the vegetation (Lutz and Chandler 1946, Remezov and Pogrebnyak 1969, Bourne and Brown 1971, Covington 1976, Mader *et al.* 1977, Raison 1980a).

There are a few studies in which an attempt has been made to document the recovery of the forest floor (biomass and nutrient content) during secondary succession. The most comprehensive studies, to date, traced the development of the forest floor on a number of sites of known age that were assumed to bear a successional relationship to each other.

In a study of forest floor recovery in the northern hardwood forests of the U.S.A. it was found that whilst leaf litter inputs to the forest floor in successional stands approached steady-state forest levels some three to four years after clear felling the organic matter and nutrient contents of the forest floor declined for 15 years after disturbance. The organic matter and nutrient content of the forest floor reached a minimum which was less than 50% of the pre-cutting levels 15 years after clear felling. The forest floor began to build up after 15 years and approached levels of biomass similar to that of the pre-cut forest after 65 years (Covington 1976).

A different model of accumulation of litter was reported by Lang who studied old field succession on the New Jersey piedmont (Lang 1978). Two patterns of litter accumulation were observed. In some old fields there was a rapid build up of litter from a field dominated by annuals to a field dominated by perennials and this level was similar to that attained by different aged shrublands and forests. The other pattern of litter accumulation was observed on some old fields dominated by perennials and showed a temporary stabilization in the early years of a litter accumulation level some 57% below that of the steady-state forest. A rise to the steady-state condition occurred after 30 years. The slower two-step rise was related to site conditions of low soil moisture and low net primary productivity.

A study of forest floor accumulation on the East Gulf Coastal plain in Mississippi showed that forest floor weights reached a maximum in 65 years. Most of the accumulation occurred in the first twenty years after forest disturbance. The weight of the forest floor decreased by 25% late in the succession. Much of the accumulation of N, P and K in the forest floor occurred in the first twenty years. The accumulation of Ca and to a lesser extent Mg in the forest floor more closely paralleled the development of dominance of hardwoods into the succession from old fields to pine forest to the final oak-hickory-pine forest climax (Hinsley 1978).

A comprehensive study of the recovery of forest floor characteristics during secondary succession in subalpine eucalypt ecosystems was undertaken by Park (1975). Park suggested that maximum weights of the forest floor are attained 55 years after the start of succession in an *Eucalyptus pauciflora* dominated stand and after 35 years in an adjacent *E. delegatensis* dominated stand in the Brindabella Range, New South Wales. The recovery of the content of major nutrients in the forest floors under the two stands followed a similar pattern in the respect that maximum weights of all major nutrients took a longer period to accumulate in the forest floor under *E. pauciflora* than under *E. delegatensis*.

Park also carried out a study of aspects of nutrient cycling between the forest floor and surface soil of 46 secondary subalpine eucalypt in which he attempted to determine successional trends in nutrient dynamics in subalpine eucalypt ecosystems (Park 1975). Unfortunately this study is open to criticism as it is possible the forest floors declined in biomass and nutrient content for some time after disturbance as has been found by other workers in a number of different secondary ecosystems (Odum 1960, Dominski



1971 (in Bormann and Likens 1979), Covington 1976, Aweto 1981b). In the absence of data showing that all of the forest floor was destroyed at the start of each succession the fitting of a positive quadratic function to Park's ecosystem data in order to calculate time from disturbance must be viewed with caution.

### 1:3:1 Secondary Succession in New Zealand Lowland Forests

A number of successional studies on lowland forest ecosystems have been undertaken in New Zealand. Most have been of a descriptive nature and very little quantitative information on vegetation structure and composition has been presented. The studies that are highly relevant to this present work are concerned with secondary succession in the Wellington region (Reid 1934, Croker 1953, Druce 1957, Esler 1967, Egunjobi 1967, 1969, 1971, Bagnall 1974, 1976 and Park 1971).

The relevance of these studies to the Marlborough Sounds is a reflection of the similarity between the two regions due to a number of factors. The original forest vegetation cover of the two areas was very similar (Cockayne 1958); the species involved in the seral pathways in the two areas are often the same; the soils are very similar in some respects and the history of the land use of the Marlborough Sounds (with regard to timber milling, firing of the vegetation and attempts at agriculture) has been similar to the pattern of land use in some areas of the Wellington region.

The study of the vegetation of an experimental catchment at Taita (Druce 1957) is the most comprehensive account of regeneration in the lowland forest ecosystem of New Zealand. Druce related the successional patterns that resulted after burning of the vegetation cover primarily to the original vegetation pattern of the catchment. Within the broad successional patterns of development to the climax forest he recognized a great deal of diversity in the regenerating communities that were present. This, Druce reasoned, was due in part to the differing responses of the predisturbance vegetation on the site and the number of burns which an area had received.

Druce's efforts to determine the history of each successional community indicated that the rate of succession to the climax forest, and what would be recognized as substantially reverted indigenous cover, was dependent upon the life spans of the pioneering species. He was thus able to assign times of persistence to the early stages of different successional pathways.

Croker (1953) related the successions occurring on the Western Hutt Hills to the original disturbance factors to the podocarp/broadleaf forest that clothed these hills at the time of European settlement. The early history of the study area was fairly well known and she estimated the ages

of the existing vegetation on the damp, south facing slopes from ring counts on increment bores obtained from a number of broadleaf species.

Successions on Kapiti Island have been studied by Esler (1967) and Bagnall (1974). The lowland successional patterns are similar to some of the coastal forest and shrubland successions observed in the Marlborough Sounds. Esler's study was a descriptive mapping account of vegetation change on Kapiti since 1902 and 1929 when the vegetation communities were previously mapped. Esler highlighted problems involved in determining the time lapse from the pioneering stage due to the telescoping of some successional pathways and the protraction of others. The accurate ageing of important successional species, other than manuka and kanuka\*, by ring counting techniques was also a problem. However he was able to assign times for the duration of early stages of succession.

In Table 1:1 successional pathways postulated in the three Wellington studies are presented. Only species combinations that are common to Wellington and the Marlborough Sounds are considered.

The time of persistence for the successional stages is usually dependent upon the life span and often on the height growth characteristics of the pioneering species. Information on the average life span of a number of pioneering species is available from the successional studies conducted around the Wellington region.

Esler (1967) considers that tauhinu has a short life span and estimates it at 10 years. Bagnall's (1974) recording of a rotten tauhinu aged at 10 years in a young kanuka shrubland (Quadrat 2c) on Kapiti Island is consistent with Esler's estimate. Bagnall (1981) postulates that it takes 15 years for tauhinu/pasture shrubland to revert to a mahoe forestland.

The life span of manuka in the Wellington region has been variously estimated as ranging from 30 to 80+ years. Esler (1967) states that manuka generally shows senility at 30-40 years. Kelly (1965) working in the Lowry Bay catchment credits manuka with a longer life span and has recorded one large manuka at 89 years but generally considers that manuka has become senile by 50-60 years when it is prone to base rot. Druce, similarly reports that manuka remains dominant on the hills at the Taita catchment for 60-70 years (Druce 1957).

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\* A list of common names and scientific names of plants is presented in Appendix I

Table 1:2. Successional Pathways in the Wellington Region

- A. Eastern Hutt Hills, Taita Catchment (after Druce 1957 and pers. comm. 1980).

Original Vegetation: Hard beech forest

1. Areas burnt prior to 1920.
  - 1 fire in beech seed year
  - a. Manuka <sup>10</sup>→manuka-hard beech <sup>30</sup>→hardbeech.\*  
1 fire in nonseed year
  - b. Manuka-(bracken) <sup>10</sup>→manuka <sup>20</sup>→manuka-(rewarewa) <sup>20</sup>→manuka-(rewarewa)-(fivefinger) <sup>10</sup>→manuka-kamahi-(rewarewa) <sup>10</sup>→kamahi-(rewarewa).  
More than 1 fire
  - c. Manuka-(bracken)-resprouted kamahi <sup>10</sup>→manuka-kamahi <sup>40</sup>→kamahi.
  - d. Bracken <sup>30</sup>→fivefinger <sup>20</sup>→kamahi.
2. Between 1920 and 1938 exotic species entered the early stages of succession.
  - a. Manuka-(bracken)-gorse-(spanish heath) <sup>10</sup>→manuka-gorse-spanish heath <sup>20</sup>→manuka-spanish heath <sup>20</sup>→manuka-fivefinger <sup>10</sup>→manuka-kamahi <sup>10</sup>→kamahi.
  - b. Manuka-bracken-gorse-spanish heath-resprouted kamahi <sup>10</sup>→manuka-gorse-kamahi-spanish heath <sup>20</sup>→kamahi-manuka-spanish heath <sup>20</sup>→kamahi.
  - c. Manuka-(bracken)-gorse-spanish heath-radiata pine <sup>10</sup>→radiata pine <sup>70</sup>→radiata pine-fivefinger <sup>30</sup>→kamahi.
3. After 1938 gorse dominated the early stage of succession.
  - a. Gorse-bracken <sup>10</sup>→gorse <sup>30</sup>→fivefinger-kamahi <sup>20</sup>→kamahi.
  - b. Gorse-spanish heath <sup>40</sup>→spanish heath-kamahi <sup>20</sup>→kamahi.

Original Vegetation: Broadleaved forest

- a. Kanuka-bracken <sup>10</sup>→kanuka <sup>40</sup>→kanuka-broadleaved spp. <sup>20</sup>→mahoe and other broadleaved spp. <sup>20</sup>→mahoe---→tawa?
- b. Tree tutu-(broadleaved spp.) <sup>50</sup>→mahoe-(broadleaved spp.) <sup>20</sup>→mahoe---→tawa?
- c. Bracken <sup>20</sup>→black treefern <sup>50</sup>→mahoe-(broadleaved spp.) <sup>20</sup>→mahoe---→tawa?

\* Only canopy species are mentioned, species placed in brackets may or may not be important.  
The numbers refer to the length of time (in years) each seral stage persists.  
Solid arrows represent observed successions, dotted arrows refer to postulated vegetation changes.

B. Western Hutt Hills, on damp, south facing slopes (after Croker 1953)

Original Vegetation: Podocarp/broadleaf forest.

1. Forest milled.

Tawa seedlings  $^{40}$  → tawa forest.

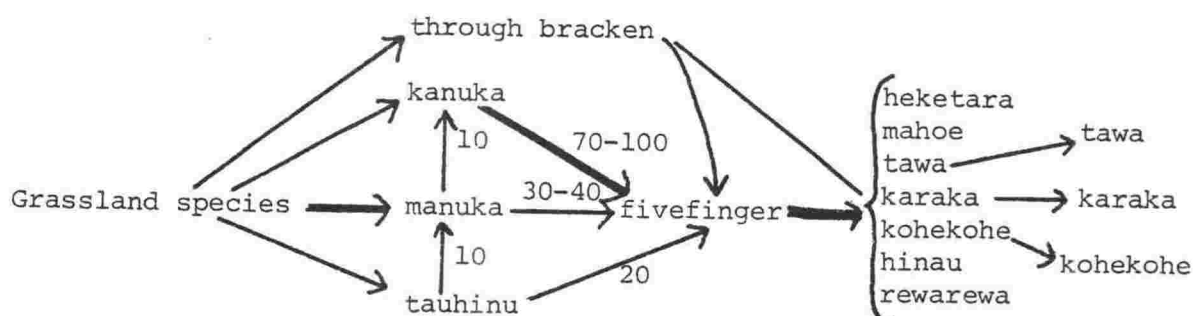
2. Forest milled and fired.

Bracken  $^{8-10}$  → karamu-mahoe  $^{45-50}$  → tawa.

3. Forest milled, fired and sown to pasture.

Pasture species → bracken  $^{4-7}$  → karamu-hangehange  $^{5-20}$  → mahoe  $^{20-50}$  → tawa.

C. Kapiti Island (after Esler 1967)



Kanuka is a longer lived species than manuka and approaches at least 80 years before it begins to become decadent (Esler 1967). Specimens occurring in forest vegetation older than 100 years were noted by Kelly (1965). He notes also that in 97 year old vegetation some trees of kanuka were still vigorous while others had sparse canopies. In 76-89 year old vegetation kanuka was old and some plants were losing their vigour. Druce (1957) recorded that kanuka scrub of 46 years was past its maximum development and was being replaced by broadleaf forest, but at least 70 years are required for the kanuka to be replaced completely by mahoe and other broadleaf species.

Gorse is reported to be prone to base rot after 25 years although older individuals than this do occur (Kelly 1965). Druce (pers. comm. 1980) states that gorse is no longer important in the Taita Catchment, this statement is in close agreement with Kelly's observation as the youngest gorse plants at Taita date from the last fire in the Taita catchment which occurred in 1950.

The life span of Spanish heath has not been recorded in the Wellington region. Druce (1957) postulated that Spanish heath-dominated vegetation would be superseded in some 30 or 40 years at Taita. This estimate appears to have been fairly accurate as Spanish heath is no longer prominent in the canopy of shrublands at Taita (pers. comm. Druce 1980).

Bracken may dominate from 8-30 or more years (Croker 1953, Druce 1957) depending upon the site and availability of seed sources of the higher plants.

Finally, successions dominated by tree tutu are superseded by mahoe and other broadleaved species within 50 years and the tree tutu specimens are moribund at this stage, hence 50 years is their likely life span (Druce 1957). The following table (Table 1:2) is a summary of the life spans of pioneering species in the Wellington region.

Table 1:3. Duration of various scrub types in the absence of fire in the lowland forest areas of the Wellington region.

<u>Pioneering Species</u>	<u>Duration Period (years)</u>
Tauhinu	10-15
Bracken	8-30+
Gorse	25-30
Spanish heath	30-40
Manuka	30-60
Kanuka	50-80+
Tree tutu	50

Beyond the Wellington region there is very little additional information on the longevity of lowland forest pioneering species. Burrows (1973) compared the ecological characteristics of manuka and kanuka and credited manuka with a life span of 30-40-(200) years and kanuka with a life span of 80-150-(250) years. His estimates of the usual life span of these two species is similar to that observed in the Wellington region; his extremes may represent ecological situations where these two are not involved in lowland forest successions.

In the Marlborough Sounds accurate historical records of vegetation change are not available for most sites and recourse must be made to ring counting techniques on woody pioneering species at each site in order to gain information on rates of succession. This method is limited to the early stages of succession unless it is known what woody pioneer initiated the succession and estimates can then be attached to the duration of the first stage of succession.

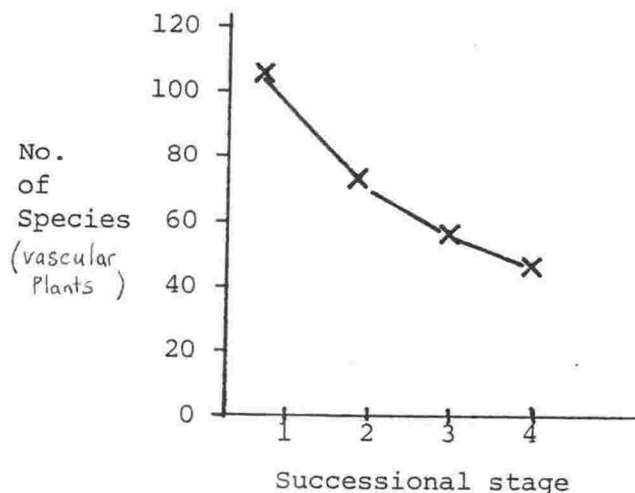
In all of the Wellington studies the assumption was made that the growth rings observed on the stem sections and wood cores are annual. Esler (1974 and pers. comm. 1977) raised the uncertainty as to the annuality of the rings of manuka. Druce (pers. comm. 1979) selected his kanuka specimens from valley and gully situations where the likelihood of summer drought was slight and hence the possibility of intra-annual rings was minimised. This policy has been followed as far as possible in this study. Although Esler's objection is still valid and especially so for ridge sites, the tree ring method of dating has been adopted as the one most likely to provide reasonable estimates for this study. The method adopted by Park (1975) that relies upon the fitting of a relative time scale to the development of the forest floor after disturbance is not considered valid for this study, especially as there is no available data on the dynamics of the forest floor of successional communities in New Zealand and studies at Hubbard Brook (Bormann and Likens 1979, Covington 1976) and at New Jersey (Lang 1978) present different models of forest floor development than the one adopted by Park in his successional study.

The New Zealand lowland forest successional studies have been limited, in the main, to an understanding of the dynamics of the vegetation at a particular site and there has been no attempt to reconcile these studies with the concepts of succession developed from overseas studies. However, a few points that are necessary to a successional theory are apparent from these studies. The authors accept that succession is directional as is

evidenced in the drawing up of successional pathways (Druce 1957, Croker 1953, Bagnall 1974, 1976, Esler 1967). Different successional pathways are accepted as leading to the same final forest type (Druce 1957, Esler 1967 and Bagnall 1976).

Druce 1957 has analysed the number of species that are present in each stage of a hard beech succession. His data on the change of species composition in this succession suggests that the species compositional change occurs by a combination of Relay Floristics and Initial Floristics (Egler 1954). Druce recognizes 4 stages in the succession to a mature self-perpetuating hard beech forest. Seven species present at the pioneer stage are present in the final stage. Eighty-one species at the pioneer stage do not proceed into the next stage. As succession proceeds new species appear at different times and other species do not continue into the next stage. The total number of species declines during the succession; the decline is greatest during the pioneering stage of succession.

Species Change In A Hard Beech Succession, Taita (after Druce 1957)



The controlling mechanisms of successional rates in the New Zealand lowland forest have not been investigated in any depth. Reference has been made to a number of studies that implicate the life span of pioneering species in determining the duration of the initial stage of succession. My studies at Tutira lead me to suggest that the rate of succession is also influenced by the life span of the consolidating species that follow the pioneering species in dominating the canopy but are not important in the later forest phases (Wassilieff 1980 unpubl. manuscript).



An important means whereby a species can come to dominate a seral stage is for it to outgrow other pioneering species (Marks 1974). If kanuka and manuka are both present in a young seral community kanuka may become dominant over the manuka for in favourable conditions kanuka grows faster and taller than manuka (Esler 1967, Burrows 1973).

Another possible means whereby kanuka gains ascendancy over manuka could be due to the manuka blight (*Canthidium walterii*). Manuka is susceptible to the blight and is sometimes weakened and killed by it, kanuka is resistant to the fungus (Burrell 1965).

Physical factors have been implicated in controlling rates of regeneration in lowland forest ecosystems in the Marlborough Sounds. Kelly (1968) and Park and Walls (1976), in discussing the rates of regeneration in the Marlborough Sounds, state that regeneration is more rapid on the southern sides of slopes than on the north facing slopes. No one factor that may be responsible for this differential growth is isolated although the implication is that the southern slopes are damper than the northern slopes. A number of possible explanations can be hypothesised, e.g.

1. rates of regeneration are directly related to soil moisture status
2. regeneration is retarded by the prevailing northwesterly and northeasterly winds
3. the dry northerly slopes carry more intense fires than the southerly slopes and thus damage to the ecosystem is always more severe on the north facing slopes.

The hypotheses are not mutually exclusive and any combination may be important in controlling rates of regeneration.

#### 1:3:2 Nutrient Cycles and Secondary Succession in New Zealand Lowland Forest Ecosystems

The study of functional aspects of forest ecosystem recovery is a field of research that has been essentially ignored in New Zealand. The only work that has been undertaken in this field is that of Egunjobi (1967, 1969, 1971) who studied aspects of primary productivity and nutrient cycling in secondary communities at the Taita Experimental Catchment. Egunjobi's study sites were located in secondary stands that had been previously studied and described by Druce (1957). The Taita studies represent the

most detailed account of secondary succession in lowland forest in New Zealand and as such serve as the main reference point for this present study.

A large part of this present investigation of secondary succession in the lowland forest ecosystem of the Marlborough Sounds has been concerned with an understanding of the relationships between soil and forest floor nutrients and the vegetation composition of seral communities. To this end it was necessary to separate out different components of the possible relationships.

The initial question to be asked was; is there a relationship between different types of successions and the nutrient status of the soils on which they occur? The reason for asking this question was that both Druce (1957) and Kelly (1965) had showed a correlation between successional community types and soil parent materials. Druce did not discuss the natural fertility of the soils that developed on these different soil parent materials but this information was later available (Atkinson 1973) and it was clear that there was an association between different vegetation types and the soils of the Taita Catchment. Successions tending toward kamahi forest are associated with strongly leached, strong-moderately acid soils derived from strongly weathered greywacke or loessial drift (Taita hill soils, Taita clay loams, Wingate hill soils and Bucks clay loams); successions tending toward mahoe-mamaku forests are associated with weakly leached, slightly acid soils derived from greywacke (Tawai steepeland soils) and successions tending toward semi-swamp forest are associated with weakly leached, moderately acid gley soils derived from loessial drift (Witako silt loams).

Kelly considered that soils of different intrinsic fertility and soil moisture holding capacity had developed on the four types of soil parent material present in the Lowry Bay catchment. Manuka, gorse, kamahi and hard beech communities were restricted to the infertile, deep "in situ" clays. Kanuka, black beech and *Coprosma lucida* dominated communities were most common on the more fertile shallow "in situ" clays. The most fertile soils were developed on alluvium and colluvium. Mahoe-mixed broadleaf communities were present on colluvial sites and vigorous stand of bracken were restricted to sites where coarse colluvium was the soil parent material. Unfortunately no measurements of soil nutrient levels were made in the Lowry Bay study (Kelly 1965).

It was felt that it was important in this present study to gain information about the available nutrient levels of the soil under a number of different types of successions. If the different types of succession are related to soil nutrient parameters then losses of critical nutrients could result in the deflection of a site from one successional path to another. This was considered to be a highly probable occurrence since soil erosion and consequent soil parent material renewal are features of the steep topography of the Marlborough Sounds and it appears that there was a period of accelerated and widespread landsliding which followed clearance of the forest cover late last century up until the 1930's (Laffan 1980).

It was necessary to include the forest floor compartment in the investigation of possible relationships between seral communities and site fertility. After disturbance and during succession there is a change in the quantity and the availability of nutrients that reach the forest floor. The nutrient status of the forest soils is dependent, in part, upon the release of nutrients from the forest floor to the lower mineral soil horizons. It is important to know how the forest floor and mineral soil respond to disturbance if we wish to maintain the nutrient status of a soil at a level which is capable of supporting and sustaining a desired ecosystem.

Information about forest floors in New Zealand is sparse. Published data on the distribution of nutrients in forest floors and forest soils in New Zealand are for the most part derived from studies of soil profiles under secondary vegetation (Ogden 1974). Our knowledge of the nature of the forest floor under mature indigenous forest is very limited and we know little of how forest floors change in physical and chemical composition after forest removal and during succession.

Two workers in New Zealand have commented upon changes in the state of the forest floor and soil horizons during secondary succession. In a study of the micromorphology of the forest floor on Taita soils at the Taita Experimental Station it was shown that a change from mor-like mulls to granular mulls occurs in the succession from *Erica lusitanica* through to *Leptospermum scoparium* shrublands and thence to a *Weinmannia racemosa* forest-land. There was a change in the distribution of organic matter from the surface of the mineral soil in the early stage of succession to a deeper incorporation into the mineral soil at the later stage of *Weinmannia* forest development. There was also an increase in soil porosity with the deeper incorporation of the organic material (Barratt 1968).

On Kapiti Island a mor-like litter was noted under *L. ericoides* stands. The litter was not well mixed with the top soil and the subsoils were compacted. On older sites where *Pseudopanax arboreus* was present in the understorey there was a reversal of the influence of the *L. ericoides* litter on the forest floor and a mull litter was present and the subsoils were not compacted (Esler 1967).

Another aspects of the relationship between site fertility and succession is the effect that different seral species have upon the nutrient status of the site. Although there have been a number of reports of soil deterioration or soil improvement due to the presence of a particular species (Duchaufour 1954, Karschon 1961, Damman 1971, Mitchell 1973), the evidence is far from clear for many reported cases.

Stone (1975) has argued that many workers may have ignored the importance of the inherent soil heterogeneity at their study sites when reporting the effects of particular species or groups of species on soil profile development, physical structure or nutrient status.

In primary successions there is usually a stage at, or near to, the beginning of vegetation succession when nitrogen inputs to the ecosystem are high. The high nitrogen input levels are never equalled again as succession progresses (Crocker and Major 1955, Stevens and Walker 1970). During secondary succession there have been some records of similar large accumulations of nitrogen in the ecosystem in the early periods of recovery (Zavitkovski and Newton 1968, Newton, El Hassan and Zavitkovski 1968). The period of rapid nitrogen accumulation is associated with the presence of a nitrogen-fixing species in the early seral stage.

At the Taita Experimental Station it was shown that the pioneering plant *Ulex europaeus* was capable of returning high quantities of nitrogen to the soil (Egunjobi 1967, 1969). Egunjobi (1969) suggested that the soil nitrogen concentration decreased during succession as succession proceeded from the nitrogen-fixing *U. europaeus* dominated shrubland to the non-nitrogen fixing *Weinmannia racemosa* forest. However this decline in soil nitrogen during secondary succession was not directly observed at Taita. The stands of *W. racemosa* forest studied by Egunjobi originated after fires in 1909 and 1921 and did not pass through an *U. europaeus* dominated phase since *U. europaeus* only became prominent in the Taita Catchment in the 1930's (Druce 1957). The present study offered the opportunity to investigate the pattern of nitrogen (and other essential elements) accumulation during secondary succession at sites where nitrogen-fixing vascular plants were not present.

#### 1:4 The Aims of the Study

This study attempts to document features of the structural and functional recovery of lowland forest ecosystems in the Marlborough Sounds Maritime Park. The hypothesis adopted at the start of the study was that the types and rates of secondary succession encountered were directly related to site fertility.

The study has been directed toward the acquisition of a field knowledge of the processes involved in the recovery of lowland forest ecosystems after disturbance.

The purpose of the research is to furnish information that will assist the people involved in the management of the ecosystems in the reserves of the Marlborough Sounds Maritime Park.

To this end the aims of the study are:

1. the documentation of different types and stages of secondary succession occurring in the lowland forest ecosystems of the Maritime Park,
2. an examination of changes in vegetation structural parameters in the course of succession,
3. an examination of some soil nutrient variables that may determine the types and rates of succession occurring on a disturbed site,
4. the documentation of the recovery of the nutrient status of the forest floor during succession,
5. an examination of the effects of different seral plant species on the forest floor and soil,
6. to compare the findings of this study with other studies conducted in similar forest ecosystems to see if common strategies of ecosystem recovery exist in the lowland forests of New Zealand,
7. to compare the findings of this study with contemporary and alternative models of secondary succession,
8. an examination of management guidelines for the Marlborough Sounds Maritime Park in the light of the findings of this study.

## CHAPTER TWO

### The Marlborough Sounds Environment

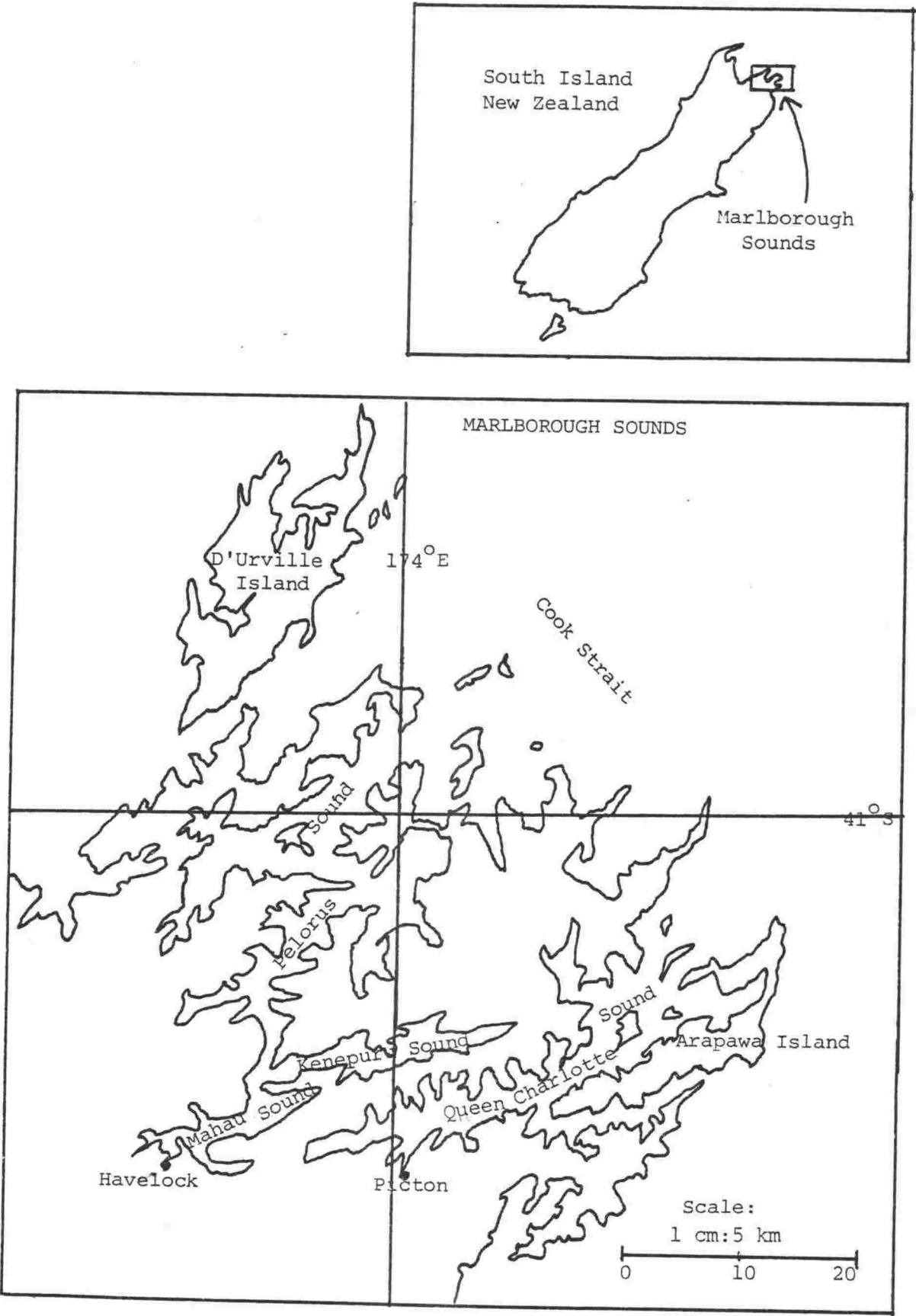
#### 2:1 Introduction

The Marlborough Sounds are located at the north eastern end of the South Island of New Zealand (Figure 2:1). The Marlborough Sounds are an intricate system of waterways that have resulted from the sea flooding of a mature landscape after the subsidence of a major earth block that was tilted toward the northeast probably during the third, main phase of the Kaikoura diastrophism (Kingma 1974).

The combined area of land and enclosed water is about 3050 square kilometers of which approximately one half is land (1480 sq. km.). The main waterways, Queen Charlotte Sound, Pelorus Sound, Kenepuru Sound, Mahau Sound, Tory Channel and French Pass represent drowned valleys. Partially drowned valleys are now deep bays. Crests of plunging spurs became islands and the tops of smaller spurs have been trimmed by wave action and are now rocky shoals and reefs. The coastline is irregular and exceeds 1450 km in length.

Relief is strong over the Sounds. The land rises steeply from sea level along the sides of the drowned valleys. Lower slopes (below 152 m) are commonly convex and often drop very steeply to the sea at a slope angle in excess of  $35^{\circ}$ . Over eighty-five percent of the land mass lies above 152 m. The middle slopes are usually straight, smooth and steep ( $25^{\circ}$ - $35^{\circ}$ ) rising to very steep, summits around 450 m - 600 m. The highest ridges of the central and western Sounds attain heights over 915 m. Mount Stokes, at 1204 m, is the highest point of the Marlborough Sounds.

Figure 2:1. Locality map



## 2:2 Geology

Paleozoic greywackes and schists are the main rocks of the Marlborough Sounds. A belt of basic volcanic and ultramafic rocks occurs within the greywackes along the western Sounds. The schistose rocks occur as a north-east trending belt of rocks, some 13 km - 10 km in width, flanked on the northwest and southeast by the less metamorphosed Pelorus Group greywackes and argillites which overlie the Marlborough Schist (Beck 1964, Vitaliano 1968).

The Marlborough Schists are of chlorite subzone ranks 2 and 3. Rocks of chlorite subzone 3 are fine grained, well foliated quartz-albite-muscovite-chlorite schists. Rocks of chlorite subzone 2 are fine grained, non-foliated quartz-albite-muscovite-chlorite schists. The metamorphism of the schist is considered to be related to their burial at great depths in the New Zealand Geosyncline. There is no stratigraphic or important structural discontinuity between the schist and adjoining greywackes (Grindley, Harrington and Wood 1961).

The Sounds are jointed, folded and faulted. Jointing is prevalent throughout the region and occurs with equal frequency in both subzones of the schists. Major cross folds are present in parts of the Sounds. Where there is intense folding in the schist, quartz veins may be present.

The major valleys and sounds have developed either along the strike of the bed where there are contrasting lithologies as on the western side of the Marlborough Sounds or along major strike orientated faults. Numerous minor faults are present.



### 2:3 Soil Parent Materials and Soils

A mapping survey of the Marlborough Sounds is being undertaken at the time of writing up of this present work. The following account of the soil parent materials of the Marlborough Sounds is based upon the preliminary results of the mapping survey (Laffan 1980).

The soils of the slopes of the Marlborough Sounds are derived in the main from weathered bed rock or unconsolidated slope deposits. The degree of weathering of rocks in the Marlborough Sounds is partly related to altitude. Weakly and moderately weathered rocks are found at altitudes above 200 m and strongly weathered rocks are found from sea level to 200 m. Shattered rock is common and is associated with the many fault lines running through the Marlborough Sounds.

Laffan recognizes three major soil parent materials of the slopes:

- (a) strongly weathered *in situ* bed rock
- (b) shattered *in situ* bed rock and
- (c) unconsolidated slope deposits

and further differentiates the latter group into (i) undifferentiated slope deposits and landslide debris, derived from strongly weathered bed rock and (ii) relict periglacial deposits and associated slope deposits.

At low altitudes unconsolidated slope deposits derived from strongly weathered bed rock are the most common type of slope deposit soil parent material. Relict periglacial deposits are common at altitudes above 200 m.

Reworked loess is incorporated into the upper part of the slope deposits. Rhyolitic glass has been identified in a deposit near Admiralty Bay at a depth of 170 cm as part of the Kawakawa Tephra Formation dated at about 20,000 yrs B.P. (Laffan 1980). The identity of loess occurring elsewhere in the Sounds has not been established.

Soft, red-weathered slope deposits and bedrock (including red saprolite) make up some promontories and lower spurs of the Sounds. The strong, deep weathering of the bedrock at lower altitudes is attributed to Late Pleistocene interglacial or interstadial periods. The origin of the undifferentiated slope deposits at the lower altitudes is possibly related to accelerated erosion during the last glaciation and to periodic mass movement and tree overturn during the Holocene. The origin of the relict

periglacial deposits is attributed to frost splitting of bedrock during the last glaciation. Solifluction and scree formation are believed to have been the means of transport of the deposits (Laffan 1980).

Most of the soils of the Marlborough Sounds are located on steep slopes, 80% of the region have slopes  $> 30^{\circ}$ . Soils on flat and rolling land (slopes from  $0^{\circ}$ - $12^{\circ}$ ) make up 10% of the region and the remaining 10% of the soils are located on hilly (slopes from  $12^{\circ}$ - $30^{\circ}$ ) land. On hilly and steep land soil depth is extremely variable but is on the average about 1 m deep.

Twelve different soil sets have been mapped in the Marlborough Sounds. Two soil moisture classes are represented; hygrous soils occur in the lower rainfall area of the Outer Sounds and hygrous-hydrous soils are associated with the higher rainfall area of the Inner Sounds (N.Z. Soil Bureau 1968).

The two main soil types are the Kenepuru steepeland soil and the Opouri steepeland soil; both belong to Southern Yellow Brown Earths. The Kenepuru steepeland soils are found on the eastern side of the Marlborough Sounds and the Opouri steepeland soils are found on the western side. Both soil types have formed on the higher rainfall areas (1270-2032 mm/yr) of the inner Sounds and occur from sea level to an altitude of 760 m. Both soil types are of low fertility.

The upland variant of the Kenepuru and Opouri steepeland soils is the Patriarch steepeland soil which occurs on very wet areas associated with the peaks and ridges of the Sounds above 760 m. The soil fertility of the Patriarch steepeland soils ranges from low to very low.

Soils of moderate fertility are found on the outer coasts of the Sounds. Three soil types are represented, they are; the Anakoha steepeland soils which are found on the eastern coast of the Sounds, the Ketu steepeland soils on the western coast of the Sounds and Arapawa steepeland soils which occur on the dry outer coast of the eastern side of Queen Charlotte Sound and also on some islands in Queen Charlotte Sound.

D'Urville Island contains the greatest number of soil types. The Yellow Brown Earths cover the greatest area of the island, however the ultramafic and basic rocks of the island have served as the parent materials of Brown Granular Loams and Clays. These are represented by Atawhai steepeland soils which are found on the western margin of D'Urville Island and Dun steepeland soils which are formed on a belt of ultramafic rocks that runs from D'Urville

Island to Croisilles Harbour in the western Sounds. The Atawhai steepland soils are of moderate fertility and the Dun steepland soils are poor soils showing characteristic chemical levels that are toxic to most plants.

The most fertile soils of the Sounds are located at the heads of bays on gently sloping fans and terraces. They are the Koromiko, Manaroa, Kaituna and Rai lowland Yellow Brown Earths. These soils cover only a small area of the Marlborough Sounds.

Silt loams are the predominant texture of the A horizon soils in all of the Sounds soils although stony loams, loams and sandy loams occur locally. The clay content increases down the profile and many of the soil types display silty clay-loam or clay loam textures in the B horizon especially where these lie on deeply weathered soil parent material.

The soils of the steep slopes are characterized by stony profiles with high clay and silt contents.

The soils on all slopes tend to have weak topsoil structures and relatively impermeable subsoils. All of the soil types with the exception of the terrace and fan soils are susceptible to sheet erosion.

## 2:4 Climate

The Marlborough Sounds experiences a mild climate with an adequate rainfall for forest growth. Full meteorological records are not available for any one site in the inner sheltered Sounds region.

There are gradients in climate across the Marlborough Sounds. The steep western and central ranges of the Sounds act as a barrier to the prevailing moisture bearing north westerlies and most of the rain is dropped on their exposed peaks and slopes. The leeward areas are relatively dry. Cook Strait acts as a funnel of the prevailing winds and causes a blustery, northeasterly and maritime environment along the outer coastal area of the Marlborough Sounds.

### Rainfall

A rainfall gradient exists across the Marlborough Sounds (Figure 2:2). The highest rainfall areas are associated with the uplands of Tennyson Inlet, Croisilles Harbour and the Mount Stokes region where an annual rainfall approaching 2500 mm is usual. A moderately heavy rainfall of 1300-2000 mm per annum falls over most of the Inner Sounds. The Outer Sounds area receives the lowest rainfall of 1000-1300 mm per annum and drought conditions can occur during mid summer.

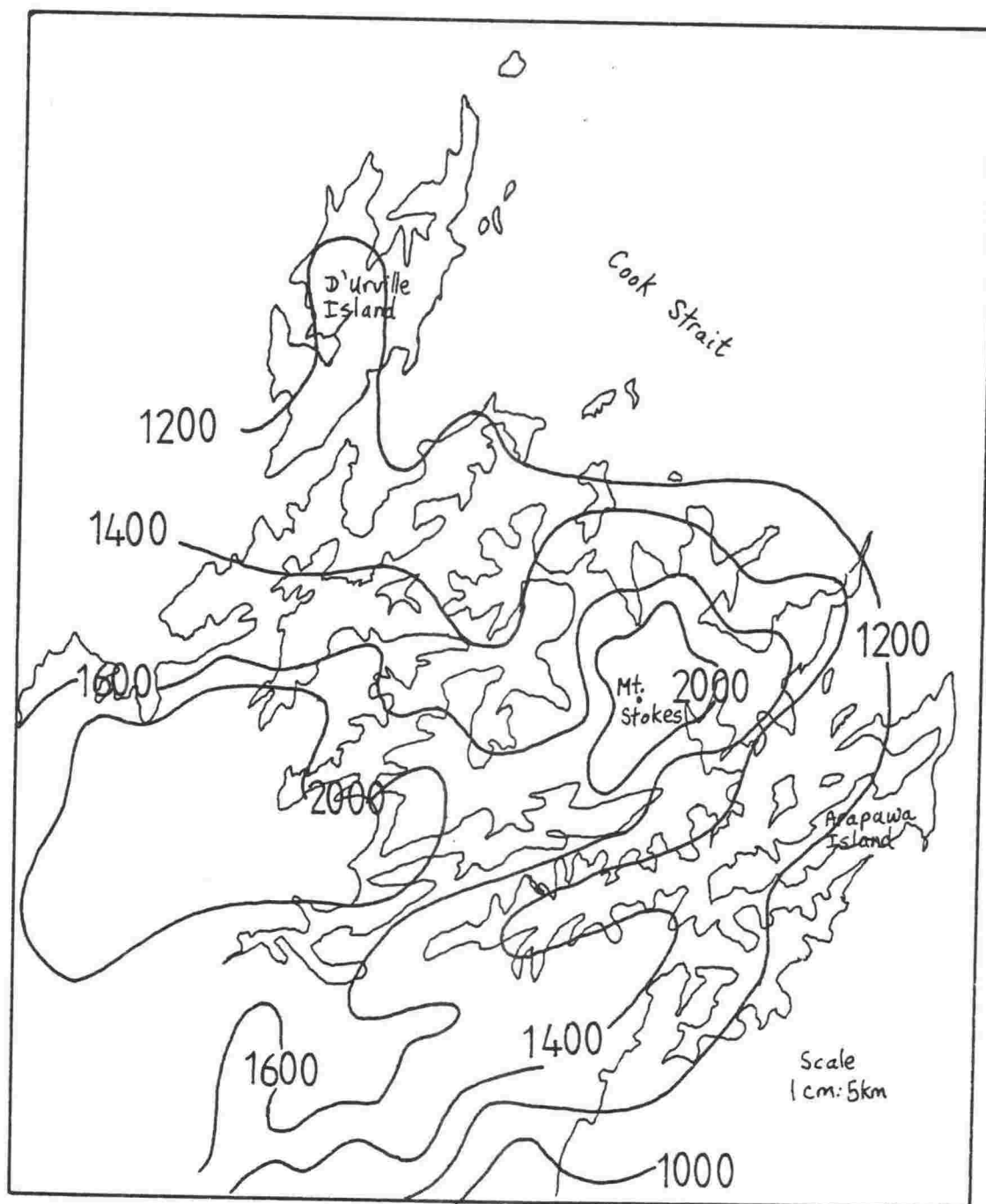
Rainfall from the northwest occasionally produces high intensities and high total falls. Snow lies on the highest peaks of the Marlborough Sounds for a few days during some winters. Snow fall at lower altitudes around 500 m has been observed (P. Buzzi pers. comm.) but is an extremely uncommon occurrence.

### Temperature

The maritime influence of Cook Strait is important in keeping coastal temperatures down. Average temperatures vary from  $9^{\circ}$ - $11^{\circ}\text{C}$  in most winter months to  $17^{\circ}$ - $18^{\circ}\text{C}$  in the summer. Temperatures can rise to  $30^{\circ}\text{C}$  and above on the warmest days. Most of the Sounds area is relatively frost free in the cooler months although the shaded slopes and valleys of the Inner Sounds can experience frequent low levels of frost.

Figure 2:2 Annual rainfall distribution in the Marlborough Sounds.

(readings in mm)



— from New Zealand Meteorological Service

Winds

The prevailing winds are from the northwest; northeasterlies and southerlies are also common. Gale force winds are common in and around Cook Strait.

## 2:5 Original Vegetation of the Marlborough Sounds

"It could probably be said that the reserves within Marlborough Sounds Maritime Park contain the best representation of lowland coastal vegetation in mid latitude New Zealand".

- G.N. Park and G.Y. Walls 1976a

The Marlborough Sounds lie within the region of Cockayne's Central Mainland Province (Cockayne 1958). The affinities of the coastal and lowland flora and their community types are with the southern part of the North Island of New Zealand rather than with any other area of the South Island (Allan 1949). The subalpine zone of Mt Stokes and the ultramafic soils of the western sounds support a distinct vegetation. The affinities of the subalpine and ultramafic flora and their associated communities are with vegetation types of the inner Marlborough and Nelson district (Sounds-Nelson Botanical District (Cockayne and Allan 1926)).

A number of papers and reports have been written about different aspects of the Marlborough Sounds vegetation. Articles on the vegetation of the outer islands of the Marlborough Sounds have been omitted from this review as these islands were beyond the realms of the study area. The following description of vegetation types is based upon reports and papers by: Martin 1932, Oliver 1943, Park 1968, Kelly 1968, Park and Walls 1976a,b, 1978, Ogle 1981 and also on personal observations (Macdonald 1976-1979). All the vegetation types of the Marlborough Sounds have not been observed by the author and in these instances the authority who first described the vegetation is noted along with the vegetation description.

### 2:5a Forests:

Five major forest associations are important in the Marlborough Sounds they are:

- 1) the coastal forest
- 2) the lowland podocarp/broadleaf forest\*
- 3) the broadleaf forest
- 4) the lowland beech forest
- 5) the beech forest above 500 m.

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\* Nomenclature of vegetation types follows Atkinson (1962) and is explained in Appendix II .

# 1) Coastal forest:

This forest association is usually dominated by kohekohe (*Dysoxylum spectabile*); it is restricted to coastal situations, areas of very little frost, low altitudes (< 300 m) and to either fertile valley soils or large boulder scree slopes. The coastal kohekohe forest occurs widely in the Outer Sounds region but limits on its distribution are quickly reached in the Inner Sounds. The kohekohe dominated association reaches its southern limit around Nydia Bay and Kenepuru Sound in the Pelorus Sound region and at Kaipakirikiri Bay in Queen Charlotte Sound.

The coastal forest is recognized by the presence of a number of tree species that have a distribution which is restricted to coastal situations around the Sounds. The species are:

karaka ( <i>Corynocarpus laevigatus</i> ),	kohekohe ( <i>Dysoxylum spectabile</i> ),
ngaio ( <i>Myoporum laetum</i> ),	wharangi ( <i>Melicope ternata</i> ),
cabbage tree ( <i>Cordyline australis</i> ),	nikau palm ( <i>Rhopalostylis sapida</i> )

and large leaved milk tree (*Paratrophis banksii*)

The coastal forest has a relatively low canopy around 10-15 m. Other species associated with kohekohe in the canopy, or in the upper understorey on fertile coastal valley sites are:

mahoe ( <i>Melicytus ramiflorous</i> )	kaikomako ( <i>Pennantia corymbosa</i> ),
putaputaweta ( <i>Carpodetus serratus</i> ),	fivefinger ( <i>Pseudopanax arboreus</i> ),
titoki ( <i>Alectryon excelsus</i> ),	hinau ( <i>Elaeocarpus dentatus</i> ),
tawa ( <i>Beilschmiedia tawa</i> ),	karaka and nikau palm.

Kohekohe usually occurs as a sole dominant in the canopy on coastal scree slopes although karaka, ngaio and wharangi may also be present.

Common understorey plants in the coastal forest are:

pigeonwood ( <i>Hedycarya arborea</i> ),	karamu ( <i>Coprosma robusta</i> )
kanono ( <i>Coprosma australis</i> ),	heketara ( <i>Olearia rani</i> )
rangiora ( <i>Brachyglottis repanda</i> ),	mahoe, kaikomako, putaputaweta and

fivefinger.

Ground cover in the valleys is often quite dense and kohekohe seedlings and small saplings are common in situations that are protected from pig (*Sus scrofa*) and possum (*Trichosurus vulpecula*). Ferns are conspicuous on the



ground floor, especially:

<i>Phymatosorus diversifolius</i> ,	<i>P. scandens</i> ,
<i>Asplenium bulbiferum</i> ,	<i>A. oblongifolium</i>
<i>A. terrestre</i> ,	<i>A. polyodon</i> ,
<i>Arthropteris tenella</i> ,	<i>Anarthropteris lanceolata</i> ,
<i>Adiantum cunninghamii</i> ,	<i>Pyrrosia serpens</i> ,
<i>Blechnum fluviatile</i> ,	<i>B. filiforme</i> ,
<i>B. chambersii</i> ,	<i>Ctenitis glabella</i> ,
<i>Hymenophyllum demissum</i> ,	<i>Pellaea rotundifolia</i> ,
<i>Pteris tremula</i> ,	<i>P. macilenta</i> ,
<i>Polystichum richardii</i> .	

The bush rice grass (*Microlaena avenacea*) is often present along with the hook grass (*Uncinia uncinata*). Sometimes lianes are present in the coastal forest; supplejack (*Ripogonum scandens*) and kiekie (*Freycinetia baueriana* ssp. *banksii* .) are the two most frequently encountered although

*Parsonsia capsularis*, *P. heterophylla*,  
*Passiflora tetrandra* and *Clematis forsteri* also occur.

The association as described is a generalisation. Communities encountered in the field are variants upon a theme. The large leaved milk tree is not present in all coastal forests as it has a restricted distribution around the outer seaward edge of the Sounds. Whau (*Entelea arborea*) is a coastal tree whose presence in the Marlborough Sounds is very limited; it was not seen by the author. Martin (1932) reports that whau appears to have been eaten out of its many former habitats around the Sounds.

Types of coastal forest present in the Marlborough Sounds are:

- a) Tawa-kohekohe/broadleaf forest
- b) (Hinau)-(tawa)/kohekohe/broadleaf forest
- c) (Pukatea)/kohekohe forest
- d) Kohekohe forest
- e) Kohekohe-mahoe/broadleaf forest
- f) Kohekohe-(tawa)-(karaka)-(titoki)/nikau-broadleaf forest
- g) Kohekohe-*Olearia paniculata* low forest
- h) (Matai)-(miro)-(rimu)-(totara)-(pukatea)/kohekohe-tawa-nikau/broadleaf forest and
- i) (Rimu)-(matai)-(miro)/kohekohe-tawa/broadleaf forest.

Types a, b and f are the common coastal forest types on sheltered valley sites. Type c occurs around alluvial stream sites. Type d occurs on colluvial scree slopes. Type c occurs on valleys and slopes that are subjected to more coastal spray than the sheltered sites of types a, b and f. Type g occurs on exposed headlands or coastal cliffs. The latter two types of coastal forest occur around the central Pelorus Sound region, they possess a very uneven canopy with huge podocarps and pukatea (*Laurelia novae-zelandiae*) emergent above the kohekohe-tawa forest.

2) Lowland podocarp/broadleaf forest:

The kohekohe dominated forest is not important away from the immediate influence of the coast. The valleys and slopes below 300 m in the Marlborough Sounds support a lowland podocarp/broadleaf forest association that is common to the southern half of the North Island and which reaches its southern limit around the Marlborough Sounds-Golden Bay area. Tawa is the dominant canopy tree with a number of podocarps emergent through the forest canopy. Rimu (*Dacrydium cupressinum*) is the most common emergent; matai (*Podocarpus spicatus*), miro (*P. ferrugineus*) and kahikatea (*P. dacrydioides*) are often present along with rimu. Pukatea is a common emergent above the tawa canopy on alluvial valley sites.

The podocarp/broadleaf forests have a complex stratified vertical structure. A three-tiered arrangement is the usual model with the podocarps occurring as emergents through a dense forest canopy. These forests contain a large number of species; epiphytes and lianes are a feature, the understorey is usually dense and many trees possess creeping surface roots on the forest floor.

Associated with tawa in the canopy are often hinau and titoki. In a layer beneath a tall forest canopy mahoe, pigeonwood, toro (*Myrsine salicina*) and kamahi (*Weinmannia racemosa*) are usually present. Sometimes these species share a low canopy with tawa and hinau.

A number of shade tolerant shrubs and tree ferns form an understorey between 2-6 m under the forest canopy. Species found here include:

karamu, konano, rangiora, heketara, putaputaweta, kaikomako, fivefinger,	
kawakawa ( <i>Macropiper excelsum</i> ),	ponga ( <i>Cyathea dealbata</i> ),
mamaku ( <i>Cyathea medullaris</i> ),	red matipo ( <i>Myrsine australis</i> ),
kohuhu ( <i>Pittosporum tenuifolium</i> )	and ramarama ( <i>Lophomyrtus bullata</i> ).

The tree fuchsia (*Fuchsia excorticata*) is common as an understorey species along stream sides.

The ground floor of the forest is covered with surface roots of the larger canopy trees. A copious fern cover is spread overtop and between the surface roots. The ferns present on the ground floor are usually the same species that are present in the coastal forest with the notable addition of the crown fern (*Blechnum discolor*) which can be very common on valley floors that experience cold air down draughts. Tree seedlings are common on the ground floor.

Supplejack and kiekie are the two most important lianes and both can often be so profuse in growth that progress through the forest is impeded. Three climbing ratas are common also; these are *Metrosideros fulgens*, *M. diffusa* and *M. perforata*. Epiphytes festoon the podocarps, the large hinaus and tawas. The epiphytic shrub puka (*Griselinia lucida*) is common along with the orchids *Dendrobium cunninghamii*, *Earina autumnalis* and *E. mucronata*. The tiny orchid *Bulbophyllum pygmaeum* has been found on a fallen rimu branch covered with large epiphytes and probably is quite common in this forest association. The perching lilies *Collospermum hastatum* and *Astelia solandri* also occur in profusion.

The areas that contain the highest proportion of podocarps are the valley flats. These areas are not well represented in the Maritime Park and are of a remnant character. They are usually found as isolated islands of forest amongst pasture land. Kahikatea which is usually restricted to alluvial valley flats occurs on quite steep slopes at Ships Cove, Queen Charlotte Sound. Totara (*Podocarpus totara*) is not common over the larger area of the Sounds. Its distribution appears to be toward the west, it is recorded as a large emergent at Fitzroy Bay (Park and Walls 1976a) and it occurs on D'Urville Island.

Community types of lowland podocarp/broadleaf forest occurring in the Marlborough Sounds are:

- a) Rimu-(matai)-(miro)/tawa-(titoki)-(hinau)/broadleaved spp. forest
- b) Kahikatea-pukatea/tawa/broadleaved spp. forest
- c) Kahikatea-rimu/nikau-kohekohe-tawa/broadleaved spp. forest
- d) Rimu-miro/hinau-kamahi forest
- e) (Rimu)-pukatea/tawa/mahoe-nikau forest
- f) Rimu-kahikatea-matai-pukatea/tawa-kamahi-mahoe-tree fern forest

- g) Rimu-rata/hinau-tawa/broadleaved spp. forest
- h) Rimu-matai-totara-miro-kahikatea/hinau-kamahi-tanekaha-mahoe forest.

Types a, c and f are typical podocarp/broadleaf forests of the valley flats and lower slopes over much of the Sounds. Types b and e are more typical of a narrow gully situation. Type d occurs on some of the broader slopes of the Sounds between 300 m and 500 m. Type h is representative of the podocarp rich forests which are found on the lower slopes on the western side of the Marlborough Sounds.

### 3) Broadleaf forest:

The distinction between the podocarp/broadleaf forests and the broadleaf forests is not always clear especially as many sites exist where there has been selective logging for the podocarp component of the forest. The broadleaf forest is similar in structure and species composition to the podocarp/broadleaf forest with the exception that there are no large podocarps present as emergents through the canopy.

Tawa and hinau are the most important canopy trees, often kamahi is present either as a member of the canopy or as an understorey tree. These forests are often found above the podocarp/broadleaf forests and on ridges and spurs.

Community types of broadleaf forest present in the Sounds are:

- a) Hinau-kamahi-tawa/broadleaved shrubs forest
- b) Hinau/kamahi-kohekohe/broadleaved shrubs low forest
- c) Pukatea/tawa-kohekohe-hinau/mahoe-kiekie-supplejack forest
- d) Pukatea/tawa/mahoe forest
- e) Kamahi-tawa forest
- f) Tawa/kohekohe forest

The types a and e are communities commonly found on high altitude slopes between 300 m and 500 m or on dry ridge and spur sites. Type b is the forest that characterizes the slopes on the islands of Queen Charlotte Sound and Pelorus Sound. Types c and d are forests that are confined to gully situations. Type f is a slope forest that occurs at lower altitudes than do types e and a.

4) Lowland beech forest:

Four species of beech (*Nothofagus* spp.) are present in the Marlborough Sounds and two types of beech hybrids also occur. Hard beech (*N. truncata*) and black beech (*N. solandri* var. *solandri*) are the two species of the lowland beech forest. Red beech (*N. fusca*) and silver beech (*N. menziesii*) are found above 300 m in the Marlborough Sounds. The two hybrids *N. fusca* x *N. solandri* var. *solandri* and *N. truncata* x *N. solandri* var. *solandri* appear to be restricted to the lowland zone.

The lowland beech forest is restricted to dry ridge or spur sites and to steep slopes. Black beech is dominant on exposed headlands and coastal ridges usually as a pure population. At some very exposed sites a hybrid population of black x hard beech can be present. Hard beech dominates on ridges away from the immediate vicinity of the coast, black beech is commonly present in the canopy, but its frequency is much less than that of hard beech.

The beech forest is of a simple structure. The canopy occurs between 8 m and 18 m depending upon exposure conditions. The forest is relatively open with a sparsely developed understorey of subcanopy trees and shrubs. Kamahi, hinau, toro, red matipo and ponga are present in the subcanopy. Among the shrubs that occur beneath the subcanopy are the two mingimingis (*Cyathodes fasciculata* and *C. juniperina*), *Coprosma rhamnoides*, *C. lucida*, fivefinger and heketara. The forest floor is clothed in a deep layer of litter and decomposing litter. Beech mycorrhiza are present through the decomposing fermentation and humus layers. A scattered fern and herb cover is present on the forest floor. The ferns *Lindsaea trichomanoides*, crown fern, *Blechnum procerum*, *Grammitis billardiera* and *Phymatosorus diversifolius* are common. The N.Z. bluebell (*Dianella nigra*), *Gahnia pauciflora* and *Astelia solandri* also feature as ground cover species. Dead branches and trunks of beech trees are a feature of the ground floor also. Many beech seedlings grow on the decomposing wood which is usually heavily clothed in moss species and the climbing rata *Metrosideros fulgens*.

Community types of lowland beech forest found in the Marlborough Sounds are:

- a) Black beech forest
- b) Hard beech-(black beech) forest
- c) Red beech x black beech forest
- d) Hard beech/southern rata-kamahi forest

Type a is restricted to exposed ridges and spurs. Type b is the main lowland beech forest type in the Sounds, it occurs on all dry ridge crests. Type c is the lowland beech forest that shows a peculiar distribution in the Marlborough Sounds. It occurs on dry ridges and spurs on the north east side of Arapawa Island (Park and Walls 1976a) and also on Kenny Isle in Pelorus Sound. No hard beech is present and the hybrid beech and kamahi are the dominant species. Type d occurs on wet ridge sites and is more prominent in the west of the Marlborough Sounds.

5) The beech forest above 500 m:

Red and silver beech are the species that dominate the forest of the higher slopes and ridges. Silver beech is the sole dominant above 1000 m on slopes and ridges, it reaches lower altitudes on ridge and spur sites. Red beech does not attain such altitudes. It often occurs as a transitional band between the lowland forest and the silver beech forest, although there are areas where it does not occur and the silver beech forest is found directly above the lowland forest.

The structure of the beech forest at higher altitudes is similar to that of the lowland beech forest. Kamahi, toro, southern rata (*Metrosideros umbellata*) and Hall's totara (*Podocarpus hallii*) occur as subcanopy trees. A sparse shrub layer consisting of broadleaf (*Griselinia littoralis*), stinkwood (*Coprosma foetidissima*), *Cyathea smithii*, horopito (*Pseudowintera colorata*) and *Pseudowintera axillaris* is usually present. Bryophytes are a conspicuous feature of these forests, they clothe the forest floor as well as the trunks of the large trees.

Community types present in the Sounds are:

- a) Silver beech/kamahi-southern rata forest
- b) Red beech/kamahi-southern rata forest
- c) Red beech-silver beech/kamahi forest
- d) Red beech-hard beech forest.

Type a is the main forest of the higher altitudes in the Marlborough Sounds. Its form varies from a tall, open-canopied forest on sheltered slopes to a short, closed-canopied forest on windswept ridges. Types b, c and d are essentially transitional forests from the lowland hard beech dominated forest to the montane silver beech forest.

Although the forest types as described would appear to exist as distinct clearly bounded communities, this is not the case. The division of the forest vegetation into community types has been adopted as a convenient means of describing the forests and the variation between types. In reality when they come together the vegetation community types intergrade to a considerable degree. The above division of the forest type provides a useful framework for the interpretation of the successional mosaic of vegetation in the Marlborough Sounds.

## 2:5b Shrublands:

A number of different types of shrubland are present in the Marlborough Sounds. The sites occupied by shrubland are subject to environmental stresses that preclude the growth of forest vegetation.

### 1) Coastal shrubland:

#### a) beaches and shores

A plant zonation sequence is often observed with shore ribbonwood (*Plagianthus divaricatus*), tauhinu (*Cassinia leptophylla*) and *Olearia solandri* on the shore fringe. Further back are flax (*Phormium cookianum*) and taller shrubs of akeake (*Dodonaea viscosa*), ngaio and mahoe, which merge into the coastal forest.

#### b) steep coastal cliffs

The steep shoreline of much of the Marlborough Sounds supports a low growing shrub community dominated by akeake, ngaio, flax, *Olearia paniculata*, taupata (*Coprosma repens*), *Hebe stricta* var. *atkinsonii* and a rich variety of herbs and ferns.

### 2) Shrubland on ultramafic soils:

This type of shrubland is found on the soils of the mineral belt on the western side of the Marlborough Sounds. Manuka (*Leptospermum scoparium*) is the dominant plant of this community. Other narrow leaved, ericiform shrubs are a feature of this community and include *Cassinia vauvilliersii*, *Coprosma propinqua*, *C. rhamnoides*, *C. sp.* (unnamed), *Corokia cotoneaster*, the mingimingi species (*Cyathodes fraseri*, *C. fasciculata*, *C. juniperina*), *Olearia serpentina*, kanuka (*Leptospermum ericoides*) and *Dracophyllum longifolium*. Small, stunted trees of kamahi, southern rata and fivefinger are also present.



The ultramafic shrubland varies in height from <1 m on exposed ridge sites to 5 m on sheltered slopes. A wide variety of herbs are found on the floor of the shrubland. Many of the herbaceous species belong to genera more commonly associated with subalpine and alpine conditions. Common herbs of the ultramafic shrubland include: *Helichrysum filicaule*, *Euphrasia cuneata*, *Craspedia* sp. (unnamed), *Gnaphalium audax*, *Senecio lagopus*, *Anisotome aromatica*, *Gentiana* sp. (unnamed), *Scleranthus biflorus*, *Celmisia gracilenta*.

### 3) Subalpine shrubland:

Mount Stokes contains the only area of subalpine shrubland in the Marlborough Sounds. Leatherwood (*Olearia colensoi*) occupies a narrow fringe above the silver beech forest. The summit of Mount Stokes is dominated by a very disturbed (pig and goat (*Capra hircus*) damage) snow tussock grassland that contains scattered shrubs of leatherwood, *Aristotelia fruticosa* var., *Dacrydium laxifolium*, *Dracophyllum longifolium*, *D. uniflorum*, *Myrsine divaricata*, *Phyllocladus alpinus*, *Pittosporum rigidum*, *Pseudopanax anomalus*, *Pseudowintera colorata* and two unnamed *Coprosma* species (included in *C. parviflora* descriptions - A.P. Druce pers. comm.).

### Other Vegetation Types of the Marlborough Sounds:

#### 2:5c Salt marsh:

A number of salt marshes are present in the Marlborough Sounds. They are confined to the heads of the larger bays. The most extensive marshes are found at the head of Pelorus, Queen Charlotte and Kenepuru Sounds. Sea grass (*Zostera muelleri*) is present on the intertidal muds. A common zonation sequence of glasswort (*Salicornia australis*), shore primrose (*Samolus repens*) and *Selliera radicans* on the lower marsh leads into a sea rush (*Juncus maritimus* var. *australiensis*) and jointed rush (*Leptocarpus similis*) zone that occupies the upper marsh.

#### 2:5d Swamp vegetation:

Swamps are not well represented in the Marlborough Sounds. Oliver (1944) describes four types from the western side of D'Urville Island:

- A brackish water swamp of sea rush, jointed rush, and *Scirpus* species at the head of Manawhakapakapa Bay,
- A fresh water swamp dominated by *Cyperus ustulatus* and large



tussocks of *Carex secta* and *C. virgata* in a low lying valley at Greville Harbour,

- A fresh water association dominated by raupo (*Typha orientalis*) at Greville Harbour and
- A raupo-*Baumea huttoni* swamp located behind sand dunes at Long Beach on the northern side of Greville Harbour.

## 2:5e Grasslands:

### 1) Coastal grassland:

The coastal tussock *Poa laevis* occurs on some very exposed, eroding coastal cliffs. Other plants include salt tolerant herbs, *Aciphylla squarrosa* and flax.

### 2) Subalpine grassland:

A small area of snow tussock grassland is present on the summit of Mount Stokes. Subalpine herbs are scattered throughout between the tussock. Williams *et al.* (1977) considers that the snow tussocks are a hybrid population of *Chionochloa flavescens* x *C. pallens* var. *pallens*.

## 2:6 Man's Effects Upon the Vegetation of the Marlborough Sounds

### 2:6a Historical perspective

The present vegetation communities in the Marlborough Sounds are a legacy of the activities of man. Less than half of the land area of the Sounds is now in forest; most of this is located above 300 m. Forest clearing commenced with the arrival of Pre-European Man in the area. The Marlborough Sounds are known to contain many sites of occupation by Pre-European Man. Recent surveys of a number of these sites have led to the suggestion that the sites have had little occupation. This archaeological work is at the field recording stage and detailed investigations with datings of time of occupation have not been made. Most of the sites recorded are small and are located directly on the foreshore area of the Sounds or adjacent coastal spurs. The evidence seems to suggest that the Pre-European Polynesian population of the Sounds area was small, located around the shore and of a transitory nature (Trotter 1977). The impact of Pre-European Man upon the vegetation of the Sounds appears to be minimal.

Ship's Cove, Queen Charlotte Sound, was Captain Cook's favourite anchorage on his three voyages to New Zealand. He visited the Cove on seven occasions between January 1770 and February 1777. His comments on the vegetation of the Cove and surrounding area indicate that the forest was in the magnificent condition that it is today at this site:

"The land about this Sound is of much height that we first saw it at the distance of 20 leagues. It consists wholly of high hills and deep Valleys, well stored with a variety of excellent Timber, fit for all purposes except Ships' Masts, for which use it is too hard and heavy."

(Captain Cook's Jnl - Wharton's Transcript)

"... and as to wood the land is here one intire forest."

(Captain Cook's Jnl - Wharton's Transcript)

This impression of the intact forested vegetation is borne out by Cook's surgeon William Anderson, who was an acute observer and visited Ship's Cove four times.

"For the hills (except a few toward the sea, which are covered with smaller bush) are one continued forest of lofty trees, flourishing with a vigour almost superior to any thing that imagination can conceive,"

(Beaglehole 1967)

Anderson notes also that in February 1777 he went to the south eastern part of the Sound to cut grass for hay. It is apparent then that not all of the Sounds area was under forest vegetation in the 1770's. Joseph Banks also commented upon the lack of forest cover in Queen Charlotte Sound in 1777:

"We found the country on our side of the bay very well wooded everywhere, but on the opposite side very bare."

and described the entrance of Queen Charlotte Sound:

"The land on both sides appeared most miserably barren."

(Jnl. of the Rt. Hon. Sir Joseph Banks ed. by  
Sir J.D. Hooker)

At the time of Cook's visits to Queen Charlotte Sound the Maori population of the Sound were using *Pteridium* rhizomes as a foodstuff. Cook's men observed "a very prodigious quantity of drying fish and much fern root." (Beaglehole 1967). In all probability the fern would have been gathered from nearby fernlands which would have been maintained by burning.

Fifty years after Cook's visits to Queen Charlotte Sound the Russian Captain F. Bellingshausen spent some 12 days in the Sound. He also noted that not all of the hills of the Sound supported forest:

"The further we penetrated up the Sound, the more did we see mountains covered not at all by woods and of a yellowish hue. Woods were confined to the lower ranges, nearer to water level."  
(from Barratt 1979)

The greater part of the forest removal has occurred since the arrival and settlement of European Man in the Marlborough Sounds. I.J.S. Bowie has traced the development of European occupation in the Marlborough Sounds in his thesis (Bowie 1964). The initial large scale land clearance occurred between 1854 and 1880 when the valley flats and lower hills were cleared for settlement and tree felling was the major occupation of the Sounds dwellers. By 1880 the millable timber supply was exhausted at the heads of the Sounds and sawmills moved into the upper reaches of the Sounds.

The next stage saw the development of farming in the Sounds during the period 1880-1910 when use of fire in clearing forest and shrublands became a regular practice for the Sounds farmer as he tried to cope with shrub invasion on his pastures and he experimented with grass mixtures and stocking levels.

By 1910 the initial fertility boost from the 'ash bed effect' over many areas in the Inner Sounds began to decline. Essentially, no large areas of land were cleared of forest after this time, with the exception of some blocks of Maori owned land; e.g. at Endeavour Inlet and Port Gore. Farming in the Sounds reached its peak during the First World War. During the 1920's the beginning of the decline of farming in the Sounds was seen especially in the older established areas of the Inner Sounds.

Farming has declined in the Sounds since 1932 through to the present. The reasons for this decline are varied and a number of opinions have been advanced. Historical factors are involved\*but even in 1918 basic biological management of the agricultural system adopted by the Sounds farmers had been attacked.

A.H. Smith writes that the decline in farming in the Inner Sounds was a natural consequence of overdevelopment, of overburning, and over clearing with too little money being spent on scrub cutting, fencing, seeding and stocking in conjunction with the burning (Smith 1918).

Bowie advances the thesis that part of the success or failure of farming in the Marlborough Sounds is a function of environmental and cultural factors operating through the soil to determine land cover. Basically he considers that soils in certain regions of the Sounds are unsuited to pasture growth (Bowie 1964, p. 63).

## 2:6b Present day vegetation of the Marlborough Sounds

Land clearing operations have been attempted on almost two thirds of the land in the Marlborough Sounds. Well grazed pastoral land makes up less than 20 percent of the area and over 40 percent of the region consists of secondary communities (Duckworth *et al.* 1976).

The varied history of land use in the Marlborough Sounds has led to a complex mosaic of vegetation types in this area. The different modifications to the forest ecosystems range from the relatively undamaging felling of a few select canopy trees to the repeated removal of all woody vegetation cover by burning and grazing. G.N. Park and G.Y. Walls have listed 67 successional types of vegetation present in the Marlborough Sounds and have related the types to seral stages and slope position (Park and Walls 1976b).

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\*Historical factors include; the 1930's Depression; the settlement of First World War veterans, inexperienced with farming methods, on units in the Sounds; increasing transport costs; no aerial application of fertiliser.

A condensation of these types is presented in order to concentrate attention on the successional types that are the most frequently encountered in the Marlborough Sounds. Some of the types presented are not listed by Park and Walls; this is, to a degree, to be expected, as initial typing of vegetation is undertaken in a relatively subjective manner. The following types are grouped on their physiognomic appearance which also corresponds to the seral stage of the succession.

SUCCESSIONAL VEGETATION TYPES OF THE MARLBOROUGH SOUNDS

- |     |             |                                     |
|-----|-------------|-------------------------------------|
| 1.  |             | Bracken/pasture                     |
| 2.  | Reverting   | Gorse/pasture                       |
| 3.  | Grasslands  | Bracken-small leaved shrubs/pasture |
| 4.  |             | Tauhinu/pasture                     |
| 5.  |             | Bracken                             |
| 6.  | Fernlands   | Gorse-bracken                       |
| 7.  |             | Bracken-(kamahi-manuka)             |
| 8.  |             | Bracken/broadleaves                 |
| 9.  |             | Gorse                               |
| 10. |             | Gorse-broom                         |
| 11. |             | Gorse-spanish heath-manuka          |
| 12. |             | Manuka/(bracken)                    |
| 13. |             | Manuka early seral                  |
| 14. |             | Manuka late seral                   |
| 15. |             | Manuka-fivefinger coastal           |
| 16. |             | Manuka-kanuka                       |
| 17. | Shrublands  | Pine/manuka                         |
| 18. |             | Manuka/spanish heath                |
| 19. |             | Tauhinu                             |
| 20. |             | Broadleaves/tauhinu                 |
| 21. |             | Kanuka                              |
| 22. |             | Tree tutu-wineberry                 |
| 23. |             | Mixed broadleaves                   |
| 24. |             | Manuka-kamahi                       |
| 25. |             | Tree tutu/mahoe-wineberry           |
| 26. |             | Black tree fern/broadleaves         |
| 27. |             | Kanuka/broadleaves                  |
| 28. |             | Kanuka-kohekohe                     |
| 29. | Forestlands | Hinau-kamahi-(rewarewa)             |
| 30. |             | Mixed broadleaves                   |
| 31. |             | Kanuka-kamahi                       |
| 32. |             | Fivefinger-kamahi                   |
| 33. |             | Black beech                         |
| 34. |             | Hard beech-kamahi                   |
| 35. | Forests     | Kamahi-(toro)                       |
| 36. |             | Mixed broadleaves                   |
| 37. |             | Mixed broadleaves-treefern          |
| 38. |             | Mahoe/kohekohe-broadleaves          |

## 2:6c Key Features of Successional Vegetation Types

### Reverting Grasslands:

These vegetation types are present on land that has been recently (within the last 15 years) retired from pastoral use. The grasses browntop (*Agrostis tenuis*), Yorkshire fog (*Holcus lanatus*) and sweet vernal (*Anthoxanthum odoratum*) are the most common species of the pastures. Vegetation types 1, 2 and 4 are found on the lower slopes. Tauhinu (*Cassinia leptophylla*) is very common in the Outer Sounds and is the primary colonizer of grazed pastures. The shrub gorse (*Ulex europaeus*) is becoming important in the early stages of succession in the Sounds. Gorse favours the less exposed conditions of the Inner Sounds. Both gorse and tauhinu are light demanding species and are only capable of entering the succession if grazing is occurring thus preventing the establishment of a dense sward of grass. If the pasture is retired from use and a heavy sward of grass is allowed to develop before gorse or tauhinu becomes established then bracken (*Pteridium esculentum*) invades the grassland by vegetative spread of its rhizomes.

At higher elevations bracken, gorse and tauhinu do not form complete canopies and other small leaved shrub species invade the pasture. The most frequently encountered pioneering shrubs at altitudes from 200-300 m are: *Coprosma rhamnoides*, manuka (*Leptospermum scoparium*), *Pseudopanax anomalus*, kaikomako (*Pennantia corymbosa*), mingimingi (*Cyathodes fasciculata*), Spanish heath (*Erica lusitanica*) and *Coprosma propinqua*.

### Fernlands:

Bracken is the dominant cover on much of the pastoral land that has been repeatedly burnt. Bracken is found on slopes, ridges and in the valleys. At altitudes below 300 m bracken quickly forms a dense cover if its rhizomes are already present in the soil prior to burning or retirement of the pasture. Bracken is usually the sole dominant for some 10 years or more. Broadleaf species establish in the bracken fernland and their presence is first noticed in winter when the bracken fronds die down.

At altitudes above 300 m and on dry ridge sites bracken does not usually form a closed canopy and kamahi (*Weinmannia racemosa*), manuka (*Leptospermum scoparium*) and Spanish heath (*Erica lusitanica*) are often present in the fernland. Regeneration to a shrubland or forest cover is slower at the higher altitudes than it is through the bracken cover on the lower slopes and valleys. There are many sites in the Sounds where advanced regeneration is present on the lower slopes and the higher slopes are still in fernland.

Gorse-bracken sites appear to be a fairly recent addition to the successional communities in the Marlborough Sounds. Most are located at the southern end of the Sounds on recent burn sites.

#### Shrublands:

A variety of shrublands are found in the Sounds. The shrubland phase is the first or second stage in the succession to forest. A feature of most of the shrublands in the Marlborough Sounds is that they are dominated by microphyllous species.

The seral shrublands were probably dominated by manuka and kanuka (*Leptospermum ericoides*) on the ridges and slopes and by tauhinu (*Cassinia leptophylla*) on the exposed coastal slopes prior to the arrival of European man in the Sounds. The introduced species: gorse (*Ulex europaeus*), broom (*Cytisus scoparius*), Spanish heath and radiata pine (*Pinus radiata*) have become prominent in the shrubland stages of succession on the slopes and ridges as a result of the activities of European man in this region.

The distribution of the introduced species is centred around areas that have had a frequent fire history. Spanish heath became established in the Sounds in the 1920's (Leonard and Beggs 1959). The shrub initially established on the eastern side of the Sounds. It is now present throughout the Marlborough Sounds although it is still most common on Arapawa Island and on the eastern side of Queen Charlotte Sound. The spread of Spanish heath across the Marlborough Sounds has been documented by Toynbee (1948) and Bowie (1963).

Gorse and broom appear to have been more recent arrivals into the Sounds. Sites burnt prior to the Second World War do not contain any evidence of the presence of gorse or broom. The large numbers of gorse seedlings coming up on the new Power Board tracks through manuka and kanuka shrublands indicate that these are areas which are capable of supporting gorse but were colonised by manuka and kanuka prior to the arrival of gorse seed.

In the valleys and gullies the successions are dominated by broadleaved species. Tree tutu (*Coriaria arborea*) and wineberry (*Aristotelia serrata*) are important colonisers. Mahoe (*Melicactus ramiflorus*), tree fuchsia (*Fuchsia excorticata*), konano (*Coprosma australis*), mamaku (*Cyathea medullaris*) and rangiora (*Brachyglottis repanda*) are common in the valleys and have grown through a pioneering sere dominated by bracken, tauhinu or broom. In very exposed, wind swept gullies tauhinu and coastal flax (*Phormium cookianum*) are

the pioneering species through which a shrubland dominated by fivefinger (*Pseudopanax arboreus*), mahoe and kohekohe (*Dysoxylum spectabile*) develops.

On the ridges and slopes manuka is the dominant shrub of early seral stages in the Sounds. Kamahi (*Weinmannia racemosa*) is often present with manuka on steep, north facing slopes. On more fertile sites kanuka plays an increasingly important role in the manuka association and it may dominate on colluvial slope deposits.

A short manuka shrubland develops on very exposed coastal ridges and slopes. This vegetation is prevented from attaining a height much greater than 1.5 m because of wind and salt damage to young shoots. Fivefinger, *Dracophyllum longifolium* and *Coprosma robusta* establish within the exposed manuka shrubland but are also subject to the wind effects and the succession is truncated at this stage as trees are unable to establish in such an exposed environment. On less exposed coastal slopes a coastal shrubland dominated by fivefinger, broadleaf (*Griselinia littoralis*), *Olearia paniculata*, heketara (*Olearia rani*) and sometimes akeake (*Dodonaea viscosa*) develops through the manuka and/or kanuka shrubland.

The dry eastern side of Queen Charlotte Sound supports a manuka shrubland that either has Spanish heath occurring as a canopy co-dominant or as an understorey shrub beneath a relatively open canopy.

Gorse and broom are the new dominants of the lower slopes around the Sounds. On higher slopes and ridges a mixed vegetation of gorse, Spanish heath and manuka occurs on recently fired slopes.

On midslopes near to an established pine source wild pines are present in profusion above a manuka canopy.

#### Forestlands:

Broadleaf forestland is a general term for the complex secondary forest that occupies the valleys or lowest slopes on coarse colluvial sites. Mahoe (*Melicytus ramiflorus*), wineberry (*Aristotelia serrata*), tree tutu (*Coriaria arborea*) and rangiora (*Brachyglottis repanda*), are often canopy dominants and tawa (*Beilschmiedia tawa*), titoki (*Alectryon excelsus*) and pukatea (*Laurelia novae-zelandiae*) may be present as seedlings or saplings. In this type of forestland the vegetation is beginning to take on the appearance of the mature podocarp/broadleaf forest with complex stratification



and a large number of plant species. Younger broadleaf forest in which tawa, titoki and pukatea are not yet present is of a more open nature. The shrubs kawakawa (*Macropiper excelsum*), pate (*Schefflera digitata*) and konano (*Coprosma australis*) are usually present. The floor cover is often rich in fern species and the large hook grass (*Uncinia uncinata*) is common.

Regenerating coastal broadleaf forestland is present on the exposed lower slopes in the Outer and Middle Sounds regions. The coastal forest

exhibit a very open canopy and have many wind thrown trees on the floor of the forest. There is an increased broadleaf tree and shrub component in the senescent kanuka forestland as compared with the younger, vigorous kanuka forestlands.

#### Forests:

Areas in the Sounds that contain secondary forests dating from disturbance since European settlement are areas that have not been subjected to repeated disturbances.

It is possible to recognize areas of recent secondary beech forest as the regenerating beech trees possess a smooth gray-white bark that is quite distinct from that of old beech trees which have a dark, thick and gnarled bark. Secondary beech forest occurs on ridges that still support some old mature black beech or hard beech trees.

Secondary hard beech-kamahi forests also occur on ridges. Some of these forests have resulted from the coppicing of kamahi after a hard beech forest has been cut over.

Kamahi-(toro) forests occur on both slope and ridge sites. Kamahi forests occupying ridge sites have developed on what was originally a hard beech or hard beech-black beech site. Although these kamahi forests do not usually contain any beech trees or saplings they are often located next to an undisturbed stand of beech forest. The lack of effective beech forest regeneration on sites that have been fired is a notable feature of the Marlborough Sounds area.

Secondary tawa forest has developed through seral forest in many isolated gullies that are flanked by manuka-kanuka forestlands on the slopes above. Some stands of tawa-mixed broadleaved forest have developed from pre-existing forest that was cut over but not completely eliminated.

Mixed broadleaved forest with a large mahoe, kohekohe and treefern component has developed in valleys and gullies through a number of different successional pathways.

## 2:7 Introduced Mammals and the Vegetation of the Marlborough Sounds

Man has affected the vegetation of the Marlborough Sounds in an indirect manner by his introduction of a number of animal species into the area. In recent years there has been some controversy over the role of introduced mammals in the forests of the Marlborough Sounds (*Arapawa Island Reserve Files, Dept. L. & S.*). Until results are available from enclosure plots which have been established in coastal forests on Arapawa Island any comments upon the evolutionary capacity of the Marlborough Sounds flora to respond to browsing pressure can only be speculative.

The following account is a brief outline of my observations of animal damage to plant communities in the Marlborough Sounds.

Sheep (*Ovis aries*) and cattle (*Bos taurus*) are responsible for damage to forest understories and for depletion of vegetation at forest margins. Sheep are often present in areas of reverting grassland. Red deer (*Cervus elaphus*) and feral pigs (*Sus scrofa*) are present throughout the Sounds. The deer are in low numbers and have little effect upon the vegetation. Pigs are responsible for local areas of disturbance to the forest floor. Usually the areas of pig rooting are fairly small but there has been severe disturbance to the forest floor in the Jacobs Bay Scenic Reserve in Pelorus Sound and the pigs are responsible for the uprooting of a *Donatia novae-zelandiae* herbfield on the summit of Mt Stokes.

Feral goats (*Capra hircus*) are numerous in the Marlborough Sounds. They are responsible for severe damage to the higher altitude forests and for the desecration of the *Chionochloa* grassland and herbfield of Mt Stokes.

Possums (*Trichosurus vulpecula*) are common on the mainland of the Marlborough Sounds. They are responsible for all canopy defoliation of the podocarp/broadleaf, coastal broadleaf and all regenerating broadleaf forests and forestlands. Their activities are not confined to canopies and they exact a high toll on broadleaf saplings and seedlings. They are especially important in virtually eliminating all kohekohe seedlings and saplings in the mainland forests.

## 2:8 Distribution of Vegetation Types in the Marlborough Sounds

A vegetation map of the Marlborough Sounds is presented (Appendix V ). Fifteen vegetation types have been mapped and where applicable they have been arranged in a seral sequence.

The map is based on field observations that ranged from extensive coverage of some areas to limited observations of vegetation cover from a distance. Only areas that were directly observed by the author have been mapped.

The map was drawn up in 1978. The changing nature of plant cover on some private land means that now (1982) areas of land have moved into different vegetation classes, for instance; - areas of fernland and tauhinu scrubland have been converted to radiata pine plantations, - areas of fertile grassland have reverted to low shrubland, - and areas of fernland and low shrubland have been brought into productive pastureland. For the most part these changes involve small areas of land.

An approximate breakdown of the different types of land cover in the Marlborough Sounds is:

Mature indigenous forest - 37% of land area  
 Secondary scrub and forestland - 10% of land area  
 Tall secondary shrubland - 18% of land area  
 Low secondary shrubland and fernland - 12% of land area  
 Reverting unimproved pastureland - 7% of land area  
 Improved pastureland - 11% of land area  
 Exotic forests - 4% of land area  
 Other (cliff vegetation, salt marsh,  
     subalpine communities, exposed rock) - 1% of land area  
     (after Duckworth *et al.* 1976).

CHAPTER THREEField and Laboratory Methods3:1 Preliminary Fieldwork

The initial part of the research programme was undertaken in the winter of 1976 and consisted of a survey of most of the reserves in the readily accessible areas of the Maritime Park. Vegetation notes were made consisting of lists of species presence with details of main species abundance and contribution to the canopy. Vegetation profiles and soil profiles were noted at a number of the sites. This reconnaissance furnished a working list of most of the successional plant communities that were present in the inner Marlborough Sounds. Soil samples were taken from a number of sites and transported to the laboratory where their soil texture and soil reaction (pH) were recorded.

### 3:2 Site Location

It was desired to select sites that would encompass the geographical range of successional lowland forest ecosystems in the Marlborough Sounds Maritime Park. There were four main constraints on this ideal being achieved. The main restraint was transport to sites. Most sites were situated where they could be reached by road transport (Goulter Bay) or by regular mail boat services (Endeavour Inlet - Resolution Bay, Cockle Cove, Ngaruru Bay). It proved possible also to hire launches for transport to Blumine Island and to Catherine Cove on D'Urville Island. Another restraint on site location was to try and minimise environmental variables affecting a successional sequence. Sites were favoured if a number of successional communities were located near to each other. The safety factor had also to be considered, as for the greater part of the field work I was alone. The final restraint was to try and locate sites with a fairly well known vegetation history or land use regime; this latter requirement was not always satisfied.

### 3:3 Sample Collection

#### 3:3:1 Vegetation:

Data was collected to provide information on the structure and composition of secondary successional communities and mature, undisturbed communities. The analysis of the population structure of the forest and shrubland communities is a well established technique in the study of forest succession (Daubenmire 1968). Usually this technique is accompanied by the analysis of the stand age of the communities sampled (stand-age analysis) for the evaluation of successional trends. It is possible to determine the successional trends from D.B.H.-distribution analysis alone (Buchholz and Pickering 1978, Zedler and Goff 1973). Both approaches were employed in this study.

#### Quadrat Analysis:

Plot size: Sampling was conducted in different sized quadrats for different vegetation types. The chosen plot sizes were required to show less than a 10% increase in the number of new species encountered for a 10% increase in plot size.

Four stand plot sizes were used:

- a) 10 m x 5 m in brackenland and shrubland
- b) 10 m x 15 m in forestland and scrubland
- c) 10 m x 30 m in beech forest, kohekohe forest and mixed coastal species forest
- d) 10 m x 40 m in rimu/tawa and tawa forest.

Basal areas and densities of trees, shrubs, saplings and seedlings were calculated from species counts and d.b.h. measurements from the quadrat data and expressed on a per hectare basis.

D.B.H. measurements were made on all specimens that were of a diameter of 2 cm and greater. Multi-stemmed trees were treated as separate entities. Basal areas were grouped into the following three size classes for each stand:

- a) small trees 3-20 cm<sup>2</sup>
- b) trees 20-100 cm<sup>2</sup>
- c) very large trees > 100 cm<sup>2</sup>

Densities of common species were grouped into 3 height classes:

- a) seedlings < 30 cm
- b) small shrubs and saplings 30 cm - 1 m
- c) shrubs and saplings 1-2 m but < 2 cm d.b.h.

and into 3 basal area classes:

- d) small trees
- e) trees
- f) very large trees.

Species diversity indices were calculated for all species >30 cm in height for each stand.

#### Point Height Intercept Analysis:

The quantity and distribution of foliage are important structural parameters that are involved in the energy, nutrient and water fluxes through forest ecosystems (Aber J.D. 1979 ). The changes in these parameters with succession were sampled by Point Height Intercept analysis (Park G.N. 1973).

The sampling instrument consisted of a sighting tube with a mirror arranged to give a right angled light path from eyelevel to the vegetation above. Cross hairs were marked on a perspex disc to give a point sight in the foliage. The optical instrument was set in a gimbal and this was placed on top of a metal rod that could be thrust into the ground at each sampling station. For all intercepts below 1.5 m a graduated rod was placed in the ground beneath the cross hairs and the sample heights read off from a marked line along the rod.

The heights at which foliage was intercepted were determined by standard trigonometric means by employing a 3 m or 6 m base line away from the metal rod and using a Suunto hypsometer for the determination of the angles to the intercept points. The species identity, height and vertical thickness of each intercept was recorded for all serai stands. In the undisturbed rimu/tawa, tawa and hard beech forests at Endeavour Inlet where the canopy occurs at heights between 15 and 25 m it was not possible to determine accurately the vertical thickness of an intercept in the canopy and only the top canopy intercept was recorded.



The sample points were selected along several parallel line transects. The direction of the first line transect was derived from random numbers. Intervals between sample stations were adjusted for different vegetation types studied to avoid repetition of similar crown parts:

- a 3 m distance was employed in forest,
- a 1 m distance was employed in shrub and forestland,
- and a 30 cm distance was employed in fern and sedgeland.

The sample size was 200 sampling stations for each site. The treatment and analysis of the P.H.I. data followed Park (1973).

#### Stand Descriptions - Vegetation

Full species listings were made for each stand and its environs. Site descriptions which followed a similar format to that employed by Kelly (1965) were recorded at each site. All observations that bore some relation to the history of the stand were noted, e.g. presence of dead trees, fire scars on trees, stumps and logs from milling activities, charcoal on and in soil, coppicing of trees and shrubs, etc. Observations were also made on the present status of the vegetation with regard to animal presence and damage, canopy form and condition and proximity of seral stands to mature forest seed source. A structural profile sketch of the stand was made.

#### 3:3:2 Site Dating:

##### a) Tree ring analysis

Two methods were employed to count the number of annual rings in the wood of the trees and shrubs present on the sites in order to gain an estimation of the probable age of the vegetation. Young stands of manuka, kanuka, tauhinu, gorse and kamahi were slashed at a sharp angle to the horizontal in the field as near to the base as possible and annual rings were counted on the site. Increment cores were taken from larger trees of manuka, kanuka, kamahi, hard beech and black beech. Manuka and kanuka proved very hard to core due to their very dense wood. All coring was done at approximately 1 m above the base as I did not have the strength to core at lower levels. Increment cores were taken with standard Swedish increment borers of 0.5 cm diameter and barrel lengths of 30.0 cm. Cores were extracted, labelled and stored in plastic drinking straws and transported back to the laboratory in a cardboard container. Cores were prepared for counting by planing with a fresh razor blade in the manner of Druce (1966)

and required a series of sandings through finer and finer grades of glass paper. All cores were mounted permanently on corrugated cardboard. Most cores were able to be counted with the naked eye. All were checked under a low power binocular microscope.

Druce (1957) has outlined the rationale behind ageing the vegetation as opposed to the individual plant and his comments are applicable to this study since the species used for the ageing of the communities are the same with the addition of *Cassinia leptophylla* in this study. A number of samples need to be taken from each community in order to gain a correct figure for the age of the stand. Problems were associated with the coring of some stands that were composed of many twisted and multi-stemmed specimens of manuka and kanuka.

False rings within annual rings are often present in manuka and kanuka from exposed or ridge situations where presumably drought conditions have led to cessation of growth for periods. This adds to the difficulty in accurately counting annual rings and the problem is quite considerable in the cores taken from the larger trees. The ages determined for the plant communities less than 40 years old are considered to be fairly accurate. The ages beyond this are considered to be approximate only. A minimum of 10 trees at each site were used for obtaining vegetation ages. It was estimated that 5 years were required for manuka and kanuka to reach 1 m in height and 10 years for kamahi and hard beech to attain 1 m. These figures were added to the number of annual rings in all estimates of the vegetation age when determined from tree cores.

#### b) Other methods

Where possible information was sought to verify the ages determined by tree ring analysis. Records of fires in reserves were consulted in the files of the Department of Lands and Survey. Residents at Endeavour Inlet and Cockle Cove provided information on the age of some of the younger sites at these locations. Aerial photographs of the Marlborough Sounds were first taken in 1942 and sets of photographs from this time up until 1972 were consulted to check fire and pasture histories of the study sites since 1942.

### 3:3:3 The Forest Floor:

The forest floor in this study was considered to consist of all organic matter lying above the mineral soil that was less than or equal to 0.2 cm in diameter. As such, the forest floor does not include dead wood composed of branches and trunks on the ground, standing dead trees, stumps or larger dead roots.

Numerous studies have stressed the importance of the forest floor to the nutrient cycles of the forest ecosystem (Gosz, Likens and Bormann 1976, Moir and Grier 1969, Reiners and Reiners 1970, Youngberg 1966). However, the majority of studies concerned with the quantification of the weight of organic matter and nutrients held in this compartment of the ecosystem have not been approached in a manner that provides a statistical measure of the large variation that is usually associated with the forest floor.

Grier and McColl (1971) intensively sampled the forest floor of a small Douglas Fir plot and calculated the number of samples required to estimate the weight of the forest floor, the water storage capacity, the Ca, Mg, N, K, Mn, and ash content and the pH of the forest floor within 10% of the mean. Their study showed that at least 30 samples of an area of  $560 \text{ m}^2$  were required to estimate the means of most properties within 10%. Smaller sample areas require many more samples for the same degree of accuracy (Bourn and Brown 1971).

It was not practical to approach this study in such a manner and thus like many other studies this work does not provide a definitive determination of the constituents of the forest floor. The sampling has been designed to try and detect differences in the forest floor between stands and to relate these differences to successional parameters.

The layers of the forest floor were removed from three randomly located quadrats of 30 cm x 30 cm dimensions.

The square was laid out and cut around with a sharp knife. The organic matter of the forest floor was separated into layers where possible. Usually it was possible to separate the undecomposed litter layer (L) from the decomposing fermentation and humus (F and H) layers beneath. All organic matter that could be separated from the mineral soil was collected by careful scraping.

Samples were placed in air tight plastic bags, labelled, sealed and transported to the laboratory. They were dried at 80°C in paper lined metal trays in a forced air oven overnight.

It was not practical to sample a very important component of the forest floor, namely the branches and logs. If the random location of the quadrat fell upon an area over which a branch or log lay then the quadrat was relocated. Hence this study represents the minimum weights of the forest floor.

### 3:3:4 Soil:

Two soil pits were dug at each study site. The pit locations were chosen to encompass the maximum variation in the profile characters at each site. Soil profiles were described (Taylor and Pohlen 1962) to a depth of 30 cm or to the C horizon if located at less than 30 cm.

Soil samples were collected from each horizon of both pits, placed into plastic bags, labelled, sealed and transported to the laboratory as rapidly as possible. Volumetric core samples were also taken from each horizon for bulk density determinations and thence calculation of elemental content of each horizon on a volumetric basis. The field core sample was taken with a stainless steel coring tube of 1 mm wall thickness, 4.8 cm internal diameter and 11 cm length. The core was pushed horizontally into the middle of each horizon on one of the walls of the soil pit and then carved out of the block with a sharp knife. The core was packed into a plastic bag, labelled, sealed and transported to the laboratory.

### 3:4 Sample Size

Forty -six plant communities were sampled for full vegetation, forest floor and soil data. Forty of these communities were composed of secondary successional vegetation, five were of undisturbed mature forest and one was of a slightly disturbed mature forest.

Only two of the three samples of the forest floor per stand were retained for chemical analysis after the dry weights had been determined for all three samples. Initial trials had shown only a small variation in the nutrient concentrations of the separate forest floor layers from any one site. Two hundred and eighty samples of forest floor layers were prepared for chemical analyses. This represents duplicates of the (L) litter and (F and H) litter layers.

Three hundred and thirty six soil samples were prepared for chemical analyses. This represented duplicate analyses of the different soil horizons from both soil pits in each sample stand.

### 3:5 Litterfall and Litter Decomposition Study

A small study was designed to try and understand some of the reasons for the differences in soil nutrient status between common secondary successional vegetation types and also to assess the role of secondary vegetation in the recovery of nutrient status of the soil after forest removal.

The study consisted of a litter fall monitoring and litter bag decomposition exercise conducted in a 25 year old manuka-kanuka stand on a lower slope in the Endeavour Inlet Scenic Reserve and in a tree tutu-wineberry stand of unknown age located in the valley adjacent to the manuka-kanuka stand.

#### 3:5:1 Litterfall Collection:

Litterfall was collected at monthly intervals for 13 months. Collections were in 40 plastic buckets per stand. Each of the buckets had a diameter of 26 cm giving a collecting area of  $531 \text{ cm}^2$  for each bucket which satisfies the recommendation that trap areas should be at least  $400 \text{ cm}^2$  (Andrzejewski, Borowski and Olszewski 1968). The buckets had drainage holes of small diameter to allow for water runoff and to minimise loss of litter through this source. The buckets were randomly placed in both stands. Recording in the manuka-kanuka stand commenced in November 1977 and continued until December 1978. Recording in the tree tutu-wineberry stand commenced in December 1977 and continued to February 1979.

Total litterfall from each bucket and each sampling period was collected and transported to the laboratory where it was dried at  $80^\circ\text{C}$  to constant weight. The litter was then sorted into leaf, twig, bark, fruit and an assorted fine fraction (frass) and weighed in these fractions. The separate fractions for each month were milled and mixed and a subsample was stored in screw top jars ready for chemical analyses.

#### 3:5:2 Litter Decomposition:

Leaves were removed from manuka and kanuka trees and mixed with freshly fallen leaf litter from an area close by the litterfall monitoring site and transported back to the laboratory where they were mixed and airdried. Exactly 20 g of the mixture of leaves and freshly fallen leaf litter were weighed into a 15 cm x 10 cm terylene bag of mesh size 0.7 mm x 0.7 mm and

then sealed with staples. Eighty bags were laid out at the litter collecting sites on the mineral soil horizon near to a collecting bucket, for ease of location. If litter had to be removed to expose the soil horizon then this was replaced over the bags. Six bags were initially removed each month at the beginning of the experiment but as time progressed the terylene bags became subject to weka (*Gallirallus australis australis*) attack and other disturbances and sometimes only 4 or 5 were collected in an intact state.

At each collection the bags were carefully removed from the soil and leaf litter and soil that had covered the bags were gently scraped away as far as possible. The decomposition bags were placed in plastic bags and transported to the laboratory where the bags and contents were oven dried at 40°C. The decomposed litter was carefully removed from each bag and the dried litter weights were measured for each bag. The decomposed samples for each month were then mixed and milled and a subsample was stored in a screw top glass jar for chemical analyses.

A similar procedure was followed for the decomposition of leaf litter study employed in the tree tutu-wineberry litter collection stand. Leaves were removed from the foliage of broadleaved trees and shrubs and mixed with freshly fallen leaves from these same trees and shrubs that were located near to the tree tutu-wineberry collection stand. After air drying in the laboratory exactly 20 g of leaf material were weighed into 15 cm x 15 cm nylon bags of 1.5 mm x 1.5 mm mesh. Collections of and treatment of the decomposed litter was as for the manuka-kanuka site.

The width of the kanuka leaves (1-2 mm) prevented the use of the larger mesh size in the manuka-kanuka decomposition trial. Collections of the tree tutu-wineberry litter from forest floor study sites revealed the presence of a large insect fauna that probably were involved in the initial stage of leaf decomposition (physical degradation) and these would have been excluded from the broadleaf litter if a smaller mesh size had been chosen for this site.

Although it was realised that decay rates of the leaf litters could not be compared quantitatively the study was undertaken to see if trends in decomposition were different at the two sites.

Collections of the decomposition bags were made at the manuka-kanuka site from November 1977-October 1978 and in the tree tutu-wineberry site from January 1978-October 1978. The study was stopped at this time as there

were no recognizable leaf fragments in the decomposition bags at the tree tutu-wineberry site, and the presence of fungal mycelia in the manuka-kanuka decomposing litter was obviously introducing large errors to the decomposition losses.

A large amount of spillage is encountered in the transport of the decomposition bags to and from the study site (Suffling and Smith 1974). Spillage losses were estimated by accurately weighing 20 g of the two types of leaf litter into 12 mesh bags of the appropriate mesh size and carrying the bags to the study sites, laying them on the ground, uplifting them and then transporting them back in plastic bags to the laboratory where they were reweighed and the spillage losses were estimated for each bag. The average percent losses were calculated for both litter types and were employed as a correction factor in the calculation of decomposition rates.



### 3:6 Physical Analysis of Soils

#### 3:6:1 Bulk Density:

The field core sample was transferred to an aluminium liner of identical internal diameter to the stainless core but only of 3 cm length and 45.3 cm<sup>3</sup> volume. The sample was carefully trimmed up flush with the liner. Two or three subsamples were able to be taken from the field core. The bulk density of the soil was calculated after oven drying (105°C) the soil for 24 hours as follows:

$$\text{B.D.} = \frac{\text{weight oven dry soil}}{\text{volume undisturbed soil}} \frac{\text{g}}{\text{cm}^3}$$

The bulk density values in g/cm<sup>3</sup> were employed in all conversions of soil weights and nutrient concentrations to a volume basis.

#### 3:6:2 Treatment of Soil Samples:

The soil samples were air dried in trays as soon as they arrived at the laboratory then they were rolled and sieved and the <2 mm fraction was retained for chemical and soil textural analyses. The <2 mm fraction was stored in screw top lid glass jars.

#### 3:6:3 Soil Texture:

Particle size distribution was carried out in duplicate on all soil samples by employing a modified Bouyoucos method for the determination of the silt and clay fraction. Determination of the fine and coarse sand fractions was by the sieving of the sand fraction left after decanting off the silt and clay suspension (Allen *et al.* 1974).

### 3:7 Chemical Analysis of Soils, Forest Floor, Litterfall and Litter Decomposition Material

#### 3:7:1 Introduction:

All analyses were made in duplicate and the mean was used in calculations. Most of the methods employed follow the New Zealand Soil Bureau Laboratory Methods (Blakemore *et al.* 1972, 1977). The moisture factor was determined on all samples and used in all calculations that report results on an oven dried basis.

#### 3:7:2 Soils

##### a. Determination of soil reaction

The Soil Bureau method was followed employing a soil:distilled water suspension of 1:2.5. Duplicate measurements of pH were made on each sample.

##### b. Determination of organic matter by loss of ignition (L.O.I.%)

Ground soil material was oven dried and weighed in silicon crucibles. The sample was heated over a bunsen burner until completely charred and then ignited at 500°C in a muffle furnace for 1 hour to determine the L.O.I.%.

##### c. Determination of oxidisable carbon

The determinations were made employing the colorimetric technique outlined by Blakemore *et al.* 1977.

##### d. Determination of exchangeable cations and cation exchange capacity (C.E.C.)

Soil Bureau Laboratory methods were followed for the leaching procedures and for the determination of individual exchangeable cations with the exception that separate standards and solutions were prepared for exchangeable sodium determinations without presence of  $\text{SrCl}_2$  (15,000 ppm Sr) as interference occurred in sodium determinations when Sr was present.

Exchangeable calcium and magnesium were determined by atomic absorption spectrophotometry using a Varian AA4 Spectrophotometer. Exchangeable potassium and sodium were analysed by flame emission using a Gallenkamp FH500 flame analyser.

e. Determination of total nitrogen

The semi-micro Kjeldahl method employed by the Soil Bureau was followed.

f. Determination of Truog soluble phosphorus

The top soil horizon from each profile was used for the determination of Truog phosphorus. The method employed by the Soil Bureau was followed.

3:7:3 Forest Floors, Litterfall and Litter Decomposition Material

a. Determination of forest floor reaction

The method employed was the same as that for the soils using a 1:2.5 litter to water ratio.

b. Determination of organic matter by loss on ignition (L.O.I.)

The method employed was the same as for soils.

c. Determination of oxidisable carbon

The Soil Bureau methods were followed employing 0.2 g of finely ground material and employing appropriate sucrose standards.

d. Determination of total calcium, magnesium, potassium and sodium

The dry ashing technique of Metson (1972) was employed and his method was followed for the preparation of the plant ash solutions. Calcium and magnesium were determined by atomic absorption spectrophotometry using a Varian Techtron AA4 spectrophotometer. Potassium and sodium were determined by flame emission on a Gallenkamp FH500 flame analyser.

e. Determination of total nitrogen

The Soil Bureau method was followed (Metson 1972). A micro-Kjeldahl digestion unit was used.

f. Determination of total phosphorus

All litterfall and litter decomposition material and some forest floor material was analysed for total P by the preparation of an ash solution of the plant material and then determining the P absorptiometrically by the vanadomolybdate method (Metson 1972).

## CHAPTER FOUR

### Vegetation Dynamics

"The interpretation of forest structure commonly looks forwards towards what it is becoming - toward some equilibrial or climax state; it is suggested here that historical interpretation is usually more realistic.

A population is more effectively explained as the outcome of past events than as a stage in development towards some end".

- John L. Harper, 1977  
from "Population Biology of Plants"

#### 4:1 Introduction

An indirect approach has usually been adopted by workers investigating forest succession (Knapp 1974, Slatyer 1977). The implicit assumption made in all indirect studies is that different aged vegetation from a number of sites can be ordered into a temporal sequence that reflects the pattern of succession that would occur on any similar disturbed site. Such an approach has failings. The most obvious failing is that there is usually very little certainty that the sites studied are similar. Any number of factors that may have a bearing on the type or rate of succession will probably differ at the study sites. The history of land use prior to disturbance, the proximity to propagule source, soil factors, exposure factors, the degree and extent of disturbance may all differ to some degree at the chosen study areas.

The life span of trees and time required for a succession to pass through a number of seral stages prohibits a direct approach from being undertaken for areas where there are no early records of the vegetation.

The method adopted in the present study was the collection of data from 40 seral communities and the comparison of seral characteristics with characters of adjacent undisturbed forest stands. The vegetation of the undisturbed stands was taken to be representative of the original vegetation of the seral stands prior to the disturbance that initiated succession. Five undisturbed stands were investigated as controls. One other stand had been marginally disturbed and was also treated as a control stand.

A brief vegetation description of the study sites is presented in section 4:2. The seral sites are arranged in a temporal order that relates to the time since the last disturbance suffered by the stand. The age of the vegetation and method of age determination are also presented. Two stands of *Coriaria arborea* - *Aristotelia serrata* forestland were unable to be aged.

The ages assigned to the vegetation of a study stand are the minimum possible ages. The age of the vegetation can only be determined if the pioneer species are still in the community (Druce 1957). If shrubland vegetation has established after a pioneer grassland or fernland sere then the ages obtained from the dating of the shrubs is not a measure of the time since disturbance.

The stands on Blumine Island are possibly examples of this type of succession. The northern and western sides of Blumine Island were farmed intensively up until the mid-1920's. The native vegetation on these two sides of the island was sparse. The island was destocked in the mid 1920's and allowed to revert to second growth (Dept. of Lands and Survey, Reserves Files). The ages of the shrubs from three study sites on the western side of the island lead one to believe that the present vegetation became established in the 1940's. The northern end of the island was occupied by military personnel in the Second World War and the possibility that fires occurred on the western side of the island during this occupation was investigated.

Photographs of the northern end of the island with western views taken in 1943 (Blenheim Office, Lands and Survey Dept.) show that the vegetation of the slopes was mainly grassland with some shrub establishment. There is no evidence to suggest that the western slopes were burnt in the 1940's and it is probable that a grassland sere of some 15-20 years duration preceeded the shrubland sere at the three Blumine Island study sites.

#### 4:2 Description of the Study Sites

##### 4:2a Vegetation and forest-floor characteristics of seral stands

(Study site name and study site name code employed to introduce each stand of vegetation).

##### Howden's Reserve 5, H.R.5

Low *Gahnia pauciflora*-dominated sedgeland. The vegetation possesses an uneven canopy, mean canopy height is 0.25 m with some emergent *Cassinia leptophylla* shrubs attaining 0.6 m. There is a patchy distribution of the sedges and a number of adventive herbs are present as the ground cover. *Nothofagus truncata* and *N. solandri* var. *solandri* stumps and logs are piled near the study area where they were removed by bulldozer. A very shallow litter layer some 1-2 mm thick covers approximately 60% of the surface area and lies directly above the mineral soil. Bare mineral soil is exposed on the remaining surface area where there is no litter or vegetation.

Age of vegetation: 2 years. The vegetation dates from land clearing operations conducted by the Marlborough Electric Power Board in 1975.

##### Ngaruru Bay 5, N.B.5

Low, dense *Leptospermum scoparium* shrubland. It possesses a very uneven canopy ranging from 0.01-2.0 m. Mean canopy height is 0.9 m. *Leptospermum scoparium* dominates the canopy, *Erica lusitanica* and *Pseudopanax arboreus* are also present. Clumps of *Gahnia pauciflora* are interspersed amongst the shrubs. Beneath the canopy there is an open ground floor cover of *Lycopodium volubile*, *Dianella nigra* and scraggy specimens of *Pteridium esculentum*. There are numerous seedlings of *P. arboreus*, *L. scoparium* and *E. lusitanica* on the ground floor. A shallow litter layer < 1 cm deep composed of *L. scoparium* leaves and twigs lies over the mineral soil for the greater area of the plot. Patches occur where there is a thick humus layer beneath the litter layer. There are dead, burnt logs and stumps of *Nothofagus truncata* at the site, some are still standing.

Age of vegetation: 12 years. The vegetation has grown up after a fire on 28 February 1963.

Ten *L. scoparium* were aged at: 8, 10, 10, 11, 11, 12, 12, 12, 12, 12 years by slash method.

##### Ngaruru Bay 6, N.B.6

Low, open *Leptospermum scoparium* shrubland located downslope from N.B.5. The vegetation has a very uneven canopy ranging from 0.01-1.7 m. *L. scoparium* and *Cyathodes fasciculata* are the canopy plants and occur as scattered, scraggy shrubs over an open understorey of *Pteridium esculentum*, *Gahnia pauciflora*, *Blechnum capense* and *Lycopodium volubile*. Numerous seedlings of *L. scoparium* and *Pseudopanax arboreus* are present. A very sparse litter layer < 0.5 cm thick lies directly over the mineral soil.

Age of vegetation: 12 years. The vegetation has grown after a fire burnt down this ridge in February 1963. It appears that the shrubs did not establish rapidly at this site.

Six *L. scoparium* were aged at: 10, 10, 11, 12, 12, 12 years by slash method.

Ngaruru Bay 7, N.B.7

Low, very dense *Leptospermum scoparium* shrubland located downslope from N.B.6. The vegetation has an uneven canopy, the mean height is 1.1 m. Specimens of *L. scoparium* attain 2.6 m. *Cyathodes fasciculata* and *Erica lusitanica* are also canopy constituents but they do not attain the height of *L. scoparium*. The ground cover is dominated by *Pteridium esculentum* and *Gahnia pauciflora* and numerous seedlings of *L. scoparium* and *Pseudopanax arboreus*. Burnt, fallen logs of *Nothofagus truncata* are present in the plot. A litter layer 1 cm deep of *P. esculentum* and *L. scoparium* fronds and leaves overlies a humus layer 2 cm deep.

Age of vegetation: 13 years. This vegetation also dates from the February 1963 fire.

Six *L. scoparium* were aged at: 10, 11, 12, 12, 13, 13 years by slash method.

Endeavour Inlet 5, E.I.5

Decaying *Cassinia leptophylla* shrubland. Very uneven canopy, mean height 0.8 m. *C. leptophylla* is a scraggy emergent above *Pteridium esculentum* and *Anthoxanthum odoratum*. *Weinmannia racemosa* is abundant as seedlings and small saplings. There is a deep litter layer composed of *P. esculentum* fronds and *Cassinia* leaf and twig material overlying the mineral soil. Fallen, charred logs of *Nothofagus truncata* are present in and near the plot.

Age of vegetation: 13 years.

Five *C. leptophylla* were aged at: 10, 10, 12, 13, 13 years by slash method. The *C. leptophylla* were rotting in the centre of the stem.

Endeavour Inlet 6, E.I.6

*Cassinia leptophylla* shrubland. Very uneven canopy, mean height 0.9 m. *Cassinia* is the dominant canopy plant although saplings of *Carpodetus serratus* and *Aristotelia serrata* are present in the canopy. A *P. esculentum* understorey occurs beneath the shrub canopy. A deep litter layer composed of *P. esculentum* fronds and *C. leptophylla* material overlies the mineral soil.

Age of vegetation: 13 years.

Eight *C. leptophylla* were aged at: 9, 10, 11, 12, 12, 12, 13, 13 years by slash method. The *C. leptophylla* were rotting in the centre of the stem.

Endeavour Inlet 1, E.I.1

*Pteridium esculentum* fernland. An uneven canopy around 0.7 m was measured in midwinter. The dense bracken fronds formed an even canopy at 2 m in mid-summer at this site. A few saplings of *Weinmannia racemosa* and *Carpodetus serratus* are present in the canopy. A deep litter layer composed of a loose assemblage of bracken fronds and petioles overlies a fermentation and humus layer of decomposing bracken material. Seedlings of *W. racemosa* are present in the F + H material.

Age of vegetation: 13 years (P. Buzzi pers. comm.).

Endeavour Inlet 2, E.I.2

*Pteridium esculentum* fernland. An uneven canopy with a mean height of 0.7 m was measured in midwinter. Bracken is the canopy dominant but scattered saplings of *Brachyglottis repanda*, *Coprosma robusta*, *Pseudopanax arboreus* and *Leptospermum scoparium* are also present. There is a deep litter and humus layer present composed of bracken fronds and petioles above the mineral soil. *Weinmannia racemosa*, *B. repanda* and *Berberis glaucophylla* seedlings are common in the dense litter layer.

Age of vegetation: 14 years (P. Buzzi pers. comm.).

Endeavour Inlet 3, E.I.3

*Pteridium esculentum* fernland. The vegetation possesses a very uneven canopy as there are a number of shrubs emergent over a bracken canopy at 1.0 m. *Leptospermum ericoides* and *Weinmannia racemosa* are the more common emergents; *Olearia rani*, *Coprosma robusta* and *Eleaocarpus dentatus* are also present. *Blechnum capense* occurs beneath the bracken canopy. There is a deep litter and humus layer present, composed of bracken material, covering the ground floor.

Age of vegetation: 16 years (P. Buzzi pers. comm.).

Sawmill Creek 1, S.C.1

Dense *Pteridium esculentum* fernland with a few scattered broadleaved species emergent over a bracken canopy of 1.5 m. There are very few species beneath the dense bracken canopy. A deep litter and humus layer composed of bracken fronds and stipes covers the mineral soil.

Age of vegetation: 16 years (P. Buzzi pers. comm.).

Resolution Bay 1, R.B.1

Low *Weinmannia racemosa* shrubland. The vegetation has an uneven canopy with a mean height of 1 m. *W. racemosa* and, to a lesser extent, *Leptospermum scoparium* are emergent over an understorey dominated by *Pteridium esculentum* and *Blechnum capense*. *Lycopodium volubile* is present beneath the bracken and *Blechnum*. There is a deep litter and humus layer composed of bracken and *Blechnum* material above the mineral soil.

Age of vegetation: 20 years.

Four *W. racemosa* were aged at: 17, 17, 19, 20 years; one *Leptospermum ericoides* was aged at: 20 years by slash method.

Tawa Bay 8, T.B.8

Low, dense *Leptospermum scoparium* shrubland. The vegetation possesses a very uneven canopy ranging from 0.01 - 3 m. *L. scoparium* is the main canopy plant but some decrepit *Cytisus scoparius* specimens are also present. An understorey is present at 1 m. *Pseudopanax arboreus*, *Coprosma rhamnoides* and *Cyathodes fasciculata* are the main understorey species. The ground flora consists of *Pteridium esculentum*, *Faesia scaberula*, *Blechnum capense* and *Lycopodium volubile*. Seedlings of *P. arboreus*, *Carpodetus serratus*, *Weinmannia racemosa* and *Pittosporum tenuifolium* are common. A shallow litter and humus layer of *L. scoparium* and *C. scoparius* material overlies the mineral soil.

Age of vegetation: 21 years.

Eight *L. scoparium* were aged at: 12, 12, 16, 18, 19, 21, 21 years by slash method. Two decrepit *C. scoparius* were aged at: 9, 9 years by slash method.



Tawa Bay 1, T.B.1

Very dense, young *Leptospermum scoparium* shrubland. The mean canopy height is 0.8 m, some shrubs attain 3 m. The canopy stems are of a spindly form. *L. scoparium* is the canopy dominant, *Weinmannia racemosa* and *Pseudopanax arboreus* are also in the canopy. Beneath the canopy and in canopy openings there is an understorey of *Gahnia pauciflora* and *Cyathodes fasciculata*. There is a ground cover of *Blechnum procerum*, *B. capense* and *Lycopodium volubile*. *W. racemosa* seedlings are present on the forest floor. There are some fallen rotting *Nothofagus* logs on the shrubland floor. There is a litter layer some 2 cm deep composed of *L. scoparium* leaves and twigs.

Age of vegetation: 23 years.

Six *L. scoparium* were aged at: 18, 19, 19, 20, 22, 23 years by slash method.

Tawa Bay 2, T.B.2

Tall, very dense *Leptospermum scoparium* shrubland. The mean canopy height is 4 m, some plants attain 6 m. *L. scoparium* is the most common species in the canopy, but *Olearia solandri* and *Cytisus scoparius* are also present. There is an understorey present from 1-1.5 m consisting of *Cyathodes fasciculata*, *Cyathea dealbata* and *Coprosma rhamnoides*. A number of broadleaved species are present as saplings and seedlings including *Brachyglottis repanda*, *Melicactus ramiflorus*, *Coprosma robusta*, *Aristotelia serrata* and *Pseudopanax arboreus*. The ground floor flora is dominated by *Pteridium esculentum*. There is a litter layer about 2 cm thick composed mainly of *L. scoparium* leaves and twigs overlying a decomposing humus layer 1 cm thick. There are a number of fallen stems of *L. scoparium*, *C. scoparius* and *Cyathodes fasciculata* on the shrubland floor and also one burnt, decomposing *Nothofagus* log.

Age of vegetation: 24 years.

Six *L. scoparium* were aged at: 18, 18, 20, 22, 24, 24 years by slash method.

Tawa Bay 6, T.B.6

Very dense *Leptospermum scoparium* and *Ulex europaeus* shrubland. There is an uneven canopy ranging in height from 1.5 to 3 m. The canopy is composed of spindly specimens of *L. scoparium* with branched *U. europaeus* shrubs interspersed between the *L. scoparium*. An understorey dominated by *Pseudopanax arboreus* and *Weinmannia racemosa* is present at a height of 1 m. The ground cover consists of scattered specimens of *Pteridium esculentum*, *Blechnum capense*, *Uncinia uncinata* and *Gahnia pauciflora*. Seedlings of *Ulex europaeus*, *Weinmannia racemosa* and *Pseudopanax arboreus* are present. There is a deep litter layer (4 cm deep) of *U. europaeus* and *L. scoparium* leaves and twigs and *Pteridium esculentum* fronds overlying a black humus layer some 2 cm deep.

Age of vegetation: 25 years.

Four *L. scoparium* were aged at: 17, 20, 23, 25 years; Two *U. europaeus* were aged at 10, 15 years; one *W. racemosa* was aged at 11 years by slash method.

Blumine Island 2, BM 2

Short, very dense *Leptospermum scoparium* shrubland. The vegetation has an uneven, relatively open canopy. The mean canopy height is 2 m. There are some *Pseudopanax crassifolius* and *P. arboreus* saplings present beneath the *L. scoparium* canopy; *Lycopodium volubile* and scattered specimens of *Pteridium esculentum* form the ground cover. This stand is undergoing self thinning as there are a number of *L. scoparium* stems lying on the shrubland floor. A shallow litter layer composed of *L. scoparium* material lies upon a thin humus layer.

Age of vegetation: 25 years.

Seven *L. scoparium* were aged at: 20, 22, 23, 23, 23, 23, 25 years by slash method.

Cockle Cove 6, C.C.6

Pole *Leptospermum scoparium* shrubland. The mean height of the vegetation is 4 m and the canopy form is open. *L. scoparium* is the canopy dominant; *Weinmannia racemosa* and *Pseudopanax arboreus* are also present in the canopy. There is no real understorey development but small saplings of *Cyathodes fasciculata*, *P. arboreus* and *W. racemosa* are present from 1-3 m. The ground cover is open and consists of a patchy distribution of *Lycopodium volubile*, *Gahnia pauciflora*, *Pteridium esculentum*, *Blechnum capense* and *Lepidosperma australe*. There are also large numbers of *L. scoparium* seedlings on the ground floor and lesser numbers of *W. racemosa* and *P. arboreus*. There is a very shallow (< 0.5 cm) litter layer of *L. scoparium* leaves and twigs lying over the mineral soil. There is an old rotting stump of *Nothofagus truncata* in the plot.

Age of vegetation: 27 years.

Five *L. scoparium* were aged at 19, 22, 25, 27, 27 years, one *W. racemosa* was aged at 27 years, by slash method.

Blumine Island 1, BM 1

Tall, dense *Leptospermum scoparium* shrubland. There is a closed canopy with a mean height of 3.7 m, however some *L. ericoides* are emergent over the *L. scoparium* and attain 6 m. The vegetation has an open understorey of *Pseudopanax arboreus* and *Coprosma rhamnoides* between 1 and 2 m. There is a ground floor cover of *Lycopodium volubile*, *Pteridium esculentum* and seedlings of *Elaeocarpus dentatus*, *Pennantia corymbosa* and *Weinmannia racemosa*. There is a shallow litter layer (< 1 cm deep) of *Leptospermum* spp. leaf and twig material overlying the mineral soil.

Age of vegetation: 30 years

Five *L. scoparium* were aged at: 25, 25, 26, 27, 30 years, one *L. ericoides* was aged at: 18 years, by slash method.

One *L. ericoides* was aged at 40 years by tree core method and is probably a fire survivor although no fire scars were noted on this specimen.

Blumine Island 3, BM 3

*Coprosma robusta* - *Leptospermum scoparium* shrubland. The vegetation has a broken canopy with a mean height of 2.9 m. *Leptospermum ericoides* is present as a canopy emergent. There is an open understorey consisting of scattered specimens of *Pteridium esculentum* and *C. robusta* saplings. There are a number of adventive species present in the ground flora and numerous *C. robusta* seedlings. A very shallow litter layer (< 0.5 cm) overlies the mineral soil.

Age of vegetation: 32 years.

Six *L. scoparium* were aged at: 23, 25, 25, 25, 30, 32 years by slash method.

Cockle Cove 1, C.C.1

Dense *Leptospermum scoparium* shrubland. The vegetation has a fairly even canopy with a mean height of 6 m. Some large canopy trees attain 9 m in height. *L. scoparium* is the most common canopy shrub but *Pseudopanax arboreus* is also represented. In some canopy gaps there are shrubs of *Ulex europaeus*. An open understorey from 1.5-3 m is present. Saplings of *P. arboreus* and *Weinmannia racemosa* are the main constituents of the understorey. There are copious seedlings of *U. europaeus* and *P. arboreus* on the shrubland floor. A number of dead *U. europaeus* and *L. scoparium* stems are present on the forest floor among clumps of *Blechnum capense* and *Dianella nigra*. A decomposing *Nothofagus* stump is present at the study site. A shallow litter layer of *L. scoparium*, *P. arboreus* and *U. europaeus* leaves and twigs overlies a 1 cm deep humus layer.

Age of vegetation: 35 years.

Six *L. scoparium* were aged at: 19, 26, 30, 34, 35, 35 years by tree core method.

Tawa Bay 4, T.B.4

Tall *Leptospermum scoparium* and *L. ericoides* forestland. The mean canopy height is 5 m, some trees attain 8 m. *L. ericoides* is just gaining dominance of the canopy. A large number of *L. scoparium* stems in the plot that have D.B.H. measurements of 2 cm or less are dead or supporting only a small amount of leaves. An understorey around 1 m in height is present. It consists of an open arrangement of *P. arboreus* and *W. racemosa* saplings and *Coprosma rhamnoides*. The forest floor flora consists of scattered specimens of *Blechnum capense* and *Pteridium esculentum* and many seedlings of *P. arboreus* and *W. racemosa*. A very thin litter and humus layer is present.

Age of vegetation: 35 years.

Five *L. ericoides* were aged at: 23, 32, 33, 33, 35 years by tree core methods.

Three *L. scoparium* were aged at: 24, 26, 26 years by tree core methods.

Cockle Cove 5, C.C.5

Pole *Leptospermum scoparium* shrubland. The canopy is uneven and has a mean height of 5.4 m. *L. scoparium* is the sole canopy species. Just below the canopy there is an upper understorey of *Pseudopanax arboreus* saplings. There is an open, low understorey with *Cyathodes fasciculata* and *Olearia rani* present below the *P. arboreus*. The ground floor vegetation is sparse. *Dianella nigra*, *Blechnum capense* and *Gahnia pauciflora* are present along with a number of seedlings of *Elaeocarpus dentatus*, *Coprosma lucida* and *Hedycarya arborea*. A shallow litter composed of *L. scoparium* and *P. arboreus* leaves and twigs directly overlies the mineral soil. There are some burnt *Nothofagus* stumps in the plot and some fallen *L. scoparium* stems with D.B.H. measurements of 3-5 cm.

Age of vegetation: 37 years.

Four *L. scoparium* were aged at: 35, 35, 36, 37 years by tree core method.

Cockle Cove 2, C.C.2

Pole *Leptospermum scoparium* shrubland. The vegetation possesses a relatively even canopy with a mean height of 6 m. There are a few canopy gaps. *L. scoparium* is the sole canopy species. There is an open understorey from 1-3 m with *Pseudopanax arboreus* and *Cyathodes fasciculata* present. The ground flora is sparse and consists of a few scraggy specimens of *Pteridium esculentum* and some *Blechnum capense*, *Dianella nigra* and *Pterostylis alobula*. There are a number of fallen *L. scoparium* stems on the shrubland floor. A deep litter layer (3 cm deep) composed of *L. scoparium* and *P. arboreus* leaves and twigs overlies a shallow humus layer.

Age of vegetation: 40 years.

Five *L. scoparium* were aged at 33, 34, 38, 39, 40 years by tree core method.

Tawa Bay 9, T.B.9

Short *Leptospermum ericoides* tree land located downslope from T.B.8. The mean height of the canopy is 3.6 m but some plants reach 5.7 m. Multi-stemmed *L. ericoides* dominate the canopy; *L. scoparium*, also, is present. There is an open understorey between 0.8 and 1.5 m consisting of *Cyathodes fasciculata*, *Pseudopanax arboreus* and *Coprosma rhamnoides*. Seedlings of *Cytisus scoparius*, *Melicytus ramiflorus*, *Coprosma robusta* and *Pseudopanax arboreus* are the main components of the ground floor vegetation. There are dead stems of *L. scoparium*, *C. scoparius* and *Cassinia leptophylla* on the forest floor amongst a shallow litter of *L. scoparium* and *L. ericoides* leaves and twigs.

Age of vegetation: 40 years.

Six *L. ericoides* were aged at: 33, 35, 37, 37, 37, 40 years by tree core method.

Ngaruru Bay 9, N.B.9

Pole *Leptospermum ericoides* tree land. The vegetation has a very even, closed canopy with a mean height of 7 m. The canopy is dominated by *L. ericoides*. Beneath the canopy there is the beginning of understorey development with *Pseudopanax arboreus* saplings present between 1 and 2 m. *Cyathodes fasciculata*, *Cyathea dealbata* and *Olearia rani* are also present in the understorey. Ground cover consists of many seedlings of *Dysoxylum spectabile*, *P. arboreus*, *Melicactus ramiflorus* and *Pennantia corymbosa*. There is no development of a herbaceous ground cover. Numerous fallen *L. ericoides* stems are present on the forest floor. These fallen stems have D.B.H. measurements around 4 cm. Self thinning of the *L. ericoides* stems is still occurring. A shallow litter layer of *L. ericoides* leaves and twigs lies directly above the mineral soil.

Age of vegetation: 40 years.

Four *L. ericoides* were aged at: 35, 39, 40, 40 years by tree core method.

Ngaruru Bay 3, N.B.3

*Leptospermum scoparium* shrubland. The canopy has a mean height of 4.5 m but some *L. ericoides* and *Pittosporum tenuifolium* reach 6 and 7 m. *Pseudopanax arboreus* is important in the canopy also. An understorey of *Cyathodes fasciculata* and *Pseudopanax arboreus* saplings occurs between 1 m and 3 m. There is a very sparse ground cover with *Lycopodium volubile* and *Dianella nigra* represented. The shrubland floor contains many fallen stems of *L. scoparium*. *L. scoparium* is undergoing self thinning and many specimens with a D.B.H. of 3 cm or less are in poor condition. A thin litter layer of *L. scoparium* and *P. arboreus* leaves and twigs clothes the forest floor and overlies the mineral soil.

Age of vegetation: 43 years.

Six *L. scoparium* were aged at: 32, 39, 40, 41, 43, 43 years by slash method.

Cockle Cove 7, C.C.7

Pole *Leptospermum ericoides* shrubland. The vegetation has a closed, even canopy with a mean height of 7.6 m. *L. ericoides* is the sole canopy dominant. There is a dense understorey with *Cyathea dealbata* and *Olearia rani* and *Pseudopanax arboreus* saplings present from 1 m to 3 m. The ground cover is dominated by *Dianella nigra*, *Gaultheria antipoda* and seedlings of *Pseudopanax arboreus*, *Carpodetus serratus* and *Melicactus ramiflorus*. There are dead stems of *L. scoparium* and *P. arboreus* in the understorey. A thin litter layer (<1 cm thick) of *L. ericoides* leaves and twigs and, in places, *Cyathea dealbata* fronds, overlies the mineral soil. There are decomposing logs and stumps of *Nothofagus* at the site.

Age of vegetation: 45 years.

Five *L. ericoides* were aged at: 33, 40, 42, 45, 45 years by tree core method.

Ngaruru Bay 8, N.B.8

Degenerating *Leptospermum ericoides* forestland. The vegetation has a very uneven, broken canopy. Although the mean height of the canopy is 4.5 m some *L. ericoides* attain 12.8 m. *Pseudopanax arboreus* and *Olearia rani* form a low canopy in the *L. ericoides* gaps. There is a relatively dense understorey present between 1 and 3 m consisting of *P. arboreus*, *O. rani*, *Brachyglottis repanda* and *Coprosma rhamnoides*. The ground flora consists of scattered clumps of *Gahnia pauciflora* and *Uncinia uncinata* and seedlings of *Melicytus ramiflorus*, *Coprosma robusta* and *P. arboreus*. There is a number of standing dead and fallen *L. ericoides* in the plot. A litter layer some 2 cm thick composed of *P. arboreus* and *L. ericoides* leaves and twigs lies above the mineral soil.

Age of vegetation: 45 years.

Five *L. ericoides* were aged at: 35, 40, 42, 44, 45 years by tree core method.

Ngaruru Bay 1, N.B.1

Tall *Leptospermum ericoides* forestland. The vegetation possesses an uneven canopy that has a mean height of 5.5 m but ranges to 9 m. *L. ericoides* is the most important species in the canopy but *Pseudopanax arboreus* is also present. An understorey composed of *P. arboreus*, *Cyathodes fasciculata* and *Cyathea dealbata* occurs between 2 and 4 m. The ground cover is dominated by *Coprosma rhamnoides*, *Dianella nigra*, scraggy specimens of *Pteridium esculentum* and seedlings of *P. arboreus* and *Olearia rani*. There are standing dead and fallen stems of *L. ericoides* in the plot. Near to the study plot are a few massive *Nothofagus truncata* trees. The forest floor has an incomplete litter cover, approximately 60% of the floor is covered with a 1 cm thick litter of *L. ericoides*, leaves and twigs which in places directly overlies the mineral soil and in other places overlies a mor humus some 3-4 cm thick.

Age of vegetation: 47 years.

Three *L. ericoides* were aged at: 42, 46, 47 years by tree core method.

Cockle Cove 8, C.C.8

Pole *Leptospermum ericoides* forestland. The vegetation has an uneven canopy with a mean height of 5.5 m. *L. ericoides* is the canopy dominant, however, *L. scoparium*, *Pseudopanax arboreus* and *Olearia rani* are also present in the canopy. There is a dense understorey of *Olearia rani*, *Cyathea dealbata* and *P. arboreus* present between 0.5 and 2 m. The ground floor cover consists principally of *Dianella nigra*, *Uncinia uncinata* and seedlings of *P. arboreus*, *M. ramiflorus* and *P. corymbosa*. There is a shallow litter layer of *L. ericoides*, *L. scoparium* and *P. arboreus* above the mineral soil.

Age of vegetation: 48 years.

Five *L. ericoides* were aged at: 43, 44, 45, 45, 48 years by tree core method.



Ngaruru Bay 2, N.B.2

*Leptospermum ericoides* forestland located downslope from N.B.1. The vegetation has an open canopy with a mean height of 6.5 m; some large *L. ericoides* attain 9.5 m. *Pittosporum tenuifolium*, *Weinmannia racemosa* and *L. scoparium* are also in the canopy. A relatively dense understorey of *P. arboreus*, *Cyathodes fasciculata*, *Brachyglottis repanda* and *Cyathea dealbata* is present between 1 and 3 m. The ground floor contains sparse plants of *Lycopodium volubile*, *Uncinia uncinata* and *Dianella nigra*, along with large numbers of *P. arboreus* and *B. repanda* seedlings. The forest floor is covered with a shallow (1 cm deep) litter layer of *L. ericoides* leaves and twigs lying above the mineral soil. There are also fallen stems of *L. ericoides* and *P. arboreus* on the forest floor.

Age of vegetation: 50 years.

Five *L. ericoides* were aged at: 44, 45, 47, 50, 50 years by tree core method.

Cockle Cove 3, C.C.3

Degenerate *Leptospermum ericoides* forestland. The forestland has a very uneven, open canopy. The mean height of the canopy is 7.6 m but some tall *L. ericoides* trees reach 16 m. There is a well developed understorey beneath the tall *L. ericoides*. *Cyathea medullaris*, *Melicytus ramiflorus* and *Pseudopanax arboreus* are common between 5 and 7 m. *Olearia rani*, *Brachyglottis repanda* and *Cyathea dealbata* occur as a lower component of the understorey and are common between 2 and 3 m. The ground floor is covered with *L. ericoides* and *Cyathea* spp. litter and there is little development of a herbaceous flora, although a number of *P. arboreus*, *M. ramiflorus*, *Corposma robusta* and *Dysoxylum spectabile* seedlings are present. Some *L. ericoides* stems have fallen to the forest floor and some dead stems of this species are still standing.

Age of vegetation: 55 years.

Four *L. ericoides* were aged at: 45, 52, 53, 55 years by tree core method.

D'Urville Island 1, D'Urv.1

Open *Leptospermum ericoides*/*Dysoxylum spectabile*-*Melicytus ramiflorus* forestland. The canopy is dominated by *L. ericoides* and has a mean height of 6.9 m, some large *L. ericoides* reach 14 m in height. There is a well developed understorey dominated by *Pennantia corymbosa*, *Dysoxylum spectabile* and *M. ramiflorus* saplings and *Cyathea dealbata*. The understorey is present between 1 and 4 m. The ground floor vegetation is dominated by mats of *Blechnum filiforme* and *Phymatosorus scandens* and clumps of *Uncinia uncinata* and *Ctenitis glabella*. There are numerous seedlings of *M. ramiflorus* and *P. arboreus* on the forest floor. There is a very thin litter layer (0.25-0.5 cm in depth) composed of *L. ericoides*, *M. ramiflorus* and *D. spectabile* leaves and twigs lying above the mineral soil.

Age of vegetation: 58 years.

Six *L. ericoides* were aged at: 45, 50, 52, 55, 57, 58 years.

D'Urville Island 2, D'Urv.2

*Leptospermum ericoides* forestland located on a ridge directly above D'Urv.1. The vegetation possesses a rather uneven canopy with a height of 6.2 m and is dominated by *L. ericoides*. *Pseudopanax arboreus* and *Weinmannia racemosa* occur to a lesser extent in the canopy. There is an open understorey present between 1 and 5 m, *P. arboreus* and *W. racemosa* are common species in this height range. *Cyathodes fasciculata* is common around the lower limits of the understorey. The ground cover is open and provides for only 60% cover of the forest floor. The ground flora consists of scraggly specimens of *Pteridium esculentum* and some *Lycopodium scariosum* and *Uncinia uncinata*. There is a thin litter layer present in places and this consists of *L. ericoides*, *W. racemosa* and *P. arboreus* leaf and twig material. This thin litter overlies a deep (F and H) layer that consists of a matted network of humus material, roots and mineral soil. There are a number of dead *L. ericoides* stems on the forest floor and a decomposing *Nothofagus* trunk.

Age of vegetation: 58 years.

Four *L. ericoides* were aged at: 45, 55, 55, 58 years by tree core method.

Goulter Bay 1, G.B.1

Tall, degenerate *Leptospermum ericoides* forestland. The vegetation possesses a very uneven, broken canopy. The mean canopy height is 9.1 m but some large *L. ericoides* attain 17.8 m. Beneath the large *L. ericoides* the canopy is composed of *Pseudopanax arboreus*, *Olearia rani*, and *Cyathea dealbata*. There is a dense understorey occurring between 1 and 5 m. The main species in the understorey are *P. arboreus*, *Coprosma australis*, *Cyathea dealbata*, and *O. rani*. A number of lianes are present including *Metrosideros perforata*, *M. fulgens*, *Ripogonum scandens*, *Passiflora tetrandra* and *Clematis australis*. The ground flora is, in the main, composed of *Uncinia uncinata* and seedlings of *P. arboreus*, *Coprosma* spp., *Dysoxylum spectabile* and *Melicytus ramiflorus*. There are a number of dead *L. ericoides* stems on the forest floor and some dead standing stems of *P. arboreus* and *Olearia rani*. A few of the larger *L. ericoides* have degenerate canopies and are dying back. There is a shallow litter of *L. ericoides* and *P. arboreus* leaves and twigs and *Cyathea dealbata* fronds overlying the mineral soil.

Age of vegetation: 70 years.

Four *L. ericoides* were aged at: 64, 68, 69, 70 years by tree core method. Some cambial rot was evident under the thick bark.

Endeavour Inlet 7, E.I.7

*Weinmannia racemosa* forestland. The forest possesses an uneven canopy, the mean height is 6.8 m. Some *W. racemosa* reach 12.8 m. *Cyathea medullaris* and *Olearia rani* are also present in the canopy. From 1-3 m there is an understorey of *Cyathea dealbata* and saplings of *Melicytus ramiflorus* and *Dysoxylum spectabile*. The ground flora is sparse and consists of clumps of *Blechnum discolor* and *Asplenium polyodon*. One of the large *W. racemosa* trees is coppicing at its base. There is a litter layer of *W. racemosa* leaves and *Cyathea* fronds that is 1.5 cm in depth; this overlies a 1 cm deep (F and H).

Age of vegetation: 70 years.

Nine *W. racemosa* were aged at: 55, 56, 56, 63, 65, 66, 68, 70, 70 years by tree core method.



Tawa Bay 5, T.B.5

Regenerating coastal broadleaf forest. Old *Leptospermum ericoides* present in canopy reaching 10.5 m. The stand possesses a very uneven canopy with *Melicytus ramiflorus*, *Macropiper excelsum* and *Cyathea dealbata*, the other main canopy trees, occurring between 5 m and 8 m. An understorey with *M. excelsum*, *Coprosma australis* and *Brachyglottis repanda* occurs between 2 m and 3 m. The ground flora consists mainly of *Blechnum filiforme*, *Uncinia uncinata* and *Microlaena avinnacea*. Seedlings of *M. excelsum*, *Pseudopanax arboreus* and *M. ramiflorus* are common. Many fallen *L. ericoides* are lying on the forest floor and some dead ones are still standing. Live *L. ericoides* are riddled with insect holes and show rotting of the cambial layer under the thick bark.

There is a shallow litter layer (< 1 cm deep) of *L. ericoides*, *M. ramiflorus* and *B. repanda* leaf and twig litter overlying the mineral soil although there is a deeper litter layer of *Cyathea* fronds and stipes near each tree fern.

Age of vegetation: 70 years.

Three *L. ericoides* were aged at: 65, 68, 70 years by tree core method.

Endeavour Inlet 4, E.I.4

*Weinmannia racemosa*-*Myrsine salicina* forest situated at the upper limit of the lowland forest. The canopy has a mean height of 6 m although some *W. racemosa* trees reach 12 m. *Myrsine salicina* shares the canopy with *W. racemosa* and a few *Pseudopanax arboreus* attain the canopy. The forest has an open understorey from 1-4 m. The main components of the understorey are *Pseudowintera axillaris*, *M. salicina*, *Coprosma australis*, *Cyathea smithii* and saplings of *Melicytus ramiflorus* and *Beilschmiedia tawa*. Epiphytes and lianes are abundant in this forest; the more common are *Tmesipteris tannensis*, *Grammitis billardieri* and *Metrosideros fulgens*. The ground floor vegetation is dominated by moss species, *Hymenophyllum* species, *Blechnum discolor*, *Metrosideros fulgens* and *Uncinia uncinata*. A litter layer of *W. racemosa* and *M. salicina* leaves and twigs overlies a 1.5 cm deep humus layer. There are a number of decomposing *Nothofagus* stumps in the plot and some of the large *W. racemosa* trees have arisen as coppice stems.

Age of vegetation: 84 years.

This forest dates from the removal of trees on a ridge during antimony mining operations in this area during the 1890's. Evidence of the bench track that ran from the head of Endeavour Inlet over the hill to Port Gore was noted at this site.

Four *W. racemosa* were aged at: 76, 80, 81, 84 years, one nearby *Nothofagus truncata* was aged at 89 years, another one could not be dated accurately as the rings on the tree cores were quite indistinct.

4:2b Vegetation and forest-floor characteristics of control sitesNgaruru Bay 4, N.B.4

Coastal broadleaf forest with a dense *Dysoxylum spectabile* canopy at 10 m and with some *Beilschmiedia tawa* and *Elaeocarpus dentatus* emergent above the *D. spectabile* at 16 m. A number of species are present in the canopy including *Pittosporum eugenoides*, *Myrsine salicina*, *Leptospermum ericoides*, *Melicactus ramiflorus*, *Laurelia novae-zelandiae*, *Carpodetus serratus* and *Cyathea medullaris*. There is an upper understorey between 4 m and 10 m dominated by *D. spectabile*; between 1 m and 4 m *D. spectabile* and *C. dealbata* dominate. The ground flora is rich in ferns; *Blechnum filiforme* is the most common, *Asplenium bulbiferum* spp. *bulbiferum* and *Phymatosorus scandens* are frequent. Seedlings of *Alectryon excelsum* and *D. spectabile* are common on the forest floor. Lianes are a feature of the stand; *Ripogonum scandens* is the most common, *Parsonsia heterophylla*, *Freycinetia baueriana* ssp. *banksii* and *Metrosideros diffusa* are also present.

A shallow litter some 1 cm thick of *B. tawa*, *D. spectabile* leaves and *Cyathea* fronds overlies the mineral soil.

In an early report on Ngaruru Bay (Lands and Survey Reserve Files) there is mention that a small settlement of one or two houses was present at the head of the bay in 1906. Five acres of cleared land were behind the houses. The rest of the bay was in a near pristine state.

Part of this stand may date from the time of the abandonment of the clearance. Further beyond the stand (up the main valley of the bay) there is no sign of human disturbance to the forest as large *B. tawa* and *E. dentatus* trees are present. This stand would thus appear to be located at the very edge of the forest clearance that was noted in 1906. The stand contains very large specimens similar to those present in the undisturbed regions of the bay as well as large trees of the light-demanding *L. ericoides* that would appear to date from the time of abandonment of the clearance.

Howden's Reserve 1, H.R.1

Tall, virgin *Nothofagus truncata* forest. The forest possesses an even canopy that ranges from 21 to 23 m. *N. truncata* dominates the canopy; there is one tree of *N. solandri* var. *solandri* that reaches the canopy in the stand. An open understorey of *Weinmannia racemosa*; *Myrsine salicina* and *M. australis* is present between 4 m and 7 m. Between 50 cm and 2 m there is a lower understorey present. *Cyathodes fasciculata* is the commonest shrub in the lower understorey; saplings of *Elaeocarpus dentatus*, *Myrsine salicina* and *Pseudopanax arboreus* are also present. A number of lianes are present in the forest; *Clematis forsteri*, *Metrosideros fulgens* and *M. perforata* are common. There is a sparse ground floor cover provided by *Asplenium oblongifolium*, *Uncinia uncinata*, *Blechnum discolor*, *Phymatosorus diversifolius* and seedlings of *N. truncata*.

A 1 cm deep litter layer of *Nothofagus* leaves and twigs overlies a shallow mor humus. The humus layer varies in depth from 0.5 cm to 2 cm and consists of a tight mat of decomposing organic matter interwoven with mycelia.

Howden's Reserve 2, H.R.2

Tall, virgin *Beilschmiedia tawa* forest. The forest has a close canopy at 15 m although there are some emergent *Dacrydium cupressinum* and *Laurelia novae-zelandiae* above the canopy. *Cyathea medullaris* and *Melicactus ramiflorus* are also present in the canopy. A tall understorey is present and is dominated by *Cyathea dealbata*, *Dysoxylum spectabile* and saplings of *B. tawa*. The ground cover is dominated by the creeping ferns *Hymenophyllum demissum* and *Blechnum filiforme*. Lianes and epiphytes are common in the forest. *Muehlenbeckia australis*, *Metrosideros perforata*, *M. diffusa*, *Parsonsia heterophylla* and *Ripogonum scandens* are common lianes. *Griselinia lucida*, *Lycopodium billardieri* and *Collospermum hastatum* are common epiphytes in this forest. Seedlings of *B. tawa*, *D. spectabile*, *L. novae-zelandiae* and *Elaeocarpus dentatus* are common on the forest floor. There is a shallow (< 0.5 cm) litter layer of *B. tawa* leaves and *Cyathea* spp. fronds lying above a shallow to moderately well developed (up to 2 cm in places) humus layer.

Howden's Reserve 3, H.R.3

Tall, virgin *Nothofagus truncata* forest with an even canopy around 24 m in height. There are a few canopy gaps present. *N. truncata* dominates the canopy but *N. solandri* var. *solandri* is present also. There is an open understorey with *Weinmannia racemosa* reaching 4 m and scattered *Cyathea dealbata* around 2-3 m. Beneath these are shrubs of *Cyathodes juniperina* and small saplings of *N. truncata*. Many seedlings of *N. truncata* are present on the forest floor and on fallen, decaying *N. truncata* logs. The rest of the ground flora is sparse and consists of scattered clumps of *Dianella nigra*, *Asplenium flaccidum* and *Uncinia uncinata*. There is a deep litter of *N. truncata* leaves overlying a very deep (up to 13 cm thick) mor humus layer of decomposing leaf litter intermeshed with mycelia.

Howden's Reserve 4, H.R.4

Tall, virgin *Dacrydium cupressinum*/*Beilschmiedia tawa* forest. *B. tawa* and *Elaeocarpus dentatus* form an open canopy at 13 m. *D. cupressinum* is present as an emergent above this canopy and reaches 30 m. There are frequent canopy gaps in this forest. A tall understorey is present around 7 m; *Weinmannia racemosa*, *E. dentatus*, *Olearia rani* and *Myrsine salicina* are the common species in this stratum. A lower understorey is present from 2-3 m; *Cyathea dealbata*, *Dysoxylum spectabile* saplings and *B. tawa* saplings are common at this level. There is almost total cover of the forest floor by *Metrosideros diffusa* and *Hymenophyllum demissum*. A number of ferns are present through this mat of creeping plants, included among these are: *Asplenium oblongifolium*, *A. polyodon*, *Blechnum discolor*, *Phymatosorus scandens*, *B. filiforme* and *Rumohra hispida*. The lianes, *Freycinetia baueriana* ssp. *banksii*, *Ripogonum scandens* and *Clematis forsteri* are common in the forest. A shallow litter layer (< 1 cm deep) of *B. tawa* and other broadleaved species leaves and twigs lies directly over the mineral soil horizon.

Cockle Cove 4, C.C.4

Virgin *Dysoxylum spectabile* coastal forest. The forest has a close, even canopy around 10.5 m, although some trees reach 13.7 m. *Dysoxylum spectabile* is the main canopy tree, there is one *Elaeocarpus dentatus* also in the canopy. A few large trees of *Melicytus ramiflorus* and *Pennantia corymbosa* are present just below the *D. spectabile* canopy. There is a dense understorey between 1 m and 3 m consisting of *M. ramiflorus* and *D. spectabile* saplings, *Cyathea dealbata* and *Macropiper excelsum*. The ground floor is completely covered by a mat of *Blechnum filiforme* and *Phymatosorus scandens*. A number of lianes are present including *Ripogonum scandens*, *Clematis forsteri* and *Freycinetia baueriana*. A very shallow litter layer of *D. spectabile* leaves overlies a network of *B. filiforme* rhizoids which are intergrated with the top centimetre of mineral soil.

Two stands were unable to be aged with any degree of confidence. These two stands are located in narrow valleys and are dominated by *Coriaria arborea*, a species that does not form distinct annual growth rings. Although nearby vegetation on the slopes above the two stands could be aged these ages could not be used as an indication of the age of the *Coriaria* dominated stands since the vegetation in the valley may have survived fires that swept the slopes and ridges above.

Tawa Bay 3, T.B.3

Tall *Coriaria arborea*-*Aristotelia serrata* forestland. The vegetation has a fairly even canopy with a mean height of 7.3 m. Some of the tall *C. arborea* and *A. serrata* reach 11 m. There is an open understorey from 3 m to just below the canopy. The common species in the understorey are *Cyathea medullaris*, *Melicytus ramiflorus* and *Brachyglottis repanda*. The ground cover is incomplete and is dominated by leaf litter. There is a sparse distribution of a few ferns including; *Pneumatopteris pennigera*, *Ctenitis velutina*, *Blechnum capense* and *B. chambersii*. There are also seedlings of *M. ramiflorus* and *Hedycarya arborea* on the ground floor. The mineral soil is exposed in many places. There are dead *C. arborea* trees in the stand. The live *C. arborea* specimens are all very large, many of their limbs have fallen off and all possess large amounts of rotten wood. A shallow litter of *A. serrata* and *C. arborea* leaves and twigs and *C. medullaris* fronds overlies the mineral soil directly at places where the litter is present.

Tawa Bay 7, T.B.7

Moderately-tall *Coriaria arborea*-*Aristotelia serrata* forestland. The vegetation has a fairly even canopy with a mean canopy height of 5 m. *Fuchsia excorticata* is present in the canopy but makes only a small contribution to crown cover. The forestland has a low, open understorey between 1 m and 2 m. *Melicytus ramiflorus* and *Cyathea medullaris* are the commonest understorey species. There is a scattered ground floor cover consisting of *Pteridium esculentum* and *Paesia scaberula* and seedlings of *M. ramiflorus*, *Pennantia corymbosa* and *Hedycarya arborea*. There is a shallow litter layer (< 1 cm) of *C. arborea*, *A. serrata* and *Cyathea medullaris* leaves and fronds overlying the mineral soil. Roots of *A. serrata* are located on the surface of the mineral soil.

Table 4:1. Age of Vegetation at Study Sites (for 1976-1977).

(a) Disturbed Stands(b) Undisturbed Stands

Study Site Code	Age (years)	Study Site Code
H.R.5	2	H.R.1
N.B.5	12	H.R.2
N.B.6	12	H.R.3
N.B.7	13	H.R.4
E.I.5	13	C.C.4
E.I.6	13	N.B.4
E.I.1	13	
E.I.2	14	
E.I.3	16	
S.C.1	16	
R.B.1	20	
T.B.8	21	
T.B.1	23	
T.B.2	24	
T.B.6	25	
B.M.2	25	
C.C.6	27	
B.M.1	30	
B.M.3	32	
C.C.1	35	
T.B.4	35	
C.C.5	37	
C.C.2	40	
T.B.9	40	
N.B.9	40	
N.B.3	43	
C.C.7	45	
N.B.8	45	
N.B.1	47	
C.C.8	48	
N.B.2	50	
C.C.3	55	
D'Urv.1	58	
D'Urv.2	58	
G.B.1	70	
E.I.7	70	
T.B.5	70	
E.I.4	84	

(c) Unknown Age Stands

T.B.3

T.B.7

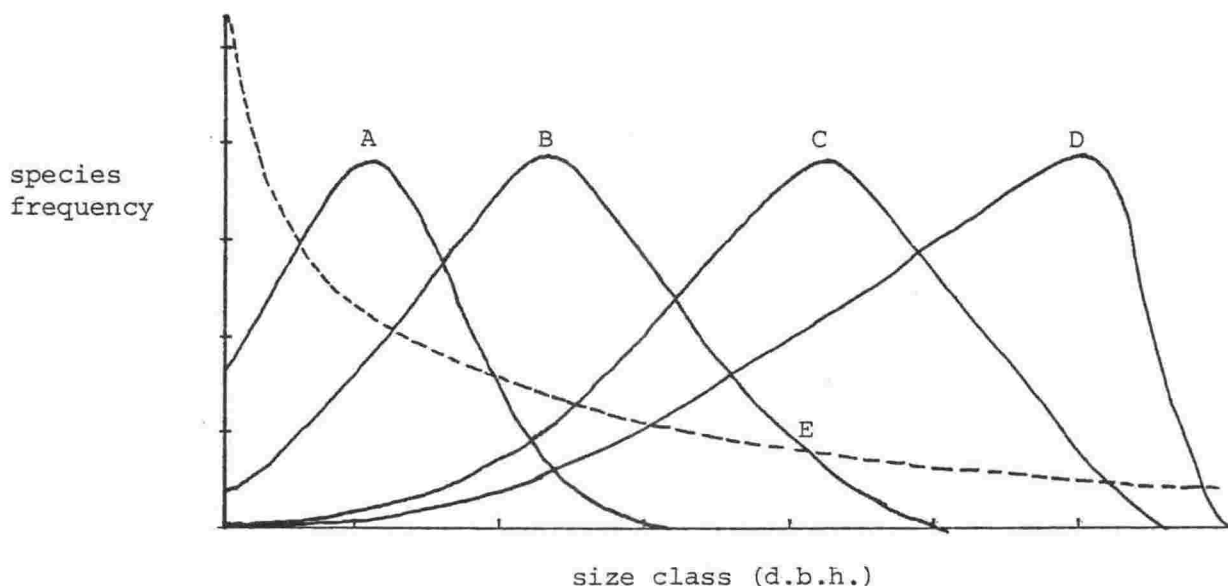
#### 4:3 Successional Pathways

Horn (1975a) asks three questions that are the basis for an understanding of a stand's vegetation dynamics;

- (i) Is the stand under invasion by species that are characteristic of supposedly later stands?
- (ii) Is there a senile population among species that supposedly belong to earlier stands?
- (iii) Are the dominant species begetting their own kind locally?

The approach adopted in an attempt to answer these questions for each stand was to employ the technique of D.B.H. - distribution analysis (Buchholz and Pickering 1978). Successional trends among canopy trees are inferred from the position of the peak in a plot of a species size (height or d.b.h.) class distribution. Considering an ideal stand of vegetation composed of different sized tree or shrub species, a frequency-size class distribution graph would have the form of Fig. 4:1 (modified from Buchholz and Pickering 1978).

Figure 4:1. Idealised Species Frequency-Size Class Distribution for Successional Stands.



A population with a majority of individuals in small d.b.h. size classes and not replacing itself at a site will exhibit a distribution similar to A. As a population ages and trees grow the pattern of tree distribution changes toward the form of D via a B-C wave-form gradient. A steady-state population with individuals in all size classes often exhibits the reverse-J shaped growth curve (Meyer 1952, Whittaker 1974, 1975) illustrated by curve E.

In a seral community where pioneering shrubs and trees are not replacing themselves other species will exhibit d.b.h.-distribution curves where peaks will occur in size classes smaller than that of the pioneering species once most of the pioneering individuals have grown into larger size classes.

The inference made from this analysis is that the population that peaks in a large diameter size class will be replaced by a population that peaks in a smaller size class. Thus the trend in direction of the succession can be determined for the stand.

Diameter and size class distributions of the most common species in the shrub and forest stands are presented (Figure 4:2 i-xlv, Table 4:2)\*.

A number of qualifications are needed when applying this technique. It is only applicable to sites that are carrying tree or shrub vegetation. Only trees that are capable of reaching the canopy are considered, e.g. *Cyathodes fasciculata* is present in many of the young and middle aged seral stages but it never reaches the canopy in the plots studied in the Marlborough Sounds. The assumption is also made that species that show no recruitment to small size classes at the time of recording will not do so at a later date.

Over half of the successional study stands possess high numbers of dead or dying trees and shrubs. This information on species death is presented in Table 4:3 and has been considered with the d.b.h. stand analysis in the drawing up of the probable successional pathways presented in Table 4:4.

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Large tables and figures are located at the end of Chapter 4 (pp. 140—195).



Table 4:3. Study Sites Possessing Dead and Dying Trees and Shrubs

Study Site	Remarks
E.I.5	<i>Cassinia leptophylla</i> dead and dying.
T.B.8	Dead <i>Cytisus scoparius</i> (one specimen died after 10 years, other specimens rotten, unable to be aged).
T.B.2	Dead <i>C. scoparius</i> , <i>Leptospermum scoparium</i> and <i>Cyathodes fasciculata</i> .
B.M.2	Dead <i>L. scoparium</i> .
C.C.1	Dead and dying <i>L. scoparium</i> , all individuals < 2 cm d.b.h. Dead <i>Ulex europaeus</i> .
T.B.4	Many dead and dying <i>L. scoparium</i> , most < 2 cm d.b.h. Dead <i>C. scoparius</i> .
C.C.5	Dead and dying <i>L. scoparium</i> .
C.C.2	Many dead and dying <i>L. scoparium</i> .
T.B.9	Dead <i>C. leptophylla</i> and <i>C. scoparius</i> .
N.B.9	Dead and dying <i>L. ericoides</i> , most 4-5 cm d.b.h.
N.B.3	Many dead <i>L. scoparium</i> < 3 cm d.b.h.
C.C.7	Dead <i>L. scoparium</i> and <i>Pseudopanax arboreus</i> .
N.B.8	Dead and dying <i>L. ericoides</i> .
N.B.1	Dead <i>L. ericoides</i> , <i>Elaeocarpus dentatus</i> and <i>P. arboreus</i> .
N.B.2	Dead and dying <i>L. ericoides</i> and <i>P. arboreus</i> .
C.C.3	Dead and dying <i>L. ericoides</i> .
D'Urv.1	Dead <i>L. scoparium</i> .
D'Urv.2	Dead <i>L. scoparium</i> and <i>L. ericoides</i> .
G.B.1	A number of dead and dying <i>L. ericoides</i> with 14-20 cm d.b.h., dead <i>P. arboreus</i> and <i>Olearia rani</i> .
T.B.5	A number of dead and dying <i>L. ericoides</i> , rotting of cambial layer noted just under the thick bark, areas of rot are soft to the touch and are pitted. Insects are present in the bark layers and between the bark and cambium.
E.I.4	Dead <i>Myrsine salicina</i> and <i>Nothofagus truncata</i> .
T.B.3	Dead and dying <i>Coriaria arborea</i> trees.



Table 4:4. Probable Successional Trends of Study Sites.



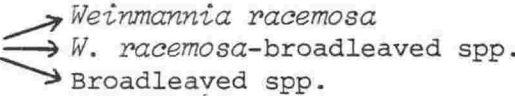
Site	Trends
H.R.5	Direct observation of stand one year after data collected from this site showed that the <i>Gahnia pauciflora</i> dominated site was then carrying a <i>Cassinia leptophylla</i> shrubland. <i>Gahnia pauciflora</i> → <i>C. leptophylla</i> .
N.B.5	<i>Leptospermum scoparium</i> -( <i>Erica lusitanica</i> ) → <i>L. scoparium</i> - <i>Pseudopanax arboreus</i> → <i>P. arboreus</i> ?
N.B.6	<i>L. scoparium</i> → <i>L. scoparium</i> -( <i>E. lusitanica</i> ) → <i>L. scoparium</i> -( <i>P. arboreus</i> ) → <i>P. arboreus</i> ?
N.B.7	<i>L. scoparium</i> → <i>L. scoparium</i> -( <i>E. lusitanica</i> ) → <i>L. scoparium</i> -( <i>P. arboreus</i> ) → <i>P. arboreus</i> ?
E.I.5	<i>C. leptophylla</i> -( <i>L. scoparium</i> ) → <i>C. leptophylla</i> / <i>Weinmannia racemosa</i> → <i>W. racemosa</i> -broadleaved spp. → <i>W. racemosa</i> ?
E.I.6	<i>C. leptophylla</i> → <i>C. leptophylla</i> / <i>Carpodetus serratus</i> -broadleaved spp. → broadleaved spp.?
E.I.1	<i>Pteridium esculentum</i> → broadleaved spp. - <i>W. racemosa</i> / <i>P. esculentum</i> → broadleaved spp. - <i>W. racemosa</i> → <i>W. racemosa</i> ?
E.I.2	<i>P. esculentum</i> → broadleaved spp. - <i>Berberis vulgaris</i> → broadleaved spp. - <i>W. racemosa</i> ?
E.I.3	<i>P. esculentum</i> → <i>W. racemosa</i> / <i>P. esculentum</i> → <i>W. racemosa</i> -broadleaved spp.?
S.C.1	<i>P. esculentum</i> → <i>Aristotelia serrata</i> -broadleaved spp./ <i>P. esculentum</i> (Observation only)
R.B.1	<i>P. esculentum</i> → <i>W. racemosa</i> -( <i>L. scoparium</i> ) → <i>W. racemosa</i> ?
T.B.8	<i>L. scoparium</i> → <i>L. scoparium</i> -( <i>Cytisus scoparius</i> ) → <i>P. arboreus</i> ?
T.B.1	<i>L. scoparium</i> → <i>L. scoparium</i> -( <i>L. ericoides</i> ) → <i>W. racemosa</i> -( <i>P. arboreus</i> )?
T.B.2	<i>L. scoparium</i> → <i>L. scoparium</i> /( <i>Coprosma rhamnoides</i> ) → <i>L. scoparium</i> /broadleaved spp. → broadleaved spp.?
T.B.6	<i>Ulex europaeus</i> -( <i>L. scoparium</i> ) → <i>L. scoparium</i> → <i>L. scoparium</i> - <i>W. racemosa</i> → <i>W. racemosa</i> -( <i>P. arboreus</i> )?
B.M.2	<i>L. scoparium</i> → <i>L. scoparium</i> /broadleaved spp. → broadleaved spp.?
C.C.6	<i>L. scoparium</i> - <i>L. ericoides</i> → <i>W. racemosa</i> - <i>P. arboreus</i> → <i>W. racemosa</i> ?
B.M.1	<i>L. scoparium</i> → <i>L. scoparium</i> / <i>P. arboreus</i> → <i>P. arboreus</i> / <i>C. robusta</i> -broadleaved spp. → <i>P. arboreus</i> -broadleaved spp.?
B.M.3	<i>L. scoparium</i> → <i>L. scoparium</i> / <i>C. robusta</i> → <i>L. scoparium</i> - <i>C. robusta</i> → <i>C. robusta</i> -broadleaved spp.?
C.C.1	<i>L. scoparium</i> / <i>Cyathodes fasciculata</i> → <i>Pseudopanax arboreus</i> / <i>C. fasciculata</i> → <i>Weinmannia racemosa</i> / <i>C. fasciculata</i> ?

Table 4:4 Continued.

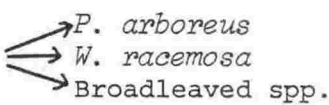
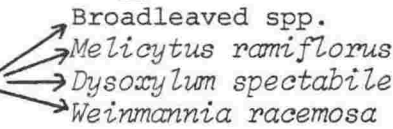
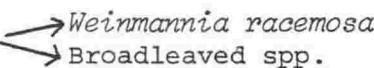
Site	Trends
T.B.4	<i>Leptospermum ericoides</i> - <i>L. scoparium</i> → <i>L. ericoides</i> → <i>L. ericoides</i> / <i>P. arboreus</i> → <i>P. arboreus</i> ?
C.C.5	<i>L. scoparium</i> → <i>P. arboreus</i> / <i>C. fasciculata</i> → <i>P. arboreus</i> - <i>Coprosma robusta</i> -( <i>Elaeocarpus dentatus</i> ) → <i>E. dentatus</i> ?
C.C.2	<i>L. scoparium</i> → <i>P. arboreus</i> / <i>W. racemosa</i> ?
T.B.9	<i>L. ericoides</i> - <i>L. scoparium</i> -( <i>C. scoparium</i> ) → <i>L. ericoides</i> → <i>L. ericoides</i> - <i>P. arboreus</i> ?
N.B.9	<i>L. ericoides</i> → <i>L. ericoides</i> / <i>P. arboreus</i> → <i>P. arboreus</i> / <i>Melicytus ramiflorus</i> -broadleaved spp. → broadleaved spp.?
N.B.3	<i>L. ericoides</i> - <i>L. scoparium</i> → <i>L. ericoides</i> - <i>P. arboreus</i> → <i>P. arboreus</i> -broadleaved spp.?
C.C.7	<i>L. ericoides</i> → <i>P. arboreus</i> - <i>Cyathea dealbata</i> → broadleaved spp.?
N.B.8	<i>L. ericoides</i> → <i>L. ericoides</i> / <i>P. arboreus</i> - <i>Olearia rani</i> → <i>P. arboreus</i> - <i>O. rani</i> ?
N.B.1	<i>L. ericoides</i> / <i>C. fasciculata</i> → <i>P. arboreus</i> / <i>C. fasciculata</i> → <i>P. arboreus</i> / <i>C. dealbata</i> → <i>P. arboreus</i> -broadleaved spp.?
C.C.8	<i>L. ericoides</i> -( <i>L. scoparium</i> ) → <i>L. ericoides</i> - <i>P. arboreus</i> → <i>P. arboreus</i> - <i>M. ramiflorus</i> → <i>M. ramiflorus</i> ?
N.B.2	<i>L. ericoides</i> → <i>L. ericoides</i> -( <i>L. scoparium</i> ) → <i>L. ericoides</i> - <i>P. arboreus</i> -broadleaved spp. → broadleaved spp.?
C.C.3	<i>L. ericoides</i> -( <i>L. scoparium</i> ) → <i>Brachyglottis repanda</i> → <i>M. ramiflorus</i> - <i>C. dealbata</i> ?
D'Urv.1	<i>L. ericoides</i> → <i>L. ericoides</i> / <i>Dysoxylum spectabile</i> - <i>Pennantia corymbosa</i> → <i>D. spectabile</i> - <i>P. corymbosa</i> → <i>D. spectabile</i> / <i>M. ramiflorus</i> -broadleaved spp.?
D'Urv.2	<i>L. ericoides</i> - <i>L. scoparium</i> / <i>C. fasciculata</i> → <i>L. ericoides</i> / <i>W. racemosa</i> - <i>P. arboreus</i> → <i>W. racemosa</i> - <i>P. arboreus</i> → <i>W. racemosa</i> ?
G.B.1	<i>L. ericoides</i> / <i>C. dealbata</i> → <i>P. arboreus</i> - <i>O. rani</i> -(broadleaved spp.) → broadleaved spp.?
E.I.7	<i>W. racemosa</i> / <i>C. dealbata</i> → <i>W. racemosa</i> - <i>C. dealbata</i> /broadleaved spp. → <i>W. racemosa</i> -broadleaved spp.?
T.B.5	Broadleaved spp.- <i>Cyathea</i> spp. → <i>M. ramiflorus</i> ?
E.I.4	<i>W. racemosa</i> - <i>Myrsine salicina</i> / <i>Pseudopanax arboreus</i> → <i>W. racemosa</i> - <i>M. salicina</i> -( <i>Belischmiedia tawa</i> )?
T.B.3	<i>Coriaria arborea</i> → <i>C. arborea</i> - <i>Aristotelia serrata</i> → <i>A. serrata</i> - <i>M. ramiflorus</i> → <i>M. ramiflorus</i> /broadleaved spp.?
T.B.7	<i>C. arborea</i> - <i>A. serrata</i> → <i>A. serrata</i> - <i>M. ramiflorus</i> → <i>M. ramiflorus</i> -broadleaved spp.?

An arrangement of the stands into three age groups shows that there are a few basic successional patterns common to the study areas.

1. Patterns exhibited by young stands (< 20 years)

- a) *Gahnia pauciflora* + *Cassinia leptophylla*   
 Pastureland   
 Weinmannia racemosa  
 Broadleaved spp.
- b) *Pteridium esculentum*   
 Weinmannia racemosa  
 W. racemosa-broadleaved spp.  
 Broadleaved spp.
- c) *Leptospermum scoparium* ± (*Erica lusitanica*) + *Pseudopanax arboreus*

2. Patterns exhibited by middle aged and older stands (> 20 years)

- a) *L. scoparium*   
 P. arboreus  
 W. racemosa  
 Broadleaved spp.
- b) *Leptospermum ericoides*   
 Broadleaved spp.  
 Melicytus ramiflorus  
 Dysoxylum spectabile  
 Weinmannia racemosa
- c) *Pseudopanax arboreus*   
 Weinmannia racemosa  
 Broadleaved spp.
- d) *Coriaria arborea*-*Aristotelia serrata* + *M. ramiflorus*-broadleaved spp.

The fate of the forests beyond these successional stages is not able to be predicted from stand analysis alone.

The classical hypothesis that colonizers prepare the way for a predictable sequence of species (Clements 1916) is not upheld by this analysis. For different stages of succession studied there is the possibility that the vegetation can develop along 1 to 4 different pathways. A multiple pathway model of succession (Cattellino *et al.* 1979) would appear to offer the most realistic approach to prediction of species composition change in the lowland forest ecosystems of the Marlborough Sounds.

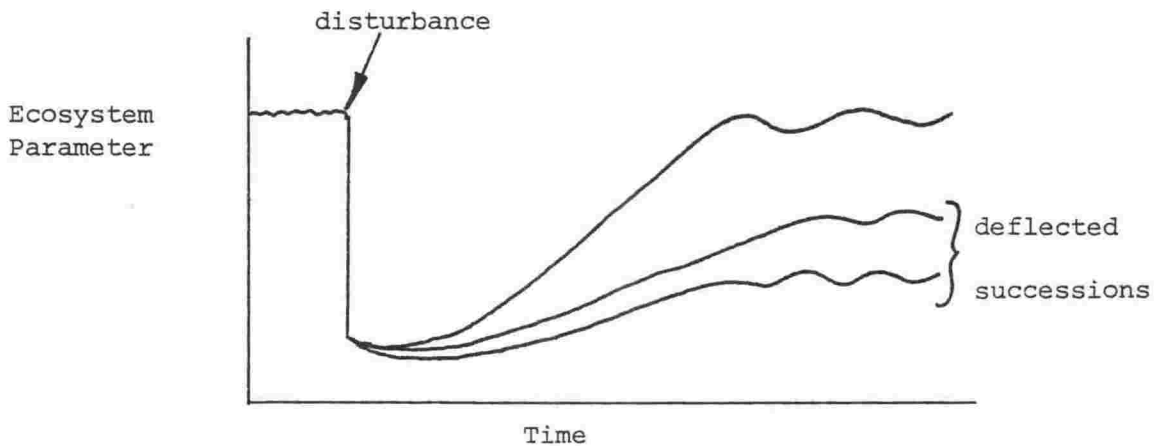
#### 4:4 Structural and Functional Trends in Secondary Succession

Theoretical models of functional and structural changes in the vegetation during succession have been proposed by a number of workers (Odum 1969, Farnworth and Golley 1974, Bormann and Likens 1979). A basic model of secondary succession shows a rapid change in ecosystem parameters immediately following disturbance and then a period of readjustment of the parameters to final levels (about which they may oscillate) similar to the levels prior to disturbance or to new final levels (about which they may also oscillate) that represent a deflected succession.

Vogl (1980) notes that in ecosystems that are not dependent upon frequent disturbances for their maintenance recovery of ecosystem parameters involve classical sigmoid recovery curves of exponential increase where the rate of recovery is slow when compared with perturbation-dependent ecosystems.

Figure 4:3 represents a possible model of steady-state ecosystem response after one disturbance event.

Figure 4:3. Model of Successional Change After One Disturbance Event.



Response of a steady-state ecosystem to a disturbance (much modified from Jordan, Kline and Sasscar 1972).

Bormann and Likens (1979) present a slightly different model for biomass accumulation during woodland succession following clearfelling. These Hubbard Brook workers recognize an initial reorganization phase following disturbance where there is a net loss of biomass. The Hubbard Brook study is one of the most detailed accounts of secondary forest succession yet undertaken and the measured slow recovery of ecosystem biomass may well be a property shared by other ecosystem parameters.

#### 4:4a Changes in Vegetation Structure During Secondary Succession

Structural and compositional parameters have been plotted against a time axis for the Marlborough Sounds study sites. No attempt has been made to try and express a mathematical relationship between the measured parameters and the time axis. Results are presented in Figure 4:4 a-r and Table 4:5a-e (p.155) (p.156)

##### (i) Canopy height

The mean canopy height increases during succession. A levelling off in canopy height occurs around 50 years. The levelling off occurs at a height which is some 33-75% less than that of the undisturbed stands. The early stages of succession possess very uneven canopies (high coefficient of variation of canopy height and sharply descending ranked canopy profiles - Figure 4:4 r) but even canopies are developed fairly rapidly after disturbance. This state may not necessarily be permanent however, for a 70 year old stand (T.B.5) possesses an uneven canopy. The unevenness results from the opening up of the canopy consequent to *Leptospermum ericoides* death. A lower canopy of broadleaved shrubs and trees is exposed in light gaps brought about by the fall of *L. ericoides*.

##### (ii) Crown cover

Crown cover recovers rapidly after disturbance and near complete cover is achieved within 10 years. Litter intercepts were included as crown cover intercepts if no living foliage was intercepted above the litter. The contribution of litter to crown cover is high in the early stages of succession rising to a maximum at 13 years and then declining to low levels by 50 years.

(iii) Vegetation space parameters

The specific vegetation space increases with succession and reaches maximum values similar to the undisturbed stands around 40-50 years. Thereafter the specific vegetation space declines reflecting a less efficient utilization of the potentially available vegetation space (as defined by the maximum canopy height) by the plants in the older seral stands.

Three structural parameters increase linearly with time. Total stand volume (T.S.V.) approaches values of low undisturbed forest by 70 years. No successional stands however approach the stand volumes possessed by tall, undisturbed forest. Total stand foliage (T.S.F.) also increases linearly with time. No seral stand possesses as much foliage as the undisturbed stands. The tall, undisturbed forests possess 2.5 x - 3 x as much foliage as the oldest seral stand studied.

As a measure of the recovery of foliage possessed by the stands during succession the total stand foliage values were expressed as a percentage of the total stand foliage possessed by stand N.B.4. The percent relative vegetation space (R.V.S.) which is a measure of this relationship increases linearly with time. No stands possess total stand foliages as great as N.B.4 although one 70 year old stand (G.B.1) possesses a R.V.S. of 91%. Thirty-five years are required for the vegetation to possess half as much foliage as N.B.4.

The R.V.S., along with some other structural parameters, could not be accurately determined for two of the tall, undisturbed forests. One of the undisturbed stands which could be measured (H.R.3) possesses a total stand foliage twice as great as N.B.4. It is probably a reasonable assumption that the total stand foliage possessed by N.B.4 is a very conservative estimate of the T.S.F. of undisturbed forest stands in the lowlands of the Marlborough Sounds.

(iv) Crown space

Crown space % is high in the initial stages of succession but declines rapidly and by 25 years the vegetation possesses similar values to that of undisturbed forests. Approximately 20% of the volume of the stand is occupied by foliage in mid to late seral stands and in undisturbed forest. Air space % is the complement of crown space %, and thus high levels of air space are attained within 25 years after disturbance.

(v) Foliage distribution

The distribution of total foliage within a stand during succession is illustrated by Figures 4:4 (l-p). The undisturbed stands, from which data were able to be gathered, have variable percentages of their total foliage occurring above 10 m. Values range from 15-90%. Only 5 seral stands have foliage occurring at heights > 10 m. Two stands have around 35% of their foliage occurring above 10 m. No stand less than 45 years old has any foliage above 10 m.

High contributions to total foliage occur in the 3-10 m height class from stands with vegetation older than 25 years. No stand less than 25 years old has any foliage occurring above 3 m. Medium to high contributions to total stand foliage are made by young and middle aged stands. Maximum contributions are made around 20-40 years. Thereafter only about 20% of the foliage occurs in the 1-3 m height class in seral stands and undisturbed forests have 1-10% of their foliage in this height class.

Young stands have most of their foliage occurring below 1 m. The youngest stand H.R.5 has most of its foliage distributed between 0 m and 0.3 m above ground level. By 30 years there is only a small percentage of a stand's foliage occurring below 1 m.

(vi) Basal area

The basal area of the stands increases during succession. Basal areas similar to undisturbed forest ( $50 \text{ m}^2 \cdot \text{ha}^{-1}$  -  $70 \text{ m}^2 \cdot \text{ha}^{-1}$ ) are attained by stands after 35 years. Two stands support very high basal areas, in excess of values attained by undisturbed forests, and it is doubtful if the site can support such high basal areas for any reasonable length of time. These two stands possess vegetation that is just beginning to undergo self-thinning.

(vii) Stem density

The number of stems, greater than 2 cm d.b.h. per hectare, increases in the early stages of succession, reaching a maximum between 25-35 years and thereafter declining to the low levels of 1,000-3,000 stems per hectare that are characteristic of the undisturbed, mature forest.

#### 4:4b Changes in species composition during succession:

The five most frequently encountered species at the study sites were *Leptospermum scoparium*, *L. ericoides*, *Pseudopanax arboreus*, *Pteridium esculentum* and *Weinmannia racemosa*. These five species' contributions to vegetation structure during succession are presented in Figures 4:5 (a-c). Trends in species composition are unclear for many of the study sites. *P. esculentum* makes medium to high contributions to crown cover during the early stages of succession. High levels of crown cover are reached by *L. scoparium* in 20-40 year old vegetation. Lower levels of *L. scoparium* crown cover are possessed by young stands of vegetation (< 20 years since disturbance). *L. scoparium* crown cover declines after 40 years and no contribution to crown cover by *L. scoparium* is made after 58 years.

*L. ericoides* crown cover % reaches a maximum in 40-58 year old vegetation. No contribution to crown cover is made by *L. ericoides* in vegetation less than 20 years old.

Relatively low levels of crown cover are contributed by *Pseudopanax arboreus*. Maximum values are reached between 45-55 years. No vegetation younger than 27 years has *P. arboreus* in the canopy. *Weinmannia racemosa* has low levels of crown cover contribution in all but the two oldest vegetation stands in which it is present.

Species % T.S.F. distributions are similar to their % crown cover distributions.

Maximum contribution to the basal area of a stand is made by *L. ericoides* in 35-60 year old vegetation. A relatively high crown cover % contributed by *L. ericoides* is possessed by the 70 year old G.B.1 stand although only a relatively low *L. ericoides* basal area is recorded from this stand. As old *L. ericoides* trees frequently have very wide, spreading crowns the Point Height method of sampling overestimates the contribution *L. ericoides* makes to the stand structure in the oldest stands.

#### 4:4c Foliage height profiles:

Major changes in point height frequency distributions are illustrated in Figures 4:6 (i-xliii). The frequency distributions of vegetation intercepts occurring in 0.5 m height intervals are plotted. The stands are arranged in order of the age of the vegetation.



The pattern of distribution of foliage recorded in this study is remarkably similar to a pattern described for a successional sequence of vegetation in the northern hardwood forests of North America (Aber 1979). The study by Aber is the only study hitherto undertaken to investigate the vertical development of forest leaf populations during secondary succession. The most obvious change in the distribution of foliage during succession is the change in total height over which the foliage is distributed. The foliage profiles of the stands change from short, concentrated distributions to tall, relatively evenly spread distributions.

The young stands have most of their foliage (including litter) distributed below 50 cm. It is not until the vegetation is about 25 years old that most of a stand's foliage occurs above 50 cm. As the vegetation ages and the canopy increases in height the distribution of foliage begins to be concentrated in the height classes near or just below the mean canopy height. There is very little understorey development under the heavily concentrated canopies. The older stands exhibit a more even distribution of foliage throughout their height profiles, although some stands still show a concentration of foliage around the mean canopy height. Understorey development has begun in the stands older than 45 years. The older seral stands and the undisturbed forests exhibit distinct strata with species foliage being distributed in separate height classes. Understorey vegetation is most developed in stands where most of the canopy species' foliage is distributed above 6 m. In such stands an understorey of broadleaved shrubs and tree ferns begins to develop with most of its foliage concentrated between 2 m and 4 m above ground level.

#### 4:4d Species contribution to foliage height profiles:

The initial stages of succession are characterised by one species contributing large amounts of foliage to the canopy and height classes above 0.5 m. E.I.5 is the only young stand where two species contribute fairly equally to foliage distribution in the tallest height classes.

The study sites dominated by *Leptospermum scoparium* are beginning to regenerate at different rates. T.B.2, at 24 years of age, shows a distribution of *L. scoparium* foliage from 1 m to 6 m with a concentration of foliage around 5-5.5 m, whilst similarly aged stands show concentration of *L. scoparium* foliage at lower heights around 1-3 m.

All of the stands possessing *L. scoparium* and *L. ericoides* and older than 25 years show little or no distribution of *Leptospermum* foliage below 1 m.

Once a complete canopy has formed no *Leptospermum* seedlings, saplings or foliage survive below 1 m.

*Cyathodes fasciculata* and *Pseudopanax arboreus* are the two most common species in the understoreys of the middle aged and older *Leptospermum* stands. *C. fasciculata* is first noted in young vegetation (13 years). *P. arboreus* is also present in young vegetation and during the successions dominated by *Leptospermum* species it rapidly extends its foliage in height although it never outgrows the *Leptospermum* canopy. Sites in the Marlborough Sounds where *P. arboreus* is the canopy dominant seem to owe their origin to the opening up of the *Leptospermum* canopy after the *Leptospermum* trees have reached the limits of their life span or to the destruction of the *Leptospermum* canopy from wind and salt burn (personal observations).

#### 4:4e Species diversity:

"Diversity relationships are to varying degrees interpretable, but they are not formally predictable".

R.H. Whittaker 1977

Different measures of species diversity were employed in this investigation of changes in species diversity during succession. Species diversity is commonly measured by the Shannon-Wiener information content index (Bazzaz 1975, Pielou 1975, Whittaker 1977), usually expressed as

$$H' = -\sum_{i=1}^S P_i \log_e P_i,$$

where  $P_i$  is a relative importance value of one species divided by the total of the importance values of all species in the sample. In this study  $H'$  was more simply calculated from the formula

$$H' = \frac{1}{N} (N \log_e N - \sum_{i=1}^S n_i \log_e n_i),$$

where  $N$  = total population,  $n_i$  = number of individuals of species  $i$  (or cover contribution of species  $i$ ) and  $S$  = number of species in the sample (Lloyd, Zar and Karr 1968).

There are two different components of species diversity (Whittaker 1977, Nicholson and Monk 1974); species richness, which is the number of species present and species evenness or species equitability, which is a measure of the evenness of distribution of individuals or importance values amongst species. It is generally accepted that  $H'$  is sensitive to fluctuations in both species richness and species evenness (Pielou 1966).

There is no agreed index that measures the species evenness component of species diversity (Hulbert 1971, Whittaker 1977).

I have used Pielou's index  $J'$  as a measure of evenness as this index has been employed in two previous studies of plant species diversity changes during secondary succession (Tramer 1975, Nicholson and Monk 1974). Whittaker (1977) has questioned the usefulness of this index. Species evenness is calculated from the formula:

$$J' = H' / \ln S.$$

Species richness as a measure of species diversity is most simply measured as  $S$ , the number of species in a sample of standard size. The measure employed in this study is one suggested by Whittaker (1977) that partially overcomes the limitation in determining  $S$  when different sized samples are used to sample communities of different structure.

Species richness  $d$  was calculated from

$$d = S / \log A, \text{ where } A = \text{sample area.}$$

A concept related to evenness is dominance, a measure of the concentration of the importance value in the highest contributing species. Dominance,  $I_D$ , in this study was calculated from the McIntosh (1967) index,

$$I_D = N - \sqrt{\frac{\sum_{i=1}^S n_i^2}{N}} / N - \sqrt{N}.$$

The parameters employed in this study were; number of species, number of species > 30 cm in height and occurring as individual plants, top hit cover for all stands and top hit cover in different height intervals. The height intervals were arbitrarily delineated at (i) > 3 m height (- canopy and upper understorey), (ii) between 30 cm and 3 m (- lower understorey) and (iii) < 30 cm (- ground floor).

Tramer (1975) in a detailed study of plant species diversity in the very early stages of old field succession found that species diversity (measured in terms of biomass contribution) decreased during succession. Tramer mentioned the importance of pre-abandonment histories of the land in causing site-to-site variations during succession in affecting species diversity levels. In all studies of plant species diversity changes during secondary succession to forest the assumption has been made that vegetation on different sites is representative of one sere (Tramer 1975).

In this study it is reasonable to assume that all sites studied are not part of one sere. The d.b.h.-distribution analysis indicated that the sites could be grouped into different pathways; also in most cases it was not possible to elucidate the pre-disturbance history of each site. Even so, some comparisons can be made between this and other studies of plant species diversity changes during succession.

In contrast to the structural parameters there were few trends clearly evident from the species diversity data during succession, (Table 4:6, Figure 4:7 a-h). Species richness  $R$  is very high and at a maximum for the youngest plot H.R.5. Species richness rapidly falls to a level considerably lower than H.R.5 where 75 species were recorded on a  $50 \text{ m}^2$  area. The undisturbed forest stands possess species richness values similar to most of the seral stands older than 12 years. A few sites have values beyond the range of the majority. The lowest value is possessed by stand S.C.1 which is almost completely dominated by *Pteridium esculentum* only 11 species were recorded from a  $50 \text{ m}^2$  area at this site.

$H'$ ,  $I_D$ , and  $J'$  values calculated for the number of species  $> 30$  cm in height show wide variation during succession. These three diversity indices show similar distribution patterns. Low values are recorded in five plots with vegetation aged between 20 and 25 years. These are plots dominated by close, pole stands of *Leptospermum scoparium* saplings. A number of young plots ( $< 20$  years) possess relatively high diversity index values. There is an apparent increase in diversity values from 25-50 years to values similar to that of the undisturbed stands. One 70 year old plot (G.B.1) has very high  $H'$  and  $J'$  values but the other seral plots  $> 50$  years old have similar values to that of the undisturbed plots.

$H'$ ,  $I_D$  and  $J'$  were unable to be calculated for the number of species for the youngest plot H.R.5 as it was difficult to determine numbers of the clumped grasses, rushes, sedges and stoloniferous herbs that were present at this site.

$H'$  only was calculated for top hit cover values for each stand as a whole and for top hit cover of each height division.  $H'$  (total top hit cover) has a similar distribution during succession to the  $H'$ ,  $I_D$  and  $J'$  values calculated from numbers of species. However, the variation in values exhibited by the undisturbed stands is much wider in the top hit cover data. Three stands, dominated by *Pteridium*, aged at 16 years, have low  $H'$  values for top hit cover.

The only clear, recognizable trend of an increase in species diversity with succession is indicated by the measurement of  $H'$  based on top hit cover data above 3 m. The species diversity of the canopy and upper understorey increases with succession. Three of the undisturbed stands, (H.R.1, H.R.3 and C.C.4), have low canopy and upper understorey cover  $H'$  values as their canopies are dominated by only one species.

There is no discernable trend in  $H'$  with succession for top hit cover values from 30 cm - 3 m and for < 30 cm. A wide scatter in points is evident during succession. This result contrasts with the findings of Loucks (1970) who found an inverse relationship between the diversity of understoreys and the diversity of overstoreys in forest stands in south Wisconsin and a curvilinear change in seedling diversity during succession in mesic forests of Wisconsin.

Species richness does not increase during succession in this study, the youngest stand studied was the richest site encountered. This finding is similar to that reported by Tramer (1975) who recorded highest species richness values in one year old vegetation. High levels of species diversity were found in relatively young stands of vegetation. High species diversity levels for temperate forests are reported as  $H' = 2.0$  and exceptionally high as  $H' = 3.0$  (Monk 1967).

Considering only the stands where *Leptospermum* species are important (open circles) a decline in species diversity is noted in the young pole stands of *Leptospermum scoparium* around 25 years. This decline is due to a low species evenness as species richness does not decline in these plots. The rise in species diversity from the 25 year old *Leptospermum* dominated plots to the 70 year old plots is also due mainly to a rise in species evenness, although the two 58 year old *Leptospermum* dominated plots (D'Urv.1 and D'Urv.2) exhibit an increase in species richness.

Species diversity as measured by  $H'$  is linearly related to species evenness  $J'$ . There is no relationship between  $H'$  and species richness. Whittaker (1977) states that " $H'$  is primarily an equitability measure". Hence  $H'$  and  $J'$  possibly both measure the same phenomenon.

In contrast to a study reported by Nicholson and Monk (1974) who found that seral changes in equitability were limited to the early stages of succession whilst species richness increased during succession, species richness is fairly constant during succession in the present study. The observed trends in species diversity during succession are due mainly to

changes in species evenness (equitability).

The *Pteridium* dominated stands have the lowest cover  $H'$  values and although there is a high degree of evenness amongst the flowering plants in these stands, as measured by  $H'$  for all individual species, there is overall low evenness in the community.

Hence a low species diversity exists only for a short period of time after disturbance to the lowland forests in the Marlborough Sounds. This period extends from the time of establishment of a complete *Pteridium* cover (estimated to be 2-3 years after disturbance based on personal observations of *Pteridium* cover on cleared Power Board tracks) until 25 years after disturbance if the site is *Leptospermum* dominated (and probably less if *Pteridium* dominated in the early seral stage). The low species diversity is not due to low species richness in the early seral stage but results from an unequal distribution of individuals, or cover, between species and one species alone is dominant in the community.

#### 4:5 Vegetation Trends at Control Sites

The broadleaved spp. dominated control stands possess structures that suggest the sites are in a dynamic state. There would appear to be no reason to assume that the present structure and composition of the forests will not change.

At site N.B.4 *Beilschmiedia tawa* is not replacing itself. There are no tall saplings or small trees of *B. tawa* at the site. *Dysoxylum spectabile* would be capable of replacing *B. tawa* as the major canopy species if present conditions were to continue.

A similar pattern of species replacement is seen at the lower stand at Howden's Scenic Reserve, H.R.2, where *B. tawa* is inadequately represented by tall saplings and small trees and where there is an adequate reservoir of small trees of *D. spectabile*, although the number of saplings of *D. spectabile* seems inadequate for later recruitment into the larger size classes.

A different pattern of vegetation replacement is indicated by stand analysis at C.C.4. *Dysoxylum spectabile* does not appear to be capable of maintaining itself as the canopy tree at this site. There is an inadequate supply of small trees of *D. spectabile* in the stand and a dearth of saplings. *Melicytus ramiflorus* and *Pennantia corymbosa* could assume dominance in the canopy if *D. spectabile* fails to replace itself.

At the higher altitude control site at Howden's Scenic Reserve, H.R.4, *B. tawa* is present in good numbers in the tall sapling and small tree size classes and appears capable of maintaining its dominance in the canopy under prevailing conditions. This site was one of the few observed in the Marlborough Sounds where all size classes of *B. tawa* were observed together.

The control *Nothofagus truncata* stands, H.R.1 and H.R.3, show a similar stand structure of low numbers of trees of *N. truncata* in the 20.1-100 cm d.b.h. size class but adequate numbers of saplings and small trees to ensure recruitment to the large tree class if release occurs subsequent to the formation of a new canopy gap.

#### 4:6 Growth Rates

##### 4:6a Height growth

Age and height determinations were made on slashed *Leptospermum scoparium* plants. Age determinations were made on the tallest, single stemmed individuals in a stand. The sample includes trees from 12 study sites (N.B.5, N.B.6, N.B.7, T.B.8, T.B.1, T.B.2, B.M.1, B.M.2, B.M.3, T.B.6, C.C.6 and N.B.3) as well as individual trees growing on the slopes around Endeavour Inlet.

The data are presented as Figure 4:8. Although there is a general trend of increase in height with age there is considerable variation in the height growth rates at different sites in the Marlborough Sounds. For example, a 25 year old tree was 2.7 m high at one site and at another site a 27 year old *L. scoparium* reached 7.2 m.

The average height growth rate of *L. scoparium* in the Marlborough Sounds is  $0.15 \text{ m.yr}^{-1}$  during the age range of 10-45 years. The range of growth rates was from  $0.09 \text{ m.yr}^{-1}$  -  $0.27 \text{ m.yr}^{-1}$ .

The average height growth rate of *L. scoparium* in the Marlborough Sounds is slower than the height growth of *L. scoparium* at the Puketurua Experimental Basin in Northland (32 km N.W. of Whangarei) where the average height growth rate was  $0.2 \text{ m.yr}^{-1}$  (range:  $0.11 \text{ m.yr}^{-1}$  -  $0.37 \text{ m.yr}^{-1}$ ) (Burke 1973). There is a lack of published information on the height growth of *L. scoparium* from other areas in New Zealand.

##### 4:6b Diameter growth

The rate of diameter growth of three species was investigated. There is a significant relationship between age and diameter for canopy trees of the three species, *Leptospermum scoparium*, *L. ericoides* and *Weinmannia racemosa* across the Marlborough Sounds. The relationship is approximately linear for much of the life of the tree (Figure 4:9). At any one site there is wide variation in d.b.h. measurements of *L. scoparium* or *L. ericoides* of the same age. The wide variation in growth rates between individual trees means that size dimensions can only be interpreted as ages in a general manner, for example; of the three species studied, trees of any one diameter may vary in age by some 30 years.



*Leptospermum scoparium* and *L. ericoides* have similar average diameter growth rates for most of their growing period:

Average diameter growth rate of *L. scoparium* =  $0.61 \text{ cm.yr}^{-1}$  (12-54 yrs)

Average diameter growth rate of *L. ericoides* =  $0.59 \text{ cm.yr}^{-1}$  (17-80 yrs)

These two *Leptospermum* species have diameter growth rates twice as fast as that of *Weinmannia racemosa*:

Average diameter growth rate of *W. racemosa* =  $0.29 \text{ cm.yr}^{-1}$  (11-104 yrs)

At sites where both *L. ericoides* and *L. scoparium* are present, *L. scoparium* is the more important (numerically and in terms of basal area contribution) for the first 40 years of the succession, then *L. ericoides* becomes the dominant species.

Stands with both *L. scoparium* and *L. ericoides* present exhibit a greater contribution by *L. ericoides* to the higher layers of foliage from quite an early period.

Although *L. scoparium* and *L. ericoides* canopy trees may show similar diameter growth rates, the extension and height growth of *L. ericoides* would appear to be more rapid than that of *L. scoparium*. *L. ericoides* is also capable of attaining greater heights than *L. scoparium* (Allan 1961) this fact, coupled with the greater longevity of *L. ericoides*, means that a shrubland initially composed of a mixture of *L. scoparium* and *L. ericoides*, where *L. scoparium* may be numerically more important, will in time give way to a *L. ericoides* dominated forestland as the *L. scoparium* succumbs under the *L. ericoides* canopy.

Data on the growth rate of *Weinmannia racemosa* from five different sites in New Zealand has been presented by Wardle (1966). The data is reproduced in a modified form in Table 4:7.

Table 4:7. Diameter Growth Rate Ranges of *Weinmannia racemosa*.  
- after Wardle 1966

Location	Site Characters	Growth Rates (cm.yr <sup>-1</sup> )
Pouakani Forest near L. Taupo	fire induced pole stand 550 m a.s.l.	0.11 - 0.25
Mt Tarawera	primary succession dating from 1886 eruption, single stemmed trees 670 m a.s.l.	0.14 - 0.42
Mt Tarawera	primary succession multi-stemmed shrubs 915 - 1100 m a.s.l.	0.15 - 0.25
Waiho, Westland	secondary succession dating from 1905 stony terrace 183 m a.s.l.	0.08 - 0.33
Wanganui Forest	coppice beneath virgin <i>Dacrydium cupressinum</i> terrace	0.04 - 0.09

Although it is not known if the Marlborough Sounds data is directly comparable with the above growth rates (the height at which the diameter measure was taken is not mentioned in Wardle's paper) it does appear that the diameter growth rate of *W. racemosa* in seral communities in the Marlborough Sounds is fairly rapid.

#### 4:7 Rates of Regeneration

Times for persistence of some seral stages could be estimated from this study. Direct observation of H.R.5 revealed that 1 year was required for a *Gahnia pauciflora* dominated sedgeland to pass into a *Cassinia leptophylla* dominated shrubland.

Ring counts of slashed *C. leptophylla* shrubs indicated that a stand of decrepit and dying *C. leptophylla* shrubland was 13 years old. A nearby stand of vigorous *C. leptophylla* shrubland was also aged at 13 years. No stands of *C. leptophylla* were found in the study areas that were older than 13 years. By 13 years the *C. leptophylla* no longer forms a complete canopy cover over an area and other broadleaved tree and shrub species are beginning to grow up between the *C. leptophylla* plants. *C. leptophylla* was never encountered in the understorey of tall shrubland and forest and it would appear that it succumbs when it is overtopped. The absence of *C. leptophylla* from the Tawa Bay study stands indicates that this species cannot compete once a closed *Leptospermum* canopy is formed. *C. leptophylla* was frequently encountered near the Tawa Bay study sites along track cuttings or in openings in the forestland, hence it is reasonable to assume that *C. leptophylla* was capable of establishing and growing over most of the Tawa Bay area if a closed vegetation canopy was not present. Twenty years would seem to be a reasonable estimate for the persistence of a *C. leptophylla* shrubland as it is absent from vegetation older than 20 years and it exhibits individual and stand degeneration at an earlier age than this.

*Leptospermum scoparium* was recorded in a 70 year old stand of vegetation (T.B.5). By 45 years, however, *L. scoparium* is no longer dominant in forestlands. The percentage contribution of *L. scoparium* to a stand's basal area can be very high in 13-40 year old vegetation, but only small percentage contributions are recorded in vegetation older than 45 years (Figure 4:5 p). *L. scoparium* does, however, contribute significantly to crown cover in 55 year old vegetation and its percentage contribution to the species foliage between 5 and 10 m is high (64%) in the 55 year old stand. Thus, although *L. scoparium* begins to decline in importance in the vegetation around 45 years it can persist and make a low contribution to total vegetation parameters for the next 25 years.

In concordance with other observations (Druce 1957, Kelly 1965, Burrows 1973, Esler 1967) the life span of *L. ericoides* in a succession is longer than that of *L. scoparium* and the contribution to vegetation parameters by *L. ericoides* is greater than that of *L. scoparium* in old stands of *Leptospermum* forestland. The oldest specimen of *L. ericoides* that could be aged from ring counts was estimated to be 80 years old. No attempt was made to try and locate individuals of *L. ericoides* older than this; many of the large specimens of *L. ericoides* proved difficult to core as they were often rotten in the centre of the trunk. The oldest stands of vegetation with a few trees of *L. ericoides* present encountered in this study were aged at 70 years, (G.B.1 and T.B.5). *L. ericoides* makes maximum contribution to a stand's basal area in 40-60 year old vegetation. Thereafter its dominance declines. The contribution made by *L. ericoides* to crown cover and to the stand foliage can still be important in 70 year old vegetation, e.g. at G.B.1, *L. ericoides* - % contribution to crown cover = 67; *L. ericoides* - % contribution to total species foliage = 50.6.

By 70 years surviving specimens of *L. ericoides* are showing signs of degeneration; wood rot is common and the condition of the canopy is ragged and open. It would not take long in these conditions for more shade tolerant species to oust *L. ericoides* in importance.

The following table is offered as estimates of the duration of seral vegetation types in the Marlborough Sounds.

Table 4:8. Duration of Seral Vegetation Types in the Marlborough Sounds (Wassilieff)

Dominant Species	Time of Duration (Years)
<i>Gahnia pauciflora</i>	1
<i>Cassinia leptophylla</i>	20
<i>Leptospermum scoparium</i>	45-55
<i>L. ericoides</i>	70-85+

These duration periods can be compared to a table prepared by Kelly (1968) based on a survey of Queen Charlotte Sound. His study was limited to a simple reconnaissance of the Queen Charlotte Sound area and to "rough estimates" of life spans of the pioneering species. Kelly acknowledges the use of the rough estimate: age of *Leptospermum* spp. =  $1.5 \times$  present good average height (in feet) for sites of moderate conditions (i.e. a height growth rate of  $20 \text{ cm.yr}^{-1}$ ).

Table 4:9. Duration of Various Scrub Types in the Absence of Fire in the Queen Charlotte Sound District.

(Kelly 1968)

Uniform scrub of	Shadier Moist Sites		Sunnier Drier Sites
<i>Cytisus scoparius</i>	10	to	15 years
<i>Pteridium esculentum</i>	15	to	30+ years
<i>Ulex europaeus</i>	20	to	30 years
<i>Erica lusitanica</i>	25	to	50 years
<i>Leptospermum scoparium</i>	35	to	60+ years
<i>Leptospermum ericoides</i>	50	to	100+ years

The estimates provided by Kelly (1968) for the *Leptospermum* species are in close agreement with my own estimates which were based on a more detailed examination of the vegetation composition and structure and site history than that undertaken by Kelly.

Kelly's estimates for the duration of the other vegetation types in his table could not be confirmed completely from my study. I was unable to locate areas of *Pteridium esculentum* and *Erica lusitanica* older than 16 years where the age of the vegetation could be verified. The fact that some 13 and 16 year old stands of *Pteridium* were supporting a "crop of emergents" i.e. sapling trees and shrubs above the *Pteridium* canopy indicates that the change from a *Pteridium* to a shrub cover would soon occur.

4:8 Discussion

The patterns of succession recognized in the present study are similar to successional pathways that have been postulated to occur in the lowland forests of mid-latitude New Zealand.

4:8a Successional pathways to broadleaved forest

Three main pathways were recognized that would lead to a mahoe-broadleaved species forest at Taita, Eastern Hutt Hills (Druce 1957). The sequence of the three pathways:

- (1) kanuka/(bracken)  $\xrightarrow{10}$  kanuka  $\xrightarrow{40}$  kanuka/broadleaved spp.  $\xrightarrow{20}$  mahoe and other broadleaved spp.  $\xrightarrow{20}$  mahoe  $\xrightarrow{10+}$  ?tawa
- (2) tutu and other broadleaved spp.  $\xrightarrow{50}$  mahoe and other broadleaved spp.  $\xrightarrow{20}$  mahoe  $\xrightarrow{30+}$  ?tawa
- (3) bracken  $\xrightarrow{20}$  black tree fern  $\xrightarrow{50}$  mahoe and other broadleaved spp.  $\xrightarrow{20}$  mahoe  $\xrightarrow{10+}$  ?tawa

is similar to that found at the study sites where a mahoe dominated or mixed broadleaved species forest is expected to occur on sites that supported an initial vegetation of kanuka, tree tutu-wineberry or bracken. Sites where black tree fern replaces bracken were not investigated in the present study (due to difficulties with age determinations) but were observed on wet southern slopes in Queen Charlotte Sound. Other bracken sites were observed (but not studied) where the tree fern *Dicksonia squarrosa* was replacing the bracken (for example, on the steep, easterly facing slopes between Scott Point and Marine Head, Queen Charlotte Sound and on the southern slopes at the head of Endeavour Inlet).

At the study sites bracken appears to give way directly to an assemblage of broadleaved species. Esler (1962) reports that there is a relatively rapid succession of *Pteridium* to broadleaved scrub in some twenty years in the Abel Tasman National Park.

The replacement of *Pteridium* dominated vegetation by broadleaved species is a pattern that has been observed at a number of sites in the Wellington region. For example on the Western Hutt Hills *Pteridium* is replaced by *Geniostoma ligustrifolium*, *Melicytus ramiflorus*, *Coprosma robusta* and other broadleaved species in lesser quantities (Croker 1953). Bagnall (1976) described the communities replacing *Pteridium* on moderate slopes at Belmont

(some 2 km south of Croker's study area), *M. ramiflorus* and *Pseudopanax arboreus* are the most important species that initially overtop *Pteridium* although *Cyathea medullaris* is locally important as a successor to *Pteridium*. On steep and stony slopes *Brachyglottis repanda* is the most common emergent above *Pteridium* at Belmont. At Lowry Bay (some 10 km south of Druce's study area at Taita) *P. arboreus*, *B. repanda*, *Pittosporum eugenoides* and *C. robusta* are the main species to replace *Pteridium* (Kelly 1965).

At Taita *Pseudopanax arboreus* is not important as a mid-seral species in the succession toward broadleaved forest. In the Marlborough Sounds *P. arboreus* is a conspicuous component of the broadleaved successions and in this respect the broadleaved successions occurring in the Marlborough Sounds are similar to the successions leading to broadleaved forest on the Western Hutt Hills, at Lowry Bay and on Kapiti Island (Croker 1953, Bagnall 1976, Kelly 1965, Esler 1967, Bagnall 1974).

Two other pathways to broadleaved forest are postulated to occur at the Marlborough study sites that are not represented at Taita. The pathways are: (1) through a *Cassinia leptophylla* pioneering stage directly to a broadleaved community and

- (2) through a *Leptospermum scoparium* pioneering stage either directly to a broadleaved community or through a *Pseudopanax arboreus* mid seral stage prior to the mixed broadleaved stage.

Bagnall (1976) suggests a successional pathway from *C. leptophylla* shrubland directly to broadleaved forest at Belmont that is similar to the pathway suggested for the Marlborough Sounds study sites. On Kapiti Island, however, it appears that *C. leptophylla* is not directly replaced by mixed broadleaved species as a shrubland or forestland dominated by either *Leptospermum scoparium*, *L. ericoides* or *Pseudopanax arboreus* develops prior to the appearance of the mixed broadleaved species as canopy dominants (Esler 1967).

Similarly on Kapiti Island a *L. scoparium* shrubland ultimately develops towards a broadleaved forest (either a *Corynocarpus laevigatus* forest, a *Beilschmiedia tawa* forest or a *Dysoxylum spectabile* forest) through a *P. arboreus* dominated mid-seral stage. This pattern of succession is similar to that occurring at study sites B.M.1 and C.C.5. There are other sites in the Marlborough Sounds where the *P. arboreus* mid-seral state is by-passed and a mixed broadleaved community develops directly through the *L. scoparium* shrubland (for example: at T.B.2, B.M.2 and B.M.3).

#### 4:8b Successional pathways to *Weinmannia racemosa* forest

Of the five main pathways to *W. racemosa* forest postulated to occur at the Marlborough Sounds study sites three involve pioneering or early seral species that are common to similar successional pathways at Taita. They are:

*Pteridium esculentum* → *W. racemosa*

*Leptospermum scoparium* → *W. racemosa*

*Pseudopanax arboreus* → *W. racemosa*

*Pseudopanax arboreus* is an important intermediary in the succession to *W. racemosa* forest at Taita and it appears that a direct succession to *W. racemosa* forest only occurs when the succession begins at a site where resprouted *W. racemosa* is present in the pioneering community (Druce 1957). Although *P. arboreus* is involved in some successions to *W. racemosa* forest at the Marlborough Sounds study sites it is not invariably present and *L. scoparium* shrubland and *P. esculentum* fernland can give way directly to a *W. racemosa* shrub forestland that originates from seed and not from *W. racemosa* resprouts.

*W. racemosa* is not important in the seral communities that have been studied on the western side of the Wellington Fault (that is: on the Western Hutt Hills (Croker 1953, Bagnall 1976), at Wilton Bush (Reid 1935) and on Kapiti Island (Esler 1967)).

Direct succession from *Leptospermum scoparium* shrubland to *Weinmannia racemosa* is reported for fire induced successions in the West Taupo area (Wardle 1966).

An important associate of *Pseudopanax arboreus* and *W. racemosa* at Taita and other seral communities in the North Island is *Knightia excelsa* (Druce 1957, Wardle 1966). *K. excelsa* enters the succession at a fairly early stage at Taita and persists with *W. racemosa* to form a long lasting forest sere. At Taita the factors that govern the distribution of *K. excelsa* are obscure (Druce 1957) and Kelly (1965) admits to being unable to understand the distribution of *K. excelsa* at Lowry Bay where apart from not thriving on dry sites there is no apparent preference of the species for aspect, slope or soil fertility.

The distribution of *K. excelsa* in the Marlborough Sounds is also a puzzle. The species is conspicuous in late successional communities in a very narrow



band across the middle Sounds region. It is prominent on the south facing slopes of Kumutoto Bay, Queen Charlotte Sound and is present across the ridge at Portage. It is present at Weka Point and Goulter Bay Scenic Reserves, Kenepuru Sound and appears again on the eastern slopes of D'Urville Island. *K. excelsa* is essentially absent from the rest of the Marlborough Sounds. (Isolated occurrences have been noted - one seedling was seen in mixed broadleaved forest at Port Underwood Saddle and one sapling was seen in kanuka forestland at Ngaruru Bay, Arapawa Island). At the one study site where *K. excelsa* was recorded, G.B.1, the species was present as seedlings and saplings in and around the study area and appeared to be expanding its range. Where *K. excelsa* is present in the Wellington region it appears to be capable of vigorous and aggressive growth in seral communities and it is hard to understand why it is not a more conspicuous element of the Marlborough Sounds seral vegetation.

Two pathways to *W. racemosa* forest postulated for the Marlborough Sounds do not seem to have any counterpart in the Wellington region. They are:

*Cassinia leptophylla* → *W. racemosa* and  
*Leptospermum ericoides* → *W. racemosa*.

*Cassinia leptophylla* is not important on the Eastern Hutt Hills although it is one of the most common pioneering species of reverting pasture land on the slopes on the western side of the Wellington Fault and on the coastal slopes of the hills above Port Nicholson. In the Wellington region *C. leptophylla* stands are thought to develop towards a mixed broadleaved forest (Esler 1967, Bagnall 1976, 1981) or to a mixed broadleaved forest with some *Nothofagus truncata* and *N. solandri* var. *solandri* (Kelly 1965).

There are no reports in the literature of *Leptospermum ericoides* giving way to *Weinmannia racemosa* in the Wellington region, however, such a pattern has been reported from fire induced successions in the West Taupo forests (Wardle 1966).

#### 4:8c Duration of successions

The duration of pioneering seres of lowland forest appear to be similar between the Marlborough Sounds and the Wellington region. It has not been possible to estimate the duration of later seral stages in the Marlborough Sounds and in fact this information is unknown for most lowland forest successions in New Zealand.

One of the problems in predicting the time for a site to recover to a vegetation type similar in composition to the nearby forests is the lack of information about the lifespan of *Pseudopanax arboreus* dominated forestland. At Taita it has been suggested that it takes 20 years for a *P. arboreus* dominated community to be replaced by *Weinmannia racemosa* forest (Druce 1957). On Kapiti Island there are sites where *P. arboreus* has dominated for several decades with no indication of the next successional change (Esler 1967).

A lowland forest secondary succession has been studied over a period of 84 years at "The Hanger", Tutira Station, Hawkes Bay (Guthrie-Smith 1969, Wassilieff 1980). "The Hanger" consists of a steep slope and a flat terrace above the slope. On the steep slope *P. arboreus* was in a very decadent state in 1980 and was no longer a major constituent of the broad-leaved forestland. The life span of *P. arboreus* on the slope was estimated to be 60 years with approximately 40 years of that as a canopy dominant. On the flat terrace above the slope *Pseudopanax arboreus* shares the canopy with *Pittosporum tenuifolium* and is still in a very vigorous state showing no sign of decline after an estimated 42 years persistence on the flat.

There is thus a need for more detailed information on the life span and time of persistence of *P. arboreus* in the canopy of seral communities before estimates can be made for duration of mid-seral stages of many areas in the Marlborough Sounds.

#### 4:8d Future development of the vegetation

The future of the forests at the study sites is unknown. There is no evidence to suggest that the seral forests of the study sites will necessarily develop into steady-state forests similar in structure and composition to the forests that previously existed on the disturbed site. In fact it is likely that a new type of forest will develop and persist at most of the study sites.

*Weinmannia racemosa* forest comes to dominate on sites that supported *Nothofagus truncata* and/or *N. solandri* var. *solandri* forest prior to disturbance. There is no indication that a *Nothofagus* forest will develop through a *W. racemosa* sere at any of the study sites. *Nothofagus* seedlings or saplings were not observed in any of the seral study stands. At many of the ecotones between undisturbed *N. truncata* forest and seral communities there was little evidence of *N. truncata* regeneration into the seral vegetation. The factors that are disadvantageous to the successful

colonization of New Zealand *Nothofagus* species into seral communities are well known, for example; *Nothofagus* seed is poorly distributed and unless the seed is water distributed downstream it usually does not land beyond the periphery of the seeding tree; seeding is irregular and mast years must coincide with forest clearance for effective colonization; rapid establishment growth of *Nothofagus* does not occur in a shaded environment (Cockayne 1926, Druce 1957).

There are sites in the Marlborough Sounds where there is evidence of effective regeneration of *N. truncata* and *N. solandri* var. *solandri* after forest disturbance. A notable area is on the ridges and spurs of Iwituaroa Scenic Reserve at the southern end of Queen Charlotte Sound. *Nothofagus* regeneration is often conspicuous along track and road cuttings through mature *Nothofagus* forest. There is no doubt that if conditions are suitable (available seed supply and an open site) *Nothofagus* regeneration can be vigorous in the Marlborough Sounds. The regeneration potential of *Nothofagus* into a disturbed community is limited if a closed vegetation establishes rapidly prior to a *Nothofagus* seed year. *Nothofagus* regeneration could occur slowly by peripheral spread from seed trees into a seral community if the seed trees are present.

The pattern of *Nothofagus* regeneration in the lowlands of the Marlborough Sounds is identical to that occurring at Taita where *N. truncata* forest does not develop under any other type of vegetation (Druce 1957). Druce treats the *Weinmannia racemosa* forest as a subclimax\* forest at Taita. The life span of *W. racemosa* is unknown although specimens have been reported that had 250 growth rings (Wardle 1966). For management purposes it is appropriate to recognize that on a human life span scale *W. racemosa* forest will be a persistent forest community in the lowlands of the Marlborough Sounds.

Forest dominated by *Melicactus ramiflorus* or a *M. ramiflorus*-mixed broad-leaved spp. forest is usually a stage in the development to *Beilschmiedia tawa* forest in the Wellington region at sites where *B. tawa* was dominant in the steady-state forest (Croker 1953, Esler 1967, Bagnall 1976). Although there are secondary *B. tawa* stands in the Marlborough Sounds that appear to have developed through a mixed broadleaved forestland or a *Leptospermum ericoides*-mixed broadleaved spp. forestland (for example; in the valleys of the eastern side of Pickersgill Island, at the south-east end of Blumine Island,

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\* Subclimax vegetation is defined as vegetation arrested by factors other than climate for an indefinite period at a stage immediately preceding the climax (Druce 1957).

Island, along an old mining track on the lower slopes at the head of Endeavour Inlet) there was no sign of *B. tawa* establishment at any of the seral study sites.

*Beilschmiedia tawa* has a very large, heavy fruit and the New Zealand Pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*) is the only bird capable of dispersing the seed (McEwen 1978). There would be little opportunity for *B. tawa* seed to arrive in *Leptospermum* dominated communities as suitable pigeon food species are not present. The mixed broadleaved communities contain a number of plant species that are utilised by the pigeon for food (for example; *Fuchsia excorticata*, *Coprosma* spp., *Aristotelia serrata*, *Melicytus ramiflorus*, *Pseudopanax arboreus*) and it could be expected that the seral broadleaved communities of the Marlborough Sounds provide an important food reservoir for the New Zealand pigeon. Although *B. tawa* seedlings were seen in some seral forestlands their occurrence was infrequent and as such was not suggestive that the pigeon was a frequent visitor to the seral forestlands. The author gained the overall impression that pigeons were more frequently encountered when she was working in tall, mature broadleaved forest (podocarp/tawa/broadleaved spp. forest, or tawa/broadleaved spp. forest) than when she was working in seral broadleaved spp. forest. Herbert (1978) has noted that large spreading trees are attractive to pigeons as perching sites and pigeon dropped seed germinates beneath these favoured trees. It is possible that the structure of the developing *Melicytus ramiflorus*-broadleaved spp. forest is unattractive to the pigeon.

An alternative explanation for the absence of *Beilschmiedia tawa* from the seral study sites may be linked to the lack of *B. tawa* regeneration in the undisturbed forests of the Marlborough Sounds. A failure of *B. tawa* to regenerate at suitable sites in recent decades has also been noted in the Wellington region (Atkinson I.E.A. pers. comm., Bagnall 1981). The reason(s) for the failure of *B. tawa* to regenerate is (are) unknown.

Podocarps were infrequently encountered in the seral communities of the Marlborough Sounds. All podocarps are dependent upon birds for seed distribution; the important distributors in the Marlborough Sounds are the New Zealand pigeon and the tui (*Prothemadera novaeseelandiae*). *Podocarpus ferrugineus* was encountered most frequently as a sapling in regenerating communities and is capable of establishing under a closed canopy. *Podocarpus dacrydioides* and *Dacrydium cupressinum* seedlings and saplings were encountered in open *Leptospermum* shrublands but the occurrences were so infrequent that it is not possible to predict how important they will be in the future forests.

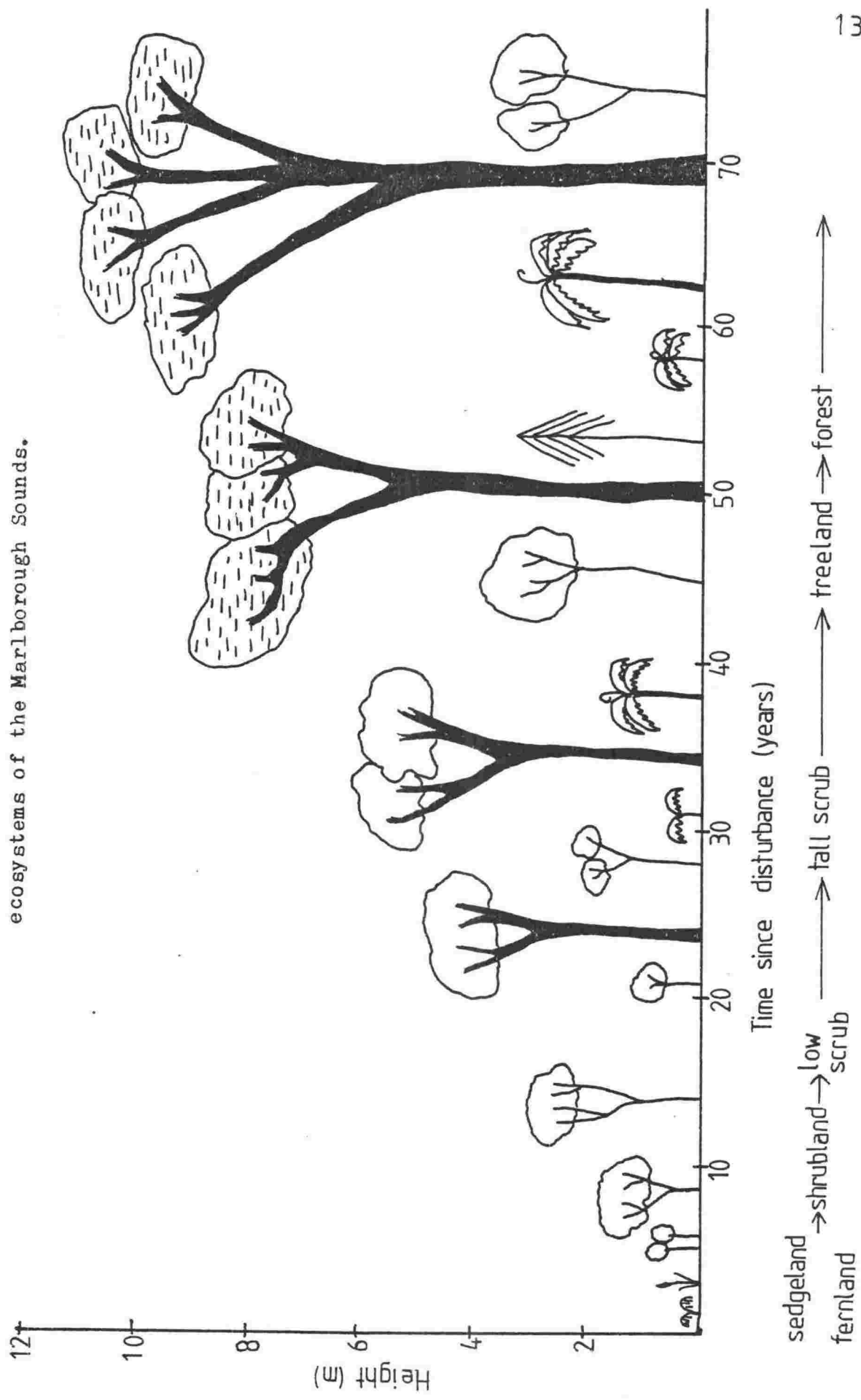
Forestlands dominated by mixed coastal broadleaves can be seral in the development to a *Dysoxylum spectabile* forest. (Esler 1967, Bagnall 1974). A noticeable feature of the *Dysoxylum* forests in the Marlborough Sounds is that effective regeneration of *D. spectabile* is only taking place on the possum (*Trichosurus vulpecula*)-free islands. For example, there is vigorous *Dysoxylum spectabile* regeneration at fertile, coastal sites on D'Urville Island, the southern half of Arapawa Island, Long Island and Pickersgill Island. Vigorous regeneration of *D. spectabile* is not apparent on the mainland of the Marlborough Sounds. The control study sites with a *D. spectabile* canopy or subcanopy (C.C.4 and H.R.2) have an unbalanced population structure with few seedlings and saplings of *D. spectabile* in the understorey. Fruit production of *D. spectabile* was good and regular during the period 1976-1980 in the Marlborough Sounds but there was ample evidence of possum damage to the fruits at mainland sites. Possum browse on the foliage of *D. spectabile* (and other broadleaved species) is noticeable on mainland stands. The possum is responsible for severe damage to young *D. spectabile* saplings. It is extremely doubtful whether the *D. spectabile* forests can maintain themselves in areas of the Marlborough Sounds that support possum populations and the possum appears capable of preventing *D. spectabile* regeneration into seral coastal broadleaved forestland.

A knowledge of the biotic factors that influence the reproduction and growth of the climax forest species of the lowlands of the Marlborough Sounds leads one to conclude that it is rather unlikely that the future forests of the study sites will be similar in structure and composition to the forests that previously occupied the sites. Similarly, some of the mature forests of the Marlborough Sounds appear to be in such a dynamic state that it is probable that the structure and composition of these forests will change quite markedly in future decades.

Although it has not been possible to predict the ultimate course of forest development on disturbed sites a model describing the expected structural changes in the development of the vegetation in the lowlands of the Marlborough Sounds has been developed. The model presents a generalised picture of the course of vegetation development over the time period of 80 years following disturbance.

The model (presented as Figure 4:10) is based on the composite data of height and basal area measurements of all the dated stands of this study. The heights are the minimum canopy heights of the first 10% canopy hits in the ranked P.H.I. canopy profile diagrams. The structural names of the different stages of vegetation follow the criteria of Atkinson 1962 (see

Figure 4:10 Model of secondary succession in lowland forest ecosystems of the Marlborough Sounds.



appendix II).

The model shows that there is rapid structural change in the first twenty years of vegetation recovery. A disturbed site is quickly colonized by vegetation of low stature which develops into, or is replaced by a, complete scrub cover within 20 years. The scrubland stage persists for some 30 years during which an understorey begins to develop. There is a short phase where a treeland dominates the site and in this stage the young trees quickly gain ascendancy over the scrub species. The final and lasting phase of forest is attained some 50 years after the commencement of secondary succession on average lowland sites in the Marlborough Sounds.



TABLE 4:2. Diameter and Size Class Distributions of Species.  
No. of individuals. ha<sup>-1</sup>.

## SERAL STANDS

Stand	Species	Height Class (m)			Basal Area (cm <sup>2</sup> )		
		<0.3	0.3-1.0	1.0-2.0	3.0-20.0	20.1-100.0	>100
		Class 1	2	3	4	5	6
N.B.5	<i>Leptospermum scoparium</i>	137 000	8 000	58 600	2 200	-	-
	<i>Pseudopanax arboreus</i>	86 300	3 000	200	-	-	-
	<i>Cyathodes fasciculata</i>	1 900	6 000	1 000	-	-	-
	<i>Erica lusitanica</i>	26 000	4 000	3 600	-	-	-
	Others	34 000	6 000	200	-	-	-
N.B.6	<i>Leptospermum scoparium</i>	420 000	6 000	3 600	800	-	-
	<i>Pseudopanax arboreus</i>	133 000	6 000	400	-	-	-
	<i>Cyathodes fasciculata</i>	10 000	38 000	-	-	-	-
	<i>Erica lusitanica</i>	1 000	11 000	400	-	-	-
	Others	31 000	8 000	400	-	-	-
N.B.7	<i>Leptospermum scoparium</i>	127 000	5 800	95 000	1 200	-	-
	<i>Pseudopanax arboreus</i>	150 000	1 600	-	-	-	-
	<i>Cyathodes fasciculata</i>	-	17 000	6 200	-	-	-
	<i>Erica lusitanica</i>	11 000	4 500	3 600	-	-	-
	Others	15 000	1 600	200	-	-	-
E.I.5	<i>Leptospermum scoparium</i>	1 300	640	400	200	200	-
	<i>Cassinia leptophylla</i>	3 200	640	3 600	4 400	800	-
	<i>Weinmannia racemosa</i>	51 000	3 200	200	-	-	-
	Others	11 500	4 500	1 400	-	-	-
E.I.6	<i>Cassinia leptophylla</i>	59 000	2 500	200	6 800	4 000	-
	<i>Carpodetus serratus</i>	1 300	1 900	2 000	200	-	-
	Others	59 000	4 500	2 800	-	-	-
E.I.1	<i>Leptospermum scoparium</i>	320	-	-	-	-	-
	<i>L. ericoides</i>	320	-	-	-	-	-
	<i>Weinmannia racemosa</i>	5 400	1 900	-	-	-	-
	Others	2 500	2 900	-	-	-	-
E.I.2	<i>Weinmannia racemosa</i>	>1000 000	1 000	200	-	-	-
	<i>Berberis glaucophylla</i>	>1000 000	1 000	800	-	-	-
	<i>Brachyglottis repanda</i>	500	200	200	-	-	-
	Others	1 000	600	1 200	-	-	-
E.I.3	<i>Leptospermum ericoides</i>	-	-	-	-	-	1
	<i>Weinmannia racemosa</i>	1 800	200	7 000	800	200	-
	Others	7 200	3 000	2 800	-	-	-
S.C.1	<i>Aristotelia serrata</i>	2 866	955	-	-	-	-
R.B.1	<i>Weinmannia racemosa</i>	1 910	8 920	10 600	1 600	200	-
	<i>Leptospermum scoparium</i>	-	-	1 000	600	-	-
	<i>Coprosma lucida</i>	-	-	-	200	-	-
	Others	640	640	-	-	-	-



TABLE 4:2 continued.

## SERAL STANDS

Stand	Species	Height Class (m)			Basal Area (cm <sup>2</sup> )		
		<0.3	0.3-1.0	1.0-2.0	3.0-20.0	20.1-100.0	>100
		Class 1	2	3	4	5	6
T.B.8	<i>Leptospermum scoparium</i>	30 570	5 100	24 200	6 200	1 800	-
	<i>L. ericoides</i>	640	640	-	200	-	-
	<i>Pseudopanax arboreus</i>	2 550	1 280	-	400	-	-
	<i>Cytisus scoparius</i>	238 850	3 190	1 200	1 200	-	-
	Others	57 320	7 000	2 000	-	-	-
T.B.1	<i>Leptospermum scoparium</i>	-	31 000	144 400	3 610	-	-
	<i>Cyathodes fasciculata</i>	2 000	-	5 050	-	-	-
	<i>L. ericoides</i>	1 000	1 000	3 610	-	-	-
	<i>Pseudopanax arboreus</i>	9 000	-	10 110	-	-	-
	<i>Weinmannia racemosa</i>	25 000	10 000	3 610	-	-	-
	Others	1 000	2 000	-	-	-	-
T.B.2	<i>Leptospermum scoparium</i>	-	-	800	2 930	2 130	2 000
	<i>Coprosma robusta</i>	11 000	1 000	270	-	-	-
	<i>C. rhamnoides</i>	269 000	17 000	3 300	-	-	-
	<i>Cyathodes fasciculata</i>	5 000	-	930	-	-	-
	<i>Aristotelia serrata</i>	12 000	1 000	-	-	-	-
	<i>Cytisus scoparius</i>	5 000	2 000	-	-	-	-
	Others	7 000	2 000	-	-	-	-
T.B.6	<i>Leptospermum scoparium</i>	-	-	51 910	8 600	480	-
	<i>Ulex europaeus</i>	51 000	-	1 280	480	1	1
	<i>Weinmannia racemosa</i>	14 650	8 920	1 750	160	-	-
	<i>Pseudopanax arboreus</i>	15 290	-	160	160	-	-
	Others	2 550	-	1 115	-	-	-
B.M.2	<i>Leptospermum scoparium</i>	1 270	1 270	45 600	37 600	1 200	-
	<i>Coprosma robusta</i>	8 920	640	400	-	-	-
	Others	16 560	1 910	1 200	-	-	-
C.C.6	<i>Leptospermum scoparium</i>	345 540	-	22 600	13 600	2 000	200
	<i>L. ericoides</i>	640	640	2 200	200	200	-
	<i>Weinmannia racemosa</i>	32 800	2 550	600	200	400	-
	<i>Pseudopanax arboreus</i>	36 000	6 400	4 000	1 400	-	-
	<i>Cyathodes fasciculata</i>	8 280	1 600	3 200	600	-	-
	<i>Coprosma lucida</i>	2 870	960	-	-	-	-
B.M.1	<i>Leptospermum scoparium</i>	2 230	-	6 670	11 900	3 070	270
	<i>L. ericoides</i>	-	-	-	-	130	-
	<i>Pseudopanax arboreus</i>	93 600	8 300	270	-	-	-
	<i>Cyathodes fasciculata</i>	2 870	4 780	530	-	270	-
	<i>Coprosma robusta</i>	124 000	320	270	-	-	-
	Others	2 550	960	-	-	-	-
B.M.3	<i>Leptospermum scoparium</i>	88 500	-	-	1 600	3 200	-
	<i>Coprosma robusta</i>	1600 000	-	8 000	4 200	1 000	-
	Others	190 000	3 200	-	-	-	-

TABLE 4:2 continued.

## SERAL STANDS

Stand	Species	Height Class (m)			Basal Area (cm <sup>2</sup> )		
		<0.3	.3-1.0	1.0-2.0	3.0-20.0	20.1-100.0	>100
		Class 1	2	3	4	5	6
C.C.1	<i>Leptospermum scoparium</i>	10 800	-	600	15 400	5 600	200
	<i>Pseudopanax arboreus</i>	116 600	13 600	10 000	2 000	1 200	-
	<i>Weinmannia racemosa</i>	2 600	24 000	5 800	400	-	-
	<i>Cyathodes fasciculata</i>	7 000	-	2 000	400	-	-
	<i>Ulex europaeus</i>	195 000	-	-	200	-	-
	Others	23 400	800	200	-	-	-
T.B.4	<i>Leptospermum scoparium</i>	538	3 770	3 500	7 000	2 300	830
	<i>L. ericoides</i>	-	-	830	1 170	2 000	1 170
	<i>Cyathodes fasciculata</i>	1 100	3 770	500	-	170	-
	<i>Pseudopanax arboreus</i>	9 150	10 200	170	-	-	-
	Others	177 500	45 700	-	-	-	-
C.C.5	<i>Leptospermum scoparium</i>	-	-	-	2 800	5 800	800
	<i>Pseudopanax arboreus</i>	24 900	14 700	8 600	5 200	-	-
	<i>Coprosma lucida</i>	38 600	4 150	-	-	-	-
	<i>Cyathodes fasciculata</i>	2 500	2 500	400	600	-	-
	Others	16 500	2 500	-	-	-	-
C.C.2	<i>Leptospermum scoparium</i>	2 600	-	-	13 000	64 000	200
	<i>L. ericoides</i>	-	400	400	-	200	-
	<i>Pseudopanax arboreus</i>	116 000	6 400	5 800	1 200	400	200
	<i>Cyathodes fasciculata</i>	3 600	1 000	200	600	-	-
	<i>Ulex europaeus</i>	56 000	4 400	-	-	200	-
	<i>Weinmannia racemosa</i>	11 200	3 200	2 400	-	-	-
	Others	27 000	3 000	-	-	-	-
T.B.9	<i>Leptospermum scoparium</i>	7 000	10 800	400	600	800	400
	<i>L. ericoides</i>	5 700	-	-	400	1 000	800
	<i>Cytisus scoparius</i>	219 000	16 000	1 400	1 000	200	-
	<i>Cyathodes fasciculata</i>	3 800	7 600	2 000	200	-	-
	Others	190 000	34 000	800	200	-	-
N.B.9	<i>Leptospermum ericoides</i>	-	-	-	400	6 000	1 200
	<i>Pseudopanax arboreus</i>	65 000	38 600	7 800	-	-	-
	<i>Melicytus ramiflorus</i>	39 600	7 000	600	-	-	-
	Others	202 000	14 000	400	-	-	-
N.B.3	<i>Leptospermum scoparium</i>	630	-	200	11 600	4 400	-
	<i>L. ericoides</i>	-	-	-	-	400	200
	<i>Pseudopanax arboreus</i>	422 000	6 400	2 600	1 400	400	200
	<i>Cyathodes fasciculata</i>	1 300	4 500	4 800	1 600	-	-
	Others	60 000	3 000	3 000	200	-	-
C.C.7	<i>Leptospermum scoparium</i>	-	-	-	-	100	-
	<i>L. ericoides</i>	-	-	-	400	1 800	1 500
	<i>Pseudopanax arboreus</i>	32 000	16 000	3 500	500	100	-
	<i>Cyathea dealbata</i>	-	3 800	1 600	-	-	-
	Others	70 000	4 100	500	-	-	-

TABLE 4:2 Continued.

## SERAL STANDS

Stand	Species	Height Class (m)			Basal Area (cm <sup>2</sup> )		
		<0.3	0.3-1.0	1.0-2.0	3.0-20.0	20.1-100.0	>100
		Class 1	2	3	4	5	6
N.B.8	<i>Leptospermum ericoides</i>	1 600	-	-	-	-	600
	<i>Pseudopanax arboreus</i>	196 000	1 600	530	200	1 000	400
	<i>Olearia rani</i>	-	640	400	600	730	130
	<i>Cyathodes fasciculata</i>	1 300	-	330	200	470	60
	Others	63 400	21 000	7 130	70	70	-
N.B.1	<i>Leptospermum ericoides</i>	3 500	-	-	-	130	540
	<i>Pseudopanax arboreus</i>	163 000	1 600	470	270	6 700	200
	<i>Cyathodes fasciculata</i>	960	3 200	2 000	940	540	-
	<i>Cyathea dealbata</i>	-	320	870	-	-	70
	Others	100 500	22 000	7 700	-	-	-
C.C.8	<i>Leptospermum scoparium</i>	-	-	-	200	400	100
	<i>L. ericoides</i>	-	-	-	-	400	500
	<i>Pseudopanax arboreus</i>	5 100	5 700	3 000	100	300	-
	<i>Melicytus ramiflorus</i>	17 200	2 900	1 600	-	-	-
	Others	-	-	700	300	-	-
N.B.2	<i>Leptospermum scoparium</i>	640	-	-	-	130	-
	<i>L. ericoides</i>	1 300	-	-	-	600	1 000
	<i>Pseudopanax arboreus</i>	140 000	16 600	8 200	-	70	-
	<i>Cyathodes fasciculata</i>	-	1 300	740	540	67	-
	Others	260 000	21 000	8 800	-	-	70
C.C.3	<i>Leptospermum scoparium</i>	-	-	-	-	200	130
	<i>L. ericoides</i>	-	-	-	-	130	270
	<i>Brachyglottis repanda</i>	-	320	70	740	740	200
	<i>Cyathea dealbata</i>	2 550	7 400	2 500	-	-	270
	<i>Pseudopanax arboreus</i>	30 900	1 600	900	870	270	130
	Others	19 000	2 550	1 400	400	130	70
D'Urv.1	<i>Leptospermum ericoides</i>	-	-	-	-	250	1 000
	<i>Pennantia corymbosa</i>	3 200	3 800	2 050	150	200	-
	<i>Dysoxylum spectabile</i>	320	1 300	1 250	250	50	-
	Others	37 000	54 000	4 700	-	50	-
D'Urv.2	<i>Leptospermum scoparium</i>	-	-	50	250	550	-
	<i>L. ericoides</i>	-	-	-	450	900	900
	<i>Weinmannia racemosa</i>	-	-	50	700	700	50
	<i>Pseudopanax arboreus</i>	-	-	50	50	100	100
	Others	-	-	2 350	350	250	150
G.B.1	<i>Leptospermum ericoides</i>	-	-	-	-	-	350
	<i>Cyathea dealbata</i>	-	1 100	1 500	-	-	300
	<i>Pseudopanax arboreus</i>	3 400	-	400	100	150	150
	<i>Olearia rani</i>	560	-	3 200	200	450	50
	Others	48 000	4 000	3 350	250	-	-

TABLE 4:2 Continued.

## SERAL STANDS

Stand	Species	Height Class (m)			Basal Area (cm <sup>2</sup> )		
		<0.3	0.3-1.0	1.0-2.0	3.0-20.0	20.1-100.0	>100
		Class 1	2	3	4	5	6
T.B.5	<i>Leptospermum scoparium</i>	-	-	-	-	-	80
	<i>L. ericoides</i>	-	-	-	-	-	80
	<i>Macropiper excelsum</i>	4 100	3 200	5 400	320	880	560
	<i>Melicytus ramiflorus</i>	2 200	6 100	2 950	80	-	80
	<i>Cyathea medullaris</i>	-	-	160	-	-	160
	<i>C. dealbata</i>	-	-	480	-	-	80
	Others	4 500	11 500	3 400	640	560	240
E.I.4	<i>Weinmannia racemosa</i>	4 800	-	100	100	140	520
	<i>Myrsine salicina</i>	-	-	520	620	690	310
	<i>Pseudopanax arboreus</i>	1 600	1 000	-	-	-	140
	<i>Olearia rani</i>	640	-	30	-	-	140
	Others	6 400	300	1 000	400	760	280

TABLE 4:2 Continued.  
STANDS UNABLE TO BE AGED

Stand	Species	Height Class (m)	Basal Area (cm <sup>2</sup> )
		3.0- 20.1-	

TABLE 4:2 Continued.

## CONTROL STANDS

Stand	Species	Height Class (m)			Basal Area (cm <sup>2</sup> )		
		<0.3	0.3-1.0	1.0-2.0	3.0-20.0	20.1-100.0	>100
		Class 1	2	3	4	5	6
H.R.1	<i>Nothofagus truncata</i>	47 900	19 000	3 800	430	130	260
	<i>Weinmannia racemosa</i>	-	-	100	200	200	130
	<i>Myrsine salicina</i>	300	600	1 400	260	60	-
	<i>Pseudopanax arboreus</i>	900	1 200	800	170	-	-
	<i>Cyathodes fasciculata</i>	4 500	1 200	330	230	100	30
	Others	5 100	8 000	2 300	270	170	-
H.R.2	<i>Beilschmiedia tawa</i>	890	250	60	-	30	270
	<i>Laurelia novae-zelandiae</i>	9 200	8 000	-	-	-	30
	<i>Cyathea dealbata</i>	130	380	480	-	-	120
	<i>Dysoxylum spectabile</i>	890	1 000	2 000	210	60	60
	Others	2 800	1 100	120	120	30	90
H.R.3	<i>Nothofagus truncata</i>	64 000	900	200	70	30	270
	<i>Weinmannia racemosa</i>	-	-	-	-	-	30
	<i>Myrsine australis</i>	500	-	-	70	30	-
	<i>Cyathodes fasciculata</i>	-	250	200	70	70	-
	Others	29 000	-	-	-	-	-
H.R.4	<i>Beilschmiedia tawa</i>	1 600	300	430	230	70	70
	<i>Weinmannia racemosa</i>	-	-	-	-	30	90
	<i>Cyathea dealbata</i>	800	-	300	-	30	300
	<i>Elaeocarpus dentatus</i>	15 000	160	170	70	90	30
	Others	15 100	320	300	200	170	200
C.C.4	<i>Dysoxylum spectabile</i>	9 100	1 600	130	130	130	900
	<i>Pennantia corymbosa</i>	63 000	21 000	-	400	260	-
	<i>Macropiper excelsum</i>	411 000	13 500	260	200	70	-
	<i>Melicytus ramiflorus</i>	51 100	42 000	3 400	70	70	-
	Others	63 000	11 900	2 800	140	70	70
N.B.4	<i>Beilschmiedia tawa</i>	-	640	200	-	-	100
	<i>Dysoxylum spectabile</i>	56 000	8 300	2 400	630	630	100
	<i>Pittosporum eugenoides</i>	-	-	-	-	30	200
	<i>Elaeocarpus dentatus</i>	960	-	60	-	-	60
	<i>Melicytus ramiflorus</i>	-	300	200	30	30	120
	Others	140 000	11 500	3 500	60	230	500

Figure 4:2 Size class distributions i-vi

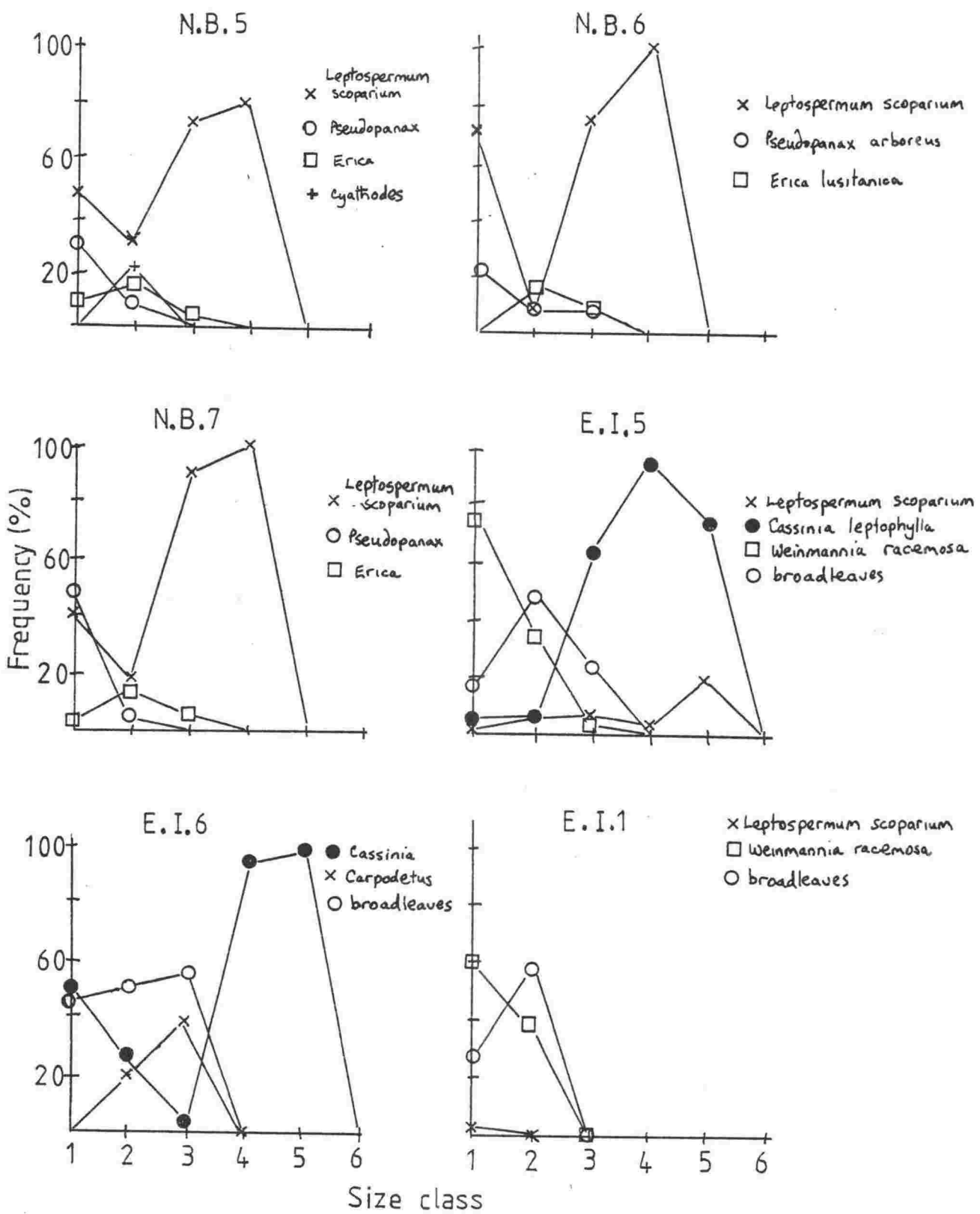


Figure 4:2 Size class distributions vii — xii

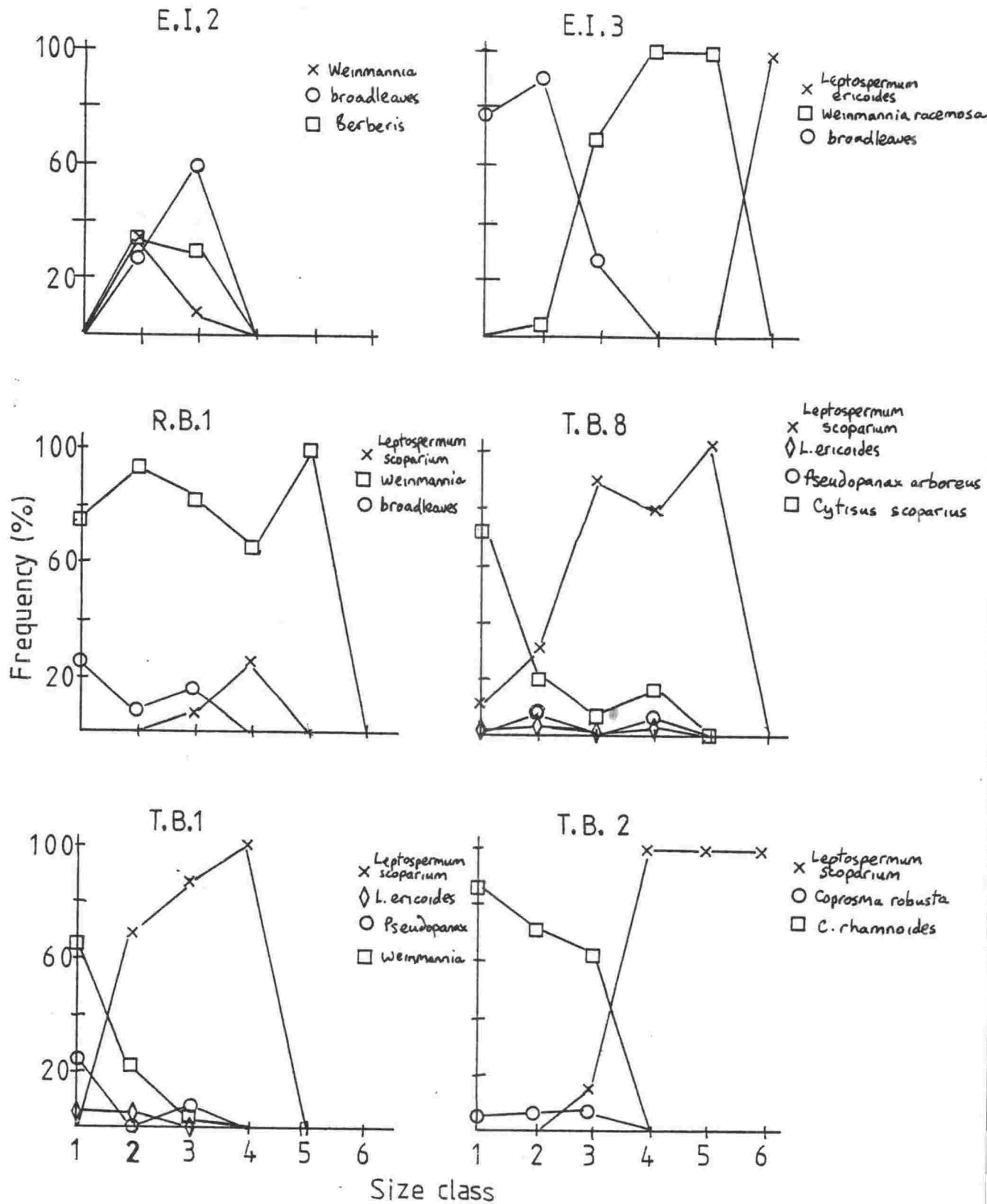




Figure 4:2 Size class distributions xiii — xviii

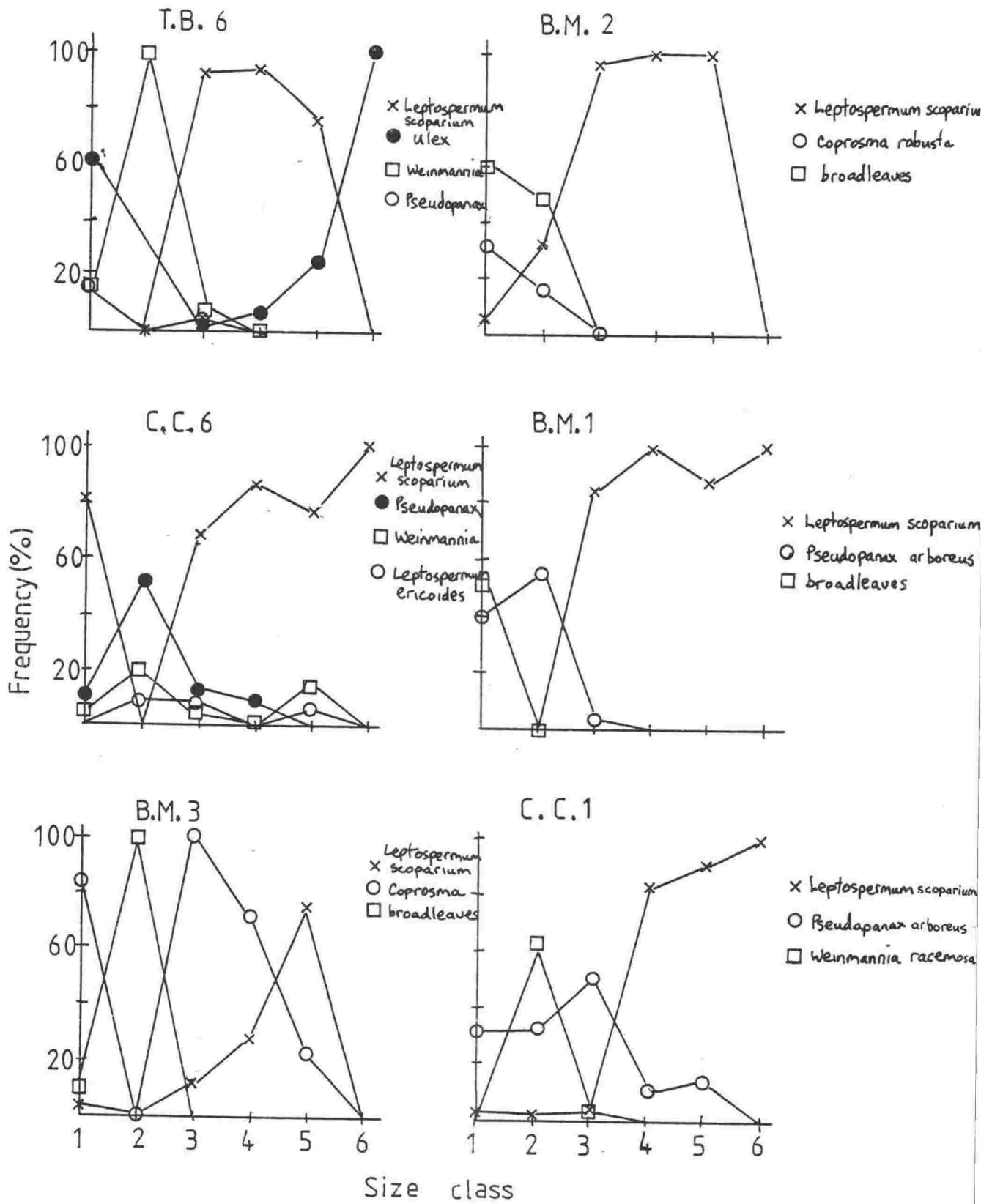


Figure 4:2 Size class distributions XIX—XXIV

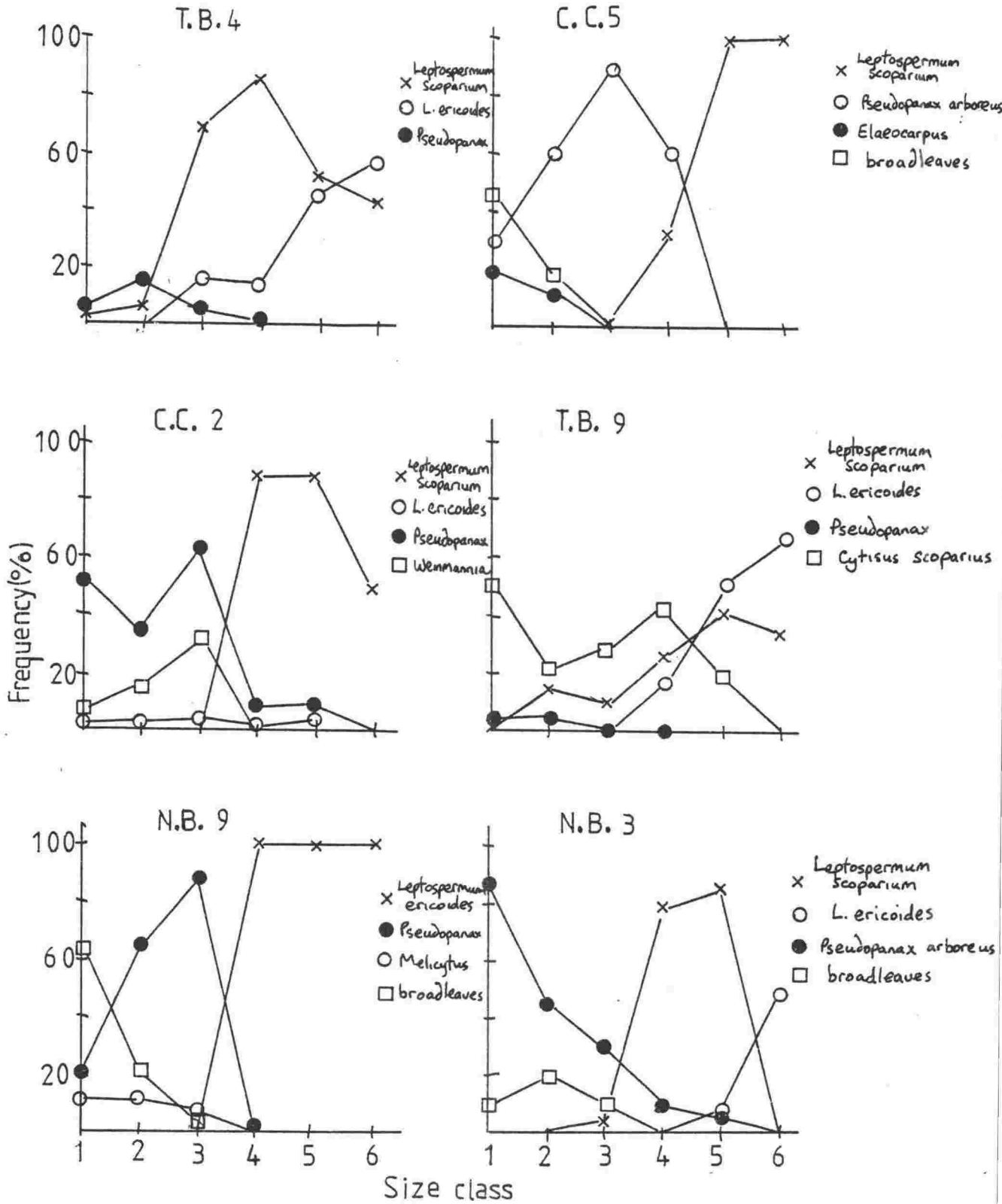


Figure 4:2 Size class distributions XXV—XXX

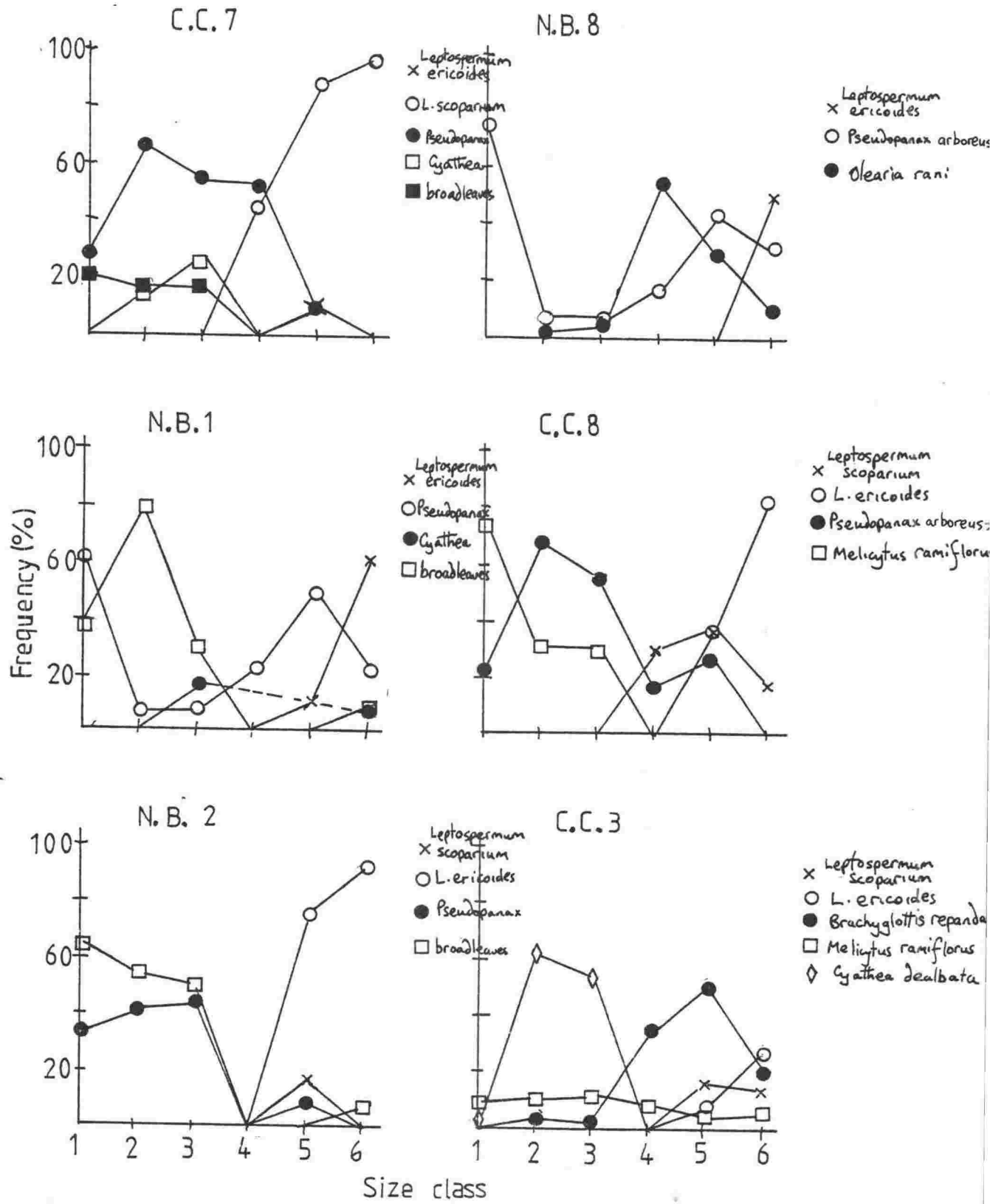


Figure 4:2 Size class distributions XXXI—XXXVI

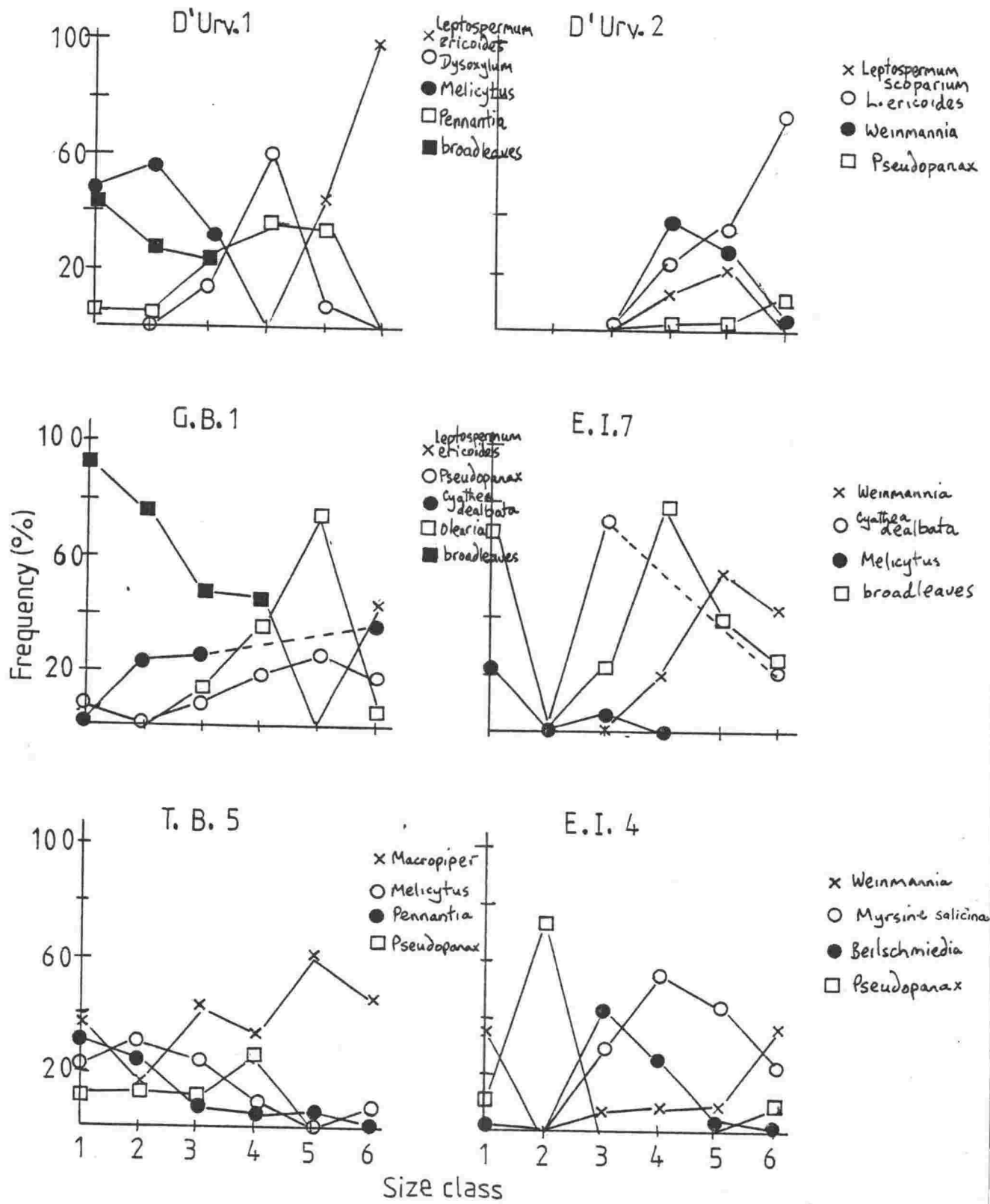


Figure 4:2 Size class distributions XXXVII— XXXVIII

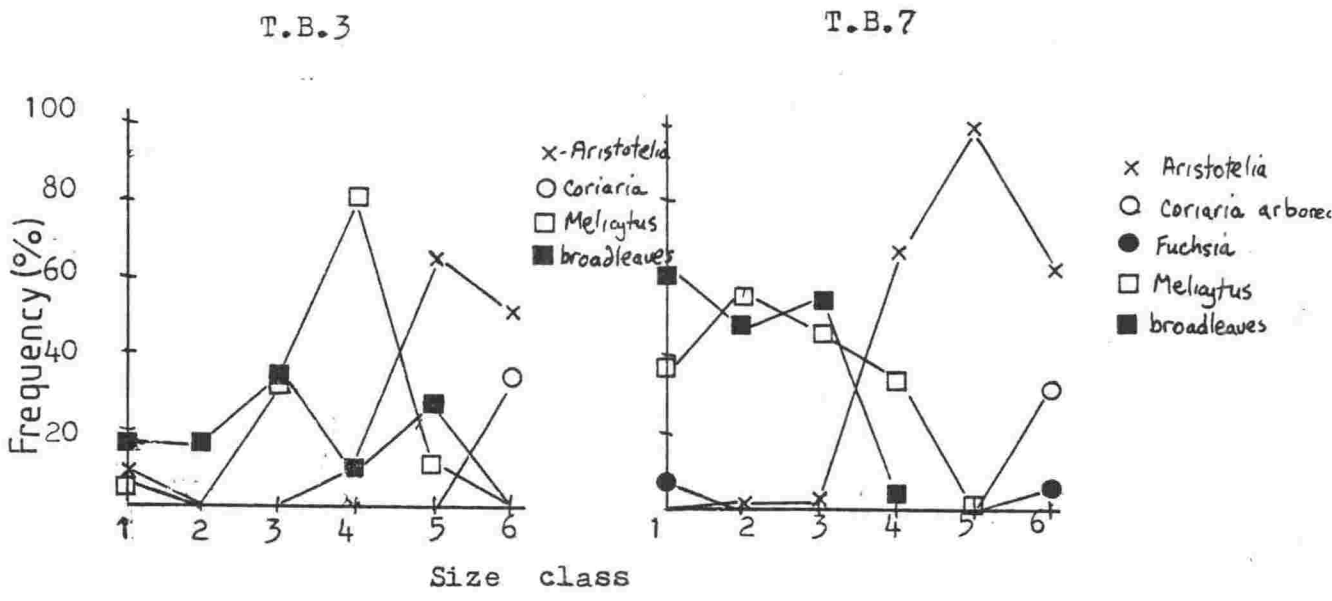


Figure 4:2 Size class distributions XXXix — xlv

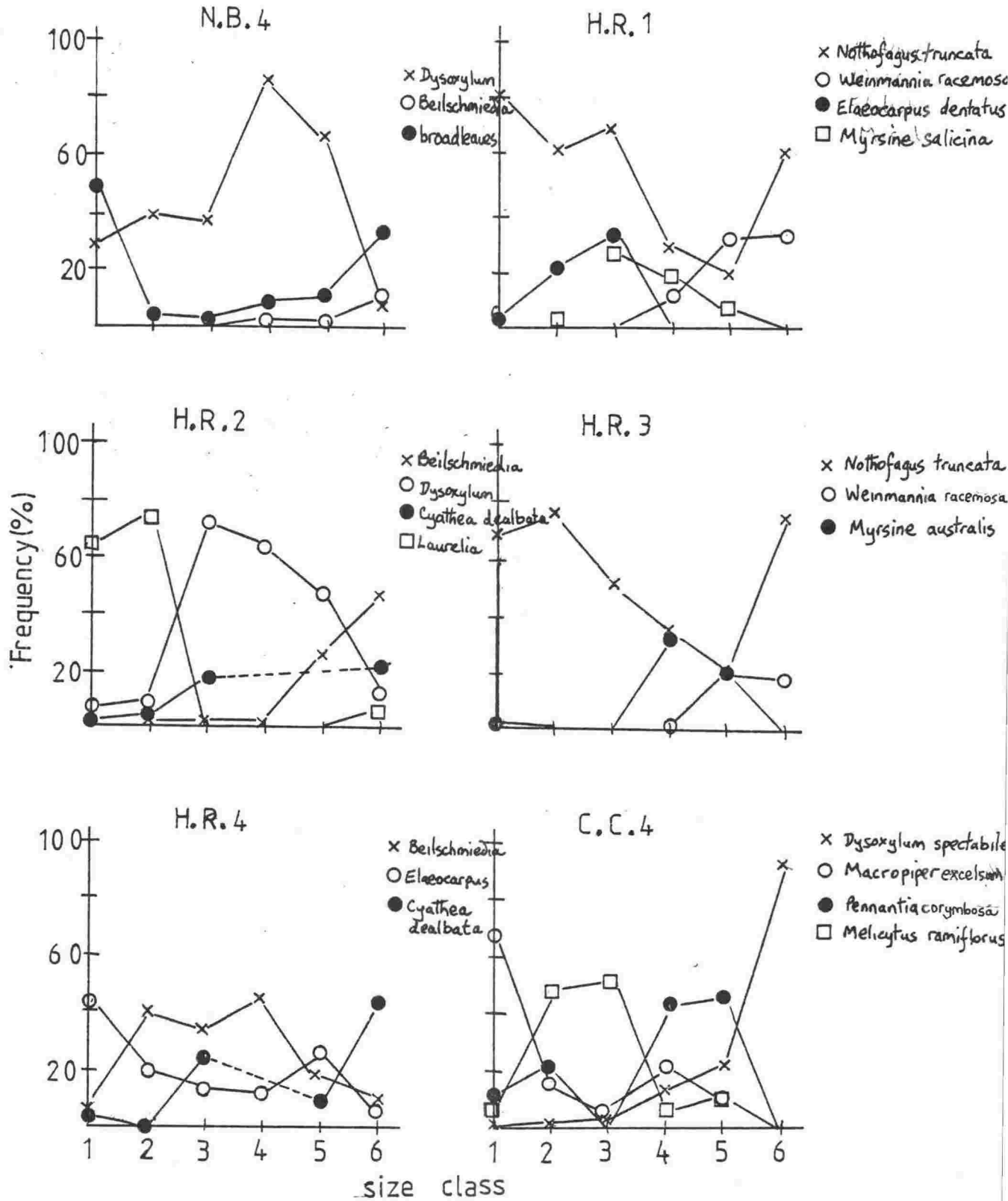


TABLE 4:5a Structural and Compositional Parameters - Young Stands (2-20 years)

	HR5	NB5	NB6	NB7	EI5	EI6	EI1	EI2	EI3	SCI	RBI
<b>Densities (no plants/ha)</b>											
<30 cm height											
30 cm - 1 m	ND	285,000	591,000	303,000	67,000	120,000	9,000	7,500	9,000	3,000	2,500
1.0 m - 2.0 m	ND	27,000	70,000	31,000	9,000	9,000	5,000	3,000	3,000	1,000	9,500
3.0 m - 20.0 cm <sup>2</sup> basal area	ND	63,000	5,000	105,000	6,000	5,000	-	2,500	10,000	-	13,000
20.0 - 100.0 cm <sup>2</sup>	-	22,000	800	1,200	5,000	7,000	-	-	800	-	2,500
>100cm <sup>2</sup>	-	-	-	-	100	4,000	-	-	200	-	200
									1		-
<b>Basal Area m<sup>2</sup>/ha</b>											
% species contribution	-	0.90	0.54	1.18	7.91	22.46	-	-	6.65	-	1.94
Leptospermum scoparium		100	100	100	13				78.2		27.1
L. ericoides									21.8		69.6
Weinmannia racemosa					87	98.7					3.2
Cassinia leptophylla											
Coprosma lucida											
<b>Canopy mean height (m)</b>											
Extreme upper height (M)	0.25	0.87	0.45	1.11	0.78	0.9	0.71	0.67	1.03	0.67	0.93
C.V. % of canopy height	0.6	1.90	1.65	2.6	2.35	3.2	1.35	1.4	4.0	1.6	2.70
	56.4	60.3	76.4	54.4	94	114	34.3	65	79	52.3	68.5
<b>Crown Cover %</b>											
% species contribution	92	99	97	100	95	98	100	100	100	100	100
Leptospermum scoparium		51	14	50							4
L. ericoides									7		14
Weinmannia racemosa	4				23	35					
Cassinia leptophylla	64	11	8	9	20		77	72	43	73	39
Gahnia pauciflora		6	17	15					15		16
Pteridium esculentum		6									
Erica lusitanica		6	4								
Blechnum capense			18	10							
Cyathodes fasciculata			26	11	29	48	21	26	21	27	16
Litter	7	10									
<b>Whole Stand</b>											
Total stand volume (units)	500	1,628	1,191	2,427	2,105	2,996	1,078	1,319	1,709	1,665	2,522
Total vegetation space (units)	282	887	387	1,197	773	467	729	716	532	836	859
Relative vegetation space %	2.8	8.7	3.8	11.7	7.6	4.6	7.2	7.0	7.8	8.2	8.4
Specific vegetation space %	57.5	54.5	32.5	49.3	36.7	31.1	67.7	54.3	31.1	50.2	34.1
Crown space %	60.5	21.9	28.1	27.2	22.6	24.2	47.1	30.9	41.2	10.6	16.1
Total Stand Foliage (units)	170	194	109	326	175	113	343	221	219	89	138
TSE % species contribution											
Leptospermum scoparium		55.8	26.9	53.1					24.5		10.1
L. ericoides											
Weinmannia racemosa					31	37.6					21.2
Cassinia leptophylla	5.7										
Gahnia pauciflora	76.2	17.5	16.8	11.2							
Pteridium esculentum	6.1	3.1	12.2	9.5	35.7		25.3	34.8	16.9	59.7	25.7
Erica lusitanica		6.7									
Blechnum capense		7.7	3.1						13.9		22.1
Cyathodes fasciculata			29.7	19.4							

cont'd

TABLE 4:5a (cont'd)

	HR5	NB5	NB6	NB7	EI5	EI6	EI1	EI2	EI3	SCI	RBI
<b>3 m - 10 m % TSF</b>											
% species contribution in this height interval						0.4			3.6		
Leptospermum ericoides						100			100		
Cassinia leptophylla											
<b>30 cm - 3 m % TSF</b>											
% species contribution	17.6	78.7	55.7	85.1	60.6	80.6	95.6	98.2	94.0	95.1	91.4
Leptospermum scoparium	0.6	52.4	42.8	60.3							5.3
L. ericoides									42.6		20.4
Weinmannia racemosa	5.8				31.0	84.4					
Cassinia leptophylla	71.0	9.5	12.1	8.7							
Gahnia pauciflora	11.6	2.6	13.2	9.7	35.7		100	92.1	27.5	100.0	25.0
Pteridium esculentum											
Erica lusitanica		5.1									
Blechnum capense		1.5	27.5	19.5					19.8		18.0
Cyathodes fasciculata											
<b>430 cm % TSF</b>											
% species contribution	82.4	21.3	44.3	14.9	39.4	18.9	4.4	1.8	3.4	4.9	8.6
Cassinia leptophylla	3.6					17.4					
Pteridium esculentum	1.7		11.0	8.2	4.5						
Gahnia pauciflora	71.3	37.3	22.8	25.8				66.7	29.2	92.3	8.3
Cyathodes fasciculata		14.5	32.4	18.6							
Leptospermum scoparium		15.7	6.9	12.4							
Blechnum capense		12.0							66.7		47.2
Erica lusitanica		9.6									
Lycopodium volubile											36.1
Weinmannia racemosa											8.3



TABLE 4:5b Structural and Compositional Parameters - Middle-aged Stands (21-40 years)

	TB8	TB1	TB2	TB6	BM2	CC6	BM1	BM3	CC1	TB4	CC5	CC2	TB9	NB9
Densities(no.plants/ha)	329,900	27,400	309,000	83,400	26,800	432,500	224,800	1,880,000	355,400	190,900	82,800	215,200	426,000	306,000
<30 cm height	17,200	31,800	23,000	8,900	3,800	12,100	14,300	3,200	38,400	63,400	23,900	18,400	68,800	59,560
30 cm - 1 m	27,400	168,200	5,330	56,200	47,200	32,600	7,730	8,000	18,600	5,000	9,400	9,000	4,600	8,800
1.0 cm - 2.0 m	8,000	3,610	2,930	9,390	37,600	16,000	11,860	5,800	18,400	8,170	8,600	14,800	2,400	400
3.0-20.0 cm <sup>2</sup> basal area	1,800	-	2,330	630	1,200	2,600	3,470	4,200	6,800	4,500	5,800	7,200	2,000	6,000
20.0 - 100.0 cm <sup>2</sup>	-	-	2,000	160	-	200	270	-	200	2,000	800	400	1,200	1,200
>100 cm <sup>2</sup>														
Basal Area M <sup>2</sup> /ha	11.68	1.90	79.24	9.95	31.06	26.08	30.27	27.34	45.41	81.37	49.59	53.42	51.76	54.39
% species contribution														
Leptospermum														
scoparium	91	100	100	63.2	100	84.5	96.7	79	81.8	35.6	91.0	80.3	21.2	100
L. ericoides	0.8					2.2	1.0		0.4	62.6		1.6	75.8	
Weinmannia racemosa				0.5		10.3			16.1		7.3	16.3		
Pseudopanax arboreus	1.1			0.5		3.1	2.3	21		1.8	1.6			
Cyathodes fasciculata														
Coprosma robusta														
Ulex europaeus				35.8										
Canopy mean height (m)	1.2	0.8	4.0	1.6	2.0	4.0	3.7	2.9	5.8	4.8	5.4	5.6	3.6	6.5
Extreme upper height (m)	3.0	3.0	6.2	3.1	3.5	7.2	6.3	4.9	9.0	8.2	7.8	7.8	5.7	9.6
C.V. % of canopy height	70	87	42	55	45	34	35	38	34	59	38	33	39	22
Crown Cover %	100	99	99	100	100	100	100	98	100	100	100	100	100	100
% species contribution														
Leptospermum														
scoparium	54	31	88	53	85	72	90	57	82	27	81	81	21	96
L. ericoides		2				5				69			67	
Weinmannia racemosa		10		5		9			2					
Pseudopanax arboreus	0.7					7			6		12	8		
Cyathodes fasciculata									1		2			
Ulex europaeus				12					3			4		
Pteridium esculentum	4			13			4							
Coprosma robusta		19	5	9	10	3	4	36	6	4	4	7	4	4
Litter	19							3						
Whole Stand														
Total Stand Vol. (units)	2,441	2,587	5,575	2,995	3,503	6,439	5,571	4,738	8,013	7,407	6,775	7,186	6,774	7,644
Total Vege. Space(units)	1,115	882	3,975	1,616	2,086	4,057	3,693	2,929	5,711	4,686	5,482	5,557	4,542	6,377
Relative Vege. Space %	10.9	8.7	39	15.9	20.5	39.8	36.2	28.7	56.0	46	53.8	54.5	44.6	62.6
Specific Vege. Space %	45.7	34.1	71.3	54	59.5	63	66.3	61.8	71.3	63.3	80.9	77.3	67.1	83.4
Crown space %	17.1	27.9	11.8	14.7	21.6	16	12.4	22.8	21.0	21.3	16.9	19.0	16.3	12.9
Total Stand Foliage(units)	191	246	469	238	451	649	458	668	1199	998	926	1056	740	823

Cont'd



TABLE 4:5c  
Structural and Compositional Parameters - Old Stands (43-84 years)

	NB3	CC7	NB8	NB1	CC8	NB2	CC3	D'Urv 1	D'Urv2	GB1	EI7	TB5	EI4
<b>Densities (no. plants/ha)</b>													
< 30 cm height	483,000	102,500	262,000	267,000	22,500	401,000	52,500	55,000	ND	52,000	28,000	10,800	13,000
30 cm - 1 m	14,000	28,000	23,000	27,000	8,600	38,900	12,000	59,000	ND	5,000	0	20,700	1,300
1.0 m - 2 m	8,600	6,200	8,400	4,900	5,300	17,700	4,900	8,000	2,500	6,000	2,100	12,600	1,700
3.0 - 20.0 cm <sup>2</sup> basal area	14,800	900	1,070	1,200	600	530	2,000	400	1,800	550	330	1,000	1,100
20 - 100 cm <sup>2</sup>	5,200	2,000	2,270	1,300	1,100	800	1,500	550	2,500	600	930	1,400	1,600
> 100 cm <sup>2</sup>	400	1,500	1,200	870	600	1,070	1,070	1,000	1,200	850	1,700	1,300	1,400
<b>Basal Area M<sup>2</sup>/ha</b>													
% species contribution	39.11	38.81	37.14	34.72	25.39	36.26	39.13	53.62	55.77	43.97	66.15	47.46	59.17
Leptospermum scoparium	66.8	0.6			17.1	2.5	7.2	0.7	4.2			2.0	
L. ericoides	15.7	98.0	43.9	49.8	77.9	86.7	26.6	96.6	72.9	39.5		5.7	
Weinmannia racemosa									10.1		52.1		44.4
Pseudopanax arboreus	14.2	1.4	28.4	24.1	3.5	0.4	17.6		6.6	12.8		6.1	10.5
Cyathea dealbata				6.0			19.8			41.3	18	14.5	
C. medullaris											8.6		
Olearia rani			16.6		1.5					6.1	5.9		7.0
Melicytus ramiflorus							3.4				2.0	23.7	
Brachyglottis repanda							24.4					4.7	
Dysoxylum spectabile								0.9			0.3		
<b>Canopy mean height (m)</b>													
Extreme upper height (m)	4.5	7.6	4.5	5.5	5.5	6.4	7.6	6.9	6.2	9.1	6.8	4.6	6.1
C.V. % of canopy height	7.0	9.7	12.8	9.0	8.2	9.5	16	13.8	12.8	17.8	12.8	10.6	12.2
	22.3	17.2	56	46.2	30.1	28	57.1	33.5	33.3	49.3	36.8	62.7	37.4
<b>Crown Cover %</b>													
% species contribution	100	100	100	100	100	100	100	100	100	100	100	99	100
Leptospermum scoparium	68				12	7	28.7		4.0				
L. ericoides	17	98	42.7	59	71	77	17.3	92.7	70	67		10.7	
Weinmannia racemosa											45.3		32
Pseudopanax arboreus	10	1	25.3	19	6		18.7		4.7	2	22.7	26.0	3
Cyathea dealbata					3		11.3	1.3	10	20		8.0	
C. medullaris										6	11.3		
Olearia rani			14.0		4								
Melicytus ramiflorus							8						
Brachyglottis repanda							10						
Dysoxylum spectabile													
Litter	-	1	3.3	4	3	-	2.7	1.3	2.7	2	-	5.2	-

cont'd

TABLE 4:5c (cont'd)

	NB3	CC7	NB8	NB1	CC8	NB2	CC3	D'Urv 1	D'Urv 2	GB1	EI7	TB5	E14
Whole Stand													
Total Stand volume (units)	6,757	9,127	8,700	8,999	8,191	8,857	15,985	12,038	9,933	16,233	10,231	9,780	5,749
Total Vegetation Space (units)	4,288	7,655	4,524	5,455	5,512	6,370	7,577	7,047	6,197	9,251	6,752	4,775	3,071
Relative Vegetation Space %	42.1	75.1	44.4	53.5	54.1	62.5	74.3	69.1	60.8	90.8	66.2	46.9	30.1
Specific Vegetation Space %	63.5	83.9	52.1	60.6	67.3	71.9	47.4	58.6	62.4	57.0	66.1	48.8	53.5
Crown Space %	16.0	18.2	19.3	21.5	18.1	15.7	66	21.2	25.5	17.2	25.4	20.2	14.8
Total Stand Foliage (units)	686	1,393	873	1,173	992	1,001	5,000	1,494	1,580	1,587	171	965	456
TSF % species contribution													
Leptospermum scoparium	48.2	-	-	-	6.5	3.8	31.5	-	0.8	-	-	-	-
L. ericoides	17.4	92.1	45.3	46.2	65.8	57.6	29.7	61.1	45.2	50.6	-	3.9	-
Weinmannia racemosa	-	-	-	-	-	7.8	-	-	22.5	-	81.8	-	36.2
Pseudopanax arboreus	10.4	2.2	21.6	22.8	7.5	-	14.1	-	12.5	2.3	-	-	-
Cyathia dealbata	-	3.6	-	-	7.9	6.7	11.2	4.0	-	25.1	8.5	15	-
C. medullaris	-	-	-	-	-	-	-	-	-	-	2.0	-	-
Olearia rani	-	0.4	15.6	-	6.7	-	-	-	-	17.4	3.1	-	-
Melicactus ramiflorus	-	-	-	-	-	-	3.7	2.2	-	-	-	32	-
Brachyglottis repanda	-	-	-	-	-	4.8	7.8	-	-	-	-	-	-
Dysoxylum spectabile	-	-	-	-	-	-	-	5.6	-	-	-	-	-
>10 m % TSF			0.4				35.6	1.8	3.5	34.3	1.1	0.3	4.2
% species contribution in this height interval													
Leptospermum scoparium							31.9	100	100	100	100		76.2
L. ericoides			100				68.1						
Weinmannia racemosa													
Melicactus ramiflorus													
3m - 10 m % TSF													
% species contribution													
Leptospermum scoparium	77.4	93.1	60.7	70.8	82.2	76.3	51.2	74.0	77.8	45.4	87.2	64.7	78.4
L. ericoides	60.6	-	-	-	8.6	5.0	39.3	-	-	-	-	-	-
Weinmannia racemosa	22.5	99.0	74.6	65.7	86.4	75.5	10.7	78.9	54.5	35.0	-	5.1	-
Pseudopanax arboreus			-			10.3			17.5	-	91.5	-	46.9
Cyathia dealbata	7.2	1.0	28.1	27.7	3.9		25.7		14.7	5.1		3.8	
C. medullaris							4.2			28.8			
Olearia rani			6.3		3.4					27.7	2.3	1.6	
Melicactus ramiflorus											3.4	43.9	
Brachyglottis repanda													
Dysoxylum spectabile													
Myrsine salicina								3.2					
Pennantia corymbosa								-					34.7
								15.9			14.7		

TABLE 4:5c (cont'd)

	NB3	CC7	NB8	NB1	CC8	NB2	CC3	D'Urv 1	D'Urv 2	GB1	E17	TB5	E14
30 cm - 3 m % TSF	20.9	5.5	37.1	27.8	15.7	21.7	13.1	20.3	16.8	19.2	10.5	33.3	15.7
% species contribution	6.3								-				
Leptospermum scoparium									53.6		8.8		2.5
Weinmannia racemosa									7.1				
Pseudopanax arboreus	24.0	16.4	10.3	14.3	16.6	12.6	6.1						
Cyathaea dealbata		43.6	2.5	17.0	35.0	47.1	64.0	21.7		66.6	68.2	3.1	
Melicytus ramiflorus							1.5	2.0					
Brachyglottis repanda			5.0			27.0	20.0					7.1	
Dysoxylum spectabile								14.8					
Cyathodes fasciculata	67.0		23.2	68.8			-	-	28.6				
Olearia rani		2.0	28.7		19.7		-	-				68.2	
Macropiper excelsum													
< 30 cm % TSF	1.7	1.4	1.8	1.4	2.1	2.0	0.1	3.9	1.9	1.8	1.1	1.6	2.7
% species contribution													
Melicytus ramiflorus								10.1					
Brachyglottis repanda			13.0			33.3							
Pteridophytes		23.3			19								37.0
Uncinia uncinata					23.8			38.5				47.8	

TABLE 4:5d

## Structural and Compositional Parameters - Virgin Stands

	HR1	HR2	HR3	HR4	CC4	NR4
<b>Densities (no.plants/ha)</b>						
<30 cm height	58,600	13,900	93,500	31,800	606,000	196,000
30 cm - 1 m	30,300	10,800	1,150	800	91,000	20,700
1.0 m - 2 m	5,400	2,700	400	1,200	7,300	6,400
3.0 - 20.0 cm <sup>2</sup> basal area	1,600	330	200	530	930	730
20 - 100.0 cm <sup>2</sup>	670	120	170	370	600	930
>100.0 cm <sup>2</sup>	430	580	370	700	100	1,100
<b>Basal Area M<sup>2</sup>/ha</b>						
% species contribution						
Nothofagus truncata	92.8		80.2			
Weinmannia racemosa	4.2		2.6			
Beilschmiedia tawa		46.2		37.7		
Cyathea medullaris		3.3		13.5		13.2
C. dealbata		10.0		21.5		2.8
Dysoxylum spectabile		3.6				
Melicytus ramiflorus					94.0	9.7
Elaeocarpus dentatus	0.1			12.8		9.0
Myrsine salicina	0.5			4.9		9.7
						9.4
<b>Canopy mean height (m)</b>						
Extreme upper height (m)	20.9	15.0	23.1	9.68	10.4	10.0
C.V. % of canopy height	23.0	30.0	25.5	30	15.7	16.0
	32.0	ND	ND	ND	16.8	26.7
<b>Crown Cover %</b>						
% species contribution	99	100	94	100	100	100
Nothofagus truncata	91		81.3			
Weinmannia racemosa				21		
Dacrydium cupressinum		8.7		9		
Beilschmiedia tawa		68.7		31		18.9
Cyathea medullaris		8.0				5.3
C. dealbata				5		-
Dysoxylum spectabile					96	5.8
Melicytus ramiflorus		2.7			-	4.7
Elaeocarpus dentatus				17	1.3	12.1
Myrsine salicina						16.8
<b>Whole Stand</b>						
Total Stand Volume (units)	23,011	27,000	25,474	25,619	13,996	16,000
Total Vegetation Space (units)	20,607	ND	23,312	11,526	10,367	10,192
Relative Vegetation Space %	ND	ND	229	113	101	100
Specific Vegetation Space %	ND	ND	91.5	76.4	74.1	63.7
Crown Space %	ND	ND	32.6	12.0	26.7	30.2
Total Stand Foliage	ND	ND	7,596	ND	2,768	3,078
<b>TSF % species contribution</b>						
Nothofagus truncata			85			
Weinmannia racemosa			0.2	40.6		
Beilschmiedia tawa				25.3		27.3
Cyathea dealbata				10.3	3.1	
Dysoxylum spectabile					83.2	19.3
Melicytus ramiflorus					1.8	4.0
Elaeocarpus dentatus				8.3		8.9
Myrsine salicina						8.1
<b>10m % TSF</b>						
% species contribution				33.0	27.9	32.8
Weinmannia racemosa				38.7		
Beilschmiedia tawa				48.3		55.1
Dysoxylum spectabile					98.4	
Melicytus ramiflorus					0.4	
Elaeocarpus dentatus				13.0		10.2

cont'd

TABLE 4:5d (cont'd)

	HR1	HR2	HR3	HR4	CC4	NB4
3m - 10m % TSF				52.8	63.5	58.6
% species contribution						
Weinmannia racemosa				56.4		
Beilschmiedia tawa				14		16.1
Cyathea dealbata				9		
Dysoxylum spectabile					86.2	33.3
Melicytus ramiflorus					2.2	8.1
Elaeocarpus dentatus				7.3		7.9
Myrsine salicina				0.4		7.8
Olearia rani				12.7		
Leptospermum ericoides						9.0
30 cm - 3 m % TSF				11.5	6.1	6.8
% species contribution						
Weinmannia racemosa				2		-
Cyathea dealbata				49	46.5	25.0
Dysoxylum spectabile					7.9	39.0
Melicytus ramiflorus					6.4	
Beilschmiedia tawa				4		3.1
<30 cm % TSF				2.7	1.4	1.8
% contribution						
Pteridophytes				50	58	59.3

TABLE 4:5e                  Structural and Compositional Parameters -  
                                     Stands unable to be Aged

	TB3	TB7
<u>Densities</u> (no.plants/ha)		
<30 cm height	19,000	27,000
30 cm - 1 m	5,000	18,500
1.0 cm - 2.0 m	3,000	5,500
3.0 - 20.0 cm <sup>2</sup> basal area	670	200
20.0 - 100.0 cm <sup>2</sup>	730	600
>100 cm <sup>2</sup>	730	1,070
<u>Basal Area</u> M <sup>2</sup> /ha	44.83	78.99
% species contribution		
Aristotelia serrata	27.1	36.3
Coriaria arborea	65.7	60.2
Fuchsia excorticata		3.5
Melicytus ramiflorus	1.3	
Brachyglottis repanda	1.4	
Cyathea medullaris	4.5	
<u>Canopy</u> mean height (m)	7.28	5.02
Extreme upper height (M)	11.3	8.0
C.V.% of canopy height	31.1	34.5
<u>Crown Cover</u> %	100	99
% species contribution		
Aristotelia serrata	63.3	60.7
Coriaria arborea	17.3	32
Melicytus ramiflorus	1.3	
Brachyglottis repanda	2.7	
Cyathea medullaris	9.3	
Litter	2.7	
<u>Whole Stand</u>		
Total Stand Volume (units)	11,737	7,291
Total Vegetation Space (units)	7,713	5,055
Relative Vegetation Space %	75.7	49.6
Specific Vegetation Space %	65.8	69.4
Crown Space %	13.4	18.0
Total Stand Foliage (units)	1,034	910
<u>TSF</u> % species contribution		
Aristotelia serrata	55.9	80.4
Coriaria arborea	6.3	8.6
Melicytus ramiflorus	9.5	
Brachyglottis repanda	16.2	
Cyathea medullaris	9.1	5.3

cont'd



TABLE 4:5e (cont'd)

	TB3	TB7
<u>&gt;10 m % TSF</u>	0.6	
% species contribution in this height interval		
<i>Aristotelia serrata</i>	70	
<i>Coriaria arborea</i>	30	
<u>3 m - 10 m % TSF</u>	73.6	60.2
% species contribution		
<i>Aristotelia serrata</i>	72.6	64.9
<i>Coriaria arborea</i>	8.5	34.5
<i>Melicytus ramiflorus</i>	5.3	
<i>Brachyglottis repanda</i>	8.3	
<i>Cyathea medullaris</i>	4.1	
<u>30 cm - 3 m % TSF</u>	24.4	37.8
% species contribution		
<i>Melicytus ramiflorus</i>	22.1	4.3
<i>Brachyglottis repanda</i>	55.3	
<i>Cyathea medullaris</i>	26.0	35.3
<u>&lt;30 cm % TSF</u>	1.4	2.6
% species contribution		
<i>Brachyglottis repanda</i>	33.3	
<i>Uncinia uncinata</i>		44.4

Figure 4:4 Vegetation structure and composition trends

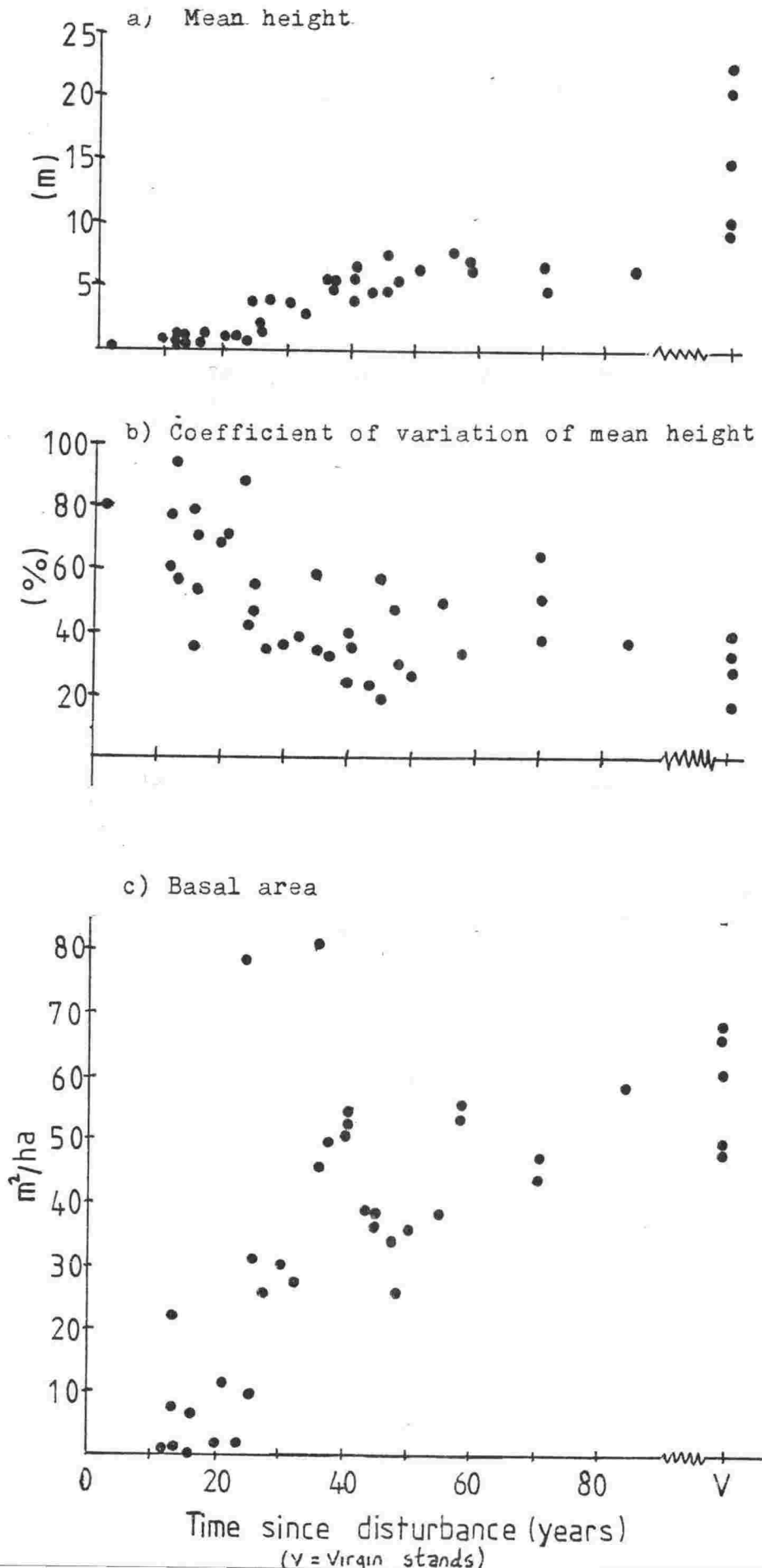


Figure 4:4 Vegetation structure and composition trends

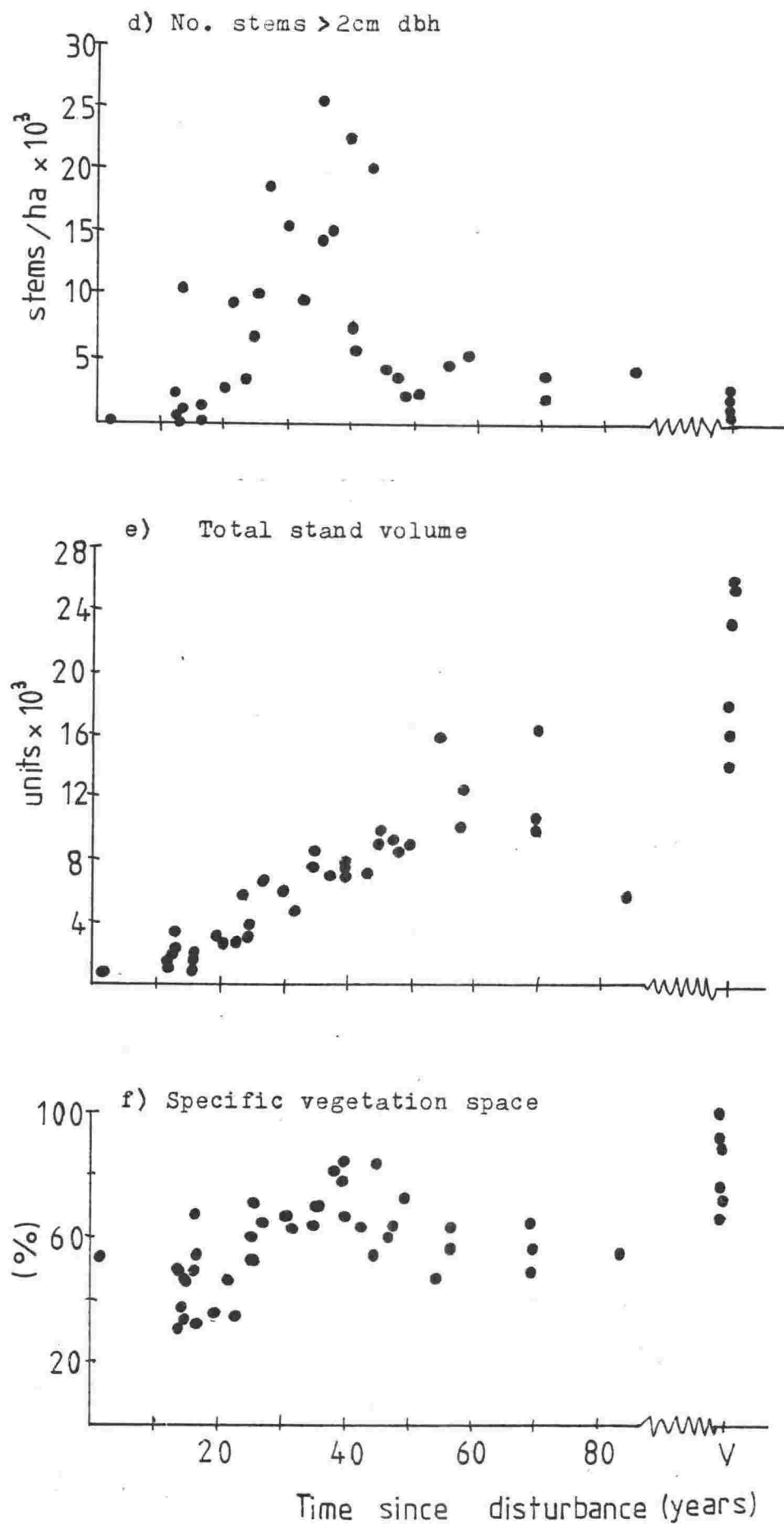


Figure 4.4 Vegetation structure and composition trends

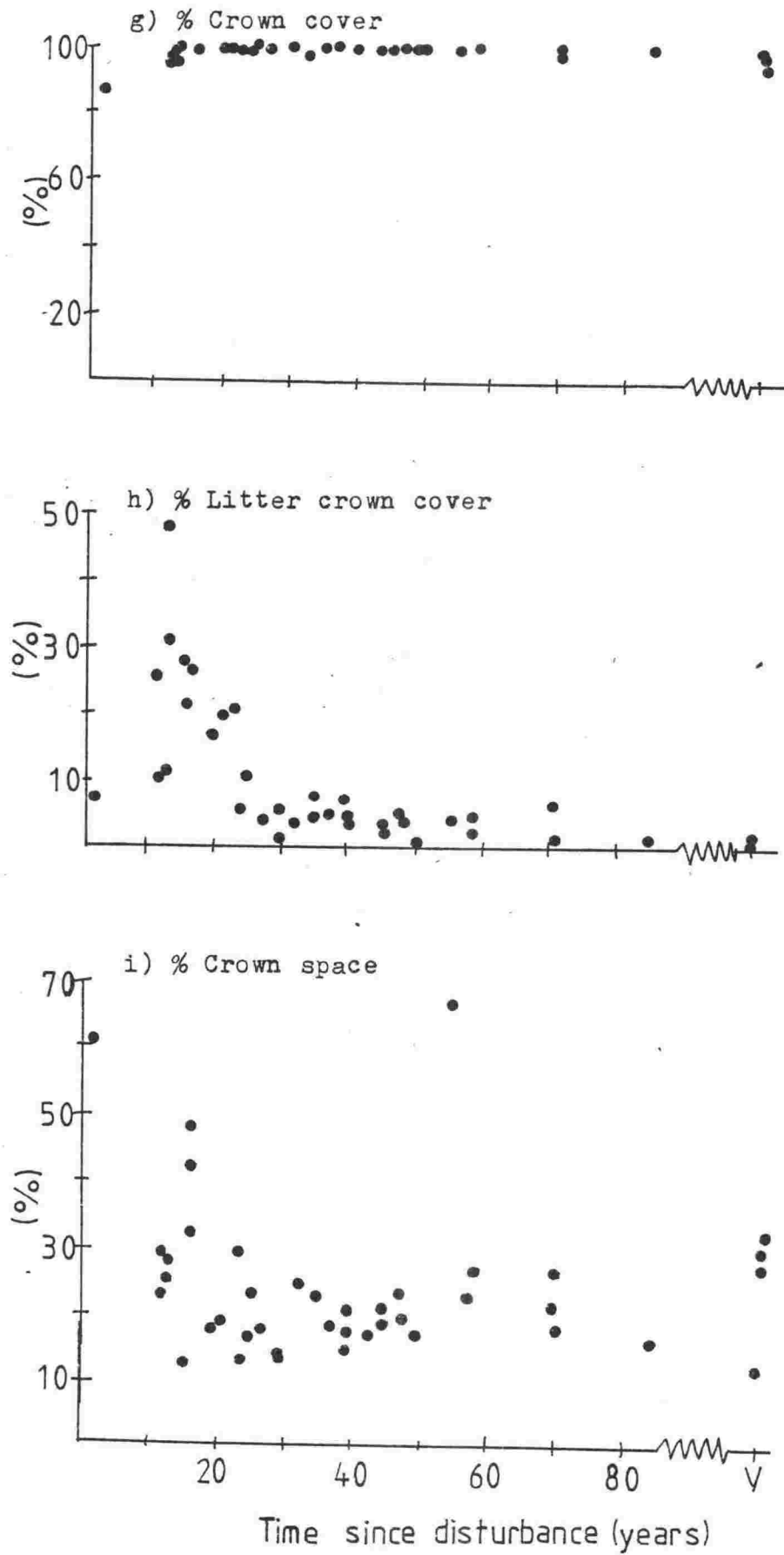


Figure 4.4 Vegetation structure and composition trends

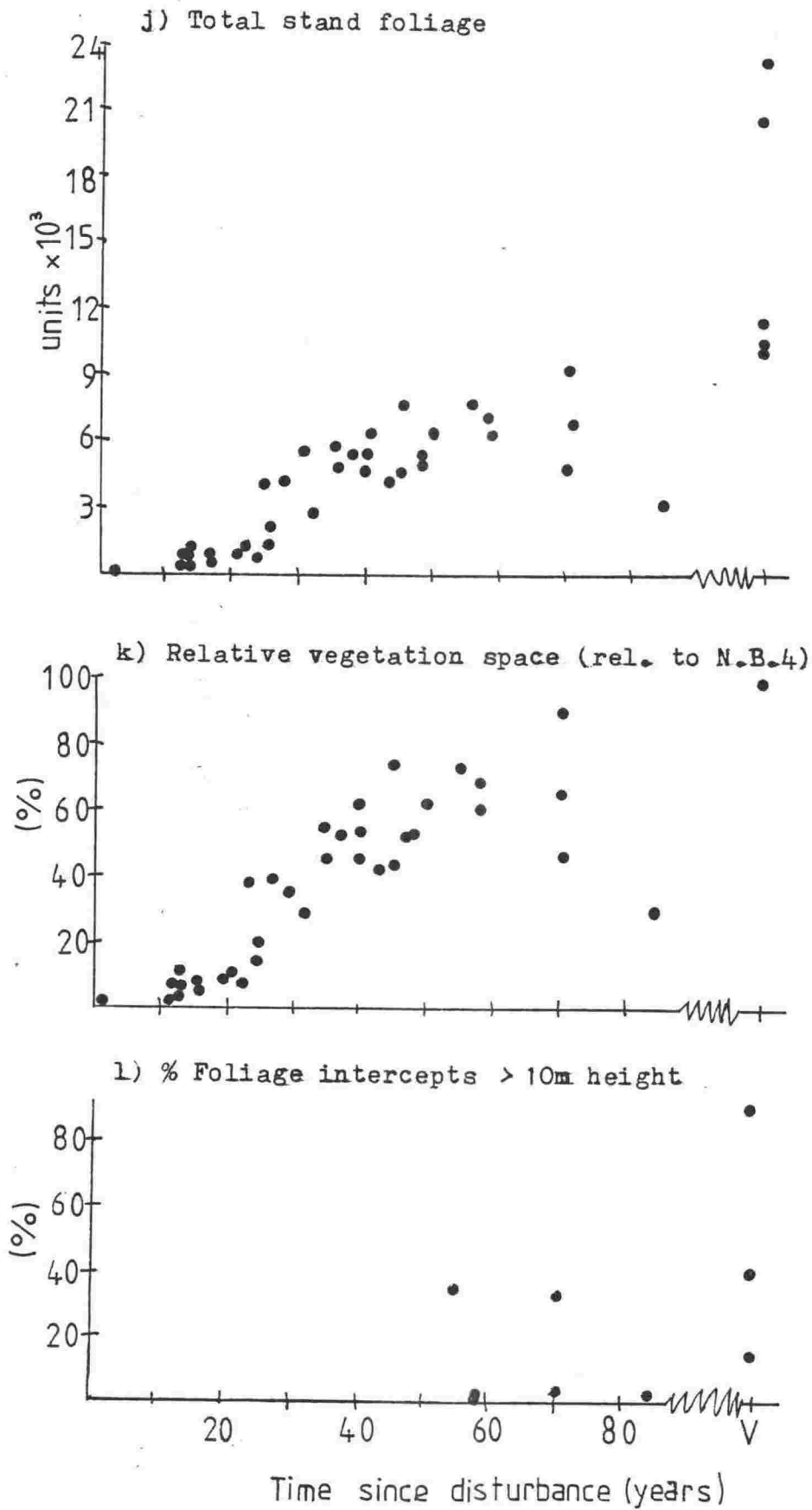


Figure 4:4 Vegetation structure and composition trends

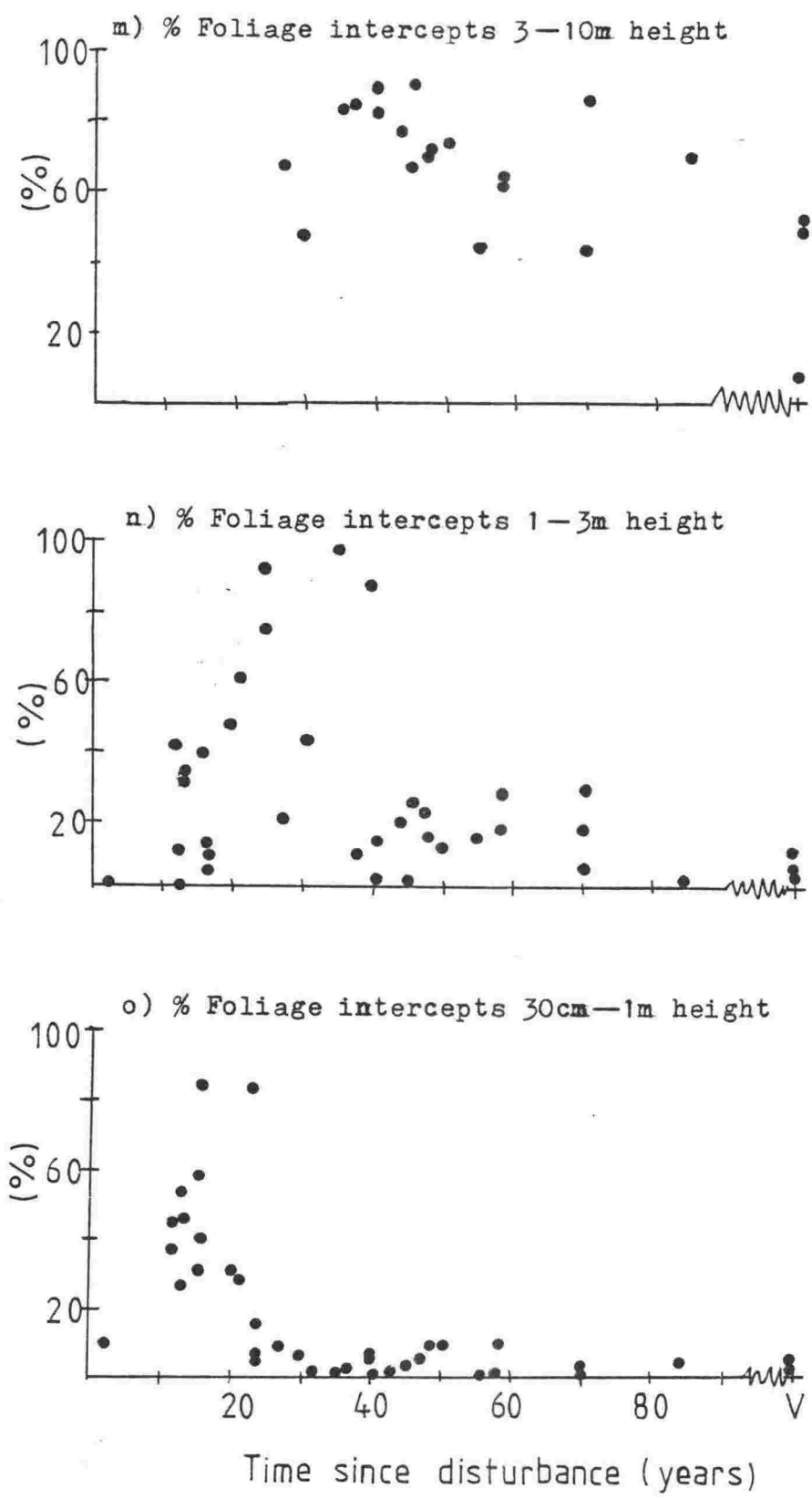
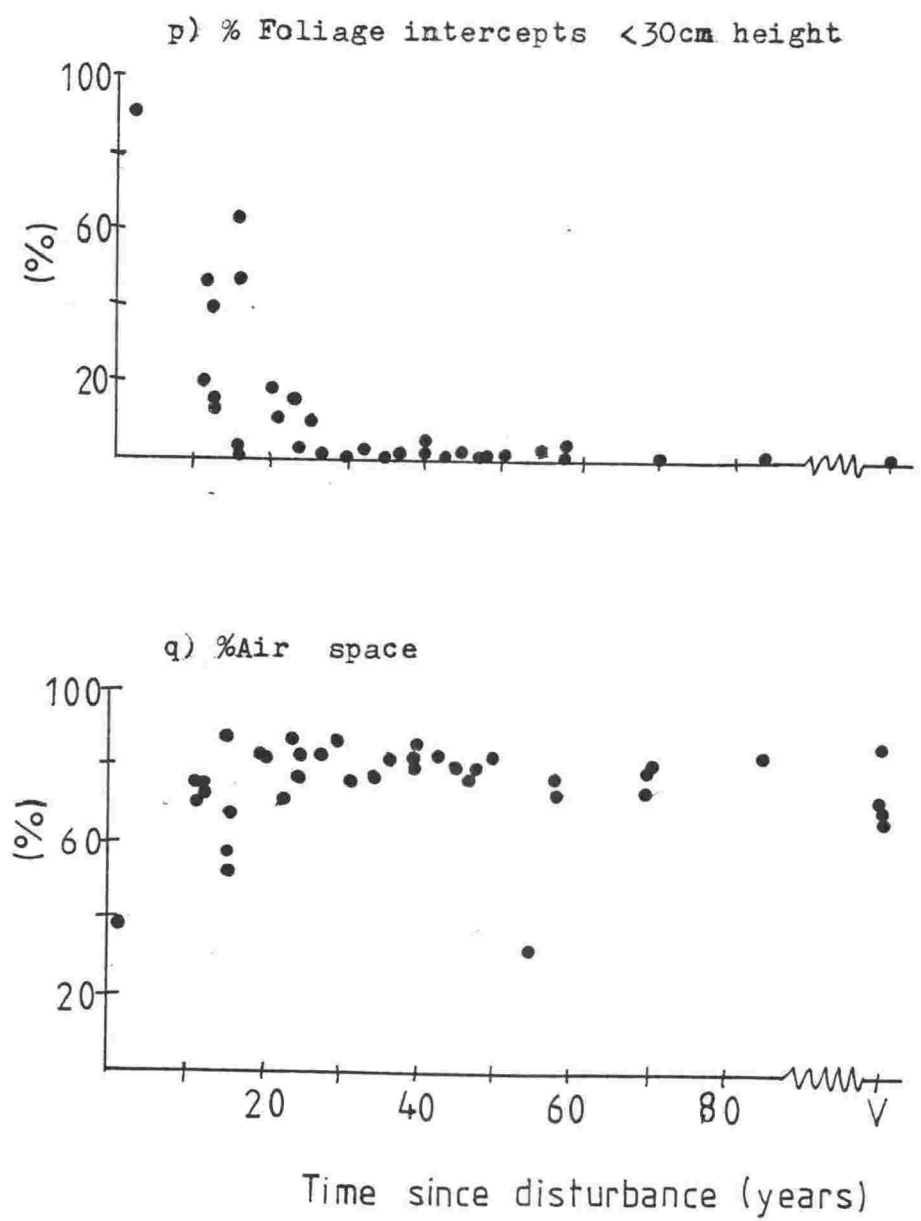


Figure 4:4 Vegetation structure and composition trends



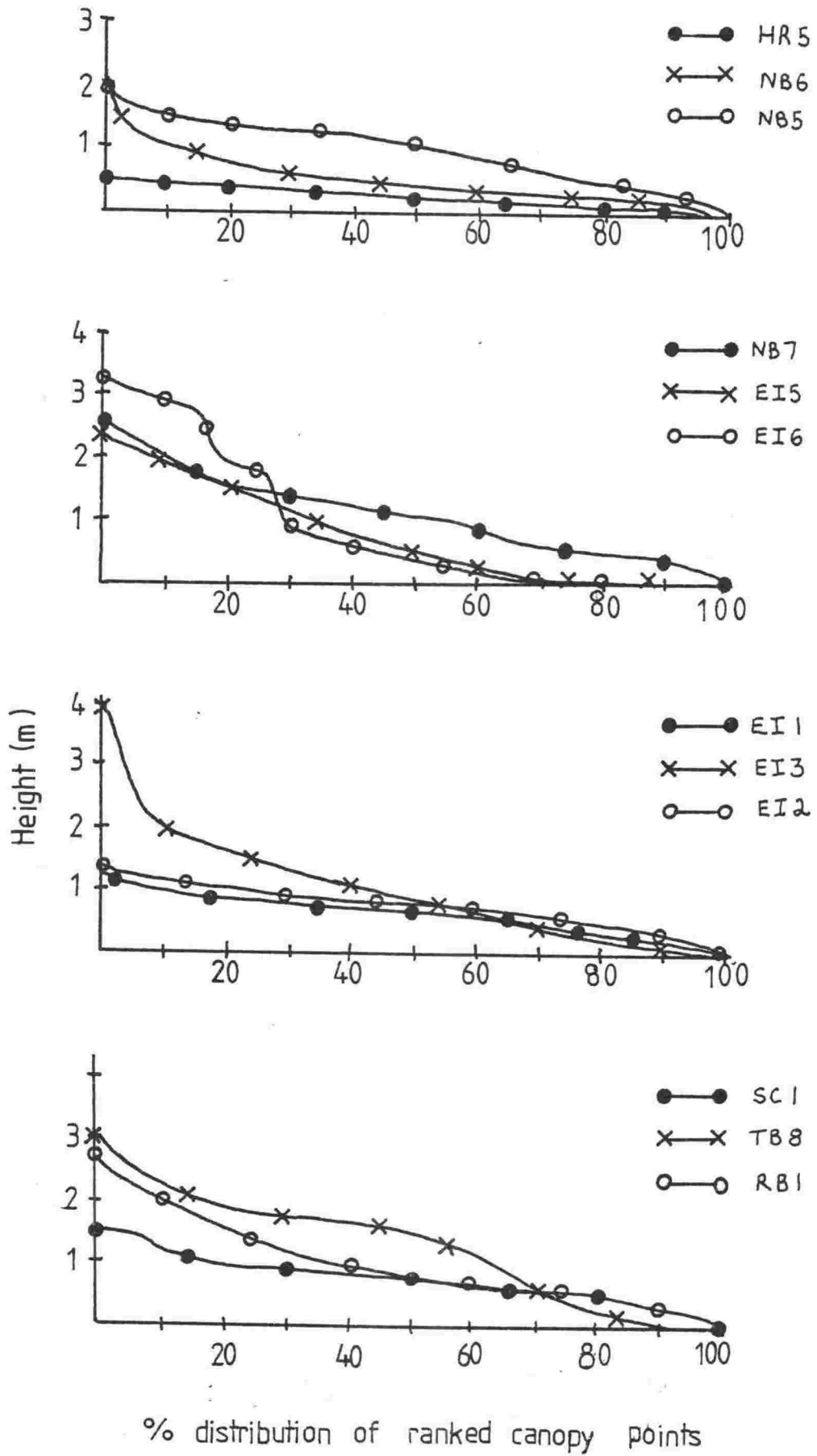




Figure 4:4r Canopy profile diagrams

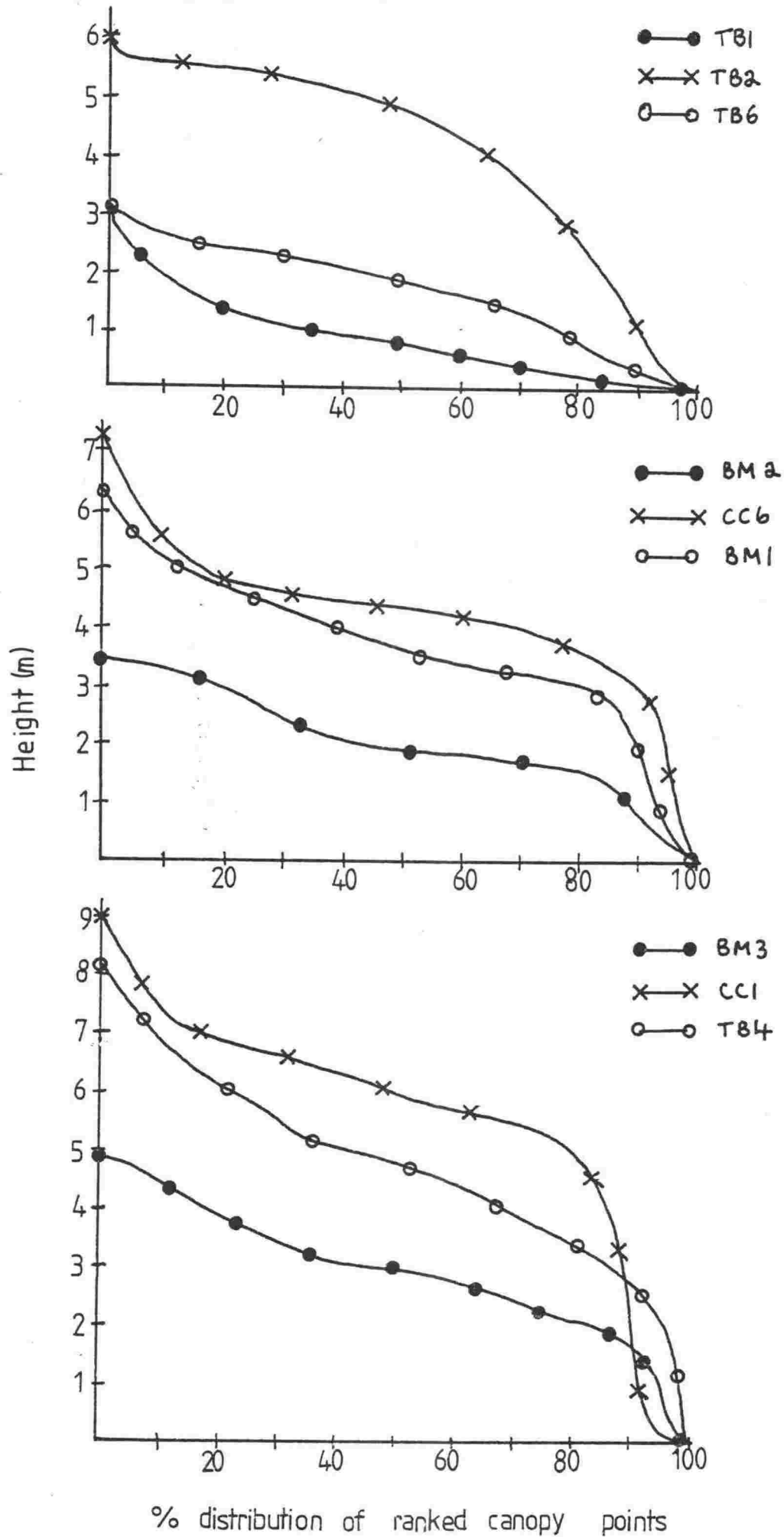




Figure 4:4r Canopy profile diagrams

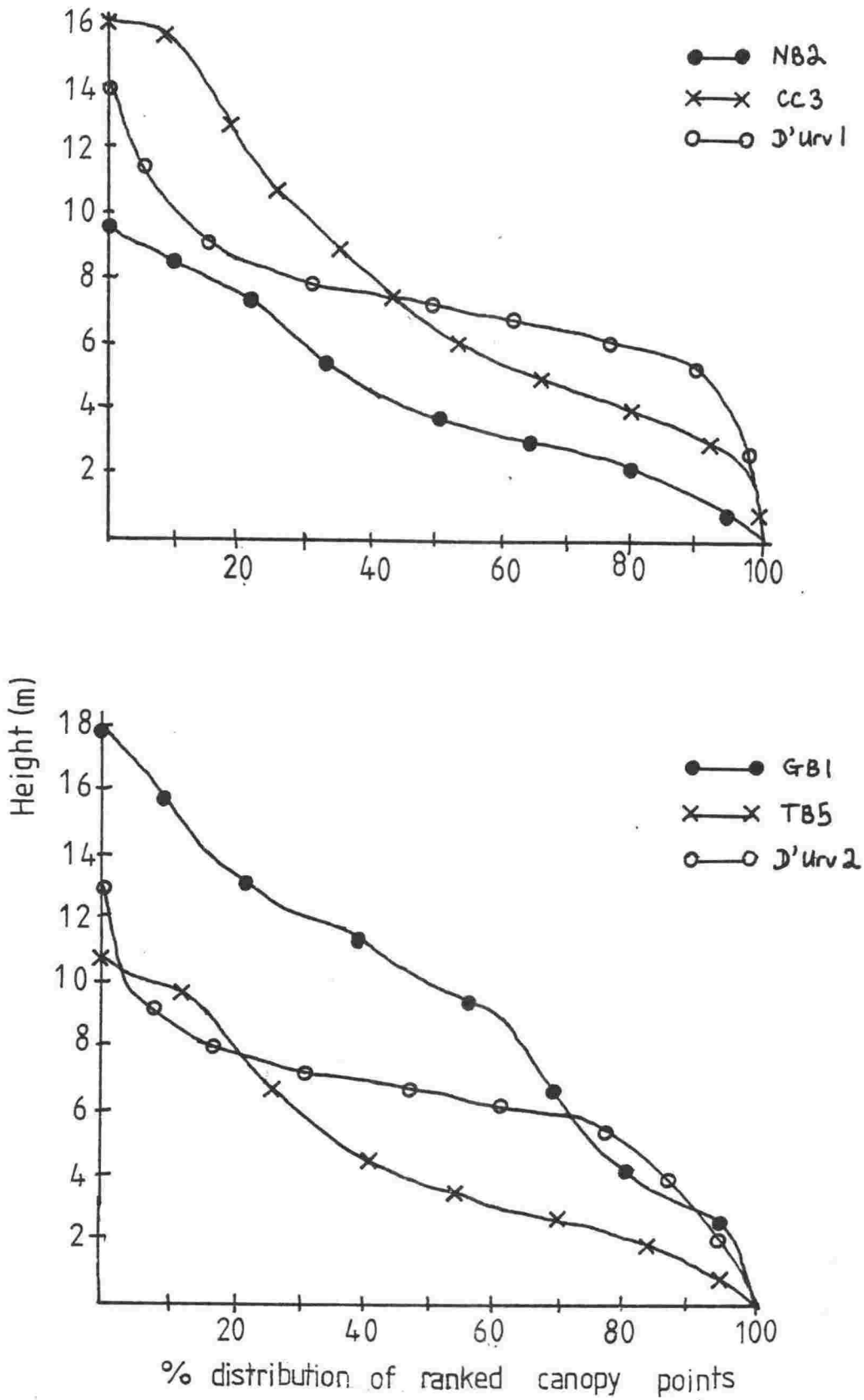


Figure 4:4r Canopy profile diagrams

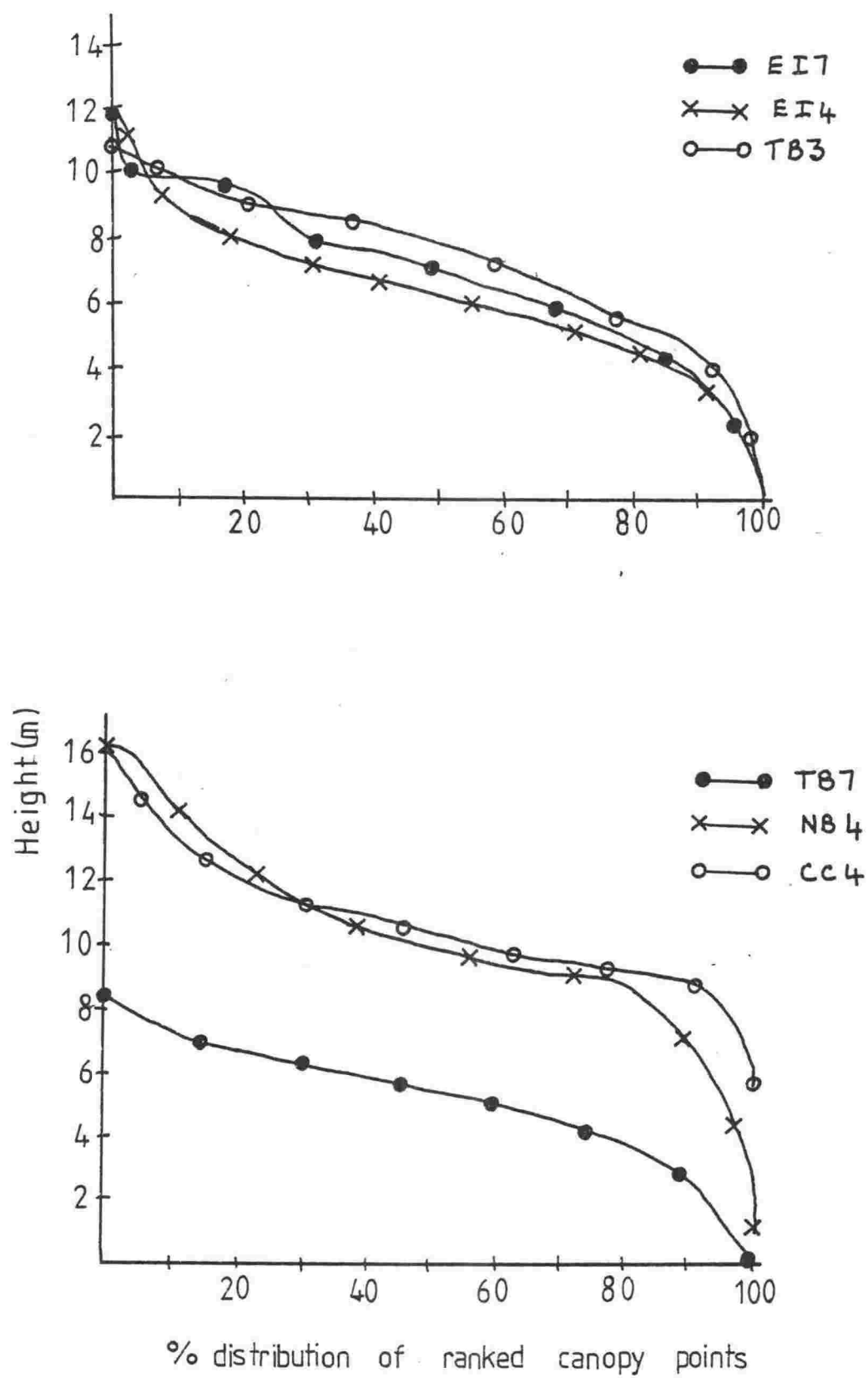


Figure 4:5 a- c Species contribution to seral stands.

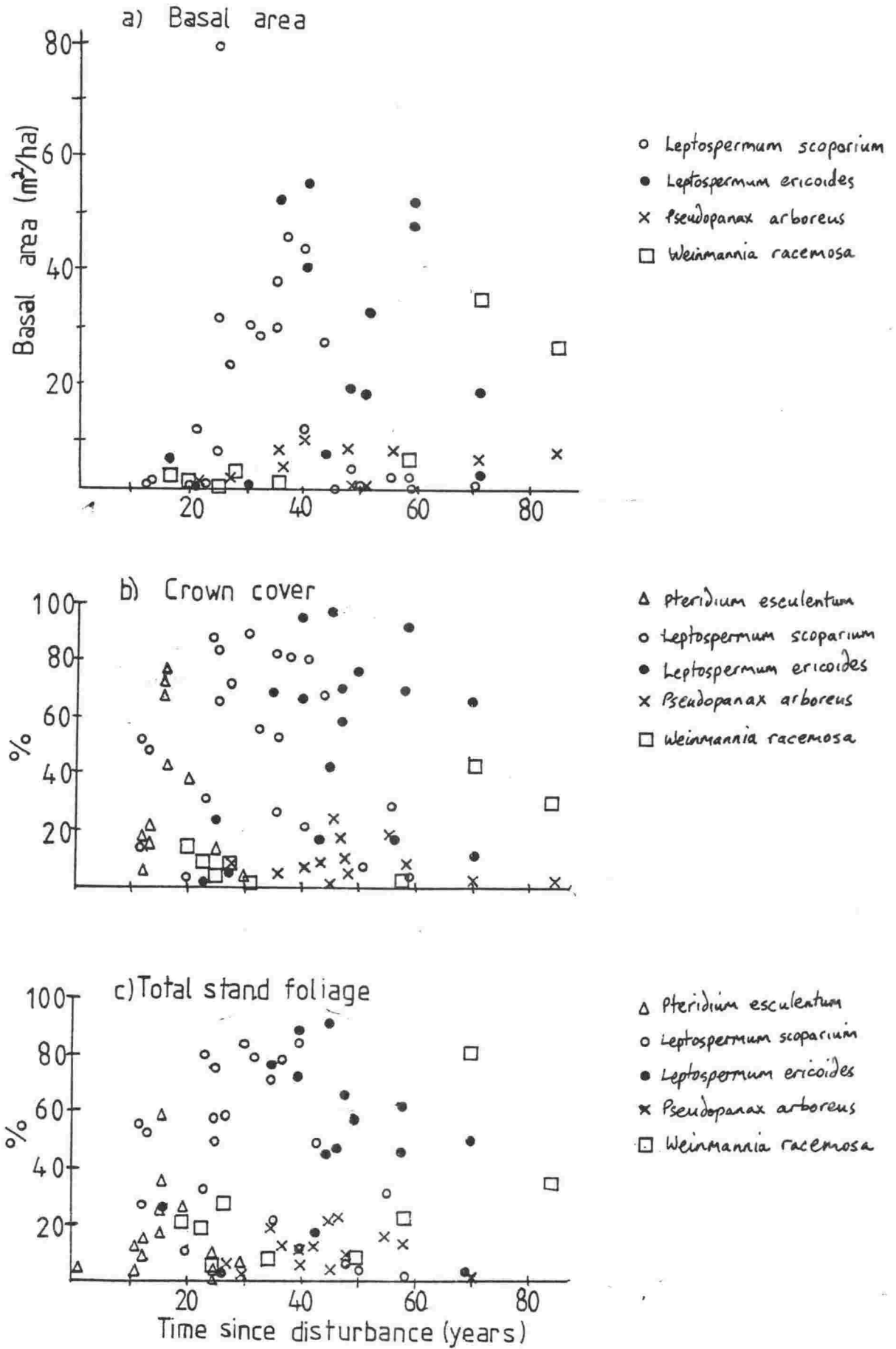
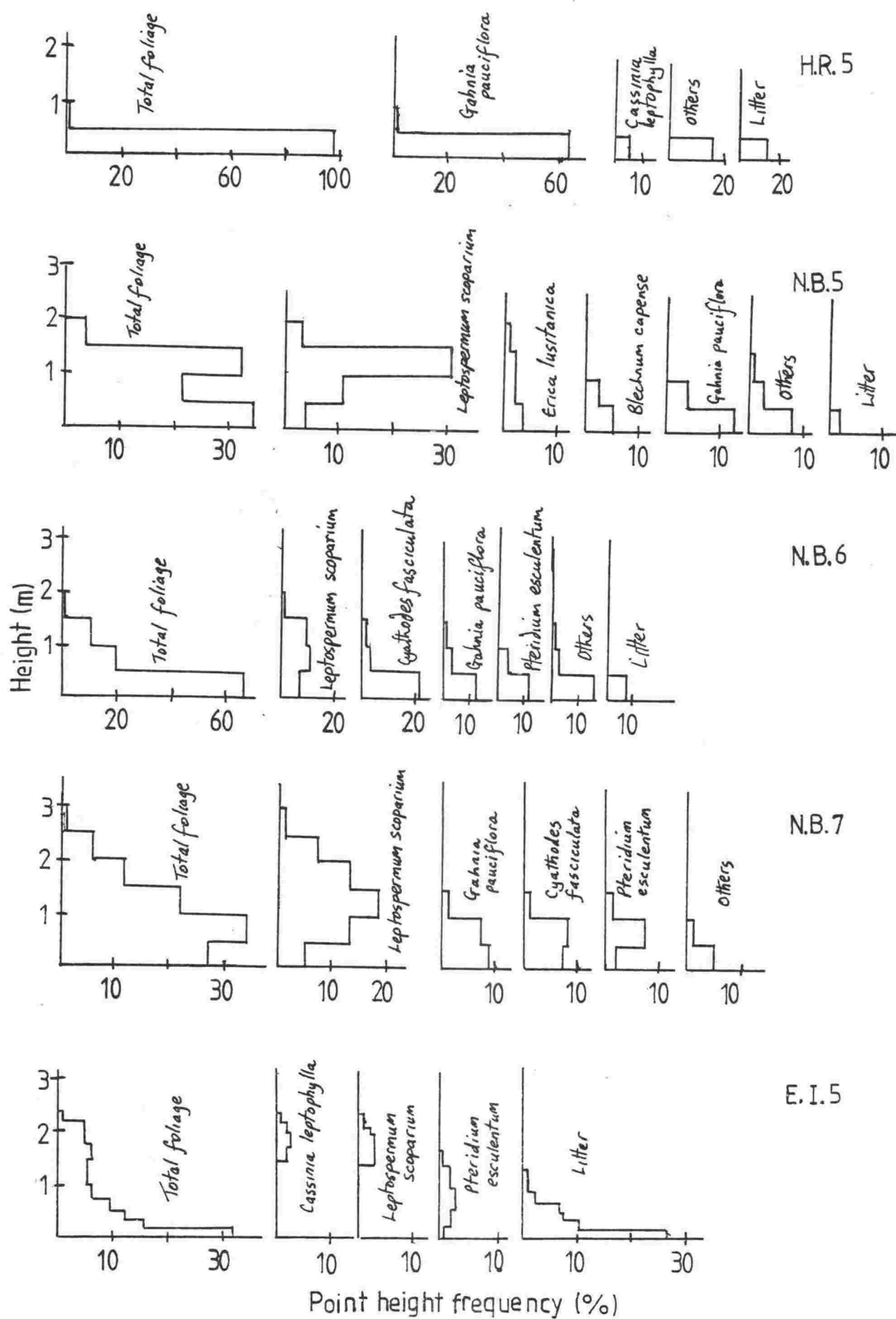


Figure 4:6 i - v



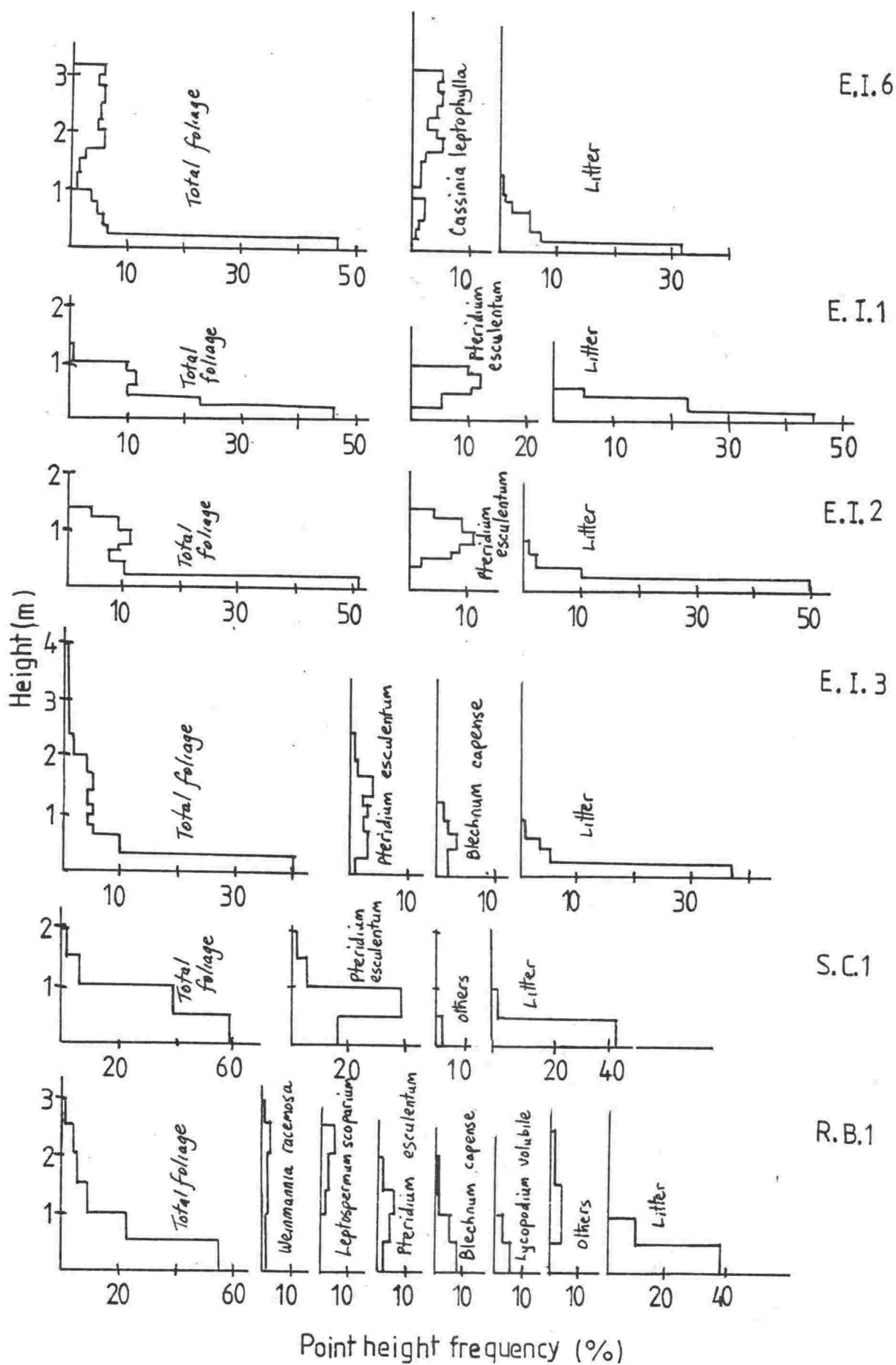


Figure 4:6 xii—xv

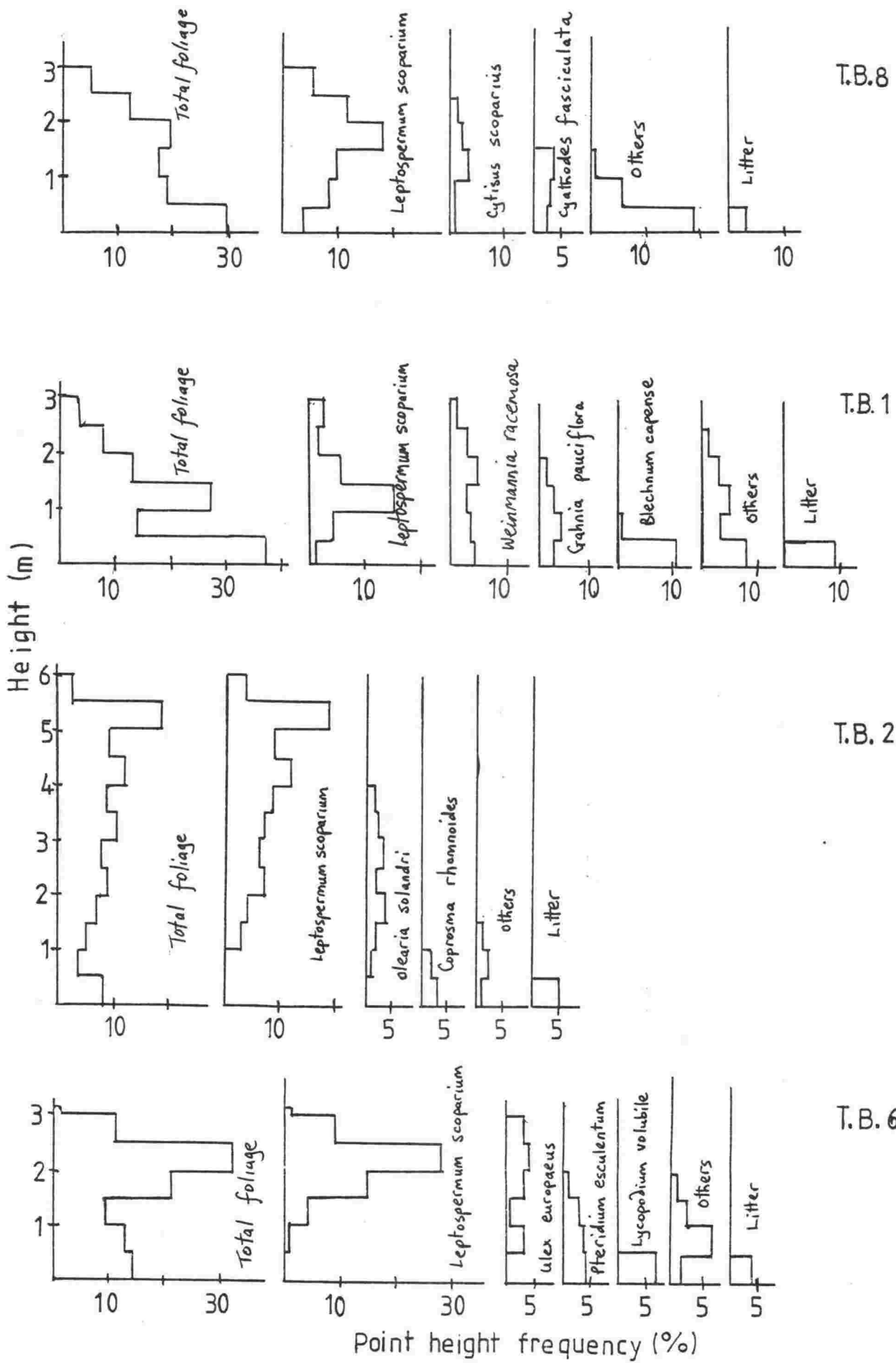




Figure 4:6 xvi—xix

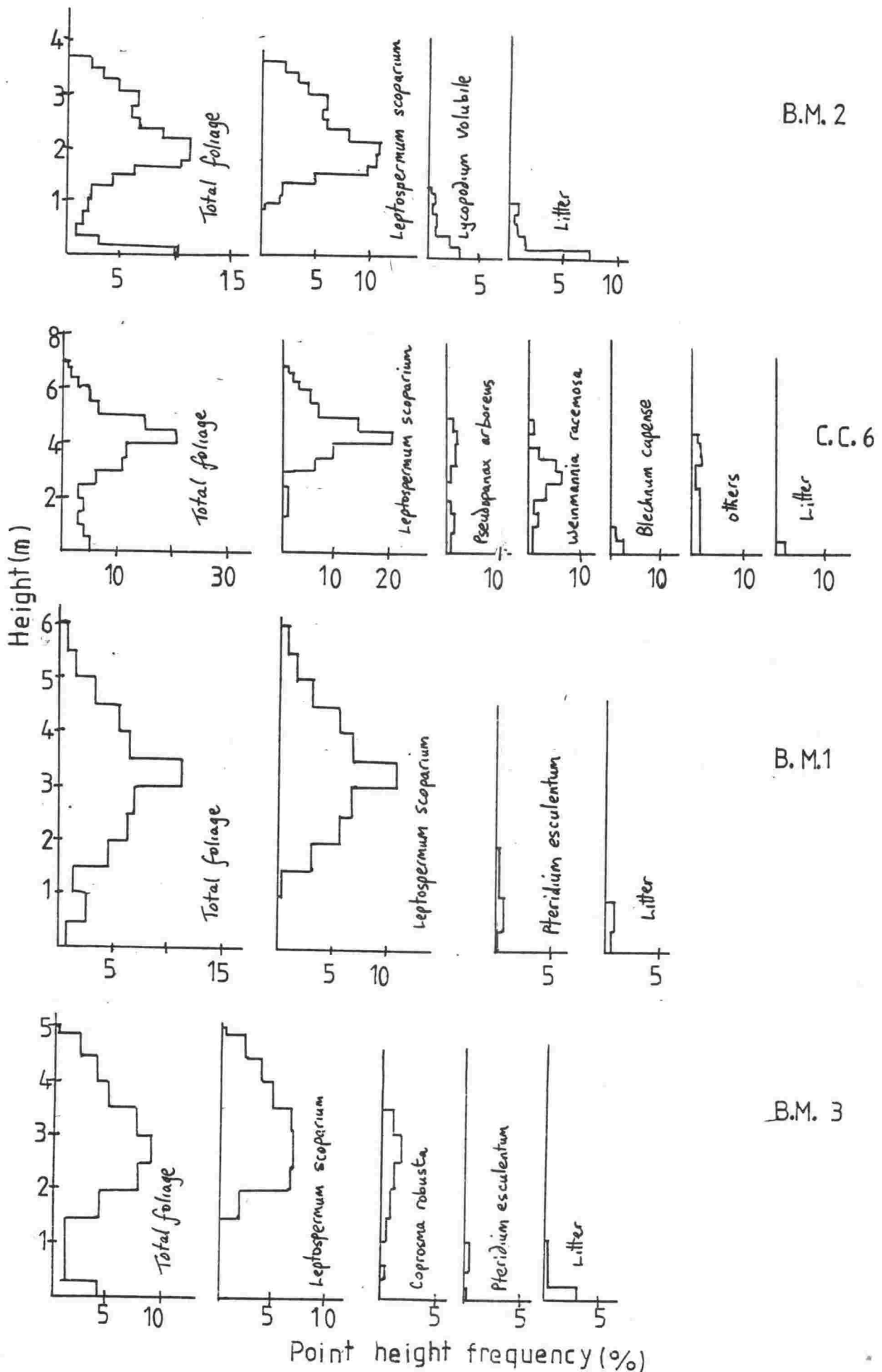


Figure 4:6 xx-xxiii

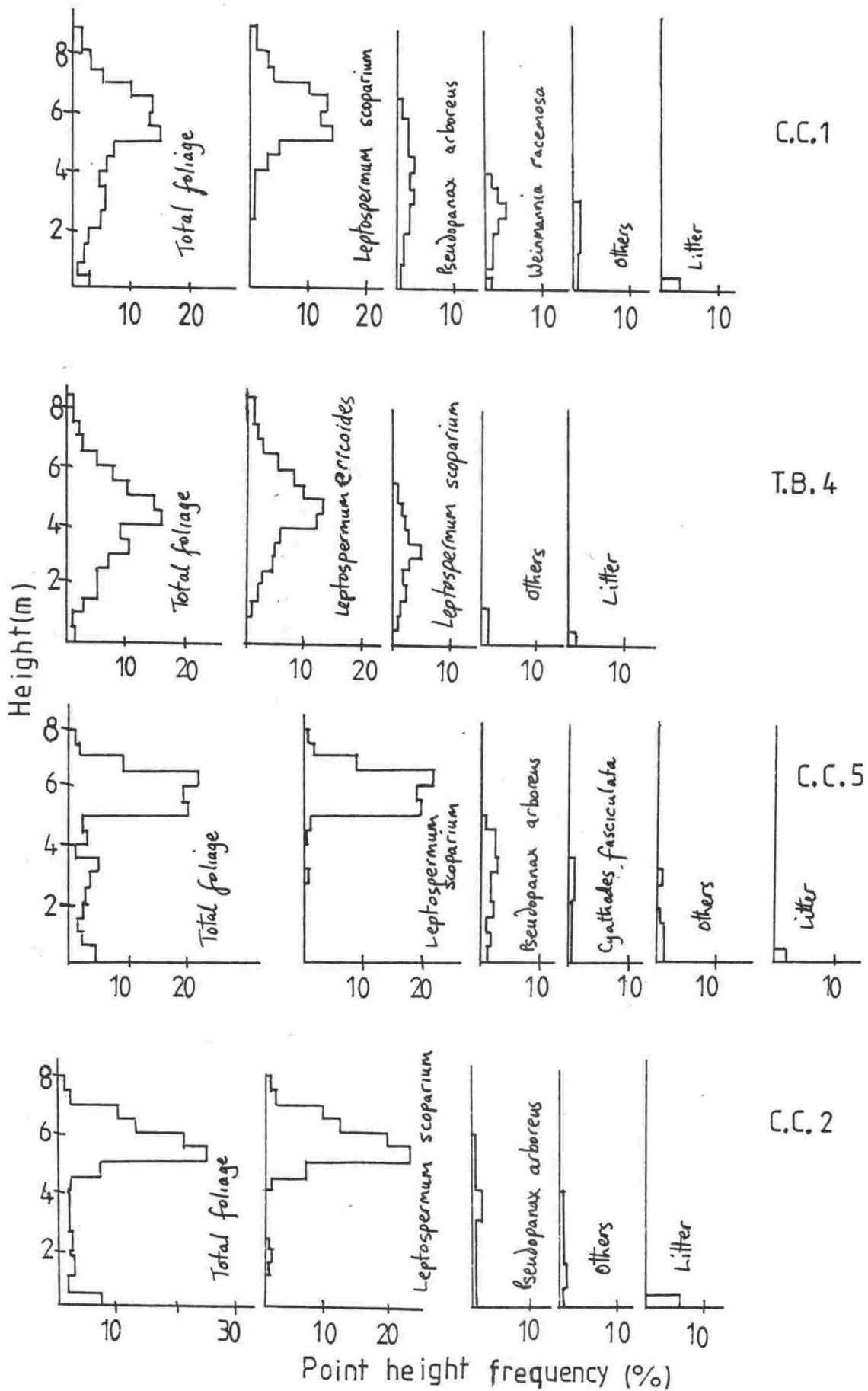


Figure 4:6 xxiv- xxvi

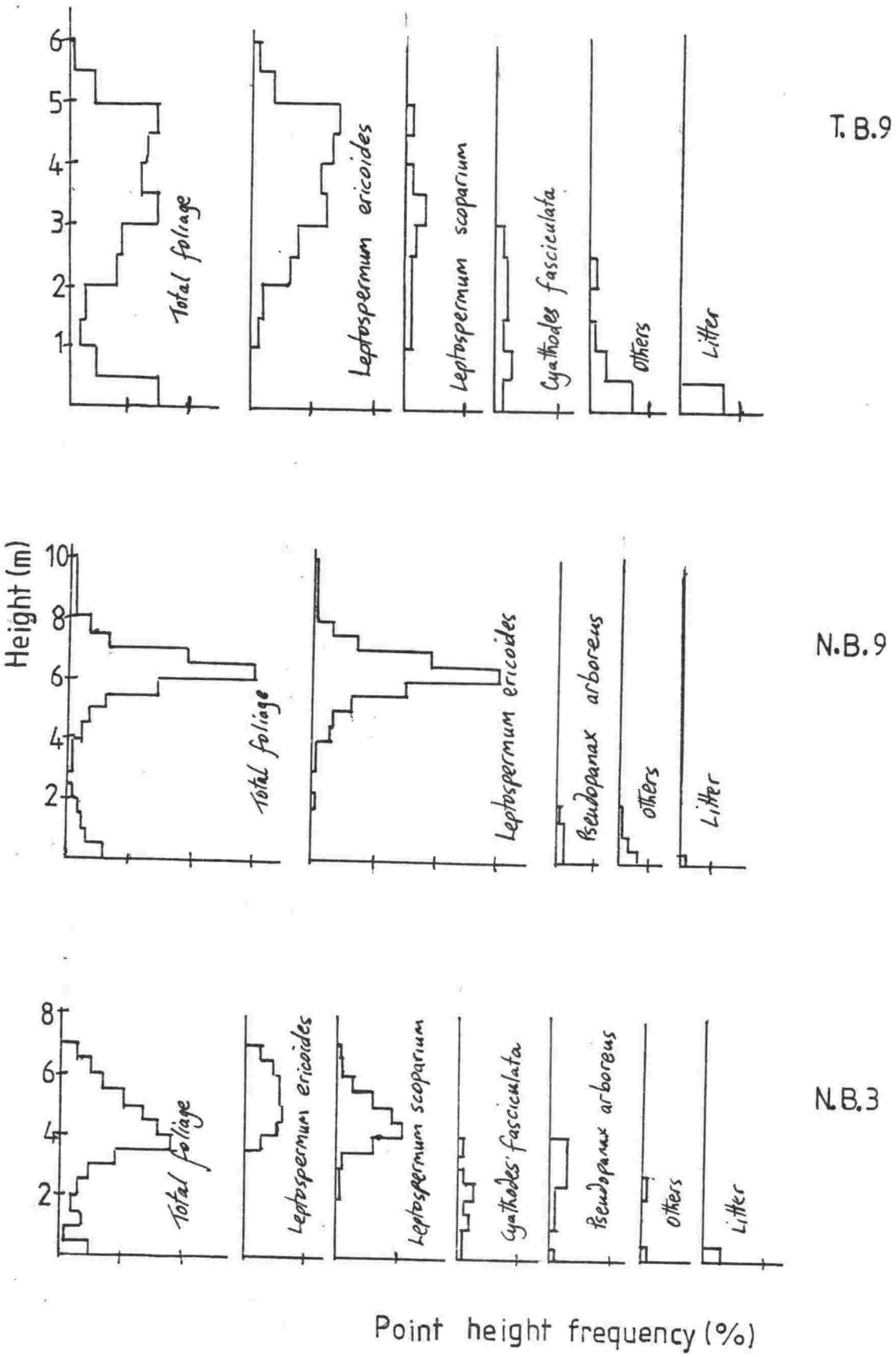


Figure 4:6 xxvii - xxix



Figure 4.6 xxx—xxxii



Figure 4:6 xxxiii—xxxv

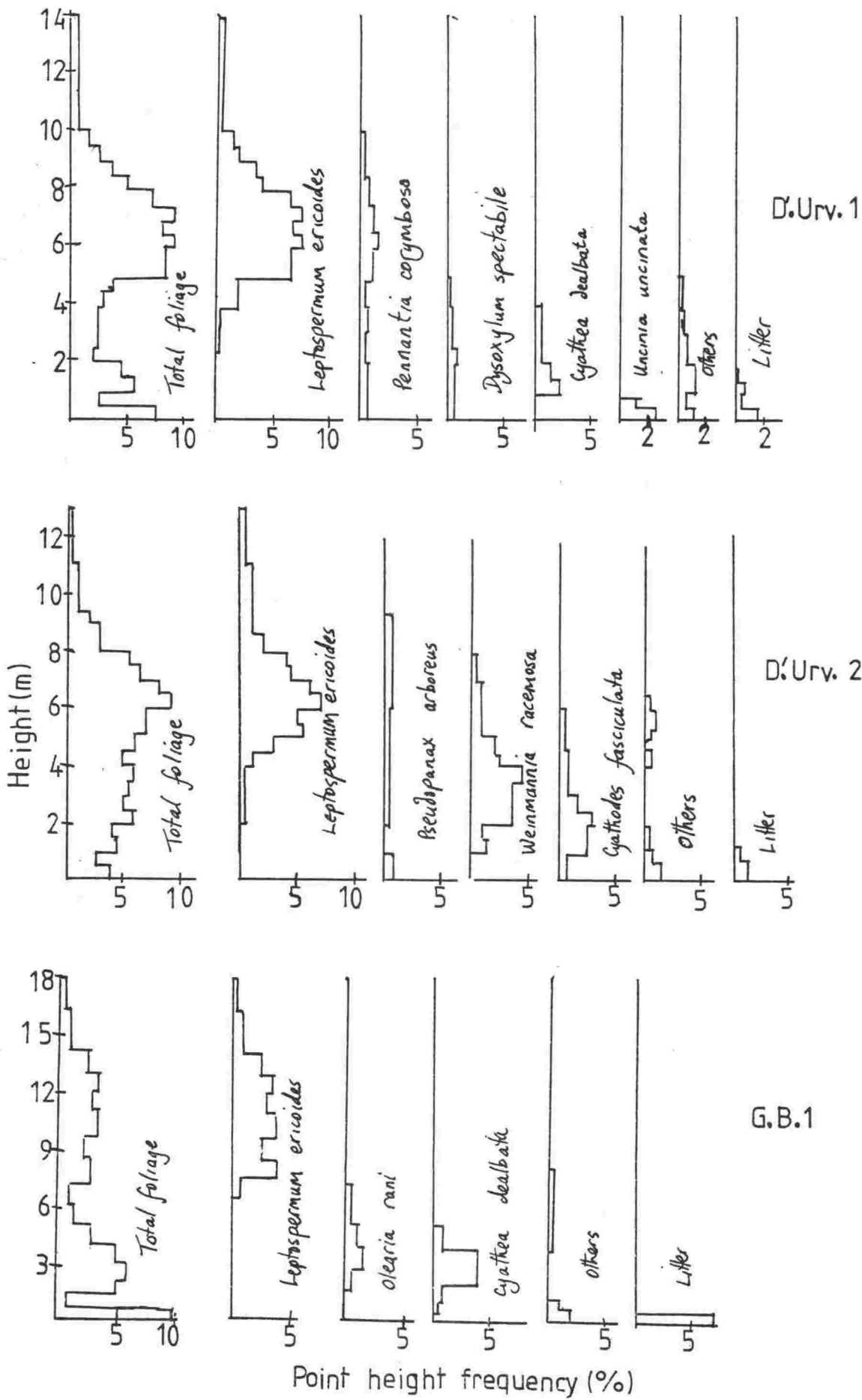


Figure 4:6 xxxvi - xxxviii

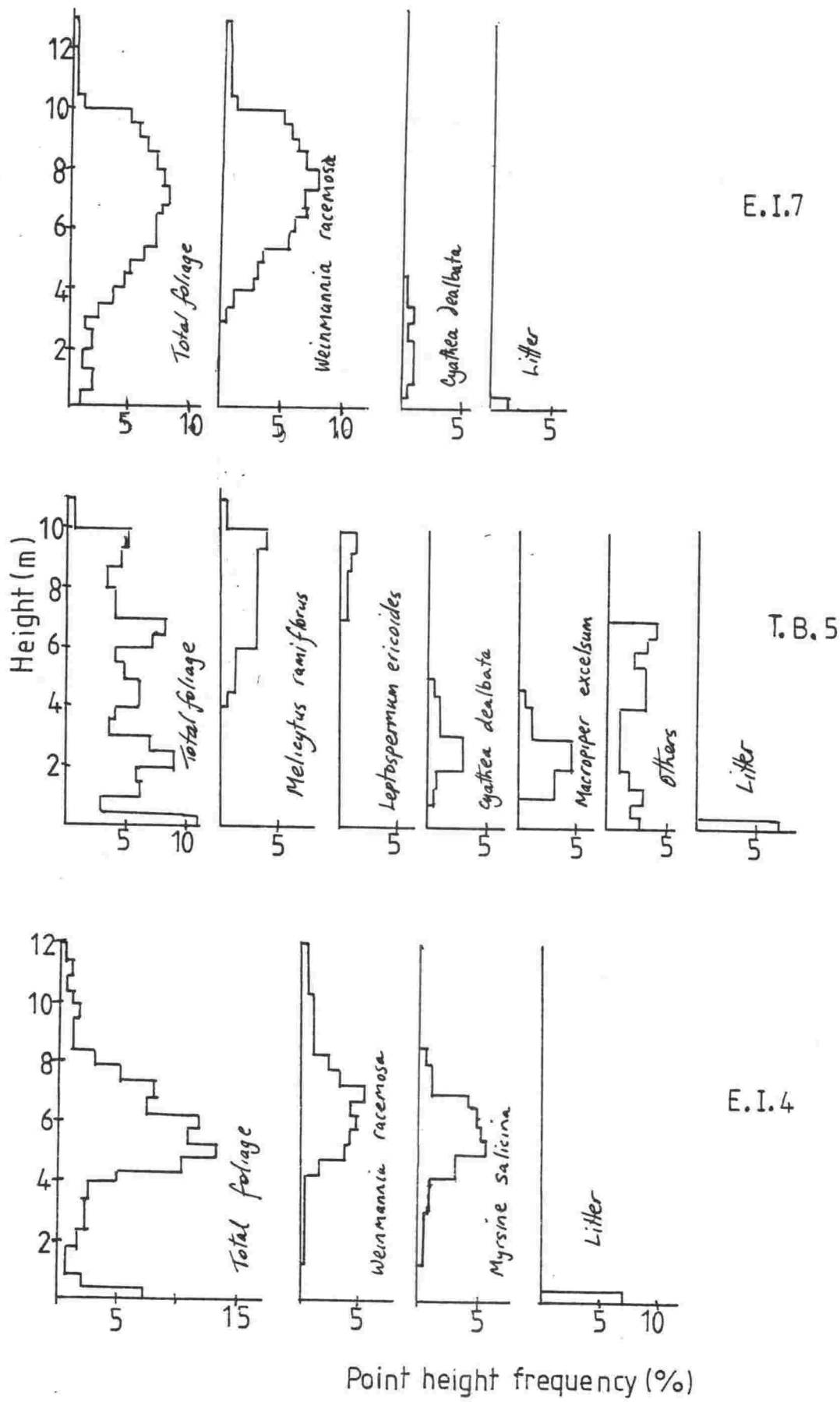
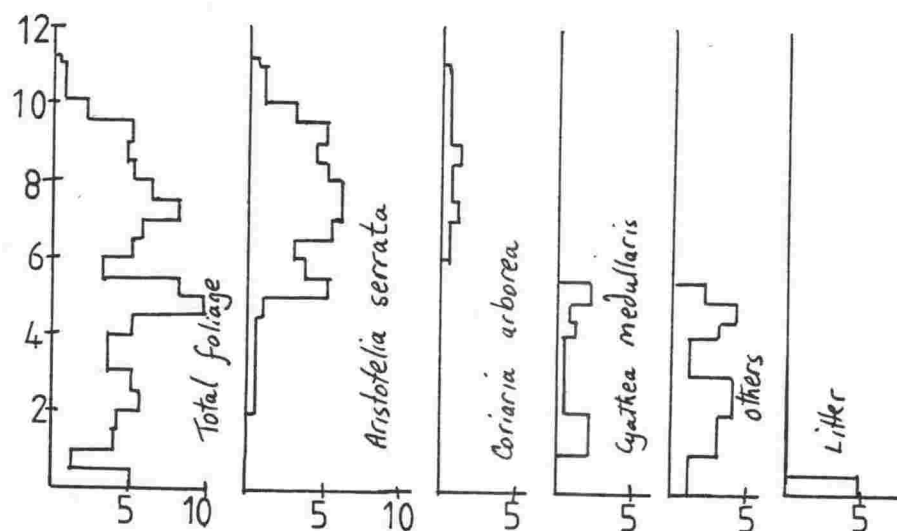
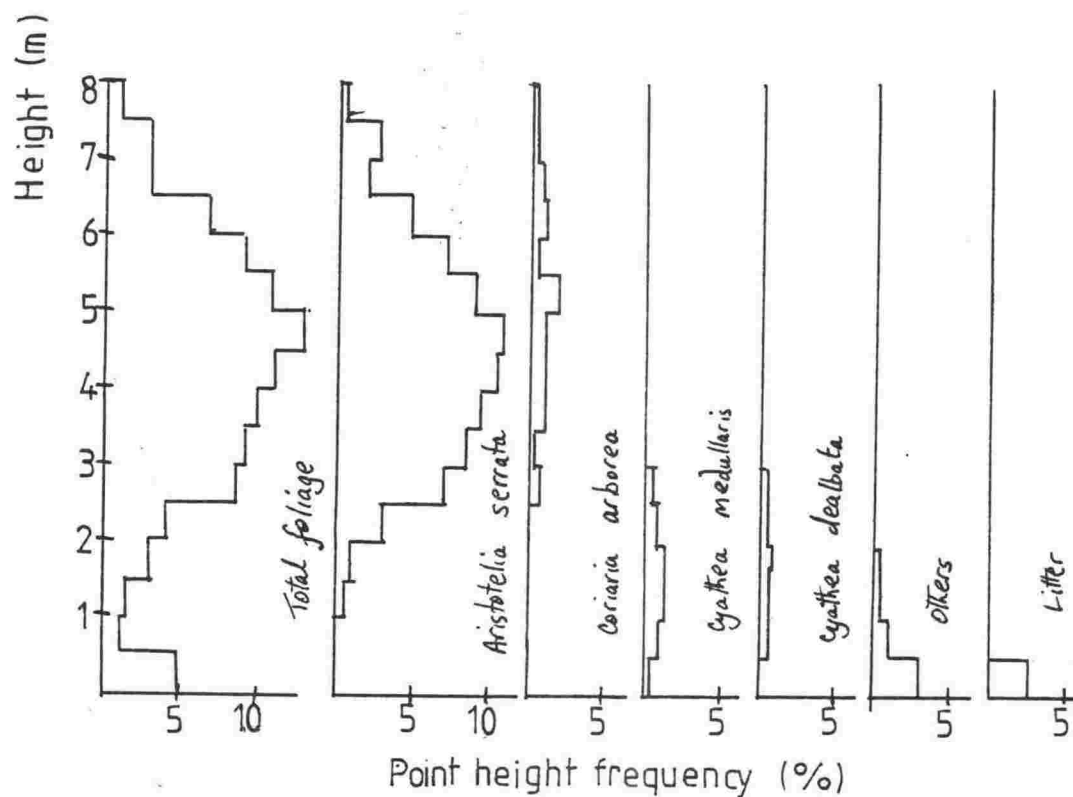


Figure 4:6 xxxix -xl



T.B.3



T.B.7



Figure 4:6 xli—xlii

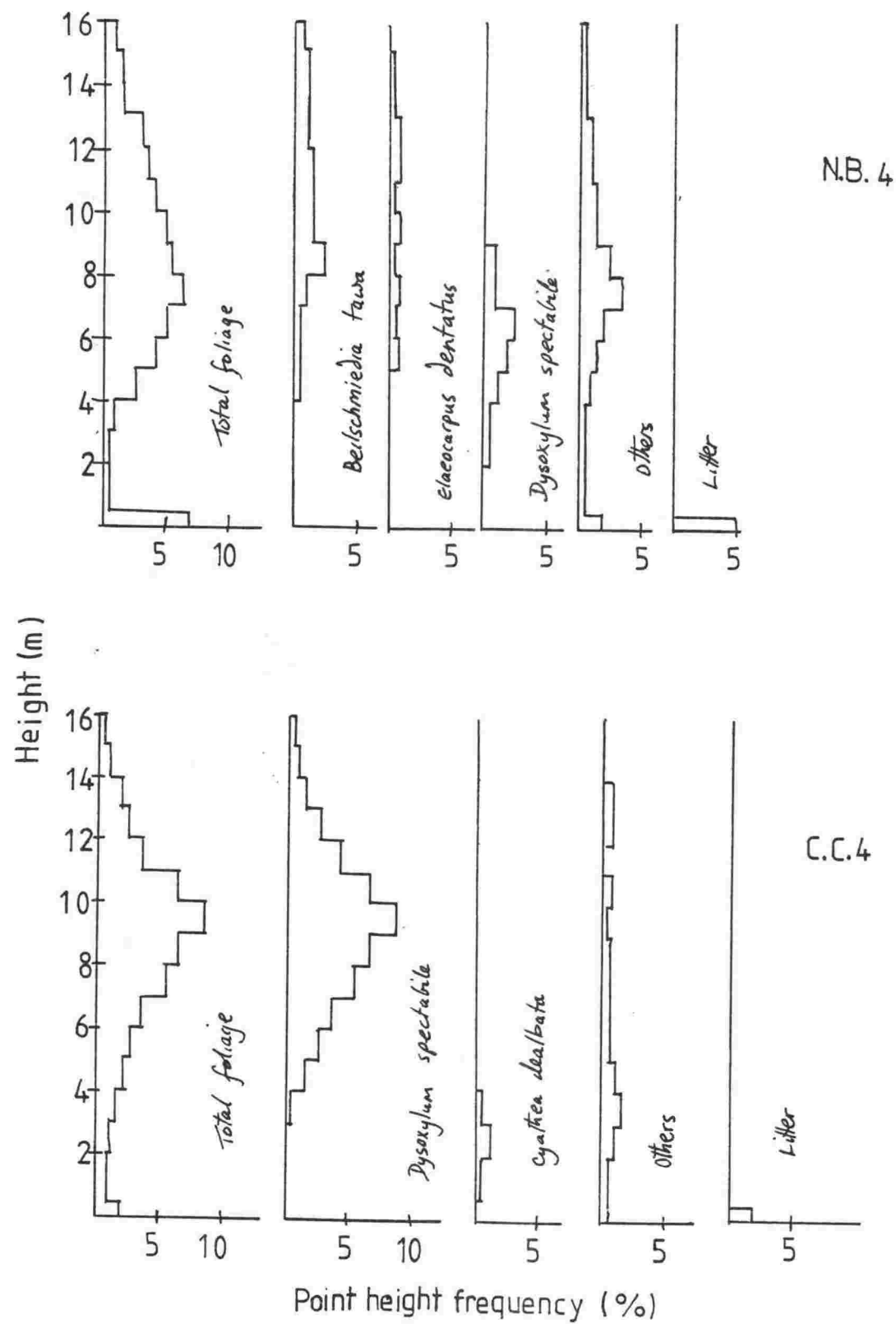
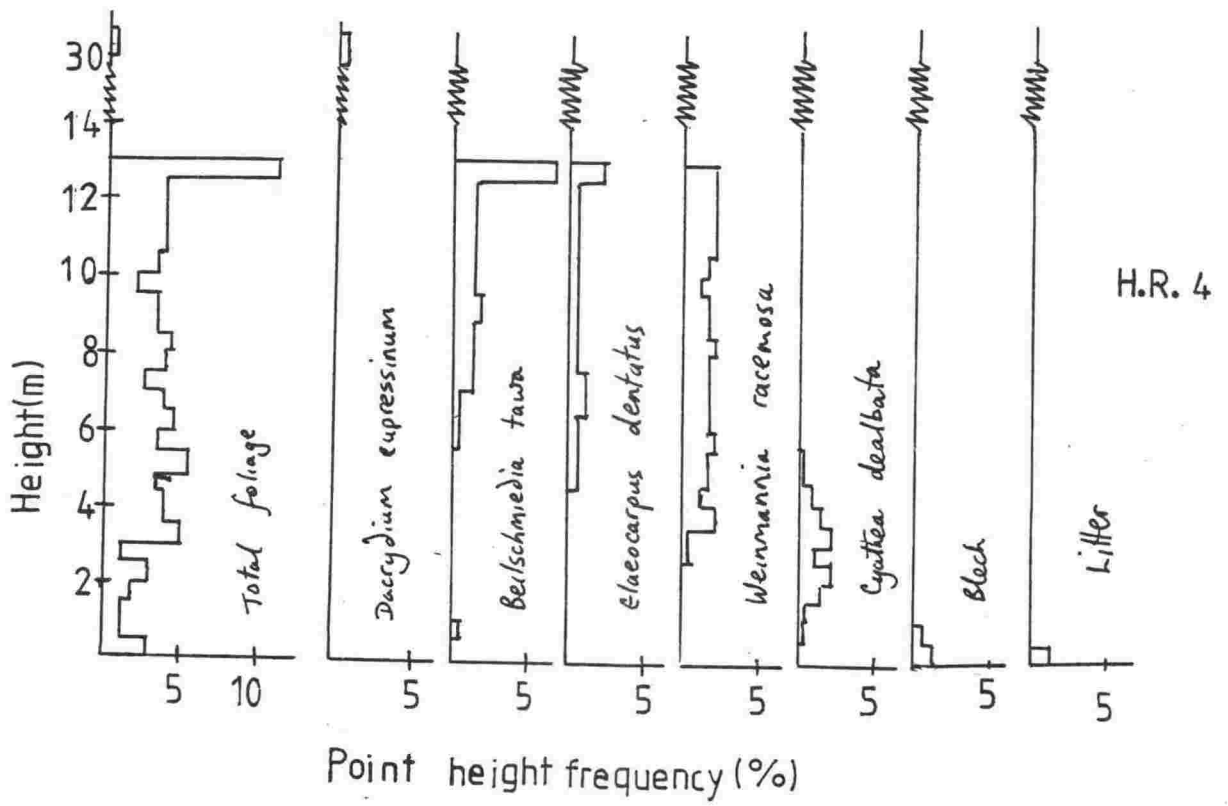


Figure 4:6 xliii



Distribution of foliage in stands H.R.1, H.R.2 and H.R.3 was unable to be determined accurately.

TABLE 4:6. Species Diversity Indices.

Stand	H' (spp. >30 cm)	J' (spp. >30 cm)	R (spp. >30 cm)	I <sub>D</sub> (spp. >30 cm)	H' (top hit cover)	H' (> 3 m cover)	H' (30 cm - 3 m cover)	H' (<30 cm cover)
H.R.5	-	-	42.38	-	2.163	-	1.282	1.996
N.B.5	1.460	0.7183	19.42	0.264	2.770	-	2.482	2.793
N.B.6	2.167	0.9863	14.13	0.438	3.060	-	2.351	3.250
N.B.7	2.634	1.1988	12.95	0.245	2.431	-	1.982	3.081
E.I.5	2.400	1.0423	19.42	0.527	3.491	-	2.273	3.612
E.I.6	2.026	0.9743	14.13	0.393	1.994	-	1.238	2.749
E.I.1	1.859	1.0375	14.13	0.371	0.707	-	0.194	1.842
E.I.2	2.256	1.2591	12.36	0.635	0.585	-	0.534	0.920
E.I.3	2.196	0.8561	15.30	0.531	2.165	-	2.056	1.117
S.C.1	0.00	0.00	6.68	0.00	0.106	-	0.00	0.650
R.B.1	0.983	0.5052	11.77	0.140	2.427	-	2.414	1.757
T.B.8	1.690	0.7692	21.78	0.324	2.508	-	1.698	3.044
T.B.1	0.971	0.5419	23.00	0.170	3.040	-	2.723	2.231
T.B.2	1.959	0.9421	20.68	0.247	1.723	0.130	2.629	2.005
T.B.6	0.935	0.4805	13.89	0.133	2.372	-	2.161	1.537
B.M.2	0.372	0.1912	18.83	0.04	1.365	0.440	1.065	0.813
C.C.6	2.034	0.8185	18.83	0.426	2.610	1.360	2.984	2.271
B.M.1	1.669	0.8577	17.37	0.376	1.502	0.106	2.355	1.972
B.M.3	1.837	1.1414	25.31	0.365	1.972	0.672	1.332	2.307
C.C.1	1.831	0.8805	12.36	0.465	0.323	1.197	1.716	2.122
T.B.4	2.202	1.0022	18.84	0.500	1.694	0.813	1.782	1.770
C.C.5	1.903	0.9152	12.95	0.402	1.938	1.101	1.108	2.855
C.C.2	2.364	0.9859	13.54	0.529	2.075	1.029	1.899	2.646
T.B.9	2.343	0.9771	20.60	0.531	2.425	0.646	2.444	2.661
N.B.9	2.085	0.7699	18.83	0.390	1.910	-	2.082	2.683
N.B.3	2.065	1.0612	17.07	0.578	2.187	1.505	1.704	2.000
C.C.7	3.008	1.0617	19.50	0.576	2.033	0.353	1.994	2.483
N.B.8	2.914	1.0510	22.52	0.566	2.976	1.850	2.595	3.007
N.B.1	3.218	1.3976	21.60	0.522	2.802	1.213	2.929	1.557
C.C.8	2.851	1.2382	15.00	0.629	2.892	1.246	2.515	2.906
N.B.2	2.599	0.8992	20.22	0.770	2.993	1.302	2.913	2.722
C.C.3	2.467	0.9348	10.11	0.507	2.806	2.747	1.621	1.000
D'Urv.1	2.719	0.9807	28.68	0.450	2.968	0.902	3.547	1.567
D'Urv.2	2.503	1.0438	24.33	0.577	2.721	1.962	2.168	2.846
G.B.1	3.580	1.2386	19.12	0.704	2.396	1.845	0.915	1.950
E.I.7	2.712	1.0573	19.30	0.566	3.044	2.389	1.728	2.560
T.B.5	2.521	0.9093	20.51	0.576	3.489	3.015	2.861	2.521
E.I.4	2.939	1.0827	16.55	0.619	3.054	2.647	2.080	0.669
H.R.1	2.246	0.8101	21.40	0.771	1.995	1.142	2.670	2.128
H.R.2	2.448	0.8829	20.37	0.493	2.912	2.584	2.836	1.854
H.R.3	2.119	0.9644	15.34	0.441	1.179	0.770	1.352	0.00
H.R.4	2.558	1.0294	19.78	0.624	3.281	3.001	2.182	2.649
C.C.4	2.593	0.9825	13.79	0.587	2.665	1.604	2.737	2.043
N.B.4	2.814	0.9932	15.34	0.537	4.163	3.602	3.466	1.969
T.B.3	2.417	1.0497	13.79	0.537	2.671	1.885	2.261	2.948
T.B.7	2.377	1.0022	19.30	0.488	2.477	0.981	2.758	2.633

\* Seral stands are ordered from youngest (H.R.5) to oldest (E.I.4).  
H.R.1 - N.B.4 represent virgin forests.  
T.B.3 and T.B.7 are seral stands that could not be aged.

Figure 4:7 Species diversity trends

- Leptospermum - dominated stands
- Non-Leptospermum - dominated stands

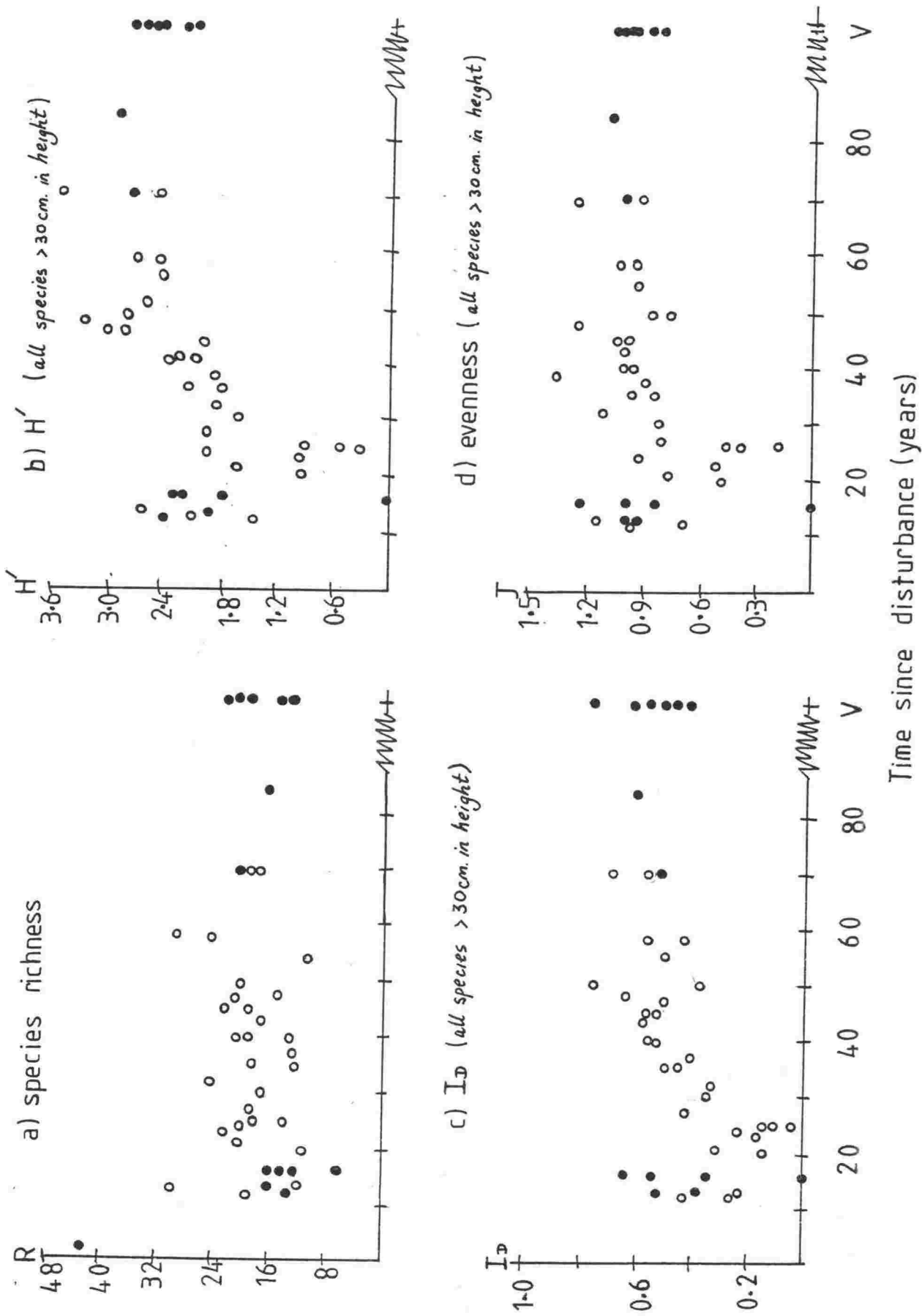


Figure 4:7 Species diversity trends

- Leptospermum-dominated stands
- Non-Leptospermum-dominated stands

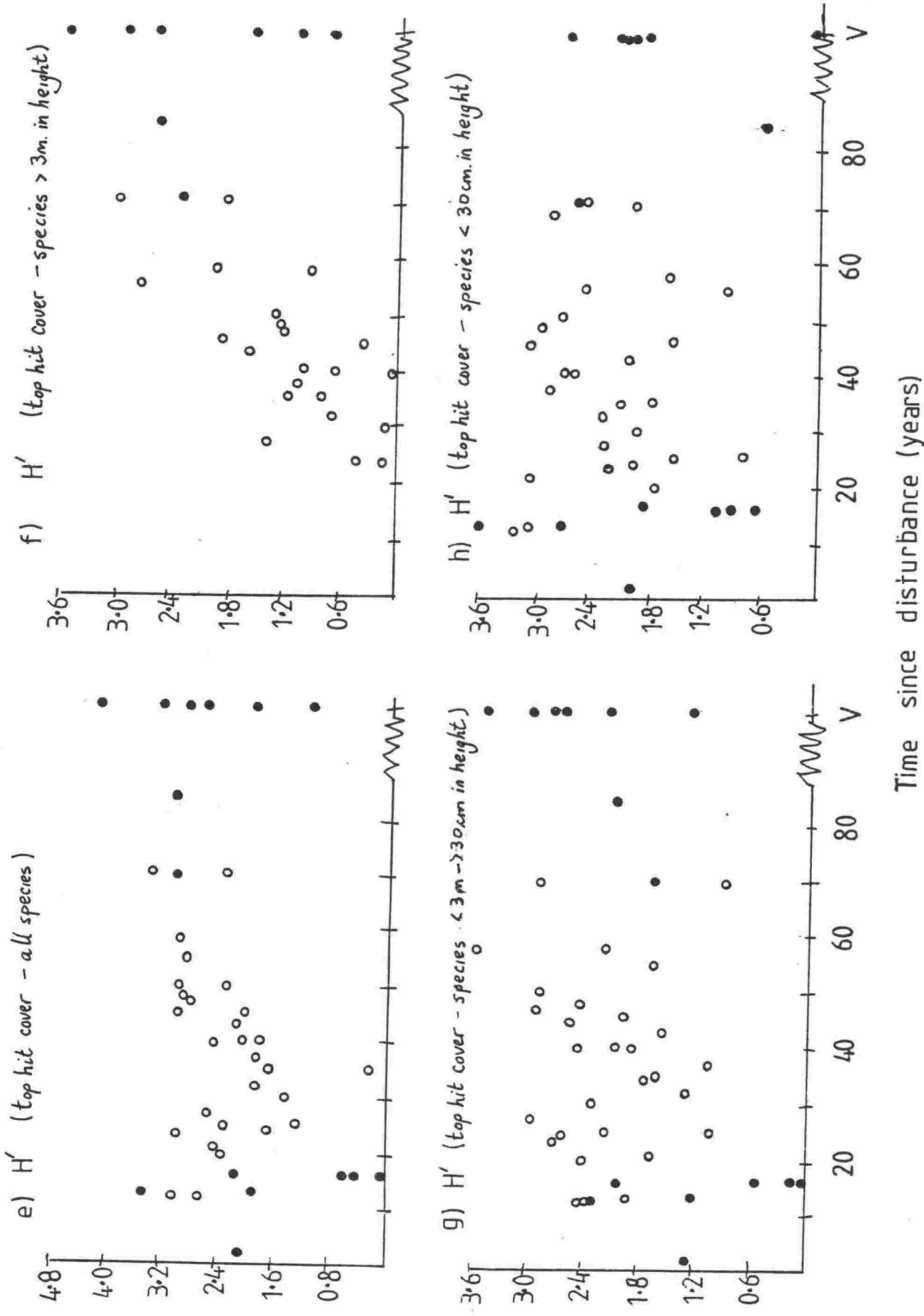


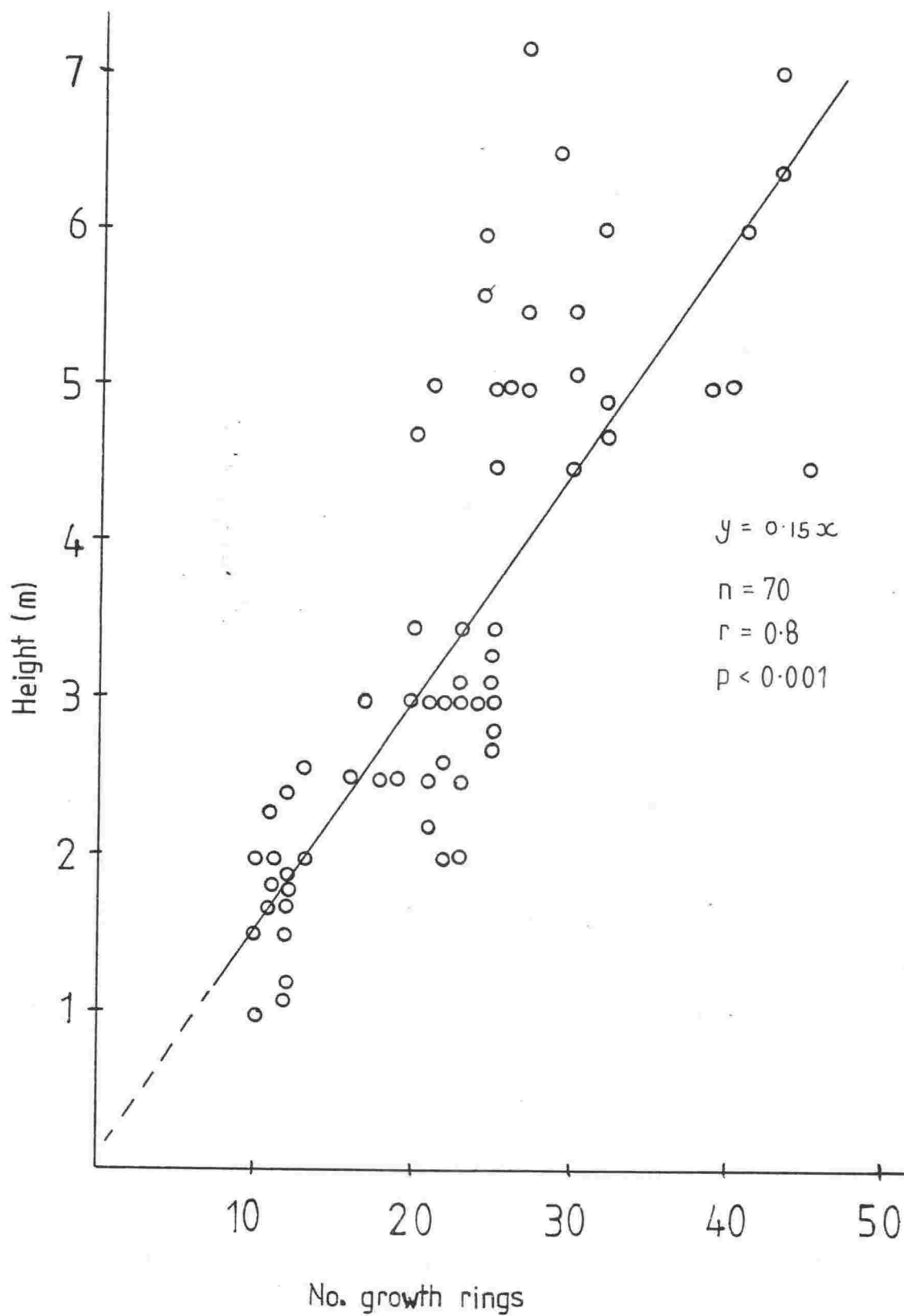
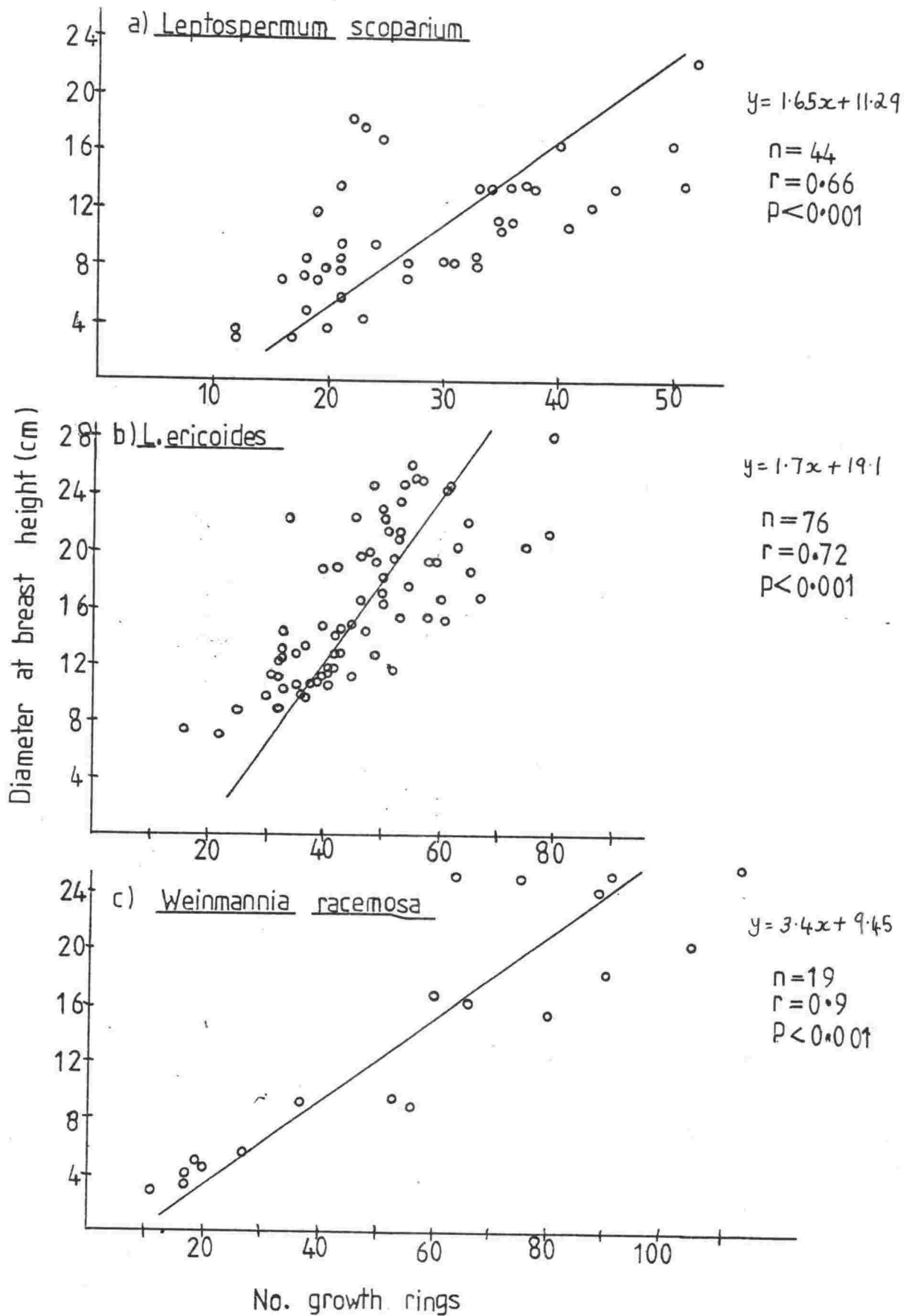
Figure 4:8 Height growth rate of Leptospermum scoparium

Figure 4:9 Diameter growth of three seral species



CHAPTER FIVEForest Floor and Soil-Vegetation Relationships During Secondary Succession5:1 Introduction

The hypothesis adopted at the start of this study was that the type and rate of vegetation recovery occurring in the lowland forest ecosystems of the Marlborough Sounds was related to the fertility of the disturbed site. This hypothesis was based on:

- (a) the observation by other workers in New Zealand lowland forests that different secondary communities were found on soils of different natural fertility (Druce 1957, Atkinson 1973, Kelly 1965),
- (b) the reports from overseas workers that the rapid regeneration of vegetation on disturbed sites was an effective mechanism of reducing nutrient losses from an ecosystem (Marks 1974, Bormann and Likens 1979),
- (c) the hypothesis that succession is a process whereby seral populations accumulate enough nutrients to allow the entry of high fertility-demanding species into the succession (Pomeroy 1970).

In a mature forest it is generally considered that the forest floor is in a steady-state condition whereby the inputs of organic matter and nutrients are balanced by the outputs (Pritchett 1979). Although no studies have been conducted into the dynamics of forest floors under mature lowland forest ecosystems in New Zealand this present study assumes that the forest floors of the undisturbed study sites are in a steady-state condition. After forest clearance there is a decline in the organic matter content of the forest floor (if some forest floor material remains after forest clearance); this is a result of both the cessation of input of litter from vegetation to the forest floor and to an increase in the rate of decomposition of the forest floor.

After forest removal the nutrients in the forest floor can be either:

- (1) lost from the ecosystem; by volatilization if forest clearance has been undertaken with the aid of fire, by rapid leaching through the root zone of the mineral soil horizons, by direct removal (bulldozing, wind and water erosion) or
- (2) retained in the ecosystem and possibly enhance soil fertility of a site by being in a more available form to plants than they were previously when bound in organic complexes in the



forest floor horizons.

Although the fate of the forest floors immediately following disturbance was unknown for all but one of the study sites, and it was recognized that the degree of disturbance suffered by any one site might have been quite different from that of other sites, it was hoped that trends of forest floor recovery during succession would be evident from sampling a number of forest floors under different types and stages of seral vegetation.

## 5:2 The Forest Floor

### 5:2:1 The nature of the forest floors

In the present study four different types of forest floor were encountered. (Forest floor descriptions of each site are presented in Appendix IV). Mor humus is formed under the undisturbed *Nothofagus truncata* and *N. solandri* var. *solandri* stands. A laminated mor develops under dense *Pteridium esculentum* stands. Mull humus is formed under the mature podocarp/broadleaf, broadleaf and coastal broadleaf forests as well as under some regenerating stands of broadleaf species. A mor-like mull is formed under the regenerating stands dominated by *Leptospermum scoparium*, *L. ericoides* and *Cassinia leptophylla*.

- (1) The mor humus under *Nothofagus truncata* possesses either distinct litter, fermentation and humus layers or a distinct litter layer and a layer where the fermentation and humus components can not be separated (F and H). The forest floor profiles of stands H.R.1 and H.R.3 (Appendix IV) are examples of these two variations.
- (2) Under dense *Pteridium* stands a mor humus is also found. The organic layer can be quite deep. This humus type is characterised by possessing a very deep litter layer in comparison to the decomposing layers. The F and H layer is usually dark brown (10 YR 3/4) or brownish-black (2.5 Y 3/2) and often melanised. A horizon soils are present in damp valley situations beneath the *Pteridium*. The A horizon soil is very friable under a dense *Pteridium* cover.
- (3) The undisturbed podocarp/broadleaf, broadleaf and coastal broadleaf forests have a mull humus profile which is similar to that found under the regenerating broadleaf stands. At these sites a shallow litter, usually less than 1 cm in depth, directly overlies a loose granular A horizon. There is no differentiation of the organic matter into litter, fermentation or humus layers with depth (L and F and H); just a scatter of leaves and twigs in different stages of disintegration and decomposition across the surface of the mineral soil. There are often faecal pellets and worm casts intermixed with the litter.

(A deep mor humus develops directly under the canopy and around the base of large *Dacrydium cupressinum* trees. The development of the mor humus is very localised and a mull humus is encountered beyond the range of the *D. cupressinum* canopy).

(4) The fourth forest floor type was encountered under many of the regenerating shrublands on the slopes and ridges dominated by *Cassinia leptophylla* and *Leptospermum* species. A thin mor-like mull humus is present. The organic material is usually 1 cm or less deep, it is composed of a litter of loose leaf and twig material that shows little sign of decomposition. Sometimes the forest floor material shows the beginning of the development of distinct layers, this occurs under a large *Leptospermum* tree where there may be an accumulation of litter above a matted decomposing layer that contains mycelia. The mor-like humus overlies a mulloid A horizon that usually possesses a granular or crumb structure.

The forest floors were differentiated in the field and only morphological criteria were considered when deciding what type of forest floor was present under a stand of vegetation. The different types of forest floor can also be defined in terms of biochemical features they possess. Two measures recorded in this present study that have been used to differentiate between the types of forest floor are the pH and C/N levels of the forest floor horizons (Table 5:1). Duchaufour (1970) classifies a mull as having a pH of 5.5 or greater and a C/N less than 20, a moder as having a pH between 4 and 5 and a C/N between 15 and 25 and a mor as having a pH between 3.5 and 4.5 and a C/N between 30 and 40 for the fermentation (F) layer and around 25 for the humus (H) layers.

If the above criteria are accepted then the organic horizons under the *Pteridium* and *Nothofagus* stands are mors on biochemical criteria. The pH levels of the forest floors under *Leptospermum* and *Cassinia* dominated stands fall within the range of moders but most of their C/N ratios are above 25. Similarly whilst the pH levels of the forest floor under the broadleaved stands are within the range of mulls the C/N levels are high and encompass the range from mull to mor.

#### 5:2:2 Recovery of forest floor biomass during succession

The oven dry weights of the forest floor (not including the wood component) are presented in Table 5:2 and the pattern of recovery of the forest floor during succession is presented in Figure 5:1a. Only the average values of the weight of the forest floor are presented in the figure. Coefficients of variation of the weights of the forest floor are high. Only 13% of the study sites had their forest floor weights estimated within 10% limits of accuracy. Twenty sites had estimated mean forest floor weights with coefficients of variation greater than 30%.

Figure 5:1 Development and nutrient content of forest floor

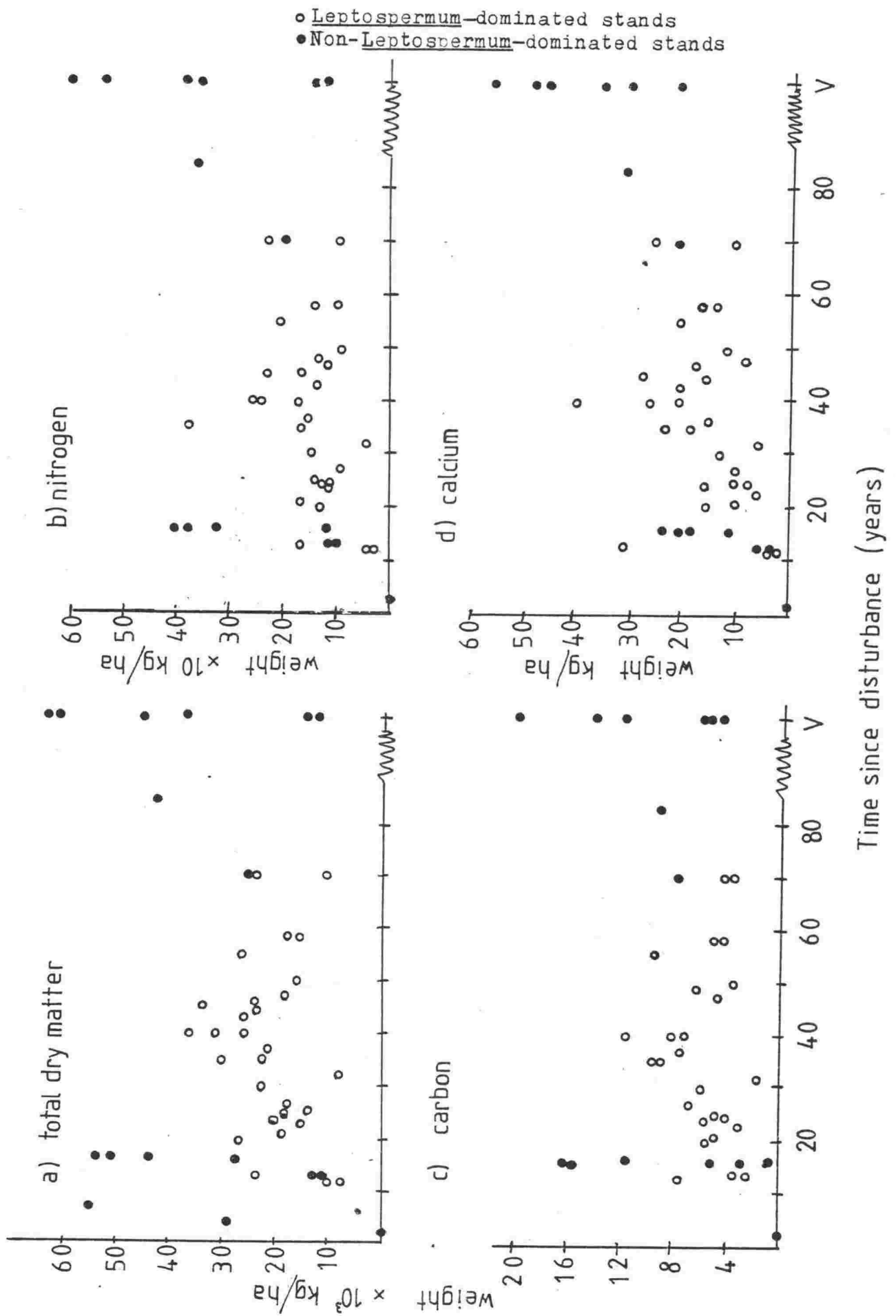
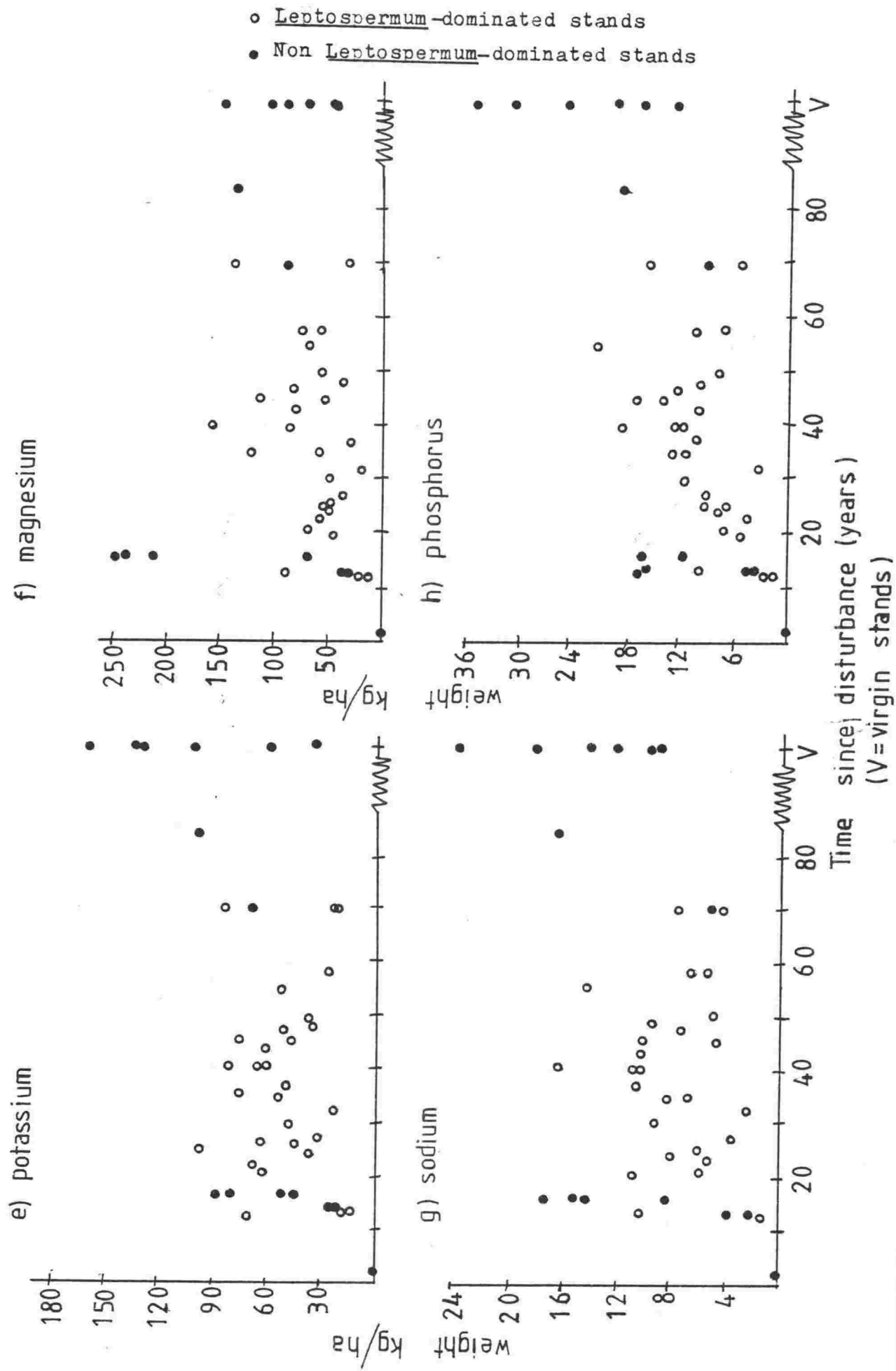


Figure 5:1 Development and nutrient content of forest floor



The sample size employed in this study is inadequate to estimate within reasonable limits the weight of the forest floor at most of the study sites. Trends are noted from this data however.

The accumulation of the forest floor is largely determined by the annual amount of litter fall minus the annual rate of decomposition (Jenny *et al.* 1949, Olson 1963). The observation by Covington and other workers in the hardwood forests of North America that the forest floor continues to decline in weight for sometime after the forest is cut-over (Covington 1976, Bormann and Likens 1979) indicated that the rate of forest floor decomposition and nutrient mineralisation exceeded the rate of input of litter to the forest floor during the early years of secondary succession.

The fate of the forest floors immediately following disturbance was unable to be studied in the present study. Disturbances that initiated the studied successions may have removed much of the original forest floor as well as the living vegetation. The youngest stand H.R.5 had had all of the original *Nothofagus truncata*-*N. solandri* var. *solandri* forest floor removed by mechanical means at the same time that the forest was removed. At two of the 12-13 year old burn sites at Ngaruru Bay forest floor development was just commencing and it would appear that all of the previous forest floor had been incinerated or washed downslope some time after the fire and prior to the growth of the seral species. Site N.B.7 however had a fairly deep forest floor with a well developed F and H layer (2 cm deep) which had the appearance of a humus that had developed under *Nothofagus* forest. This site, situated in a sheltered concavity, may have only carried a relatively light fire that burnt all standing vegetation and only the surface litter layer. At all of the other study sites it was not possible to estimate to what extent the forest floor had been disturbed at the beginning of the succession.

There are two main patterns of forest floor accumulation in this study. Sites dominated by *Pteridium esculentum* show a rapid recovery of forest floor biomass. Additional information on litter weights under *Pteridium* cover has been provided for two stands at Tennyson Inlet, Pelorus Sound by Dr. J.R. Bray (pers. comm.). One stand was dominated by 4.5 year old *Pteridium*, the other stand was composed of 7 year old *Pteridium*; these litter weights have been presented in Figure 5:1a.

Sites dominated by the *Leptospermum* and *Cassinia* species show slower rates of forest floor accumulation; the forest floor weights attained by the *Pteridium* stands are never equalled in the *Leptospermum* and *Cassinia*

shrub and forest stands.

The fate of the forest floor in the *Pteridium* stands is not known. The inferred direction of secondary succession at these sites is toward broadleaf forest and it is reasonable to assume that the weight of the forest floor will decline to levels similar to those of broadleaf forest. The *Pteridium* litter and humus will decompose with time and the forest floor inputs will be from broadleaf species.

There is a trend toward a decline in the weight of the forest floor in the *Leptospermum* dominated stands after 40 years of succession. This decline in the forest floor could be due to a lowering of the litter input to the forest floor, or to a more rapid decomposition of the forest floor, or a combination of the two factors. The decline in forest floor occurs at the same time that the contribution of *L. scoparium* to the basal area and crown cover of a stand begins to decline and the contribution of *L. ericoides* and *Pseudopanax arboreus* to a stand's basal area and crown cover begins to increase.

The *Leptospermum* dominated successions that were initiated by the destruction of *Nothofagus* forest do not attain the forest floor weights possessed by mature *Nothofagus truncata* forest. Similarly, the weights of forest floor possessed by the mature undisturbed podocarp/broadleaf and broadleaf forest of Howden's Reserve, Endeavour Inlet are never equalled by the seral shrub and forestlands in the first eighty years after disturbance.

At sites where it proved possible to resolve the forest floor into its component layers the lower decomposed layer was usually denser than the a litter layer. Processes of degradation and decomposition in litter and humus occur at different rates. The humus layer represents a pool of material that is more resistant to decomposition than the litter and over a time period the humus layer accumulates relative to the litter layer (Minderman 1968).

Two studies have been undertaken in the Wellington region that provide information about forest floor weights under secondary vegetation in New Zealand. At the Taita Experimental Station litter weights under young stands (4, 7 and 10 years old) dominated by *Ulex europaeus* ranged from 8,800 kg/ha to 11,810 kg/ha. The forest floor weights under intermediate aged stands (16, 21 and 33 years old) of *Ulex europaeus* and *Leptospermum scoparium* ranged from 3,170 kg/ha to 18,410 kg/ha and were similar to, or

lower than, the recorded weights of forest floor under vegetation of a comparable age in the Marlborough Sounds.

The forest floor weights of older stands (45 and 57 years old) dominated by *Leptospermum scoparium* and *Weinmannia racemosa* were 6,880 kg/ha and 11,730 kg/ha respectively, <sup>(Egunjobi 1969)</sup> and were much lower than the weights recorded from similar aged stands in the Marlborough Sounds.

A secondary stand of *Nothofagus truncata* was studied by Miller at Keith George Memorial Park, Silverstream, Wellington. The stand was 110 years old and had a forest floor weight of nearly 17,000 kg/ha (Miller 1963); this value is considerably less than the weights of the forest floor under undisturbed *N. truncata* stands in the Marlborough Sounds.

The values of the forest floor weights in the mature podocarp/broadleaf and broadleaf stands are similar to, or slightly higher than, the weights reported from steady-state hardwood forests in temperate regions of the world (Rodin and Bazeliovich 1967, Bourn and Brown 1971, Mader *et al.* 1977).

#### 5:2:3 The nutrient content of the forest floor

Total nitrogen, calcium, magnesium, potassium, sodium, phosphorus and organic carbon concentrations were determined on duplicate samples of forest floor layers at two sites in each stand. Nutrient weights were calculated from the average weights of each forest floor layer. The concentration of elements and weights of each element in the forest floor of the study stands are presented in Tables 5:1 and 5:2.

Only the average value of the nutrient concentration is presented. Concentrations of duplicates were only accepted if the levels were within acceptable limits of each other.\* Samples were reanalysed if the values obtained were outside acceptable limits. The concentration of the nutrients studied was remarkably similar in both of the forest floor samples at each study stand. The overall variation in the weight of the forest floor at any one study stand far outweighed the nutrient content variability of any one forest floor layer.

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\* Analyses were repeated when the difference between duplicates relative to their mean values exceeded 5% of N, C, exch. Ca, Mg and K and 10% for exch. Na and Truog P.



### 5:2:3a Nitrogen in the forest floor

In the present study only three seral sites contained a vascular nitrogen-fixing species in any quantity (*Coriaria arborea* in T.B.3 and T.B.7 and *Ulex europaeus* in T.B.6). Some other vascular nitrogen-fixing plants (*Trifolium* spp., *Lotus* spp., and *Cytisus scoparius*) are present in small quantities at some of the other study sites. However, the nitrogen-fixing plants are not conspicuous elements of this study's flora and hence the study offered the opportunity to observe the course of secondary succession in the absence of a period of rapid nitrogen accumulation.

Nitrogen concentrations in the litter layers range from 0.38-1.49%. Sites that possessed discrete L and F and H layers usually had lower N concentrations in the litter layer than in the decomposing F and H layer. However, the lowest N concentration recorded was from the humus layer of undisturbed *Nothofagus truncata* forest. This H layer contained a quantity of mineral soil and the low N concentration partially reflects the mixed composition of the layer. The highest N concentrations were found in the L and F and H material under the secondary *Coriaria arborea-Aristotelia serrata* stands; average N concentrations for the two stands were 1.4 and 1.49%.

The rate of nitrogen accumulation in the forest floor layers of all the stands (Figure 5:1b) is directly related to the rate of litter accumulation. A linear regression of the two variables yielded a significant positive correlation

$$(r = 0.928, n = 45, p < 0.001).$$

There is no large accumulation of N in the forest floor during the early stage of succession. The two sites dominated by *Coriaria arborea* do not appear to exhibit a different pattern of nitrogen accumulation in their forest floors from that shown by the other study sites.

Weights of N in the forest floor range from 0 kg/ha (at H.R.5, where no forest floor had developed) to 608 kg/ha (under undisturbed *Nothofagus truncata* forest). Most of the seral sites had N weights in the range 150-250 kg/ha in the forest floor.

### 5:2:3b Carbon in the forest floor

Organic carbon concentrations in the litter range from 21-41%. The organic C content of the decomposing layers is less than that of the litter; values range from 6% in the H layer under undisturbed *Nothofagus truncata* forest to 36% in the F layer of the same forest. Average litter C contents are around 30% and average F and H C contents are around 25%.

The rate of C accumulation in the forest floor (Figure 5:1c) is directly related to the rate of forest floor accumulation ( $r = 0.901$ ,  $n = 45$ ,  $p < 0.001$ ).

High weights of C in the forest floor are found under the *Pteridium esculentum* stands; weights of carbon can reach 16,000 kg/ha in 16 year old vegetation. The highest weight of C in the forest floor is under one of the undisturbed *Nothofagus truncata* stands where there is 21,390 kg of C/ha.

The *Leptospermum* dominated stands have weights of C in their forest floors in the range between 2,000-10,000 kg/ha. Maximum values of C accumulated in the forest floor occur approximately 40 years after disturbance, thereafter the weight of C in the forest floor declines in the *Leptospermum* dominated stands.

### 5:2:3c Carbon:Nitrogen ratio of the forest floor

The C:N ratio serves as an indicator of the stage of decomposition of organic matter (Ulrich 1971). Plant material that is fully humified has a C:N value near to 10. During the process of decomposition the carbon of the forest floor serves as an energy source for decomposers and the nitrogen is used for the construction of cellular organic compounds. Material with a high N content is usually more rapidly decomposed than material having a low N content (Bocock 1964, Anderson 1973). Other factors may influence the ability of micro-organisms to cause litter breakdown (e.g. lignin content, polyphenol content, phosphorus content, base concentrations and physical nature of the material (Pritchett 1979)), hence, the relationship between rate of litter decomposition and nitrogen content is not a direct one when different plant materials are considered.

When the C:N ratio of decomposing material is around 30:1 nitrogen mineralisation is usually rapid (Russell 1973, Duchaufour 1970). Nitrogen mineralisation proceeds at a slower rate as the C:N ratio narrows.

The C:N ratios of the forest floor materials sampled in this study fall into three broad categories:

- (1) very high C:N ratios (> 50) exhibited in the litters of the *Pteridium esculentum* stands and the mature *Nothofagus truncata* forests,
- (2) high C:N ratios (30-50) exhibited in the litters of the *Leptospermum* dominated stands and the undisturbed podocarp/ broadleaf and broadleaf stands,
- (3) moderate-low C:N ratios (< 30) exhibited by the litters of the *Cassinia leptophylla* dominated shrublands and the *Coriaria arborea-Aristotelia serrata* forestlands.

The C:N ratios narrow in the decomposing layers of the forest floor and values around 20-30 are shown by the stands that have high and very high C:N ratios in their litters.

The C:N ratios of the litters and decomposing layers do not exhibit any trend with succession.

#### 5:2:3d Cation Content of the forest floor

Total Mg, Ca, Na and K concentrations were determined in the forest floor materials.

The concept of cation exchangeability in the litter and F and H layers is not a useful one; potentially, all the cations are capable of being released during decomposition and moving into the mineral soil horizons (Ogden 1974, Gadgil *et al.* 1976).

The total cation content of the forest floor reflects the nature of the different types of forest floor.

The concentration of K and Ca is low in the mor litter and F and H layers under *Pteridium esculentum*. The K and Mg content in the forest floor under *Nothofagus truncata* is low, although the Ca content of the

litter is of a moderate level.

The mull litter layers are high in K, Mg and Ca. Na concentrations are fairly constant within the contrasting forest floor types.

The mor-like mull forest floors under the *Leptospermum*-dominated and *Cassinia* stands are generally intermediate in total cation content between the mull and mor types. Low concentrations of cations are present in the young *Leptospermum scoparium* stands N.B.5 and N.B.6.

The pattern of accumulation of the cations on the forest floor, like that of C and N, is directly related to the litter biomass accumulation. There is a significant correlation between the weight of the forest floor and the weight of each cation in the forest floor;

weight Ca in forest floor:weight of forest floor

$r = 0.743, n = 45, p < 0.001$

weight Mg in forest floor:weight of forest floor

$r = 0.773, n = 45, p < 0.001$

weight Na in forest floor:weight of forest floor

$r = 0.56, n = 45, p < 0.001$

weight K in forest floor:weight of forest floor

$r = 0.701, n = 45, p < 0.001.$

There is a fairly constant weight of K in the forest floor in the seral stands (weights are generally between 25-75 kg/ha). Highest weights of K in the forest floor are found in the mature *Nothofagus truncata* forests and a mature podocarp/broadleaf forest where values are between 130-160 kg/ha.

The greatest weights of Mg in the forest floor are under the *Pteridium* stands where values in excess of 200 kg/ha of Mg are held. Most of the other seral sites and the undisturbed sites have weights of Mg in the forest floor that are between 30 and 100 kg/ha. Very low weights of Mg are recorded in the forest floor of young *Leptospermum* stands at Ngaruru Bay where levels are less than 15 kg/ha.

Weights of Na in the forest floor range between 2 and 24 kg/ha. Forest floor weights of Ca in the *Leptospermum*-dominated stands tend to increase during succession up to 40 years after disturbance to a maximum of 400 kg/ha, thereafter levels fall to values around 100-250 kg/ha. High to very high weights of Ca are found in the forest floors of the undisturbed forests and levels between 200-560 kg/ha are attained.

#### 5:2:3e Phosphorus content of the forest floor

Phosphorus concentrations in the forest floor range from 0.02% to 0.12%. Moderate to high values ( $> 0.05\%$ ) occur under podocarp/broadleaf, coastal broadleaf and *Aristotelia-Coriaria* stands. Low to moderate phosphorus levels occur in all the other seral stands and in the *Nothofagus truncata* forest floors.

The weight of P on the forest floor is also directly correlated with the biomass of the forest floor, ( $r = 0.813$ ,  $n = 45$ ,  $p < 0.001$ ).

Maximum weights of P in the forest floor material occur under the mature podocarp-broadleaf and broadleaf forests at Howdens's Reserve; values of 31 and 35 kg/ha of P were recorded respectively.

The lowest weights of P are held in the forest floors of young *Leptospermum* and *Cassinia* stands and in the 32 year old *Leptospermum* stand B.M.3 which has a very shallow forest floor. Less than 5 kg/ha of P is held in these forest floors.

TABLE 5:1. Chemical Analyses - Forest Floors

Site	Horizon	pH	Total N (%)	Organic C- (%)	C/N	K (%)	Mg (%)	Na (%)	Ca (%)	P (%)
E.I.1	L	-	0.59	36	61	0.20	0.42	0.03	0.51	0.04
	F+H	4.55	0.90	29	32	0.15	0.51	0.03	0.45	0.03
E.I.2	L	-	0.63	37	58	0.25	0.40	0.04	0.41	0.03
	F+H	4.45	0.76	26	34	0.12	0.47	0.03	0.32	0.02
E.I.3	L	-	0.68	34	50	0.11	0.50	0.04	0.42	0.05
	F+H	4.6	0.79	22	27	0.10	0.55	0.03	0.50	0.03
E.I.4	L	4.8	0.81	41	51	0.26	0.31	0.04	0.80	0.05
	F+H	4.55	0.90	16	18	0.22	0.31	0.04	0.71	0.04
E.I.5	L+F+H	4.65	0.85	11.5	14	0.21	0.22	0.03	0.48	0.03
E.I.6	L+F+H	4.8	0.92	7.5	8	0.26	0.35	0.02	0.36	0.04
E.I.7	L	5.2	0.73	38	52	0.32	0.26	0.02	1.00	0.04
	F+H	-	0.84	24	29	0.21	0.41	0.02	0.65	0.03
T.B.1	L	-	0.70	21	30	0.35	0.41	0.04	0.48	0.03
	F+H	5.6	0.78	20	26	0.15	0.33	0.03	0.43	0.04
T.B.2	L+F+H	5.55	0.60	28	47	0.50	0.24	0.04	0.77	0.04
T.B.3	L+F+H	5.7	1.40	23	16	0.36	0.40	0.04	1.53	0.06
T.B.4	L	-	0.89	33	37	0.21	0.44	0.02	0.74	0.05
	F+H	5.3	1.32	30	23	0.28	0.39	0.03	0.58	0.04
T.B.5	L+F+H	5.55	0.90	16	18	0.35	0.53	0.03	0.99	0.06
T.B.6	L+F+H	5.05	0.93	27	29	0.33	0.36	0.03	0.55	0.05
T.B.7	L+F+H	4.95	1.49	26	18	0.35	0.47	0.04	1.23	0.07
T.B.8	L+F+H	4.9	0.85	26	31	0.35	0.37	0.03	0.59	0.04
T.B.9	L	-	0.60	24	35	0.32	0.41	0.03	0.80	0.04
	F+H	5.45	0.75	22	29	0.21	0.44	0.03	0.72	0.03
H.R.1	L	4.05	0.72	39	54	0.22	0.21	0.04	1.14	0.05
	F+H	3.85	0.80	28	35	0.31	0.14	0.04	0.48	0.04
H.R.2	L	5.2	0.81	22	27	0.25	0.31	0.03	1.45	0.09
	F+H	4.95	1.09	14	13	0.13	0.22	0.04	1.21	0.08
H.R.3	L	4.3	0.72	40	56	0.20	0.18	0.04	1.32	0.04
	F	4.25	1.06	36	40	0.30	0.17	0.04	0.47	0.04
	H	-	0.26	6	23	0.18	0.11	0.02	0.11	0.03
H.R.4	L	5.45	0.74	35	47	0.28	0.22	0.02	1.08	0.05
	F+H	-	1.1	14	13	0.19	0.25	0.02	0.86	0.06
R.B.1	L	-	0.38	36	95	0.25	0.20	0.04	0.61	0.03
	F+H	5.15	0.55	12	22	0.20	0.14	0.04	0.55	0.02
S.C.1	L	4.25	0.53	29	55	0.20	0.36	0.03	0.43	0.05
	F+H	4.85	0.44	16	36	0.19	0.22	0.03	0.45	0.04
N.B.1	L+F+H	5.65	0.5	20	40	0.23	0.35	0.03	0.73	0.05
N.B.2	L	5.0	0.62	25	40	0.25	0.37	0.03	0.85	0.05
	F+H	-	0.51	20	39	0.20	0.28	0.03	0.72	0.05
N.B.3	L+F+H	5.25	0.56	31	55	0.26	0.32	0.04	0.80	0.04
N.B.4	L+F+H	5.55	0.91	39	43	0.25	0.29	0.06	1.40	0.08
N.B.5	L+F+H	4.75	0.5	32	64	0.20	0.11	0.02	0.38	0.03
N.B.6	L+F+H	4.25	0.41	22	54	0.22	0.13	0.02	0.45	0.03
N.B.7	L	4.45	0.69	32	46	0.29	0.32	0.03	1.27	0.05
	F+H	4.45	0.68	32	47	0.29	0.29	0.06	1.27	0.03
N.B.8	L	5.25	0.72	33	46	0.25	0.32	0.03	0.87	0.05
	F+H	-	0.65	27	42	0.20	0.32	0.03	0.80	0.05
N.B.9	L	4.65	0.7	30	43	0.27	0.36	0.04	0.85	0.06
	F+H	-	0.66	24	36	0.19	0.30	0.04	0.78	0.03

TABLE 5:1 Continued

Site	Horizon	pH	Total N (%)	Organic		K (%)	Mg (%)	Na (%)	Ca (%)	P (%)
				C (%)	C/N					
C.C.1	L+F+H	5.1	0.73	40	55	0.25	0.25	0.03	1.0	0.05
C.C.2	L+F+H	5.3	0.77	38	49	0.19	0.26	0.05	1.2	0.06
C.C.3	L+F+H	5.3	0.75	34	45	0.18	0.23	0.05	0.74	0.08
C.C.4	L+F+H	6.45	1.10	36	33	0.78	0.32	0.07	2.6	0.12
C.C.5	L+F+H	4.7	0.73	36	49	0.24	0.12	0.05	0.73	0.05
C.C.6	L+F+H	4.8	0.53	35	66	0.18	0.17	0.02	0.59	0.05
C.C.7	L+F+H	4.6	0.72	38	53	0.20	0.21	0.02	0.65	0.06
C.C.8	L+F+H	4.6	0.7	33	47	0.20	0.19	0.05	0.50	0.05
G.B.1	L+F+H	5.05	0.90	35	39	0.23	0.26	0.04	1.02	0.05
B.M.1	L	5.15	0.53	23	43	0.26	0.23	0.04	0.69	0.05
	F+H	-	0.66	13	20	0.18	0.20	0.04	0.54	0.05
B.M.2	L+F+H	5.0	0.54	24	44	0.35	0.25	0.03	0.57	0.05
B.M.3	L+F+H	5.25	0.59	20	34	0.28	0.24	0.03	0.65	0.04
D'Urv.1	L	5.85	0.77	33	43	0.21	0.57	0.04	1.23	0.07
	F+H	-	1.06	27	25	0.15	0.45	0.04	0.99	0.03
D'Urv.2	L+F+H	4.95	0.55	24	44	0.15	0.30	0.03	0.82	0.06

TABLE 5:2. Forest Floor Weights.

Site	Horizon	oven dry weight	Average weight (kg/ha)						
		$\bar{x} \pm 1.s.d(t/ha)$	N	C	K	Mg	Na	Ca	P
E.I.1	L	1.72 $\pm$ 0.47	101.1	6192	34.4	72.2	5.2	87.7	6.9
	F+H	3.39 $\pm$ 0.48	304.1	9662	50.9	172.9	10.2	152.6	10.2
		5.11 $\pm$ 0.95	405.2	15854	85.3	245.1	15.4	240.3	17.1
E.I.2	L	2.13 $\pm$ 0.27	134.1	7775	53.3	85.2	7.5	87.3	9.4
	F+H	3.28 $\pm$ 1.17	250.6	8528	39.4	154.2	9.8	105.0	6.6
		5.41 $\pm$ 1.44	384.7	16303	92.7	239.4	17.3	192.3	16.0
E.I.3	L	1.66 $\pm$ 0.52	112.2	5644	18.3	78.0	6.6	69.7	8.3
	F+H	2.74 $\pm$ 1.66	217.6	5960	27.4	137.0	8.2	137.0	8.2
		4.40 $\pm$ 2.18	329.8	11604	45.7	215.0	14.8	206.7	16.5
E.I.4	L	0.95 $\pm$ 0.12	75.2	3895	24.7	29.5	3.8	76.0	4.8
	F+H	3.35 $\pm$ 2.94	300.5	5193	73.7	103.9	13.4	237.9	13.4
		4.30 $\pm$ 3.06	375.7	9088	98.4	133.4	17.2	313.9	18.2
E.I.5	L+F+H	1.31 $\pm$ 0.68	111.4	1507	27.5	28.8	3.9	62.9	3.9
E.I.6	L+F+H	1.11 $\pm$ 0.27	102.1	833	28.9	38.9	2.2	40.0	4.4
E.I.7	L	1.27 $\pm$ 0.38	92.7	4826	40.6	33.0	2.5	127.0	5.1
	F+H	1.34 $\pm$ 0.08	112.6	3149	28.1	54.9	2.7	87.1	4.0
		2.61 $\pm$ 0.46	205.3	7975	68.7	87.9	5.2	214.1	9.1
T.B.1	L	0.86 $\pm$ 0.20	60.2	1806	30.1	35.3	3.4	41.3	2.6
	F+H	0.65 $\pm$ 0.04	50.7	1300	9.8	21.5	2.0	28.0	2.6
		1.51 $\pm$ 0.24	110.9	3106	39.9	56.8	5.4	69.3	5.2
T.B.2	L+F+H	2.01 $\pm$ 0.11	121.1	5729	100.5	48.2	8.0	154.8	8.0
T.B.3	L+F+H	1.40 $\pm$ 0.45	196.0	3234	50.4	56.0	5.6	214.2	8.4
T.B.4	L	0.70 $\pm$ 0.20	62.3	2310	14.7	30.8	1.4	51.8	3.5
	F+H	2.3 $\pm$ 0.21	316.9	6969	64.4	89.7	6.9	133.4	9.2
		3.0 $\pm$ 0.41	379.2	9279	79.1	120.5	8.3	185.2	12.7
T.B.5	L+F+H	2.57 $\pm$ 0.98	230.5	4061	90.0	136.2	7.7	254.4	15.4
T.B.6	L+F+H	1.43 $\pm$ 0.36	132.4	3861	47.2	51.5	4.3	78.7	7.2
T.B.7	L+F+H	0.98 $\pm$ 0.16	146	2548	34.3	46.1	3.9	120.5	6.9
T.B.8	L+F+H	1.88 $\pm$ 0.33	160.4	4944	65.8	69.6	5.6	110.9	7.5
T.B.9	L	0.94 $\pm$ 0.21	56.5	2258	30.1	38.6	2.8	75.3	3.8
	F+H	2.67 $\pm$ 0.67	200.1	5874	56.0	117.4	8.0	192.1	8.0
		3.61 $\pm$ 0.89	256.6	8132	86.1	156.0	10.8	267.4	11.8
H.R.1	L	1.33 $\pm$ 0.40	95.8	5187	29.3	27.9	5.3	151.6	6.7
	F+H	3.29 $\pm$ 1.21	263.2	9212	102.0	46.1	13.2	157.9	13.2
		4.62 $\pm$ 1.61	359.0	14399	131.3	74.0	18.5	309.5	19.9
H.R.2	L	0.99 $\pm$ 0.32	80.2	2178	24.8	30.7	3.0	143.6	8.9
	F+H	2.78 $\pm$ 1.69	303.0	3892	34.8	61.2	11.1	336.4	22.2
		3.77 $\pm$ 2.01	383.2	6070	59.6	91.9	14.1	480.0	31.1
H.R.3	L	2.11 $\pm$ 0.98	151.9	8440	42.2	38.0	8.4	278.6	8.4
	F	3.45 $\pm$ 0.40	365.7	12420	103.5	56.9	13.8	162.2	13.8
	H	0.89 $\pm$ 0.21	23.1	534	16.0	9.8	1.8	9.8	2.7
		6.45 $\pm$ 1.59	540.7	21394	161.7	104.7	24.0	450.6	24.9
H.R.4	L	1.83 $\pm$ 0.81	135.4	6405	51.2	40.3	3.7	197.6	9.2
	F+H	4.30 $\pm$ 2.80	473.0	6020	81.7	107.5	8.6	369.8	25.8
		6.13 $\pm$ 3.61	608.4	12425	132.9	147.8	12.3	567.4	35.0



TABLE 5:2 Continued.

Site	Horizon	oven dry weight	Average weight (kg/ha)						
		$\bar{x} \pm 1.5 \cdot d$ (t/ha)	N	C	K	Mg	Na	Ca	P
R.B.1	L	0.90 $\pm$ 0.27	34.2	3240	22.5	18.0	3.6	54.9	2.8
	F+H	1.84 $\pm$ 1.17	101.2	2208	36.8	25.8	7.4	101.2	2.7
		2.74 $\pm$ 1.44	135.4	5448	59.3	43.8	11.0	156.1	5.5
S.C.1	L	0.60 $\pm$ 0.21	31.8	1740	12.0	21.6	1.8	25.8	3.0
	F+H	2.19 $\pm$ 0.40	96.4	3504	41.6	48.2	6.6	98.6	8.8
		2.79 $\pm$ 0.61	128.2	5244	53.6	69.8	8.4	124.4	11.8
N.B.1	L+F+H	2.39 $\pm$ 1.20	119.5	4780	55.0	83.7	7.2	174.5	12.0
N.B.2	L	1.02 $\pm$ 0.33	63.2	2550	25.5	37.7	3.1	86.7	5.1
	F+H	0.61 $\pm$ 0.39	31.1	1220	12.2	17.1	1.8	43.9	3.1
		1.63 $\pm$ 0.72	94.3	3770	37.7	54.8	4.9	130.6	8.2
N.B.3	L+F+H	2.57 $\pm$ 0.81	143.9	7969	66.8	82.2	10.3	205.6	10.3
N.B.4	L+F+H	1.51 $\pm$ 0.64	137.4	5889	37.8	43.8	9.1	211.4	12.1
N.B.5	L+F+H	0.79 $\pm$ 0.25	39.5	2528	15.8	8.3	1.6	30.0	2.4
N.B.6	L+F+H	1.01 $\pm$ 0.34	41.4	2222	22.2	13.1	2.0	45.5	3.0
N.B.7	L	1.38 $\pm$ 0.13	95.2	4416	40.0	44.2	4.1	175.3	6.9
	F+H	1.07 $\pm$ 0.07	72.8	3424	31.0	31.0	6.4	135.9	3.2
		2.45 $\pm$ 0.02	168.0	7840	71.0	75.2	10.5	311.2	10.1
N.B.8	L	1.96 $\pm$ 0.28	141.1	6468	49.0	62.7	5.9	170.5	9.8
	F+H	1.44 $\pm$ 0.25	93.6	3888	28.8	46.1	4.3	115.2	7.2
		3.40 $\pm$ 0.53	234.7	10356	77.8	108.8	10.2	285.7	17.0
N.B.9	L	1.67 $\pm$ 0.2	116.9	5010	45.1	60.1	6.7	142.0	10.0
	F+H	0.85 $\pm$ 0.17	56.1	2040	16.2	25.5	3.4	66.3	2.6
		2.52 $\pm$ 0.37	173.0	7050	61.3	85.6	10.1	208.3	12.6
C.C.1	L+F+H	2.27 $\pm$ 0.34	165.7	9080	56.8	56.8	6.8	227	11.4
C.C.2	L+F+H	3.13 $\pm$ 0.48	241.0	11894	62.9	86.1	16.6	397.2	18.8
C.C.3	L+F+H	2.84 $\pm$ 1.3	213.0	9656	51.1	65.3	14.2	210.2	21.3
C.C.4	L+F+H	1.35 $\pm$ 0.27	148.5	4860	105.3	43.2	9.5	351.0	16.2
C.C.5	L+F+H	2.12 $\pm$ 0.39	154.8	7632	50.9	25.4	10.6	154.8	10.6
C.C.6	L+F+H	1.83 $\pm$ 0.18	96.9	6405	32.9	31.1	3.7	108.0	9.2
C.C.7	L+F+H	2.36 $\pm$ 0.42	169.9	8968	47.2	49.6	4.7	153.4	14.2
C.C.8	L+F+H	1.87 $\pm$ 0.84	130.9	6170	37.4	35.5	9.4	93.5	9.4
G.B.1.	L+F+H	1.07 $\pm$ 0.39	96.3	3745	24.6	27.8	4.3	109	5.4
B.M.1	L	0.78 $\pm$ 0.23	41.3	1794	20.3	17.9	3.1	53.8	3.9
	F+H	1.53 $\pm$ 0.67	101.0	4131	27.5	30.6	6.1	82.6	7.7
		2.31 $\pm$ 0.90	142.3	5925	47.8	48.5	9.2	136.4	11.6
B.M.2	L+F+H	1.95 $\pm$ 0.15	105.3	4680	68.3	48.8	5.9	111.2	9.8
B.M.3	L+F+H	0.77 $\pm$ 0.57	45.4	1848	21.6	18.5	2.3	50.1	3.1
D'Urv.1	L	0.53 $\pm$ 0.16	40.8	1749	11.1	30.2	2.1	65.2	3.7
	F+H	0.99 $\pm$ 0.09	104.0	2673	14.9	44.6	4.0	98.0	3.0
		1.52 $\pm$ 0.25	145.7	4422	26.0	74.8	6.1	163.2	6.7
D'Urv.2	L+F+H	1.75 $\pm$ 0.5	96.3	4200	26.3	52.5	5.3	143.5	10.5

### 5:3 The Soils

The present study encompassed three different soil types of steep-land Yellow Brown Earth, namely: Arapawa silt loams, Kenepuru silt loams, Opouri silt loams. It was soon apparent that the scale of soil mapping used in the Soil Survey of the Marlborough Sounds was too gross to account for the different soil profiles encountered within any one catchment.

The soils of the study sites have been resolved into five broad categories based on topographical position. The five categories correspond to a generalised relief catena that is the basic landform of the low altitude regions of the Marlborough Sounds. The categories are:

- (1) soils of valley floors and terraces
- (2) soils of gentle, lower slopes
- (3) soils of steep, rubbly, colluvial slopes
- (4) soils of steep, fine textured, upper slopes
- (5) soils of ridges and spurs.

The corresponding "original" vegetation types of the five categories are:

- (1) (podocarp)/broadleaf forest or coastal broadleaf forest
- (2) (podocarp)/broadleaf forest or broadleaf forest (tawa dominant)
- (3) broadleaf forest (mahoe dominant or kohekohe dominant)
- (4) kamahi-hinau forest
- (5) beech forest

The aim of the present study has not been to provide a pedological interpretation of the different soils encountered but to try and relate the different vegetation types of the study areas to some soil parameters. The study has focused on the nutrient content of the soils in the zone in which the majority of roots and rhizoids are distributed.

Soil profile descriptions for each stand are presented in Appendix . A number of trial soil pits were dug at each site. Only one soil profile is described from the sites where the pit profiles were of a similar form. At sites where different soil profiles were encountered the two extreme profiles are described. Major differences in soil pits at any one site were usually concerned with the depth of the A horizon or the distribution of stones throughout the profile.

Soil nutrient data are presented in Tables 5:3 and 5:4. Average soil nutrient concentrations were calculated from duplicate analyses of separate horizons for two soil pits at each site. Soil nutrient contents were calculated by multiplying the soil nutrient concentration by the soil volume (derived from bulk density measurements) of each profile to a depth of 30 cm. Mechanical analyses are presented in Table 5:5.

#### 5:3:1 Soil nutrient concentrations

Soils of the valley floors and terraces: sites H.R.2, N.B.4, S.C.1.

These soils possess a fairly deep A horizon (average depth 13.5 cm) of a sandy loam or silt loam texture. Small schist rocks are usually present. The soils of the A horizons are moderately acid (pH range 5.0-5.75) and have medium to high C/N ratios. Measured soil nutrients, with the exception of exchangeable Na and Truog P, are at medium levels. Exchangeable Na and Truog P levels are low. The B horizons are silt loams and both small and large rocks are present throughout. The soil reaction of the B horizon is strongly acid (range 4.8-5.2). Soil nutrients, with the exception of exchangeable Mg, are in low concentrations. Exchangeable Mg levels are at medium concentrations.

Soils of gentle lower slopes: sites H.R.4, N.B.2, N.B.9, E.I.1, E.I.2, E.I.3, E.I.5, E.I.6, T.B.2, T.B.4, T.B.8.

The soils possess a deep A horizon (typically between 15-20 cm). They contain a high sand fraction and are mostly loamy sands with a friable structure. Some profiles contain rocks in the A horizon. The A horizons are moderately or strongly acid (pH range 4.65-5.3). Organic C levels are in the low to medium range, total N levels are low and C/N ratios are typically high (range 12-20). The cation exchange capacity levels of the A horizons are medium with low concentrations of exchangeable Ca and Na, medium Mg levels and high exchangeable K levels. Truog P levels are low or very low.

The B horizons are friable loamy sands or silt loams. Most profiles contained rocks in the B horizon. The soil is strongly acid (pH range 4.7-5.3) and contains low or very low levels of available soil nutrients.

Soils of steep colluvial slopes: sites C.C.3, C.C.4, D'Urv.1, N.B.8,  
T.B.3, T.B.5, T.B.7, T.B.9.

These soils have A horizons of variable depths, some profiles have shallow A horizons (around 6 cm in depth) whilst other A horizons extend beyond a depth of 30 cm. The A horizons are all loamy sands and rocks are abundant throughout the profile. The A horizons are moderately to strongly acid (pH range 4.9-5.7). Organic C concentrations are typically of a medium level although two sites have low concentrations. Total N levels are medium and most C/N ratios are low or medium (range 12-20). Cation exchange capacity levels of the A horizons are medium or high and exchangeable cations are at medium or high levels. Truog P levels are low or very low.

The soils of the B horizons are loamy sands or silt loams and large rocks are present throughout the horizon. They are strongly to moderately acid (pH range 4.4-5.7) and contain moderate levels of exchangeable cations.

Soils of steep, fine textured upper slopes: sites C.C.6, C.C.7, C.C.8,  
N.B.1, N.B.7, B.M.1, B.M.2,  
T.B.1, E.I.4, E.I.7, R.B.1,  
D'Urv.2.

The soils of the steep upper slopes have A horizons of variable depth, most are less than 20 cm deep and some are very shallow (around 4 cm deep). The A horizons contain more silt and clay than the preceeding three soil types and are silt loams. Rocks and schist chips are present in the A horizons of some of the profiles. The horizon is strongly to extremely acid (pH range 4.35-5.3) and is leached of nutrients. Exchangeable Mg is the only measured nutrient in good supply at all sites. Organic C levels are low or medium, total N levels are low and most C/N ratios are in the medium to very high range (range 9-33).

The B horizon soils are also silt loams and have a well developed nut structure. They are strongly to extremely acid (pH range 4.25-5.3) and are leached of nutrients.

Soils of ridges and spurs: sites H.R.1, H.R.3, H.R.5, C.C.1, C.C.2, C.C.5,  
G.B.1, N.B.3, N.B.5, N.B.6, B.M.3, T.B.6.

These soils contrast strongly with the previous four soil types in a number of ways. The A horizon, if present, is typically quite shallow (around 10 cm deep) and contains a high clay component. The soils are silt loams with a strongly developed nut structure. Penetration of the soil with

a spade was quite difficult. Rocks are absent from the A horizon. The A horizons are strongly acid (pH range 4.5-5.3) and low in available nutrients. Organic C levels are low or very low, total N levels are low and C/N ratios range from low to high (range 9-37). Cation exchange capacity levels are typically of medium levels. Exchangeable Ca levels are low or very low. Exchangeable Mg levels are variable, some sites have low levels while other sites have high levels. Exchangeable K and Na levels range from very low to medium. Truog P levels are very low.

The B horizons of the ridges and spurs are either silt loams or clay loams and are very difficult to penetrate with a spade. At some sites rocks are present in the B horizon. The soils are extremely acid (pH range 4.35-5.05). All measured soil nutrients are in low or very low concentrations with the exception of exchangeable Mg which occurs in moderate levels at most sites.

#### 5:3:2 Soil nutrient contents

The nutrient contents of the soils within the five relief groups are more variable than the soil concentrations of any one element (Table 5:4). The greater variability of the soil nutrient contents is due, in the main, to the variation in horizon depth and bulk density of the soils in each relief group.

The general trend of soil nutrient status is observed however, with a lower nutrient content in the soils of the ridge and spur sites than the other sites. Highest nutrient contents are possessed by soils on colluvial slopes. Soils of the valleys and terraces, the gentle lower slopes and the steep upper slopes possess soil nutrient contents intermediate between that of the soils of the ridges and spurs and the soils of colluvial slopes.

TABLE 5:3a. Chemical Analyses - A Horizon Soils

Site	pH	Total N (%)	Organic C (%)	C/N	Exch. K (me %)	Exch. Mg (me %)	Exch. Na (me %)	Exch. Ca (me %)	CEC (me %)	Truog Sol. P (mg %)
E.I.1	5.2	0.28	5.7	20	1.14	3.0	0.15	3.8	22.0	0.8
E.I.2	4.65	0.35	6.9	20	1.18	2.6	0.32	3.5	18.25	0.5
E.I.3	5.0	0.30	4.7	19	1.00	2.7	0.20	2.2	23.0	0.6
E.I.4	4.5	0.44	10.0	23	0.20	1.4	0.40	2.3	25.7	0.8
E.I.5	4.95	0.26	4.2	16	0.63	2.1	0.15	4.4	23.25	1.0
E.I.6	5.05	0.42	6.8	16	0.76	1.5	0.25	2.3	20.25	1.2
E.I.7	4.85	0.21	4.6	22	0.50	2.0	0.10	4.0	19.85	1.2
T.B.1	4.8	0.11	2.55	23	0.50	2.0	0.12	1.3	17.5	0.5
T.B.2	5.2	0.21	3.1	15	0.99	2.4	0.19	4.2	17.5	0.7
T.B.3	5.3	0.33	3.35	10	1.05	2.7	0.16	6.8	21.0	1.4
T.B.4	5.3	0.25	3.0	12	0.13	1.0	0.20	0.8	17.35	0.8
T.B.5	5.3	0.26	2.7	10	1.02	4.6	0.20	10.5	24.25	0.9
T.B.6	5.0	0.26	4.8	19	0.53	2.9	0.16	4.6	22.9	0.6
T.B.7	5.1	0.47	4.2	9	0.96	2.5	0.18	4.8	23.2	1.4
T.B.8	4.85	0.22	3.4	16	0.76	1.6	0.14	1.1	15.2	0.9
T.B.9	5.0	0.25	3.0	12	0.81	1.9	0.15	2.9	19.75	0.9
H.R.1	4.5	0.09	3.3	37	0.08	0.8	0.16	0.4	17.5	0.7
H.R.2	5.0	0.33	4.6	14	0.31	2.3	0.16	5.2	27.5	0.4
H.R.3	4.55	0.11	2.0	18	0.12	0.8	0.20	0.1	16.25	0.8
H.R.4	5.1	0.26	5.1	20	0.36	2.7	0.26	4.7	27.25	1.4
H.R.5	4.8	0.09	2.3	26	0.25	1.4	0.20	1.0	16.0	0.2
R.B.1	4.8	0.17	5.6	33	0.53	2.6	0.20	2.7	28.5	0.8
S.C.1	5.05	0.35	6.4	18	1.09	2.9	0.22	5.4	24.5	0.5
N.B.1	5.2	0.25	8.5	34	1.22	5.9	0.69	12.3	20.5	0.6
N.B.2	5.5	0.32	4.85	15	0.95	5.4	0.48	8.7	19.5	0.7
N.B.3	5.2	0.11	0.13	14	0.57	3.7	0.34	6.4	14.75	0.7
N.B.4	5.75	0.29	3.6	12	0.70	4.6	0.38	9.0	16.2	0.7
N.B.5	5.0	0.16	4.3	27	0.35	3.0	0.30	6.5	21.8	0.6
N.B.6	4.9	0.15	3.7	25	0.49	3.4	0.30	8.0	23.6	0.8
N.B.7	4.9	0.19	3.0	16	0.98	5.3	0.40	9.7	17.5	0.7
N.B.8	5.55	0.34	6.5	19	1.23	5.7	0.64	10.0	30.5	0.6
N.B.9	5.2	0.25	4.8	19	0.51	3.3	0.30	6.1	22.65	0.7
C.C.1	4.6	0.2	4.3	18	0.36	1.6	0.26	2.8	17.2	0.5
C.C.2	-	-	-	-	-	-	-	-	-	-
C.C.3	5.2	0.19	2.9	15	0.35	4.2	0.34	11.5	15.0	0.2
C.C.4	5.7	0.17	3.4	20	1.30	5.0	0.31	17.2	23.7	0.4
C.C.5	5.0	0.20	1.85	9	0.49	4.8	0.45	5.0	19.5	0.4
C.C.6	4.55	0.15	2.6	17	0.25	1.4	0.20	1.2	15.6	0.2
C.C.7	5.3	0.13	2.2	17	1.20	5.3	0.36	5.2	20.8	0.2
C.C.8	4.9	0.19	2.3	12	0.36	3.5	0.39	3.0	14.1	1.0
G.B.1	4.95	0.10	2.5	25	0.48	3.0	0.63	7.1	19.3	0.4
B.M.1	4.9	0.12	1.95	16	0.46	3.3	0.35	5.0	16.5	0.4
B.M.2	5.15	0.18	1.6	9	0.79	4.8	0.40	4.0	17.25	0.7
B.M.3	5.3	0.16	1.6	10	0.53	2.1	0.41	3.6	15.5	0.4
D'Urv.1	4.9	0.29	3.7	13	1.06	4.0	0.61	8.4	27.2	1.2
D'Urv.2	4.35	0.23	5.0	22	0.82	2.2	0.40	4.1	23.12	1.6

TABLE 5:3b. Chemical Analyses - B Horizon Soils

Site	pH	Total N (%)	Organic C (%)	C/N	Exch. K (me %)	Exch. Mg (me %)	Exch. Na (me %)	Exch. Ca (me %)	CEC (me %)
E.I.1	5.2	0.14	2.35	17	0.34	0.57	0.14	0.8	15.0
E.I.2	4.8	0.12	1.95	16	0.12	0.23	0.05	0.2	11.5
E.I.3	-	-	-	-	-	-	-	-	-
E.I.4	4.7	0.15	3.7	25	0.15	0.61	0.18	0.7	11.6
E.I.5	5.0	0.15	2.7	18	0.34	0.90	0.11	2.4	10.9
E.I.6	4.9	0.19	2.6	14	0.41	0.75	0.09	1.2	10.6
E.I.7	4.9	0.15	3.35	22	0.21	0.26	trace	0.4	12.6
T.B.1	5.3	0.09	1.2	13	0.30	0.61	0.08	0.9	14.9
T.B.2	5.3	0.08	1.4	18	0.54	1.06	0.10	0.9	11.9
T.B.3	5.25	0.17	1.65	10	0.49	1.13	0.08	2.7	16.3
T.B.4	4.7	0.06	1.3	22	0.08	0.61	0.10	0.4	17.4
T.B.5	5.7	0.12	1.2	10	0.41	1.40	0.08	3.3	18.1
T.B.6	4.85	0.12	1.4	12	0.24	1.20	0.09	0.9	11.8
T.B.7	5.3	0.20	2.6	13	0.36	1.01	0.09	1.6	14.2
T.B.8	5.2	0.11	1.95	18	0.32	0.81	0.11	0.8	11.2
T.B.9	5.2	0.19	2.0	11	0.41	0.85	0.08	0.8	12.6
H.R.1	4.9	0.07	1.7	24	0.06	0.41	0.06	0.2	17.2
H.R.2	4.8	0.27	3.5	13	0.12	1.05	0.10	1.4	18.4
H.R.3	5.05	0.08	1.7	21	0.05	0.31	0.08	0.2	10.5
H.R.4	5.0	0.14	2.2	16	0.06	0.60	0.12	0.45	25.0
H.R.5	-	-	-	-	-	-	-	-	-
R.B.1	4.9	0.07	0.6	9	0.21	1.06	0.10	0.8	16.1
S.C.1	4.9	0.28	3.95	14	0.61	1.32	0.11	1.4	14.2
N.B.1	4.9	0.08	0.9	11	0.61	1.36	0.14	2.8	11.3
N.B.2	5.05	0.06	0.45	8	0.42	1.81	0.21	1.4	12.5
N.B.3	4.45	0.05	0.9	18	0.26	1.44	0.15	2.6	11.1
N.B.4	5.2	0.10	0.6	6	0.17	2.70	0.48	3.1	11.8
N.B.5	4.95	0.06	0.5	8	0.16	1.30	0.15	2.0	21.2
N.B.6	4.6	0.06	0.7	12	0.21	1.65	0.11	3.0	10.9
N.B.7	4.9	0.11	0.4	3	0.46	2.10	0.15	2.2	12.2
N.B.8	5.4	0.10	0.6	6	0.78	3.50	0.49	1.5	15.3
N.B.9	5.0	0.08	0.8	10	0.16	1.41	0.11	1.6	16.5
C.C.1	4.35	0.04	0.65	16	0.16	0.57	0.02	0.2	16.0
C.C.2	4.5	0.1	2.35	24	0.22	1.06	0.15	0.5	18.2
C.C.3	5.2	0.06	0.8	13	0.16	1.81	0.14	2.7	10.6
C.C.4	5.45	0.08	0.3	4	0.21	1.95	0.09	4.6	11.8
C.C.5	4.6	0.06	0.6	10	0.22	1.89	0.20	1.5	14.3
C.C.6	4.4	0.06	0.4	7	0.10	0.31	0.08	0.6	8.8
C.C.7	4.8	0.06	0.6	10	0.5	2.1	0.18	1.3	10.2
C.C.8	4.85	0.07	0.4	6	0.12	1.09	0.11	0.8	9.3
G.B.1	4.4	0.04	0.6	15	0.11	1.03	0.31	1.6	11.4
B.M.1	5.05	0.03	0.6	20	0.20	3.00	0.31	3.6	15.3
B.M.2	5.0	0.05	0.8	16	0.28	1.30	0.24	1.4	13.5
B.M.3	5.0	0.05	0.55	11	0.43	1.45	0.28	1.8	14.1
D'Urv.1	-	-	-	-	-	-	-	-	-
D'Urv.2	4.25	0.10	1.2	12	0.40	1.35	0.20	0.9	13.9



TABLE 5:4a. Chemical Analyses - Nutrient Weights (kg/ha). A Horizon Soils.

Site	Depth (cm)	Total N	Organic C	Exch. K	Exch. Mg	Exch. Na	Exch. Ca	Truog P
E.I.1	15	4410	89 788	702	577	128	1197	10
E.I.2	23	5550	109 391	732	503	117	1111	11
E.I.3	30	6750	128 250	880	741	104	990	14
E.I.4	9.5	4598	104 513	82	179	96	481	8
E.I.5	14	3413	55 120	362	377	51	1294	15
E.I.6	20	5040	81 598	356	220	69	552	11
E.I.7	4	815	17 844	76	95	9	310	4
T.B.1	15	1799	41 689	320	399	45	425	3
T.B.2	20	4200	61 992	774	586	87	1680	14
T.B.3	6	1980	20 097	246	198	22	816	9
T.B.4	20	6400	76 800	130	312	118	410	5
T.B.5	8	2184	22 670	348	489	40	1831	8
T.B.6	13.5	3370	62 210	269	459	48	1192	8
T.B.7	21	10660	95 300	851	692	94	2177	32
T.B.8	28	6468	99 930	874	574	95	647	12
T.B.9	20	5250	63 000	665	487	73	1218	19
H.R.1	8	99	3 616	34	107	40	88	8
H.R.2	17	5021	69 993	184	427	56	1582	6
H.R.3	12	1874	34 069	80	166	78	34	14
H.R.4	8	1872	36 729	101	237	43	677	4
H.R.5	-	-	-	-	-	-	-	-
R.B.1	20	3400	111 996	415	634	92	1080	16
S.C.1	15	4305	78 738	524	435	62	1328	6
N.B.1	12.5	2969	100 946	465	702	155	2399	6
N.B.2	14	4211	63 842	489	867	145	2290	9
N.B.3	9	1040	14 179	211	427	74	1210	7
N.B.4	8.5	3081	38 239	291	596	93	1913	6
N.B.5	10	1920	51 610	164	439	83	1560	8
N.B.6	0.5	80	1 981	6	22	4	86	0.4
N.B.7	11	2445	38 607	493	162	118	2497	9
N.B.8	15	5508	105 313	781	1127	239	3240	10
N.B.9	10	2750	52 800	219	443	76	1342	8
C.C.1	11	2904	52 040	170	242	72	678	9
C.C.2	-	-	-	-	-	-	-	-
C.C.3	27	5643	86 112	406	1522	232	6831	6
C.C.4	15	2805	56 100	839	1007	118	5676	7
C.C.5	14.5	3306	30 581	317	968	171	1653	3
C.C.6	21.5	3290	57 007	214	375	101	526	22
C.C.7	30	4719	79 846	1703	2347	301	3775	7
C.C.8	20.5	4479	54 913	332	1007	212	1415	17
G.B.1	8	880	22 000	153	299	118	1159	3
B.M.1	17	2387	38 789	358	801	160	1989	8
B.M.2	19.5	4001	35 569	687	1302	205	1778	5
B.M.3	26	5034	50 340	652	806	297	2265	16
D'Urv.1	30	9135	116 563	1306	1537	442	5292	38
D'Urv.2	4	966	21 001	135	113	39	344	7



TABLE 5:4b. Chemical Analyses - Nutrient Weights (kg/ha) - Soil to a Depth of 30 cm.

Site	Total N	Organic C	Exch. K	Exch. Mg	Exch. Na	Exch. Ca	Truog P
E.I.1	6930	132 088	941	702	186	1485	27
E.I.2	6474	123 976	768	525	126	1142	27
E.I.3	6750	128 250	880	741	104	990	30
E.I.4	8288	195 533	226	362	198	825	27
E.I.5	6053	102 640	596	570	95	2138	19
E.I.6	6978	108 118	519	313	90	797	15
E.I.7	4793	106 686	294	179	15	523	13
T.B.1	2867	61 849	517	524	76	726	9
T.B.2	5120	78 092	1017	734	114	1887	22
T.B.3	6468	54 417	752	562	71	2242	17
T.B.4	7180	93 700	171	409	148	514	16
T.B.5	5352	54 350	771	940	89	3574	23
T.B.6	4267	72 675	339	568	63	1327	15
T.B.7	12541	121 040	991	814	114	2494	39
T.B.8	6710	104 220	901	596	100	682	19
T.B.9	7340	85 000	841	601	93	1394	31
H.R.1	1101	55 976	107	261	83	211	28
H.R.2	8654	117 086	248	599	87	2439	37
H.R.3	3789	74 767	127	257	123	130	39
H.R.4	5876	99 649	169	273	122	934	39
H.R.5	324	8281	352	615	166	691	7
R.B.1	4121	118 176	499	768	116	1245	21
S.C.1	8925	143 913	918	701	104	1790	18
N.B.1	4677	120 161	974	1056	223	3594	18
N.B.2	5430	72 986	823	1316	243	2859	17
N.B.3	2300	36 859	467	869	161	2520	17
N.B.4	5704	53 977	465	1460	383	3539	19
N.B.5	3366	63 660	315	821	166	2524	11
N.B.6	2240	27 174	301	747	95	2245	4
N.B.7	4995	47 879	910	756	198	3517	19
N.B.8	7338	116 293	1339	1908	445	3789	27
N.B.9	4670	72 000	370	856	137	2110	20
C.C.1	3907	68 342	327	417	84	778	20
C.C.2	3600	84 600	310	466	124	360	22
C.C.3	5908	89 640	434	1619	247	7069	27
C.C.4	4365	61 950	999	1470	158	7470	23
C.C.5	4469	42 206	483	1415	260	2234	14
C.C.6	3902	61 087	254	413	120	649	31
C.C.7	4719	79 846	1703	2347	301	3775	21
C.C.8	5310	59 663	388	1165	242	1605	26
G.B.1	1971	38 368	271	642	313	2032	9
B.M.1	2863	48 305	482	1381	273	3131	20
B.M.2	4642	45 817	827	1505	275	2137	14
B.M.3	5290	53 156	738	897	330	2449	19
D'Urv.1	9135	116 563	1306	1537	442	5292	45
D'Urv.2	4086	58 441	623	627	182	906	17

TABLE 5:5. Mechanical Analyses (soil &lt; 2 mm).

Site:Horizon	Clay %	Silt %	Fine sand %	Coarse sand %	Texture
E.I.1:A	4	36	49	11	loamy sand
E.I.1:B	16	30	33	21	silt loam
E.I.2:A	1	15	77	7	sand
E.I.2:B	28	44	26	2	silt loam
E.I.3:A	21	39	34	6	silt loam
E.I.3:B	21	40	35	4	silt loam
E.I.4:A	8	32	36	18	loamy sand
E.I.4:B	22	42	30	6	silt loam
E.I.5:A	6	28	42	24	loamy sand
E.I.5:B	14	27	19	40	sandy loam
E.I.6:A	0	14	29	57	sand
E.I.6:B	4	22	36	38	loamy sand
E.I.7:A	6	26	40	28	loamy sand
E.I.7:B	14	24	33	38	loamy sand
T.B.1:A	14	44	29	13	silt loam
T.B.1:B	34	41	24	1	silty clay loam
T.B.2:A	10	36	29	25	silt loam
T.B.2:B	22	36	30	12	silt loam
T.B.3:A	2	22	56	18	loamy sand
T.B.3:B	8	30	46	16	loamy sand
T.B.4:A	10	28	44	18	loamy sand
T.B.4:B	23	47	23	7	silt loam
T.B.5:A	6	24	44	26	loamy sand
T.B.5:B	24	46	24	6	silt loam
T.B.6:A	12	32	46	10	silt loam
T.B.6:B	40	38	19	3	silty clay loam
T.B.7:A	1	24	52	23	loamy sand
T.B.7:B	2	29	46	23	loamy sand
T.B.8:A	20	44	31	5	silt loam
T.B.9:A	0	13	39	48	sand
T.B.9:B	15	36	29	30	silt loam
H.R.1:A	12	40	39	9	silt loam
H.R.1:B	25	21	44	10	silt loam
H.R.2:A	10	42	40	8	silt loam
H.R.2:B	9	33	47	11	loamy sand
H.R.3:A	20	41	35	4	silt loam
H.R.3:B	25	33	32	10	silt loam
H.R.4:A	6	18	55	21	loamy sand
H.R.4:B	10	23	44	23	loamy sand
H.R.5:B	33	41	22	4	silty clay loam

TABLE 5:5 Continued.

Site:Horizon	Clay %	Silt %	Fine sand %	Coarse sand %	Texture
R.B.1:A	3	45	42	10	sand
R.B.1:B	16	34	26	14	silt loam
S.C.1:A	3	45	42	10	silt loam
S.C.1:B	8	36	18	38	silt loam
N.B.1:A	6	19	55	20	loamy sand
N.B.1:B	20	33	36	11	silt loam
N.B.2:A	16	32	36	16	silt loam
N.B.2:B	40	38	20	2	silty clay loam
N.B.3:A	36	30	31	3	clay loam
N.B.3:B	16	46	36	2	silt loam
N.B.4:A	2	20	62	18	loamy sand
N.B.4:B	24	29	39	9	silt loam
N.B.5:A	16	34	28	20	silt loam
N.B.5:B	31	37	26	6	silty clay loam
N.B.6:A	16	34	43	17	silt loam
N.B.6:B	20	40	34	6	silt loam
N.B.7:A	14	26	39	21	sandy loam
N.B.7:B	6	23	50	21	loamy sand
N.B.8:A	23	39	33	5	silt loam
N.B.8:B	32	34	33	1	clay loam
N.B.9:A	10	26	56	8	sandy loam
N.B.9:B	4	34	59	3	loamy sand
C.C.1:A	13	43	32	12	silt loam
C.C.1:B	34	40	25	1	silty clay loam
C.C.2:B	5	27	49	19	loamy sand
C.C.3:A	8	36	46	10	silt loam
C.C.3:B	20	40	34	6	silt loam
C.C.4:A	1	19	63	17	sand
C.C.4:B	16	47	31	6	silt loam
C.C.5:A	8	34	44	14	loamy sand
C.C.5:B	30	43	26	1	silt loam
C.C.6:A	8	38	42	12	silt loam
C.C.6:B	22	47	30	1	silt loam
C.C.7:A	1	12	73	14	sand
C.C.7:B	30	33	24	13	clay loam
C.C.8:A	19	45	32	4	silt loam
C.C.8:B	22	41	32	5	silt loam
G.B.1:A	4	16	76	4	loamy sand
G.B.1:B	16	40	41	3	silt loam

TABLE 5:5. Continued.

Site:Horizon	Clay %	Silt %	Fine sand %	Coarse sand %	Texture
B.M.1:A	20	42	32	6	silt loam
B.M.1:B	30	34	30	6	clay loam
B.M.2:A	39	31	28	2	clay loam
B.M.2:B	26	40	27	7	silt loam
B.M.3:A	8	42	44	6	silt loam
B.M.3:B	26	44	28	2	silt loam
D'Urv.1:A	2	20	39	39	loamy sand
D'Urv.2:A	40	10	41	9	sandy clay
D'Urv.2:B	14	42	40	4	silt loam

#### 5:4 Relation of Vegetation Successions to Soil Pattern

One of the objectives of this study was to investigate whether the successions occurring at the study sites were related to the measured soil parameters. Although there is an unique assemblage of canopy plants and potential canopy plants at each study site there appear to be two broad lines of forest development. Some sites are tending towards a mixed broadleaf species-dominated forest with a significant *Melicytus ramiflorus* + and/or *Dysoxylum spectabile* component. Other sites are tending toward a forest dominated by *Weinmannia racemosa*. There are some other sites where the direction of succession is not yet clear.

The successional pathways inferred from the study sites were related to the relief position and soil parameters of the sites.

Soils of the valley floors and terraces and the steep colluvial slopes either support a mixed broadleaf forest or an assemblage of plants that are tending toward this type of forest. *Leptospermum scoparium* is not important in the early stages of succession at these sites.

Soils of the lower and upper slopes and ridges support vegetation that tends towards either; a *W. racemosa* dominated forest or, a mixed *M. ramiflorus*-broadleaf dominated forest. *L. scoparium* is important in the early seral stages at some of these sites.

It was not possible to delineate absolutely soils that were associated with successions tending towards a *W. racemosa* forest or a mixed broadleaf species forest by employing the measured soil parameters as the only variables. One relationship was noted; all sites that support vegetation that is tending toward a *W. racemosa* forest possess low or very low exchangeable Calcium levels in the A horizon. There are other sites, however, with low or very low exchangeable Ca levels in the A horizon that support a vegetation that is progressing toward a mixed broadleaf species forest. On the less leached soils of some ridges and the leached soils of some of the slopes the balance between a *W. racemosa*-directed succession or a mixed broadleaf species sere is not clear and is not directly related to the soil parameters measured in this study.

### 5:5 Rates of Regeneration on Different Soil Types

Another aim of this study was to investigate the hypothesis that rates of regeneration were related to soil nutrient contents, or more specifically, that fertile sites exhibit more rapid rates of regeneration than infertile sites.

The most obvious measure of regeneration rate is the time taken for the vegetation to attain a steady-state (climax) condition. With regard to the present study there is no evidence to suggest that the successions are proceeding towards a forest composition identical to that of the adjacent undisturbed forests. Also, there is no reason to believe that any of the study sites have attained a forest composition or form that will be duplicated when the present canopy dominants die.

Since it has not been possible to follow any succession to a steady-state in this study another measure of regeneration rate is needed in order that different types of succession can be compared. If stands are arranged in a chronosequence rates of regeneration can be obtained by measuring the change in a vegetation parameter over a time interval. The vegetation parameters employed must show a steady increase for most or all of the succession (Major 1974). In the present study vegetation parameters that increase with time are height measures, total stand volume and total stand foliage (Figure 4:4 a,e,j).

For the purposes of this study rates of regeneration have been taken as the height growth rate of a stand of vegetation. This approach allowed for the comparison of different types of succession that were proceeding along different pathways and dominated by different pioneering species.

Two height growth rate indices were employed. They were derived by

- (1) dividing the average canopy height of the vegetation of each stand by the age of the vegetation, and by
- (2) dividing the minimum height of the tallest 10% of the canopy hits of each stand by the age of the vegetation.

The latter index was employed as the physiognomy of the stands is dominated by the tallest plants present at each site.

The height growth rates ( $\text{m, yr}^{-1}$ ) so obtained are present in Table 5:6.

TABLE 5:6. Height Growth Rate Indices of Seral Stands.

Stand	Vegetation Type	Age (yrs)	Canopy Height (m) $\bar{x} \pm 1 \text{ S.D.}$	Minimum Height of Tallest 10% Canopy Hits (m)	Index 1 (m/yr)*	Index 2 (m/yr)*
<u>VALLEY FLOORS AND TERRACES</u>						
S.C.1	bracken fernland	16	0.67 $\pm$ 0.35	1.28	0.04 $\pm$ 0.02	0.08
<u>GENTLE LOWER SLOPES</u>						
N.B.2	kanuka forestland	50	6.40 $\pm$ 1.79	8.50	0.13 $\pm$ 0.04	0.17
N.B.9	kanuka forestland	40	6.46 $\pm$ 1.42	7.60	0.17 $\pm$ 0.04	0.19
E.I.1	bracken fernland	13	0.71 $\pm$ 0.24	0.78	0.04 $\pm$ 0.02	0.06
E.I.2	bracken fernland	14	0.67 $\pm$ 0.44	1.12	0.04 $\pm$ 0.03	0.08
E.I.3	bracken fernland	16	1.03 $\pm$ 0.81	2.08	0.06 $\pm$ 0.05	0.13
E.I.5	<i>Cassinia</i> shrubland	13	0.78 $\pm$ 0.73	1.95	0.06 $\pm$ 0.06	0.15
E.I.6	<i>Cassinia</i> shrubland	13	0.90 $\pm$ 1.14	2.85	0.07 $\pm$ 0.08	0.22
T.B.2	manuka shrubland	24	3.98 $\pm$ 1.67	5.50	0.17 $\pm$ 0.07	0.23
T.B.4	manuka- kanuka forestland	35	4.81 $\pm$ 2.84	7.00	0.14 $\pm$ 0.08	0.20
T.B.8	manuka shrubland	21	1.22 $\pm$ 0.85	2.10	0.06 $\pm$ 0.04	0.10
<u>STEEP COLLUVIAL SLOPES</u>						
C.C.3	kanuka forestland	55	7.6 $\pm$ 4.33	15.40	0.14 $\pm$ 0.08	0.28
D'Urv.1	kanuka forestland	58	6.93 $\pm$ 2.36	9.85	0.12 $\pm$ 0.04	0.17
N.B.8	kanuka forestland	45	4.52 $\pm$ 2.53	7.65	0.10 $\pm$ 0.06	0.17
T.B.5	coastal broadleaf forest	70	4.56 $\pm$ 2.87	9.80	0.07 $\pm$ 0.04	0.14
T.B.9	kanuka forestland	40	3.61 $\pm$ 1.41	5.20	0.09 $\pm$ 0.04	0.13

TABLE 5:6 Continued

Stand	Vegetation Type	Age (yrs)	Canopy Height (m) $\bar{x} \pm 1 \text{ S.D.}$	Minimum Height of Tallest 10% Canopy Hits (m)	Index 1 (m/yr)*	Index 2 (m/yr)*
<u>STEEP, FINE TEXTURED UPPER SLOPES</u>						
C.C.6	manuka shrubland	27	4.0 $\pm$ 1.36	5.40	0.15 $\pm$ 0.05	0.20
C.C.7	kanuka shrubland	45	7.62 $\pm$ 1.30	9.00	0.17 $\pm$ 0.03	0.20
C.C.8	kanuka forestland	48	5.49 $\pm$ 1.65	7.70	0.11 $\pm$ 0.03	0.16
N.B.1	kanuka forestland	47	5.50 $\pm$ 0.25	8.95	0.12 $\pm$ 0.01	0.19
N.B.7	manuka shrubland	13	1.11 $\pm$ 0.60	1.95	0.09 $\pm$ 0.05	0.15
B.M.1	manuka shrubland	30	3.67 $\pm$ 1.29	5.10	0.12 $\pm$ 0.04	0.17
B.M.2	manuka shrubland	25	2.00 $\pm$ 0.90	3.25	0.08 $\pm$ 0.04	0.13
T.B.1	manuka shrubland	23	0.79 $\pm$ 0.78	1.85	0.03 $\pm$ 0.03	0.08
E.I.4	kamahi-toro forest	84	6.08 $\pm$ 2.25	9.25	0.07 $\pm$ 0.03	0.11
E.I.7	kamahi forestland	70	6.80 $\pm$ 2.52	9.80	0.10 $\pm$ 0.04	0.14
R.B.1	kamahi shrubland	20	0.93 $\pm$ 0.64	2.20	0.05 $\pm$ 0.03	0.11
D'Urv.2	kanuka forestland	58	6.21 $\pm$ 2.05	8.70	0.11 $\pm$ 0.04	0.15
<u>RIDGES AND SPURS</u>						
H.R.5	<i>Gahnia</i> sedgeland	2	0.25 $\pm$ 0.14	0.40	0.13 $\pm$ 0.07	0.20
C.C.1	manuka shrubland	35	5.77 $\pm$ 1.96	7.35	0.16 $\pm$ 0.06	0.21
C.C.2	manuka shrubland	40	5.57 $\pm$ 1.84	7.20	0.14 $\pm$ 0.05	0.18
C.C.5	manuka shrubland	37	5.39 $\pm$ 2.05	7.40	0.15 $\pm$ 0.06	0.20
G.B.1	kanuka shrubland	70	9.13 $\pm$ 4.47	15.40	0.13 $\pm$ 0.06	0.22
N.B.3	manuka shrubland	43	4.51 $\pm$ 0.99	6.45	0.11 $\pm$ 0.02	0.15
N.B.5	manuka shrubland	12	0.87 $\pm$ 0.52	1.56	0.07 $\pm$ 0.04	0.13
N.B.6	manuka shrubland	12	0.45 $\pm$ 0.34	0.96	0.04 $\pm$ 0.03	0.08
B.M.3	coprosma-manuka shrubland	32	2.93 $\pm$ 1.11	4.50	0.09 $\pm$ 0.03	0.14
T.B.6	manuka-gorse shrubland	25	1.58 $\pm$ 0.87	2.75	0.06 $\pm$ 0.03	0.11

\* Index 1 - Mean growth rate of stand  $\pm$  1 S.D. (m/yr)

Index 2 - Growth rate of tallest 10% canopy hits (m/yr)



The height growth rates were compared with the measured soil parameters and were related to the topographic positions of the stands. No relationships were evident between either of the regeneration rate indices and the soil parameters. The average height growth rate is constant between the vegetation of the ridges, upper and lower slopes and the colluvial sites, although it does vary between stands on any one topographic position.

(Relationships were also investigated between total stand volume and total stand foliage measures and soil concentrations and topographic position. Results were similar to those presented for the height growth indices, i.e. the regeneration rates are similar for seral stands on ridges, slopes and colluvial sites and there is no relationship between regeneration rates and measured soil nutrient contents).

## 5:6 Discussion

The majority of the successions studied owe their origins to fire. All of the study sites, with the exception of H.R.5 and possibly E.I.4, have had at least one fire through them within the last 100 years.

Substantial nutrient losses from an ecosystem can occur when the vegetation is burnt. The nutrient losses can occur at the time of the fire, by volatilization of nitrogen, calcium, magnesium, potassium, phosphorus and sulphur (Harwood and Jackson 1975, Grier 1975, Raison 1980b). Nutrient losses also occur after the fire as nutrients can be washed downslope after rain, ash can be blown from the site, nutrients can be lost from the rooting zone of the plants by leaching into the deep soil horizons.

It has not been possible to estimate the amount of nutrient loss from any site, since all sites were disturbed prior to the start of the present study. Each site would have a unique history with regard to the extent and severity of disturbance suffered. In a qualitative sense it is possible to identify the sites that have suffered the severest nutrient losses from their soil profiles. Three sites have suffered soil truncation; at site H.R.5 all vegetation, forest floor and A horizon material were bulldozed off the site; sites C.C.2 and C.C.7 do not possess an A horizon, their upper soil horizons are B horizons (illuvial horizons). Some of the other sites, especially in the Tawa Bay and Endeavour Inlet Scenic Reserves, have a history of repeated firing; the result of trying to control the second growth that established on poor pasture land. All of these sites may have suffered considerable nutrient loss from the ecosystem.

There is no method available with which one can quantify the seriousness of the loss of soil nutrients from an ecosystem (Stark 1977). Sites on infertile soils and with slow weathering—parent materials, low atmospheric nutrient inputs and slow organic matter breakdown rates are especially vulnerable to nutrient loss from the ecosystem since nutrient recovery will be slow. A measure of the vulnerability of the study sites to nutrient loss from the ecosystem is given by the ratio of the amount of available nutrient stored in the forest floor and the top 1 cm of soil (the vulnerable zone for most land use activities) to the amount of available nutrient stored in the forest floor and the effective rooting zone of the soil (considered to be 30 cm in this present study). Table 5:7 is a summary of the percentage of available nutrients stored in the 'vulnerable' zone of each study site.

TABLE 5:7. Proportion of nutrients in forest floor and top 1 cm soil :  
nutrients in forest floor and soil to a depth of 30 cm.

Site	N	C	K	Mg	Na	Ca	P <sub>T</sub>
E.I.1	9.5	14.8	12.9	29.9	11.9	18.6	66.3
E.I.2	9.1	12.7	14.5	34.2	15.7	17.9	61.1
E.I.3	7.8	11.3	8.1	25.1	15.5	19.1	56.7
E.I.4	9.9	9.9	33	30.7	12.7	23.2	71.4
E.I.5	5.8	4.7	7.2	8.3	5.7	3.1	25.5
E.I.6	5.0	4.5	8.5	14.2	6.2	8.1	32.2
E.I.7	8.2	10.8	24.2	41.8	37	39.6	76.2
T.B.1	7.8	9.1	11	14.4	10.4	12.2	63.5
T.B.2	6.3	10.5	12.5	9.9	10.2	11.7	39.5
T.B.3	7.9	11.4	11.4	14.4	12.2	14.3	57.6
T.B.4	9.2	12.7	34.2	25.7	9.1	29.4	69.6
T.B.5	9.0	11.8	16.6	18.3	13.2	12.6	70.1
T.B.6	8.7	11.1	17.4	13.8	11.6	11.9	52
T.B.7	5.2	5.7	7.3	9.2	7.1	8.7	21.7
T.B.8	5.7	7.8	10.0	13.5	8.5	16.9	40.9
T.B.9	6.8	12.1	12.9	23.8	13.9	19.7	41.4
H.R.1	25.4	21.1	57	26.1	23.3	61.6	75.6
H.R.2	7.5	8.3	22.9	16.9	17.2	56.5	84.7
H.R.3	16.1	25.2	58.3	32.8	20.7	78	67.5
H.R.4	13	15.2	48.3	42.2	13.2	43.4	91.7
H.R.5	3.4	3.3	3.3	3.3	3.3	3.3	3.3
R.B.1	7.2	8.9	14.3	9.3	12.3	15.0	29.0
S.C.1	4.6	7.0	9.1	12.8	11.3	11.1	67.8
N.B.1	7.4	10.3	8.9	12.3	8.7	9.7	67.9
N.B.2	7.2	10.9	8.5	8.5	6.1	9.8	51.1
N.B.3	10.6	21.3	16.9	13.7	10.8	12.5	64.7
N.B.4	8.6	17.4	14.3	7.6	5.1	6.3	69.7
N.B.5	6.8	11.6	9.7	6.3	5.9	7.3	17.3
N.B.6	8.5	17.2	11.8	7.9	9.1	8.9	10.0
N.B.7	6.9	20.4	11.8	10.8	10.2	14.1	56.5
N.B.8	7.9	13.7	9.2	9.1	5.7	12.3	66.3
N.B.9	9.3	15.6	22.9	14.9	15.3	17.3	64.5
C.C.1	9.1	17.8	18.8	22.8	18.4	26.8	67.3
C.C.2	9.4	15.2	19.6	18.5	14.7	54.0	84.4
C.C.3	6.9	12.9	13.7	9.9	11.4	9.1	79.8
C.C.4	7.4	12.9	14.6	7.3	10.3	9.3	72.8
C.C.5	8.3	19.5	13.7	6.4	8.3	11.3	77.7
C.C.6	6.3	13.4	15.0	10.9	6.8	17.6	32.8
C.C.7	6.7	13.1	5.9	5.3	4.8	7.1	67.3
C.C.8	6.4	13.4	12.7	7.1	7.8	9.6	39.4
G.B.1	10	15.4	14.8	9.7	6.0	11.9	66.7
B.M.1	9.4	15.1	13.0	6.7	6.6	7.8	61.7
B.M.2	6.5	12.9	11.6	7.4	5.8	9.0	69.9
B.M.3	4.5	6.9	6.2	5.4	4.1	5.5	19.8
D'Urv.1	4.9	6.9	5.2	7.8	4.6	6.2	18.0
D'Urv.2	8.1	15.1	9.2	11.9	8.0	21.9	70.9

A substantial percentage of the nutrients readily available to plants is located in the forest floor and top 1 cm of soil of the study sites.

Nitrogen is the one nutrient studied that has adequate reserves located in the soil profile. Most seral stands had less than 10% of their available nitrogen capital distributed in the forest floor and top 1 cm of soil. The two undisturbed *Nothofagus* stands however had in excess of 10% of their available nitrogen reserves located in the 'vulnerable' zone.

The majority of seral and undisturbed stands had high percentages of exchangeable cations and organic carbon located in the forest floor and top 1 cm of soil. The *Nothofagus* stands had a high nutrient investment in the forest floor and top 1 cm of soil; available potassium and calcium are especially concentrated in this region.

There is a very high concentration of available phosphorus in the 'vulnerable' zone. The high concentration of available phosphorus in the upper portion of the soil horizon may well be an exaggeration. True phosphorus levels are probably not an accurate measure of the phosphorus that is available to the plants and other forms of phosphorus (e.g. absorbed on clay minerals) distributed in the soil profile may be readily available to forest species.

Although a number of seral sites had less available nutrients in the forest floor and soil (to a depth of 30 cm) than that found under mature, undisturbed forests there were some seral sites that possessed more available nutrients in the forest floor-soil zone than that of the undisturbed forests.

There was no discernible trend in the recovery of any soil nutrient measured as:

1. quantity of nutrients in forest floor and top 1 cm of soil,
2. quantity of nutrients in forest floor and A horizon,
3. quantity of nutrients in forest floor and soil to a depth of 30 cm.

during succession.

The variation in the nutrient content, depth of horizons, severity of disturbance at the study sites masked any trends of soil nutrient loss or gain that could be associated with succession.

Egunjobi, in his study of nitrogen distribution in successional stands at Taita, showed that the nitrogen-fixing shrub *Ulex europaeus* was responsible for influencing soil nitrogen concentrations during the early stages of secondary succession (Egunjobi 1969).

The nitrogen content (kg/ha) of the litter and soil to a depth of 28 cm was highest in the youngest *Ulex* dominated stands, intermediate in the middle aged stands of *Leptospermum scoparium* and *U. europaeus* and lowest in the oldest *L. scoparium* and *Weinmannia racemosa* stands. The weights of nitrogen in the litter and soil of the *U. europaeus* dominated stands reported by Egunjobi are not exceptional or even high when compared to the present study. Nitrogen weights of 137 kg/ha and 129 kg/ha were reported from the forest floors (litters) of four and seven year old *U. europaeus* stands at Taita. Older seral stands had weights of N in the forest floor similar to, or lower than that of stands of equivalent age in the Marlborough Sounds.

The nitrogen concentration of forest floor material under vascular nitrogen-fixing plants was similar at Taita and at the Marlborough Sounds sites (1.4-1.5%). The N concentration of *Leptospermum* litter in the Marlborough Sounds was lower than that reported from under vegetation of similar composition at Taita.

The high nitrogen content of most forest floors in the Marlborough Sounds results from the high biomass of forest floors under many of the Marlborough Sounds sites. Whereas most sites at the Marlborough Sounds had forest floor weights in excess of 15,000 kg/ha, the sites at Taita only averaged 9,550 kg/ha.

The nitrogen content of the soils under the young *U. europaeus*-dominated stands at Taita are similarly not exceptional when compared to the soils under younger regenerating stands in the Marlborough Sounds. The highest value of N, to a depth of 28 cm, in the soil profile at Taita was 5,476 kg/ha which falls into the medium range of the nitrogen content of the Marlborough Sounds soils. Soil profile N content at Taita, under *U. europaeus*, is much lower than the soil N content in the profile under the vascular N-fixers at the Marlborough Sounds where values between 6,500 and 12,500 kg/ha were recorded. The lowest N soil contents at Taita to a depth of 28 cm were recorded under the oldest stands. The values of 2,684 and 2,968 kg/ha are comparable to that of the soils of some of the less fertile upper slope and ridge sites studied in the Marlborough Sounds.

The overall impression gained from the present study is that most of the seral slope and ridge sites studied in the Marlborough Sounds are more productive than similarly aged stands at Taita.

In a study of nutrient accumulation in seral stands of *Pinus banksiana* and mixed hardwoods in New Brunswick, Canada, MacLean and Wein (1977b) were unable to find any trends in forest floor development or nutrient accumulation in the forest floor and mineral soil (to a depth of 25-30 cm) with succession. As in the present study the great variation in depth of organic horizons and nutrient content of soil between stands masked any trends of nutrient recovery with succession. Their conclusion that there is a need for well designed research to address specific questions about the long term effect of disturbance on nutrient cycles is especially apt when applied to the New Zealand lowland forest ecosystem. Whilst the evidence from the present study would suggest that tree growth has not been limited at any one stand site by the measured soil nutrients, it has been impossible to predict the long term consequences of further disturbance to a site. This has been due to a number of factors, amongst which the lack of knowledge about the nutrient requirements of our indigenous shrub and tree species and the uncertainty about the availability of nutrients in forest soils to plants have been the main barriers to prediction.

The fact that many of the seral stands have over 10% of their available nutrient capital invested in the forest floor and top centimetre of the soil horizon indicates that there could be a drain on the ecosystem's nutrient reservoir with further disruption to the forest floor.

CHAPTER SIXNutrient Cycling Fluxes in Adjacent *Leptospermum scoparium*-*L. ericoides*  
and *Coriaria arborea*-*Aristotelia serrata* communities.6:1 Introduction

Structural and compositional characteristics of successional communities in the Marlborough Sounds have been documented in the previous two chapters. In recent years a number of studies have attempted to define succession in functional terms (Zavitkovski and Newton 1971, Lang 1973, Ashton 1975, Park 1975, Edmonds, R. 1979 and Bormann and Likens 1979). These studies have sought to document the manner in which rates of mineral cycling, hydrological cycling, photosynthesis, respiration, etc., change during succession or are restored to steady-state levels.

A small study was designed to complement the investigations of the structure and composition of the vegetation and standing state of the forest floors in the successional stands. Investigations of the nutrient status of the forest floors and soil horizons had revealed differences in quantity and quality of the nutrients between seral vegetation types at different sites. The study involved the monitoring of litter fall and leaf litter decomposition in two adjacent seral communities. The aim of the study was to investigate the role of different seral species in restoring and maintaining nutrient levels in the disturbed ecosystems.

## 6:2a The environment of the study area

The study area was located on the south facing slopes on the northern side of Endeavour Inlet, in the Tawa Bay Scenic Reserve.

Endeavour Inlet is a sheltered bay in Queen Charlotte Sound. It is protected from north easterly winds by the hills which rise to 823 m between Resolution Bay and Endeavour Inlet. The Mount Stokes-Mount McMahon mountain ridge system protects Endeavour Inlet from the full effects of southerly winds. Winds are funnelled down the valley at the head of Endeavour Inlet and the north westerly winds that come down the valley are the prevailing winds of the Inlet.

The Inlet experiences an annual rainfall of 1600 mm at sea level.

The two vegetation communities studied are located on a slope and an adjacent gully at an altitude of 120 m.

The vegetation cover of the two study stands is typical of regenerating communities on slopes and in gulleys over much of the Endeavour Inlet area that was originally cleared for agriculture.

## 6:2b Study site descriptions

### (i) Seral *Leptospermum* shrubland

The shrubland is located on a gentle ( $5-10^{\circ}$ ) mid-slope, grid reference: NZMS1 S:16 468474.

The community is a *Leptospermum ericoides*-*L. scoparium* shrubland.

The vegetation has a closed canopy with an average height of 5.3 m. Some *L. ericoides* trees reach 9.8 m. *Leptospermum scoparium* is numerically more important than *L. ericoides* and makes a greater contribution to the basal area of the stand:

No. <i>L. scoparium</i> plants > 2 cm d.b.h./ha	=	4040
No. <i>L. ericoides</i> plants > 2 cm d.b.h./ha	=	320
Basal area ( $\text{m}^2/\text{ha}$ ) <i>L. scoparium</i>	=	41.48
Basal area ( $\text{m}^2/\text{ha}$ ) <i>L. ericoides</i>	=	18.59



There is very little understorey development, only a few scattered *Cyathodes fasciculata* shrubs and *Cyathea dealbata* ferns are present.

The ground floor vegetation is sparse with some etiolated specimens of *Pteridium esculentum* in light gaps and *Lycopodium volubile* scrambling over the ground floor and climbing up *Leptospermum* stems.

A thin litter layer of *Leptospermum* leaf and twig material overlies the mineral soil. There are a number of dead *Leptospermum scoparium* stems with d.b.h. measurements between 2 cm and 5 cm lying on the forest floor and a number standing of similar dimensions supporting very little photosynthetic material.

Tree cores of *L. ericoides* and *L. scoparium* were taken and the community appears to be approximately 30 years old. There is evidence of an old fence line along the southern side of the study plot.

#### Soil profile description:

L + F + H	0 - 1 cm	litter and decomposing material of <i>Leptospermum</i> spp. twigs and leaves.
A hor	1 -18 cm	dark brown (10 YR 3/4) firm silt loam, moderately developed fine nut structure, roots abundant to 15 cm, bracken rhizomes at 18 cm, indistinct boundary to
B hor	18-40 cm	yellow brown (10 YR 5/8) firm, silty clay loam, moderately developed nut structure, roots present to 35 cm, schist chips (approx. 5 x 3 x 1 cm <sup>3</sup> ) throughout horizon.

Soil Parent Material: Marlborough schist

#### (ii) Seral *Coriaria-Aristotelia* forestland

The forestland is located on a steep (25-30°) colluvial mid-slope gully immediately to the east of the seral *Leptospermum* study site.

The community is a tall *Coriaria arborea-Aristotelia serrata* forestland. The forestland has a closed, relatively even canopy with a mean height of 9.2 m. Some of the canopy trees attain 14.5 m. *Coriaria arborea* and *A. serrata* make equal contributions to the canopy, there is also a slight contribution to the canopy from *Cyathea medullaris*. Although *A. serrata* is numerically more important than *C. arborea* it makes a smaller contribution to the basal area of the stand:

No. <i>Aristotelia serrata</i> plants > 2 cm d.b.h./ha	=	880
No. <i>Coriaria arborea</i> plants > 2 cm d.b.h./ha	=	680
Basal area (m <sup>2</sup> /ha) <i>A. serrata</i>	=	17.85
Basal area (m <sup>2</sup> /ha) <i>C. arborea</i>	=	22.44

An understorey of broadleaved tree and shrub species and tree ferns is present between 1 m and 5 m. The most common understorey species are *Brachyglottis repanda*, *Melicytus ramiflorus*, *Cyathea dealbata* and *C. medullaris*. The ground floor vegetation is sparse and consists of a scattered fern cover. There are a number of decomposing branches and stems of *Coriaria arborea* on the forest floor. A thin litter layer of *B. repanda*, *C. arborea*, *A. serrata* and *Cyathea* spp. leaf, twig and frond material lies directly above the mineral soil.

The community was unable to be aged.

#### Soil profile description:

L + F + H	0 - 1 cm	leaf and twig material.
A hor	1 -10 cm	dark brown (10 YR 3/4) friable loamy sand, well developed crumb structure, roots abundant, schist rocks common, indistinct horizon to
B hor	10-30 cm	dull yellow brown (10 YR 5/4) firm loamy sand, well developed crumb structure, roots abundant, large schist rocks present, indistinct boundary to
C hor	30+ cm	large schist rocks.

Both sites show evidence of recent slipping. A debris avalanche slip occurred in December 1977 directly above the *Leptospermum* plot. Slip debris spread onto one end of the study plot. The head of the slip was 5 m across and approximately 6 m deep, the debris spread for a distance of 14 m.

The *Coriaria-Aristotelia* stand is subject to constant soil movement. Stones are abundant at the surface of the soil. Each month one or two of the litter collecting buckets had slid against the retaining stakes and sometimes they had tipped over. Many of the litter bags were carried away from the site where placed and were usually located some distance downslope lodged in a litter heap behind a rock or tree obstacle.

Methods of sampling, sample treatment and chemical analyses of forest floor and litter material were described in Chapter 3.

## Results

The results of the study are presented in Figures 6:1-6:7. The data are tabulated in in the text.

### 6:3 Above Ground Structure of the Vegetation

Direct sampling of the above ground biomass was not undertaken. A relative estimate of the above ground biomass of the stands is given by comparing basal areas and vegetation space parameters of the two vegetation types. Reiners and Reiners (1970) employed tree basal area as a convenient index of litter production in an ecosystem and showed that for three ecosystems (oak forest on a sandy plain, open white cedar-black ash on a marginal fen and white cedar swamp) in Minnesota there was a marked convergence in function (expressed as energy flow, measured by calorific content of litterfall) relative to the basal area of each forest. Fox, Fox and McKay (1979) reported a direct relationship between annual litterfall and site basal area for seral *Eucalyptus pilularis*-*Angophora costata* communities at Seal Rock, N.S.W., Australia.

Olson (1963) considered that since litterfall is "generally related to the quantity of photosynthetic machinery in the system, it is an index of ecosystem productivity". Park (1975) found a close relationship between annual litterfall weights and vegetation space of two adjacent successional montane eucalypt communities.

In the present study the vegetation space parameters have been derived from Point Height Intercept Analysis (Park 1973). Two hundred point stations were employed in each vegetation type. Basal area data was derived from the diameter at breast height measurement of all tree and saplings > 2 cm d.b.h. in a 10 m x 30 m plot at each site.

Throughout this chapter the relative distribution of above ground structural parameters, nutrients and total weights of the two vegetation types is expressed by the ratio of the value in the *Leptospermum ericoides*-*L. scoparium* stand relative to the value in the *Coriaria arborea*-*Aristotelia serrata* stand, i.e. (Lspp/C.-A.) ratio.

The structural features of the vegetation in the *Leptospermum* spp. shrubland and the *Coriaria*-*Aristotelia* forestland are summarised in the following table.

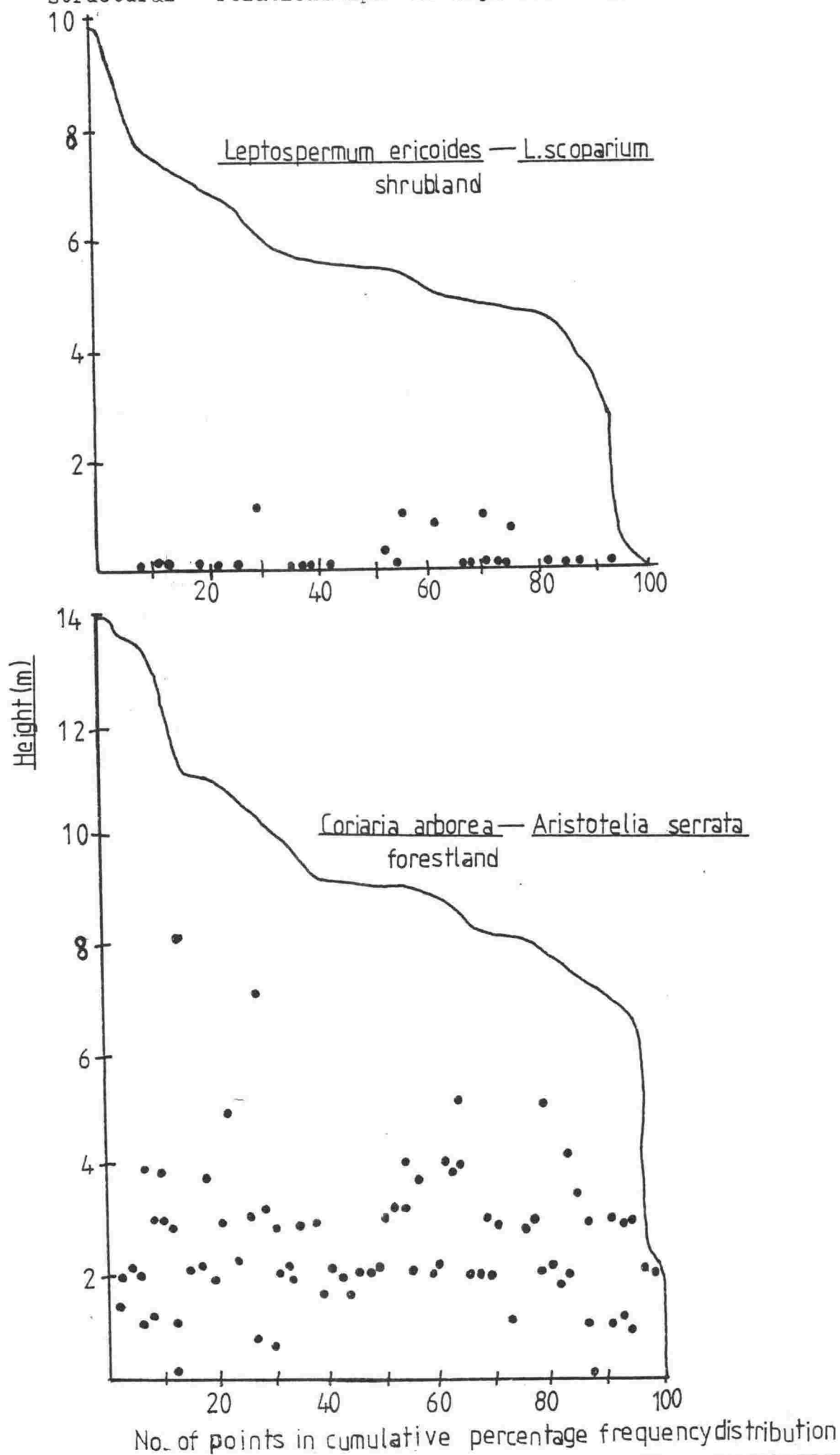
Table 6:1. Structural Features of Vegetation in a *Leptospermum ericoides*-*Leptospermum scoparium* shrubland and an adjacent *Coriaria arborea*-*Aristotelia serrata* forestland.

Parameter	<i>L. ericoides</i> - <i>L. scoparium</i>	<i>C. arborea</i> - <i>A. serrata</i>	<i>L. spp.</i> / <i>C.-A.</i>
Basal area (m <sup>2</sup> /ha)	60.07	48.69	1.23
No. stems > 2 cm d.b.h.	4360	3000	1.45
Maximum height (m)	9.8	14.5	0.68
Average height (m)	5.3	9.2	0.58
Total stand volume (units)	8104	13655	0.59
Total vegetation space (units)	5137	9541	0.54
Total stand foliage (units)	1474	2576	0.57
Specific Vegetation Space (ratio)	63	70	
Annual litter fall (tonnes/ha)	7.8	10.1	0.77

The *Leptospermum ericoides*-*L. scoparium* shrubland is dense and supports a high basal area. The vegetation is undergoing self thinning, there are a number of fallen *L. scoparium* stems on the forest floor.

The *Leptospermum* stand supports just over half the amount of foliage possessed by the *Coriaria-Aristotelia* stand. Understorey vegetation was intercepted at 69% of the intercept stations in the *Coriaria-Aristotelia* forestland (Figure 6:1). In contrast only 6% of the intercepts encountered understorey vegetation under the *Leptospermum* canopy. Ground floor cover is better developed in the *Leptospermum* stand than in the *Coriaria-Aristotelia* forestland. Ground floor vegetation was intercepted at 22% of the point stations in the *Leptospermum* stand but only at 4% of the stations under the *Coriaria-Aristotelia* canopy.

Figure 6:1 Simplified P.H.I. diagrams (Park 1973) of vegetation structural relationships in adjacent seral stands.



#### 6:4 Concentration and Weight of Nutrients on the Forest Floor

The concentrations and weights of nutrients in the forest floors of both stands are presented in Table 6:2 and Table 6:3.

The weight of the forest floor (oven dried at 80°C for 24 hrs) is higher in the *Leptospermum* stand than in the *Coriaria-Aristotelia* stand. Although the nutrient content of the *Coriaria-Aristotelia* forest floor material is higher than that of the *Leptospermum* forest floor material there is a greater weight of all nutrients in the *Leptospermum* forest floor.

Table 6:2. Biomass and Concentration of Nutrients in the Forest Floor

Vegetation	Biomass (tonnes/ha) *	Concentration (% oven dried material							
		C	N	K	Mg	Na	Ca	P	C/N
<i>Leptospermum ericoides</i> - <i>L. scoparium</i>	17.9(1.0)	28	0.8	0.28	0.22	0.04	0.67	0.05	35
<i>Coriaria arborea</i> - <i>Aristotelia serrata</i>	7.0(0.7)	25	1.5	0.32	0.35	0.05	1.31	0.10	17
L. spp./C.-A.	2.56		0.53	0.88	0.63	0.80	0.51	0.50	2.1

\*Standard Errors in parentheses (n = 6).

Table 6:3. Weight of Nutrients in the Forest Floor

Vegetation Type	Weight (kg/ha)					
	N	K	Mg	Na	Ca	P
<i>Leptospermum ericoides</i> - <i>L. scoparium</i>	143.2	50.1	39.4	7.2	119.9	9.0
<i>Coriaria arborea</i> - <i>Aristotelia serrata</i>	105.0	22.4	24.5	3.5	91.7	6.3
L. spp./C.-A.	1.4	2.2	1.6	2.1	1.3	1.4

The independent distribution of the elements in the two forest floors is best described by the L. spp./C.-A. ratios of concentrations and weights. Relative to dry weight the quantity of nutrients in the forest floor is lower in the *Leptospermum* stand, especially for Ca, N and Mg.

## 6:5 Seasonal Fluxes in Litter Fall

Results are presented in Figure 6:2 and Tables 6:4a and b.

### 6:5a Weight of litter fall

The annual litter fall weights of both stands are very high. The % contribution of the leaf litter to the total annual litter fall is similar for both stands and is approximately 70%. The contribution of the leaf litter to the monthly litter fall varies from lows of 55% in the *Coriaria-Aristotelia* stand and 47% in the *Leptospermum* stand to highs of 89% in the *Coriaria-Aristotelia* stand and 92% in the *Leptospermum* stand.

There is a seasonal peak in litter fall in both stands. Peak litter-fall in the *Coriaria-Aristotelia* stand occurs in spring; the peak leaf fall also occurs in spring and extends into early summer. The leaf fall amount declines rapidly in late summer to low levels in autumn and winter. Twig fall is not markedly seasonal in the *Coriaria-Aristotelia* stand. High twig falls occur in summer, winter and spring months.

Peak litter fall in the *Leptospermum* stand occurs in late summer. (This is the time of peak leaf fall.) The peak litter fall is a very obvious phenomenon and the forest floor is covered by the leaf litter. (The following December the author noted a heavy *Leptospermum ericoides* leaf fall when camped in a *L. ericoides* grove in the Wairarapa. A nylon tent was clothed in *L. ericoides* leaf litter overnight). Leaf fall in the *Leptospermum* stand declines during autumn and winter and reaches a minimum in September. Twig and capsule litter fall is not markedly seasonal; highest falls occur in winter and spring months.

The twig fall does not appear to be related to heavy winds. Heavy twig fall in one stand does not coincide with the heavy twig fall in the adjacent stand, with the possible exception of the October fall.

The seasonal pattern of leaf fall recorded at the two sites is similar to that reported by other workers in New Zealand's indigenous forests. There is a marked peak of leaf fall in summer and a low in winter. This pattern has been reported by Miller (1963), Wardle (1970) and Bagnall (1972) for *Nothofagus* spp. forests and by Daniel (1975) for a podocarp-rata-broadleaf forest. Daniel (1975) reports that similar patterns of leaf fall have been recorded in warm temperate evergreen forest in Japan and in warm temperate forests in Australia.



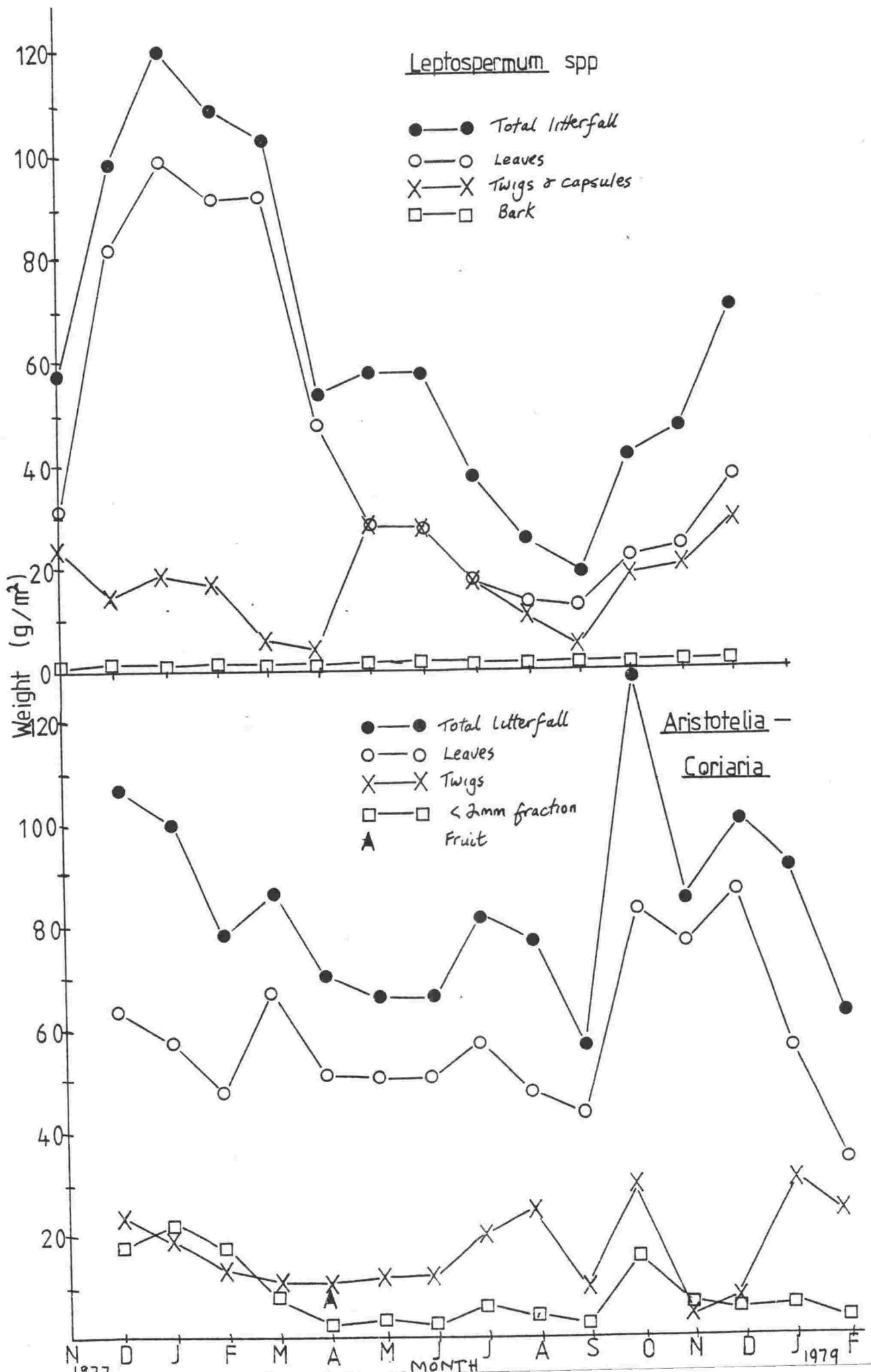
Table 6:4a. Litter Fall Weights ( $\text{gm/m}^2$ ) - *Leptospermum* stand.

Month	Total	Leaves	Bark	Twigs and Capsules
Nov	58.34	32.50	1.45	24.39
Dec	99.00	82.82	2.09	14.09
Jan	121.04	100.46	1.21	19.37
Feb	110.38	92.50	0.66	17.22
Mar	103.73	95.29	1.62	6.82
Apr	54.02	48.79	0.65	4.58
May	59.40	29.17	1.10	29.13
Jun	59.40	29.17	1.10	29.13
Jul	38.18	18.11	1.37	18.70
Aug	25.56	14.18	0.52	10.86
Sep	19.74	12.97	1.03	5.74
Oct	42.59	22.49	1.14	18.96
Nov	47.82	25.20	1.32	21.30
Dec	71.00	39.31	1.48	30.21
Tonne/ha/yr	7.80	5.51	0.41	2.15

Table 6:4b. Litter Fall Weights ( $\text{gm/m}^2$ ) - *Coriaria-Aristotelia* stand.

Month	Total	Leaves	Chaff	Twigs and Branches	Fruit
Dec	107.24	64.22	18.54	24.48	
Jan	100.26	58.15	22.61	19.50	
Feb	78.94	47.36	17.80	13.78	
Mar	87.24	67.87	8.86	10.51	
Apr	70.50	50.90	2.13	10.24	7.23
May	65.84	50.53	3.29	12.02	
Jun	65.84	50.53	3.29	12.02	
Jul	82.03	56.73	5.62	19.68	
Aug	76.49	47.31	3.98	25.20	
Sep	56.26	43.37	2.70	9.19	
Oct	129.68	83.13	16.29	30.26	
Nov	84.98	75.63	5.12	4.23	
Dec	100.54	87.07	6.06	7.41	
Jan	91.19	55.86	5.29	30.62	
Feb	62.05	34.13	3.10	24.82	
Tonne/ha/yr	10.07	6.98	1.06	2.03	

Figure 6:2 Monthly fluxes in litterfall in two adjacent seral stands.



6:5b Concentration of nutrients in litter fall

Leaf material was analysed separately from the other components of the litter fall which <sup>here</sup> was pooled together for each stand. Data on the fluxes in the concentrations of total nutrients in the litter fall for each stand are presented in Figures 6:3a and 6:3b and Table 6:5a and 6:5b.

All elements were present in higher concentrations in the leaf litter fraction of the *Coriaria-Aristotelia* litter fall than in the combined twig and chaff component. In the *Leptospermum* litter fall only the N and P concentrations were consistently higher in the leaf litter than in the combined twig, capsule and bark component of the litter fall.

Element concentrations, with the exception of Na, are higher in the *Coriaria-Aristotelia* leaf litter. Potassium levels, however, are within the same range for much of the year between the two stands' leaf fall. Sodium and K occur in greater concentrations in the *Leptospermum* twig and bark component of the litter fall than in the *Coriaria-Aristotelia* twig and chaff litter.

Ratios of the maximum concentrations recorded in the leaf and twig components of the litter are presented in Table 6:6. The independent behaviour of the elements in their distributions in the litter components is evident from the different ratios of each element.

Table 6:6. Ratios of the Maximum Concentrations Recorded in the Leaf and Twig Components of the Litter Fall in a *Leptospermum ericoides*-*L. scoparium* shrubland and *Coriaria arborea*-*Aristotelia serrata* forestland.

Element	L. spp./C.-A. (leaf concentration)	L. spp./C.-A. (twig concentration)
N	0.43	0.35
K	0.86	1.32
Mg	0.40	0.81
Na	2.50	3.67
Ca	0.49	0.73
P	0.60	0.40

Table 6:5a. Concentration (% dry weight) of Total Nutrients in Litter  
Fall - *Leptospermum* stand.

Month	Fraction	N	K	Mg	Na	Ca	P
Nov	Leaf	0.73	0.2	0.16	0.10	0.68	0.05
	Twig + Bark	0.45	0.15	0.14	0.11	0.50	0.02
Dec	Leaf	0.70	0.29	0.17	0.12	0.60	0.06
	Twig + Bark	0.51	0.23	0.17	0.11	0.62	0.03
Jan	Leaf	0.70	0.42	0.19	0.16	0.56	0.07
	Twig + Bark	0.44	0.19	0.15	0.10	0.51	0.03
Feb	Leaf	0.63	0.43	0.13	0.15	0.69	0.06
	Twig + Bark	0.40	0.18	0.13	0.11	0.52	0.03
Mar	Leaf	0.57	0.40	0.13	0.09	0.68	0.07
	Twig + Bark	0.46	0.23	0.16	0.06	0.53	0.02
Apr	Leaf	0.71	0.26	0.15	0.05	0.63	0.06
	Twig + Bark	0.48	0.21	0.12	0.05	0.60	0.03
May	Leaf	-	-	-	-	-	-
	Twig + Bark	-	-	-	-	-	-
Jun	Leaf	0.84	0.20	0.12	0.08	0.65	0.05
	Twig + Bark	0.41	0.29	0.10	0.07	0.69	0.02
Jul	Leaf	0.88	0.25	0.14	0.07	0.70	0.06
	Twig + Bark	0.48	0.14	0.11	0.05	0.63	0.03
Aug	Leaf	0.81	0.44	0.18	0.06	0.55	0.06
	Twig + Bark	0.56	0.28	0.17	0.03	0.55	0.04
Sep	Leaf	0.72	0.46	0.14	0.06	0.55	0.05
	Twig + Bark	0.52	0.21	0.13	0.04	0.61	0.04
Oct	Leaf	0.78	0.60	0.16	0.09	0.50	0.09
	Twig + Bark	0.48	0.25	0.14	0.08	0.53	0.03
Nov	Leaf	0.79	0.53	0.18	0.10	0.65	0.08
	Twig + Bark	0.50	0.26	0.13	0.11	0.62	0.03
Dec	Leaf	0.75	0.35	0.20	0.09	0.69	0.07
	Twig + Bark	0.52	0.21	0.15	0.09	0.54	0.04

Table 6:5b. Concentration (% dry weight) of Total Nutrients in Litter  
Fall - *Coriaria-Aristotelia* stand.

Month	Fraction	N	K	Mg	Na	Ca	P
Dec	Leaf	1.40	0.22	0.30	0.05	1.21	0.08
	Twig + Chaff	0.94	0.15	0.21	0.02	0.95	0.05
Jan	Leaf	1.41	0.24	0.35	0.06	1.37	0.09
	Twig + Chaff	0.92	0.11	0.2	0.02	0.88	0.06
Feb	Leaf	1.37	0.32	0.32	0.05	1.18	0.12
	Twig + Chaff	0.86	0.16	0.14	0.03	0.69	0.03
Mar	Leaf	1.45	0.22	0.39	0.04	1.36	0.11
	Twig + Chaff	0.94	0.14	0.16	0.02	1.00	0.06
Apr	Leaf	2.07	0.18	0.41	0.05	1.50	0.13
	Twig + Chaff	0.77	0.16	0.20	0.03	0.91	0.04
May	Leaf	-	-	-	-	-	-
	Twig + Chaff	-	-	-	-	-	-
Jun	Leaf	1.80	0.23	0.27	0.03	1.34	0.09
	Twig + Chaff	0.97	0.15	0.16	0.01	0.90	0.05
Jul	Leaf	1.86	0.18	0.29	0.04	1.41	0.08
	Twig + Chaff	1.10	0.11	0.14	0.02	0.86	0.04
Aug	Leaf	1.77	0.43	0.34	0.05	1.26	0.11
	Twig + Chaff	1.08	0.17	0.19	0.01	0.79	0.07
Sep	Leaf	1.85	0.48	0.31	0.06	0.91	0.09
	Twig + Chaff	1.61	0.18	0.15	0.03	0.75	0.08
Oct	Leaf	1.83	0.70	0.30	0.05	1.07	0.11
	Twig + Chaff	1.52	0.19	0.12	0.02	1.01	0.06
Nov	Leaf	1.76	0.61	0.34	0.04	1.10	0.12
	Twig + Chaff	1.41	0.18	0.11	0.02	0.75	0.10
Dec	Leaf	1.82	0.45	0.38	0.03	1.25	0.14
	Twig + Chaff	1.21	0.22	0.19	0.02	0.93	0.09
Jan	Leaf	1.69	0.41	0.50	0.03	1.27	0.15
	Twig + Chaff	1.06	0.21	0.21	0.01	0.93	0.04
Feb	Leaf	1.71	0.39	0.36	0.04	1.42	0.11
	Twig + Chaff	1.21	0.17	0.14	0.02	0.91	0.05

Figure 6:3a Monthly fluxes in concentration of total nutrients in litterfall in Leptospermum spp. stand

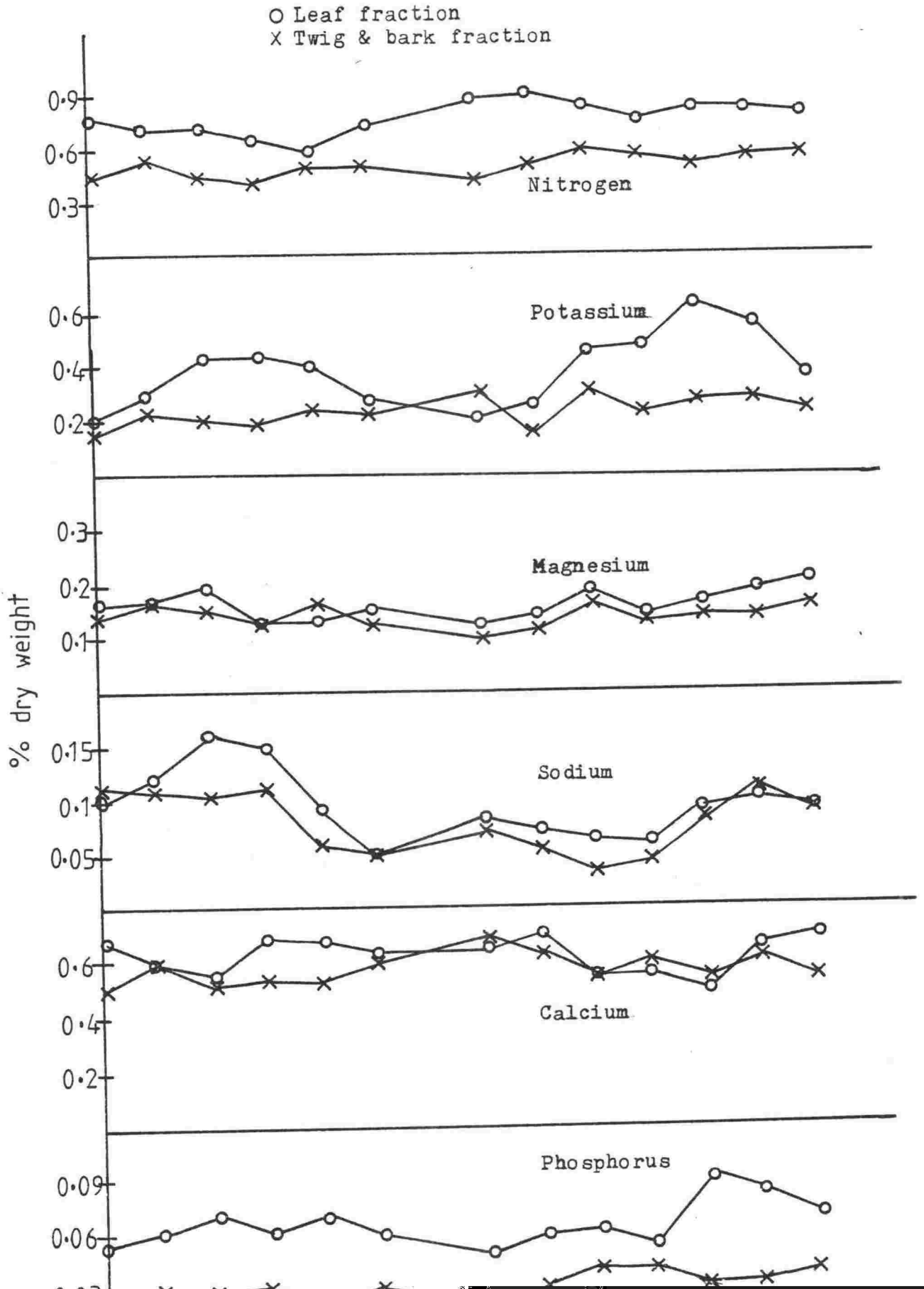
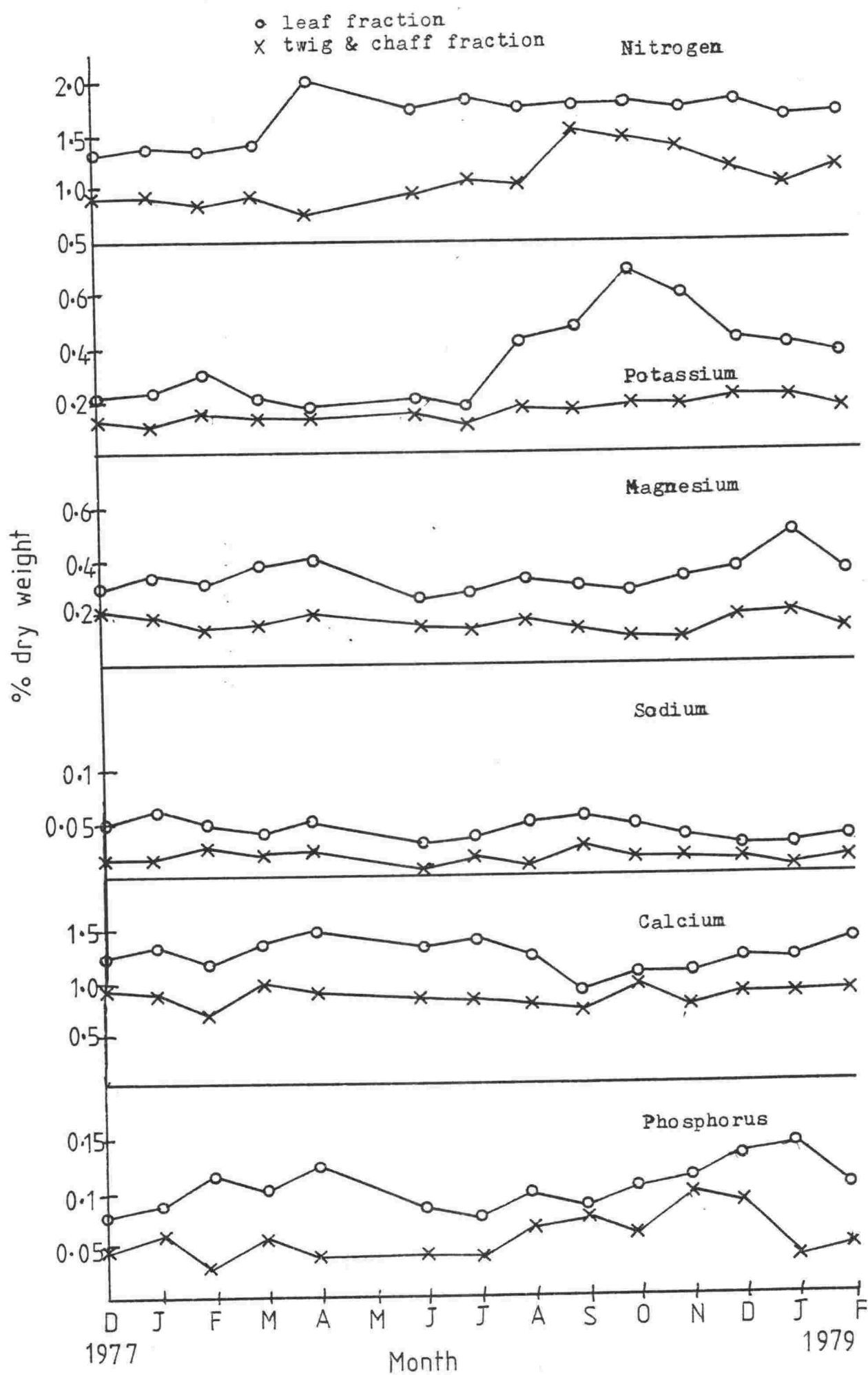


Figure 6:3b Monthly fluxes in the concentration of nutrients in  
Coriaria-Aristotelia litterfall



### 6:5c Seasonal fluxes in the concentration of nutrients in litter fall

Although each element exhibits fluctuations in concentrations in the leaf and twig components of the litter fall only Na and K exhibit any seasonal pattern of nutrient flux. Fluctuations in concentration levels are to be expected since the concentrations of the elements at the time of sampling are affected by a number of factors, especially:

- a) element conserving transfers involving the withdrawal of elements from leaves into other parts of the plant prior to leaf fall,
- b) leaching of mobile elements from leaves still attached to the tree,
- c) leaching and decomposition from the litter in collection buckets prior to collection and
- d) atmospheric inputs onto the collected litter.

Low levels of Na and K are recorded in the leaf litter of *Leptospermum* during the winter months. Low levels of K are recorded in the *Coriaria-Aristotelia* leaf litter during the early winter months but there is a marked increase in the K content of the litter from August to October. The October K peak is recorded in both ecosystems and possibly represents an accumulation of K in the litter from the leaf leachate of the trees during a wet month.

Nitrogen levels of *Leptospermum* leaf litter are lowest in the months of maximum leaf fall, this may indicate a nitrogen conserving mechanism by the *Leptospermum* trees. No other element shows a decline in concentration during the months of maximum leaf fall in either ecosystem.

There is an increase in N concentration of twig and chaff material during spring in the *Coriaria-Aristotelia* stand. The N concentration increase does not occur in the leaf litter and is not coincident with an increase in N in the woody fraction of the *Leptospermum* litter fall. The increase is probably accounted for by a larger contribution of twig and frass material from *Coriaria* than from *Aristotelia* and other broadleaved shrubs and tree ferns.



#### 6:6 The Weight of Nutrients in the Litter Fall

The monthly returns of nutrients to the forest floor in the litters of the *Leptospermum* and *Coriaria-Aristotelia* stands are presented in Figure 6:4 and Tables 6:7a and 6:7b. The annual return of elements in the litter fall is an average over the collection period.

There is a greater quantity of elements, with the exception of Na, returned in the annual fall of *Coriaria-Aristotelia* litter than in the annual fall of *Leptospermum* litter. Greater quantities of N, Mg, Ca and P are returned to the forest floor each month in the *Coriaria-Aristotelia* litter. During autumn and early winter the quantity of K returned in the litter fall of the two study stands is similar. It is only during the winter months that amounts of Na returned in the *Coriaria-Aristotelia* litter fall are greater than that returned in the *Leptospermum* fall.

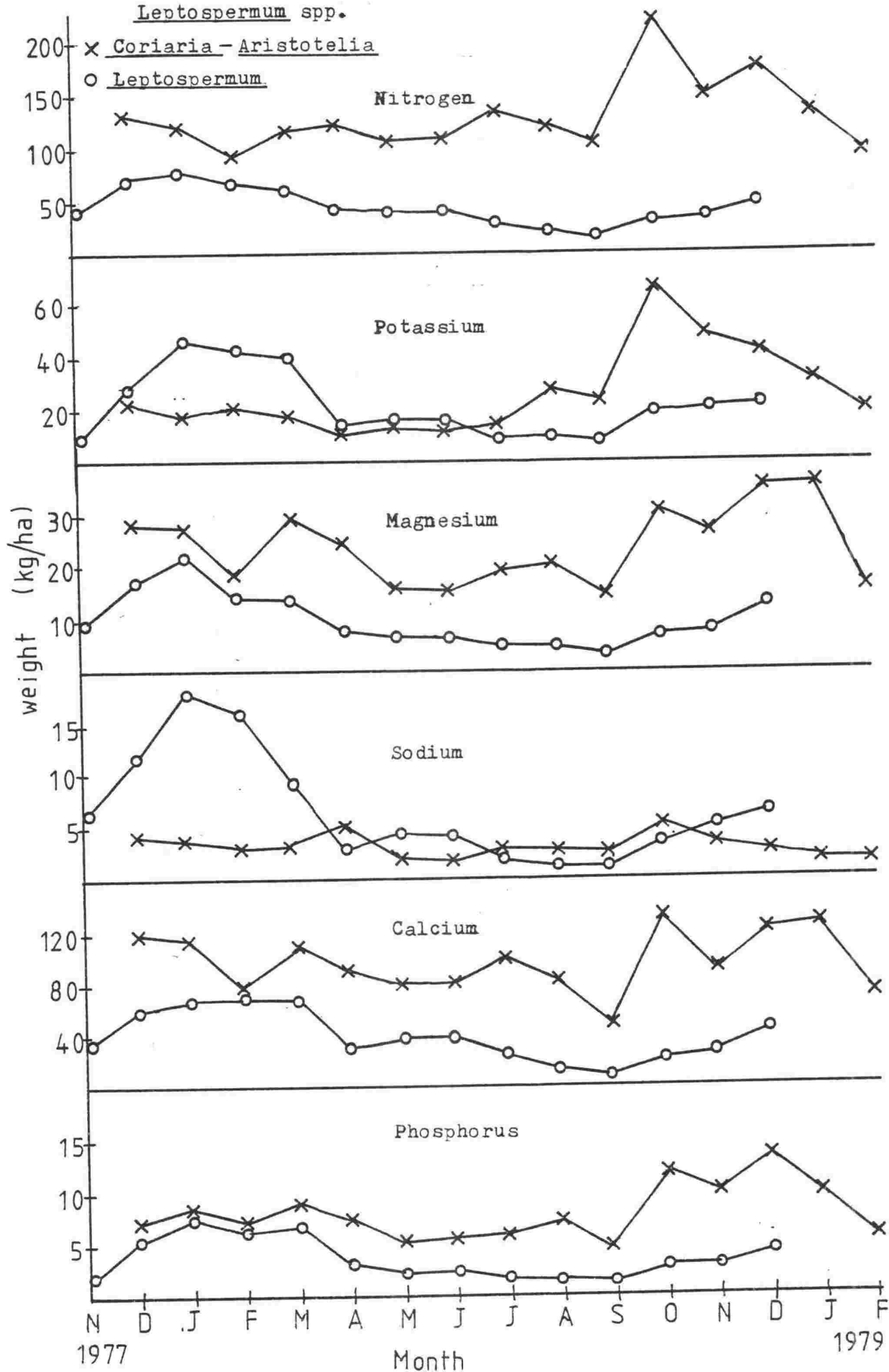
Table 6:7a. Total Nutrient Weight in Litter Fall (kg/ha) - *Leptospermum* stand.

Month	N	K	Mg	Na	Ca	P
Nov	35.38	10.40	8.82	6.34	35.02	2.15
Dec	66.22	27.74	16.83	11.72	59.72	5.46
Jan	79.38	46.10	22.18	18.13	66.76	7.70
Feb	65.43	43.00	14.35	15.85	73.13	6.09
Mar	58.20	40.06	13.74	9.09	69.27	6.84
Apr	37.15	13.79	7.95	2.70	33.88	3.09
May	36.89	14.60	6.52	4.45	39.82	2.06
Jun	36.89	14.60	6.52	4.45	39.82	2.06
Jul	25.57	7.34	4.75	2.27	25.34	1.69
Aug	17.86	9.43	4.48	1.19	14.13	1.31
Sep	12.86	7.39	2.70	1.05	11.26	0.92
Oct	27.19	18.52	6.41	3.63	21.90	2.62
Nov	31.22	19.24	7.48	5.01	30.40	2.70
Dec	45.96	20.41	12.61	6.39	44.23	4.02
Kg/ha/yr	49.4	25.1	11.6	7.9	48.4	4.2

Table 6:7b. Total Nutrient Weight in Litter Fall (kg/ha) - *Coriaria-Aristotelia* stand.

Month	N	K	Mg	Na	Ca	P
Dec 1977	130.35	20.58	28.30	4.07	118.58	7.29
Jan 1978	120.73	18.59	28.77	4.23	116.73	7.76
Feb	92.04	20.21	19.58	3.32	77.67	6.63
Mar	116.62	17.64	29.57	3.11	111.67	8.63
Apr	120.45	12.30	24.79	5.14	94.19	7.40
May	105.80	13.92	16.09	1.67	81.48	5.32
Jun	105.80	13.92	16.09	1.67	81.48	5.32
Jul	133.35	12.99	19.99	2.78	101.75	5.55
Aug	115.25	25.30	21.63	2.66	82.66	7.24
Sep	99.38	22.96	15.22	2.96	48.39	4.85
Oct	222.89	67.03	30.53	5.09	135.97	11.93
Nov	146.29	47.81	26.74	3.22	90.20	10.02
Dec	174.77	42.14	35.65	2.88	121.37	13.40
Jan 1979	132.46	30.44	35.47	2.04	128.36	9.82
Feb	92.14	18.06	16.20	1.93	73.87	5.18
Kg/ha/yr	152.7	30.7	29.2	3.7	117.2	9.3

Figure 6:4 Monthly fluxes in weight of total nutrients in litterfall in adjacent stands of Coriaria-Aristotelia and Leptospermum spp.



## 6:7 Comparison with other Litter Collection Studies in the Indigenous Forests of New Zealand.

Biomass and nutrient data from the present study and from other litter collection studies in the indigenous forests of New Zealand are presented in Table 6:8 .

The weights of annual litter fall reported from the Marlborough Sounds are the highest weights yet recorded in New Zealand (Will (1959) reports high litter fall weights of 10,304 kg/ha/yr for a 39 year old *Pinus radiata* stand and 9,206 kg/ha/yr for a 43 year old *Pinus nigra* stand at Whakarewarewa forest, Central Volcanic Plateau, North Island but his data are not directly comparable with the present study or with other New Zealand studies as Will reported litter fall weights as air dry weights).

The weight of the annual litter fall in the *Aristotelia-Coriaria* stand is in the range hitherto only reported from highly productive rain forests (Nye 1961, Bray and Gorham 1964, Bevege 1978).

It is not possible to assess accurately whether the litter fall values recorded in the Marlborough Sounds seral stands are typical values of annual litter fall as the study was very limited in its duration. A high variability in total annual litter fall was recorded over a seven year period in a *Nothofagus truncata* stand (Miller 1963). The major annual variation in the *N. truncata* litter collection study appeared to be related to the flowering of *Nothofagus*; heavy flowering of *Nothofagus* in one year coincided with a heavy spring litter fall in the same year (Bagnall 1972). The phenomenon of irregular flowering is not applicable to the present study. All canopy species in both stands flower regularly and well each year.

The weather of the 1977-1978 collection period did not appear atypical of the weather usually experienced in Endeavour Inlet. No prolonged extremes of climate were experienced during the collection period.

It is possible that the sample size employed in the present study is smaller than that required for an accurate estimation of the annual litter fall. The sample size is smaller than that employed in the comparable New Zealand studies. Individual collections from each bucket from the two study sites were made for the first collection month. The sample size, of 40 buckets of 28 cm diameter at each site, appeared adequate for sampling the < 28 cm long litter; yielding an error of 9% of the mean for the *Coriaria*-

*Aristotelia* stand and 8.2% of the mean for the *Leptospermum* stand. In a similar study conducted in a *Quercus petraea* woodland it was found that 20 funnels each of 20 cm diameter gave an error of  $< 5\%$  of the mean for leaf litter (Carlisle, Brown and White 1966).

Hence, although the duration of the study and the size of collection are obvious constraints on the data presented, it is felt that the values reported are true representations of the litter fall of the two stands.

The nutrient weights of the litter fall of the *Leptospermum* stand are similar to the weights reported by Daniel and Adams (pers. comm.) from the virgin podocarp-rata-broadleaf forest in the Orongorongo Valley, near Wellington. The forest studied by Daniel (1975) is similar in structure and composition to the virgin podocarp/broadleaf forest that formerly covered, the valleys and lower slopes of Endeavour Inlet. (The absence of rata, *Metrosideros robusta*, from the Endeavour Inlet forests is the notable difference between the two sites).

With the exception of Ca the nutrient weights in the litter fall of the *Leptospermum* stand are higher than the values reported from *Nothofagus truncata* forests (Miller 1963, Levett 1978).

The return of nutrients, with the exception of Na, to the forest floor in the litter of the *Coriaria-Aristotelia* forestland is considerably greater than in the litter of other forests in New Zealand. The quantity of N in the litter is especially notable and is a reflection of the nitrogen-fixing ability of *Coriaria arborea*.

It would appear that the seral communities studied are returning a greater quantity of nutrients to the forest floor than the mature (climax) forests would at the study sites. Even if it is not a valid assumption to extrapolate the litter fall characteristics of mature forests of the Wellington and Westland regions to the forests of the Marlborough Sounds, it is apparent that the successional communities are performing an important role in the recovery of nutrient cycling ability of disturbed ecosystems.

Table 6:8. Biomass and Nutrient Content of Litter Fall in New Zealand Forests.

Vegetation (source)	Location (altitude)	Biomass	Annual Litter Fall kg/ha/yr					P
			N	Ca	Mg	K	Na	
<i>Nothofagus truncata</i> (Miller 1963)	Silverstream, Wellington (240 m)	6026	37	70.6	11.2	9.0	5.6	2.5
<i>Nothofagus truncata</i> (Levett 1978)	Granville Forest, Westland (210 m)	7252	40.1	62.4	9.6	10.4	4.2	2.8
Podocarp-rata- broadleaf (Daniel and Adams unpublished)	Orongorongo Valley, Wellington (140 m)	6865	44.2	50.7	11.8	20.1	-	2.8
Podocarp/hardwood (Levett 1978)	Hochstetter Forest, Westland (250 m)	4489	30.9	29.7	9.4	11.4	3.3	2.1
<i>Nothofagus solandri</i> var. <i>solandri</i> (Bagnall 1972)	Lake Ponui, S.W.	5688						
	Wairarapa (60 m)	4970						
<i>Nothofagus solandri</i> var. <i>cliffortioides</i> (Wardle 1970)	Cragieburn Range (850 m)	3710						
	(1340 m)	3062						
	Kaweka Range (1340 m)	3568						
<i>Leptospermum</i> spp. (Wassilieff)	Marlborough Sounds (120 m)	7801	50.7	47.2	11.6	22.7	8.5	4.3
<i>Aristotelia-Coriaria</i> (Wassilieff)	Marlborough Sounds (120 m)	10069	153.9	123.9	31.8	31.7	3.6	10.1

## 6:8 Decomposition of Leaf Litter

There are a number of methods available for estimating the decomposition rate of leaf litter (Singh and Gupta 1977). One of the more acceptable methods can only be applied to vegetation where the forest floor has attained an equilibrium state between additions from litter fall and losses from decomposition. In this instance the decomposition rate ( $k$ ) is calculated by dividing the annual litter production weight ( $L$ ) by the weight of the forest floor at steady-state ( $X_{ss}$ ),

$$\text{i.e.} \quad k = \frac{L}{X_{ss}} \quad (\text{Olson 1963})$$

This method is not valid for vegetation stands where the forest floor is actively accumulating or disappearing.

Direct decomposition methods are employed for ecosystems that are not in a steady-state. In the present study the litter bag technique was employed to investigate the flux of nutrients in decomposing *Coriaria-Aristotelia* leaf litter and decomposing *Leptospermum ericoides*-*L. scoparium* leaf litter. The decomposition study ran concurrently with the litter collecting exercise and was conducted in the same areas.

A litter bag decomposition study can yield lower rates of litter decomposition than that given by other direct methods (Witkamp and Olson 1963, Anderson 1973) but is the only suitable method available for small leaf material like *Leptospermum* leaves.

## Results

### 6:8a Dry matter and nutrient concentration fluxes in decomposing leaf litter

Data on the concentration of nutrients and fluxes in dry matter of decomposing leaf litter are presented in Tables 6:9a and 6:9b and Figures 6:5a and 6:5b.

There was a rapid decline in the weight of *Coriaria-Aristotelia* litter, after 10 months 76.7% of the material had disappeared from the litter bags. The experiment was terminated after the 10th month in the *Coriaria-Aristotelia* stand. Very little recognisable leaf material was left in the bags after 10 months on the forest floor. The remaining material was mainly soil particles and insect frass.

Table 6:9a. Monthly Fluxes in Concentration of Total Nutrients in Decomposing *Leptospermum* spp. Leaf Litter (% dry weight). (Means of 4 samples/collection)

Month	N	K	Mg	Na	Ca	P
Oct 1977	0.90	0.60	0.21	0.15	0.61	0.07
Nov	0.91	0.27	0.16	0.10	0.58	0.07
Dec	1.03	0.18	0.18	0.07	0.59	0.07
Jan 1978	1.02	0.19	0.20	0.06	0.67	0.07
Feb	1.05	0.18	0.24	0.05	0.77	0.065
Mar	1.15	0.21	0.20	0.05	0.69	0.06
Apr	1.21	0.20	0.22	0.06	0.73	0.06
May	-	-	-	-	-	-
Jun	1.32	0.15	0.19	0.03	0.86	0.06
Jul	1.42	0.15	0.17	0.025	0.84	0.07
Aug	1.39	0.32	0.16	0.025	0.75	0.06
Sep	1.46	0.50	0.17	0.02	0.62	0.075
Oct	1.48	0.48	0.20	0.02	0.63	0.075
Nov	1.46	0.31	0.18	0.02	0.65	0.06
Dec	1.50	0.29	0.19	0.015	0.66	0.06
Jan 1979	Experiment discontinued.					

Table 6:9b. Monthly Fluxes in Concentration of Total Nutrients in Decomposing *Coriaria-Aristotelia* Leaf Litter (% dry weight). (Mean of 4 samples/collection)

Month	N	K	Mg	Na	Ca	P
Dec 1977 (initial)	1.87	0.50	0.35	0.03	1.20	0.15
Jan 1978	2.05	0.31	0.40	0.02	1.23	0.19
Feb	2.44	0.23	0.41	0.03	1.25	0.17
Mar	2.54	0.18	0.29	0.03	1.80	0.14
Apr	2.90	0.22	0.30	0.02	1.60	0.15
May	-	-	-	-	-	-
Jun	2.25	0.55	0.36	0.02	1.04	0.16
Jul	2.78	0.50	0.31	0.01	1.20	0.165
Aug	2.45	0.51	0.40	0.01	1.15	0.13
Sep	2.80	0.49	0.35	0.01	1.00	0.16
Oct	3.50	0.48	0.27	0.01	0.90	0.18
Nov 1978	Experiment discontinued.					



Figure 6:5a Monthly fluxes in concentration of total nutrients in decomposing Leptospermum leaf litter.

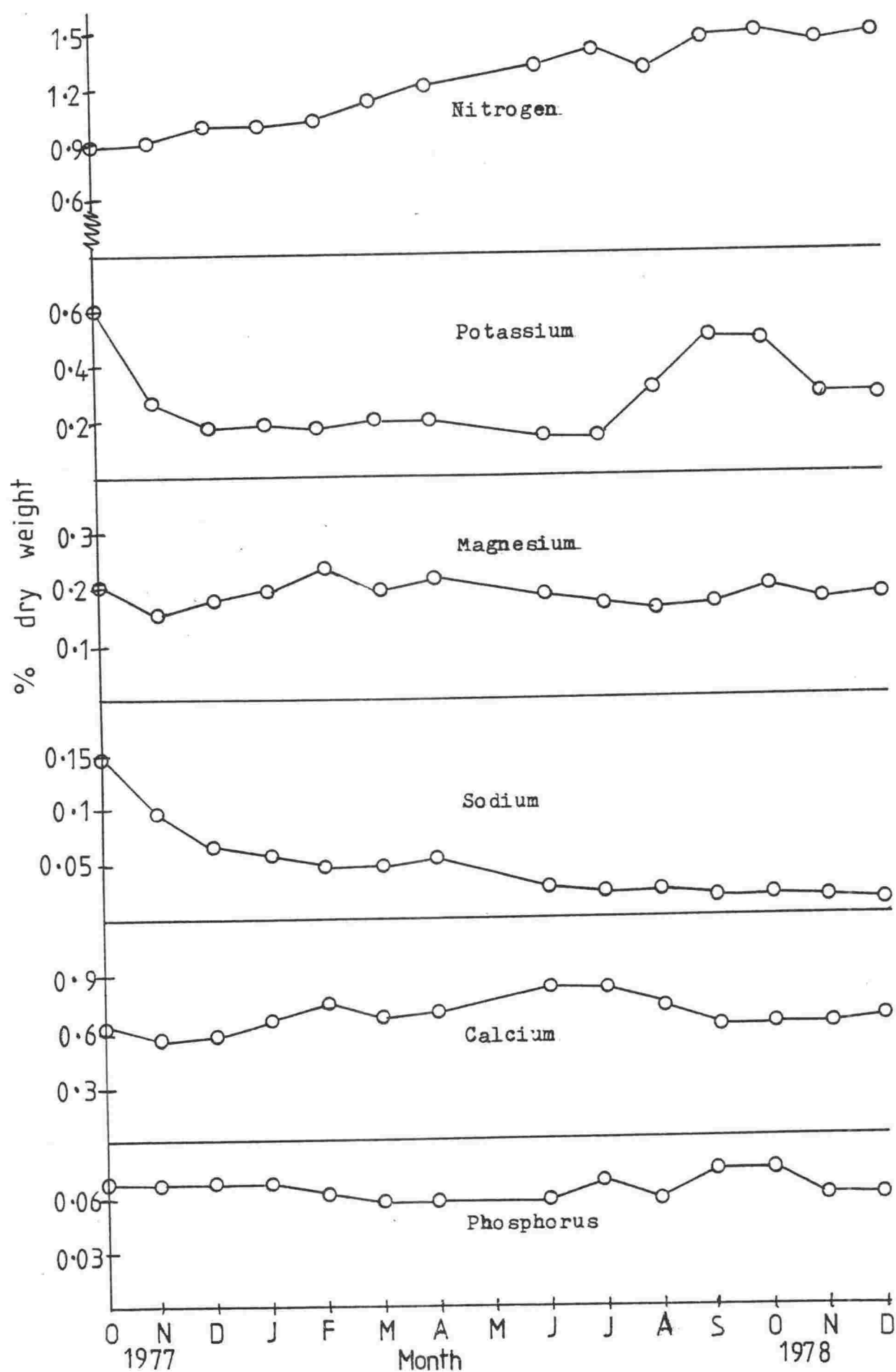
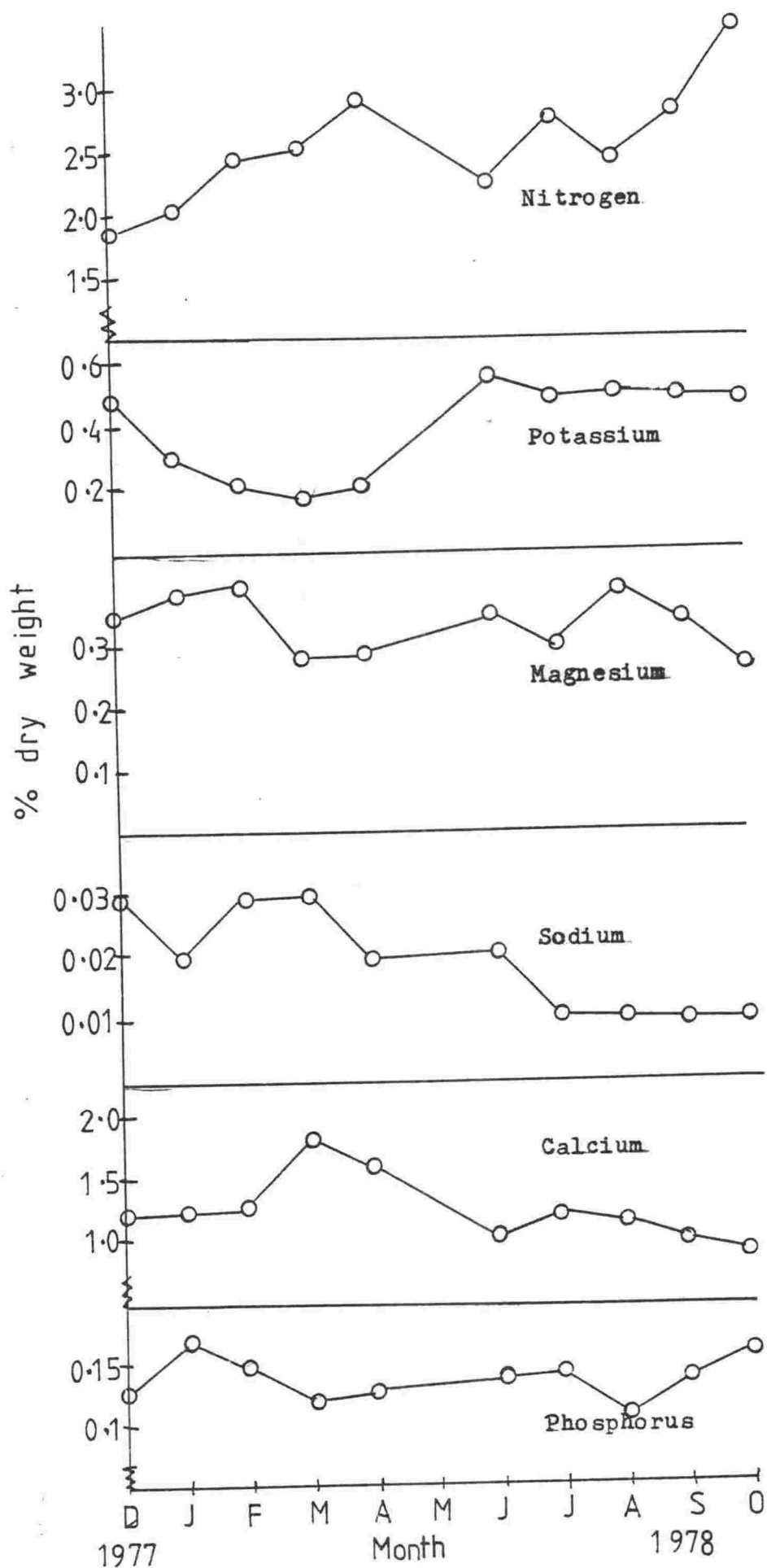


Figure 6:5b Monthly fluxes in concentration of total nutrients in decomposing Coriaria-Aristotelia leaf litter.



The decomposition study continued for 14 months in the *Leptospermum ericoides*-*L. scoparium* stand. After 14 months on the forest floor 50% of the mixed *Leptospermum* leaf litter had disappeared from the litter bags (44% loss of dry weight in 10 months). There were still recognizable leaf fragments and even entire leaves in the *Leptospermum* litter bags 14 months after having been placed on the forest floor. The *Leptospermum* litter bags were all riddled with fungal mycelia by this time and it was apparent that the decomposition rate of *Leptospermum* could not be measured accurately since new material was being added to the litter.

Both communities exhibited similar trends in concentration of nutrients during decomposition. Potassium concentrations declined rapidly in both litters and then rose to high levels similar to the initial concentrations during winter. Sodium concentrations declined rapidly in the decomposing *Leptospermum* leaf litter and remained at low levels. There was an overall loss of Na from decomposing *Coriaria-Aristotelia* leaf litter in which the rate of Na loss was less than that from the *Leptospermum* litter. Nitrogen concentrations increased with time in both litters. There was a steady gain in N in the *Leptospermum* leaf litter throughout the 14 month study period. The N concentration in the *Coriaria-Aristotelia* litter showed fluctuations during the winter months but there was an overall increase in N content from an initial value of 1.87% to 3.50% ten months later.

Magnesium, P and Ca concentrations in both types of leaf litter fluctuated around the initial levels. The concentration fluctuations were not synchronous for the elements in either litter type.

#### 6:8b. The weight of nutrients in decomposing leaf litter

There was a decline in weight of all elements in both litter types (Figures 6:6a and 6:6b and Tables 6:10a and 6:10b). Continuous weight declines were only exhibited by Na. Potassium weights recovered from an initial decline in both litters; moderate levels were maintained in both the *Leptospermum* and *Coriaria-Aristotelia* leaf litters despite the progressive dry matter weight decline of the decomposing litter. The increase in weight of K in the two litter types was not synchronous. The pattern of loss of Ca, Mg, and P was similar in the two litters. The weight declines of Ca, Mg and P were closely correlated with the dry matter loss of the two litter types. The N decline was closely correlated with loss of dry matter in the *Coriaria-Aristotelia* leaf litter but this pattern was not evident in the *Leptospermum* litter where high levels of nitrogen were maintained despite progressive loss in dry weight.

Table 6:10a. Monthly Fluxes in Biomass and Total Nutrients in Decomposing *Leptospermum* spp. Leaf Litter. (Mean of 4 samples/collection)

Month	Biomass (g)	N	K	Mg	(mg) Na	Ca	P
Oct 1977	10.000	90.0	60.0	21.0	15.0	61.0	7.0
Nov	8.396	76.4	22.7	13.4	8.4	48.7	5.9
Dec	8.110	83.5	14.6	14.6	5.7	47.8	5.7
Jan	8.003	81.6	15.2	16.0	4.8	53.6	5.6
Feb	7.822	82.1	14.1	18.8	3.9	60.2	5.1
Mar	7.222	83.0	15.2	14.4	3.6	49.8	4.3
Apr	7.999	96.8	16.0	17.6	4.8	58.4	4.8
May	-	-	-	-	-	-	-
Jun	6.466	85.4	9.7	12.3	1.9	55.6	3.9
Jul	5.969	84.8	9.0	10.1	1.5	50.1	4.2
Aug	5.695	79.2	18.2	9.1	1.4	42.7	3.4
Sep	5.107	74.6	25.5	8.7	1.0	32.2	3.8
Oct	5.753	85.1	27.6	11.5	1.1	36.2	4.3
Nov	5.436	79.4	16.9	9.8	1.1	35.3	3.3
Dec 1978	5.004	75.0	14.5	9.5	0.8	33.0	3.0
<u>Correlation</u>							
<u>coefficient</u>							
(r)calculated							
for relation-							
ship between							
biomass decline							
and nutrient							
loss							
significance (p)							
		0.52	0.48	0.92	0.91	0.81	0.95
		0.05	0.1	<0.001	<0.001	<0.001	<0.001

Table 6:10b. Monthly Fluxes in Biomass and Total Nutrients in Decomposing *Coriaria-Aristotelia* Leaf Litter. (Means of 4 samples/ collection).

Month	Biomass (g)	N	K	Mg	mg Na	Ca	P
Dec 1977	10.000	187	50.0	35.0	3.0	120	15.0
Jan 1978	8.622	177	26.9	26.9	1.7	106	16.4
Feb	5.862	143	13.5	24.0	1.8	73	9.9
Mar	5.025	128	9.0	14.6	1.5	90	7.0
Apr	6.869	199	15.1	15.1	2.0	109	10.3
May	-	-	-	-	-	-	-
Jun	4.072	92	22.2	14.7	0.8	42	6.5
Jul	3.173	88	15.9	9.5	0.6	38	5.2
Aug	3.363	82	17.2	13.5	0.3	39	4.4
Sep	3.107	87	15.2	10.9	0.3	31	5.0
Oct	2.326	81	11.2	6.3	0.2	21	4.2
<u>Correlation coefficient</u>							
(r) calculated for							
relationship between		0.92	0.74	0.93	0.94	0.94	0.97
biomass decline and							
nutrient loss							
significance (p)		<0.001	<0.01	<0.001	<0.001	<0.001	<0.001

Figure 6:6a Monthly fluxes in weight and nutrient content of decomposing Leptospermum leaf litter.

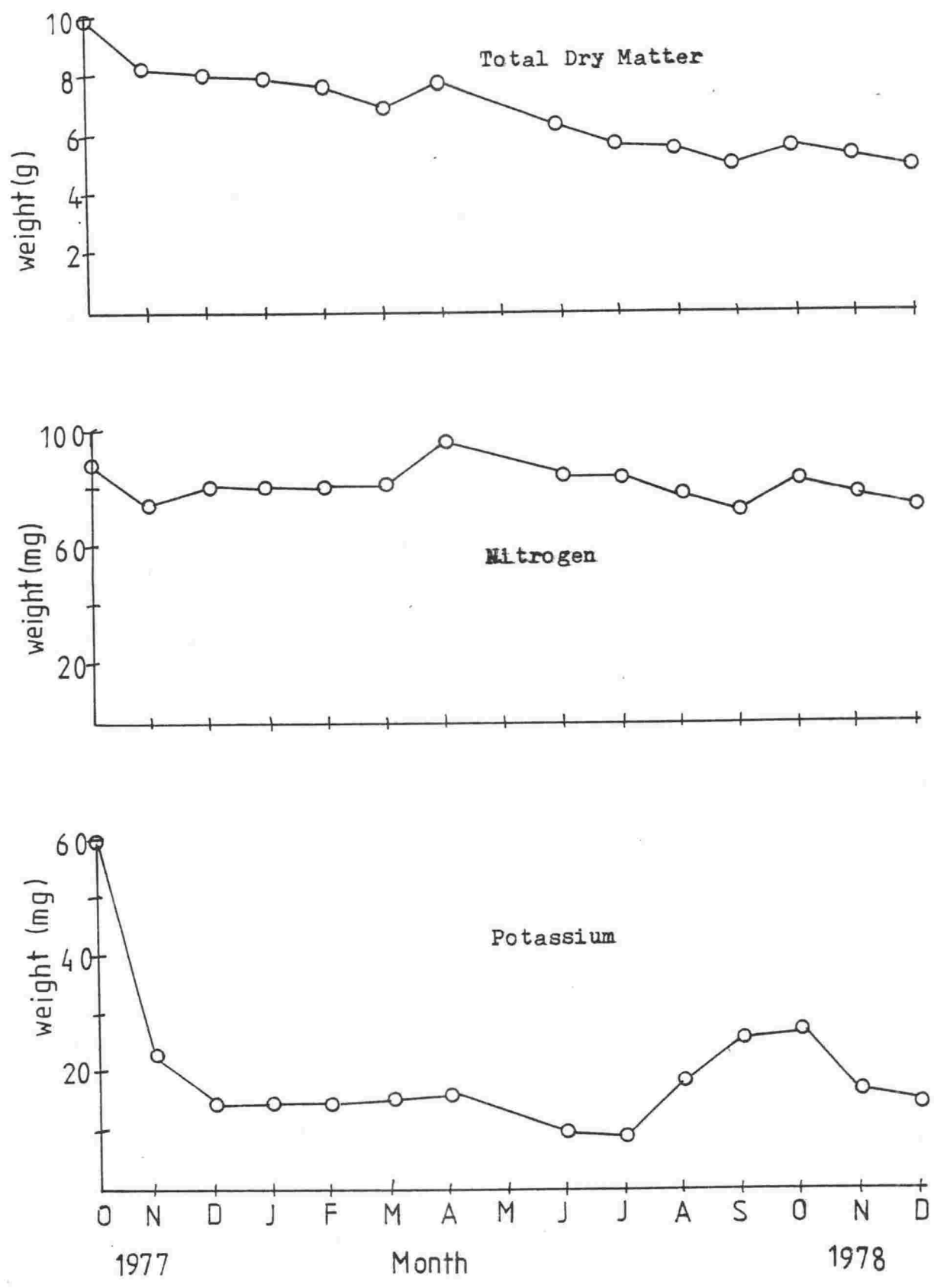


Figure 6:6a Monthly fluxes in weight and nutrient content of decomposing Leptospermum leaf litter.

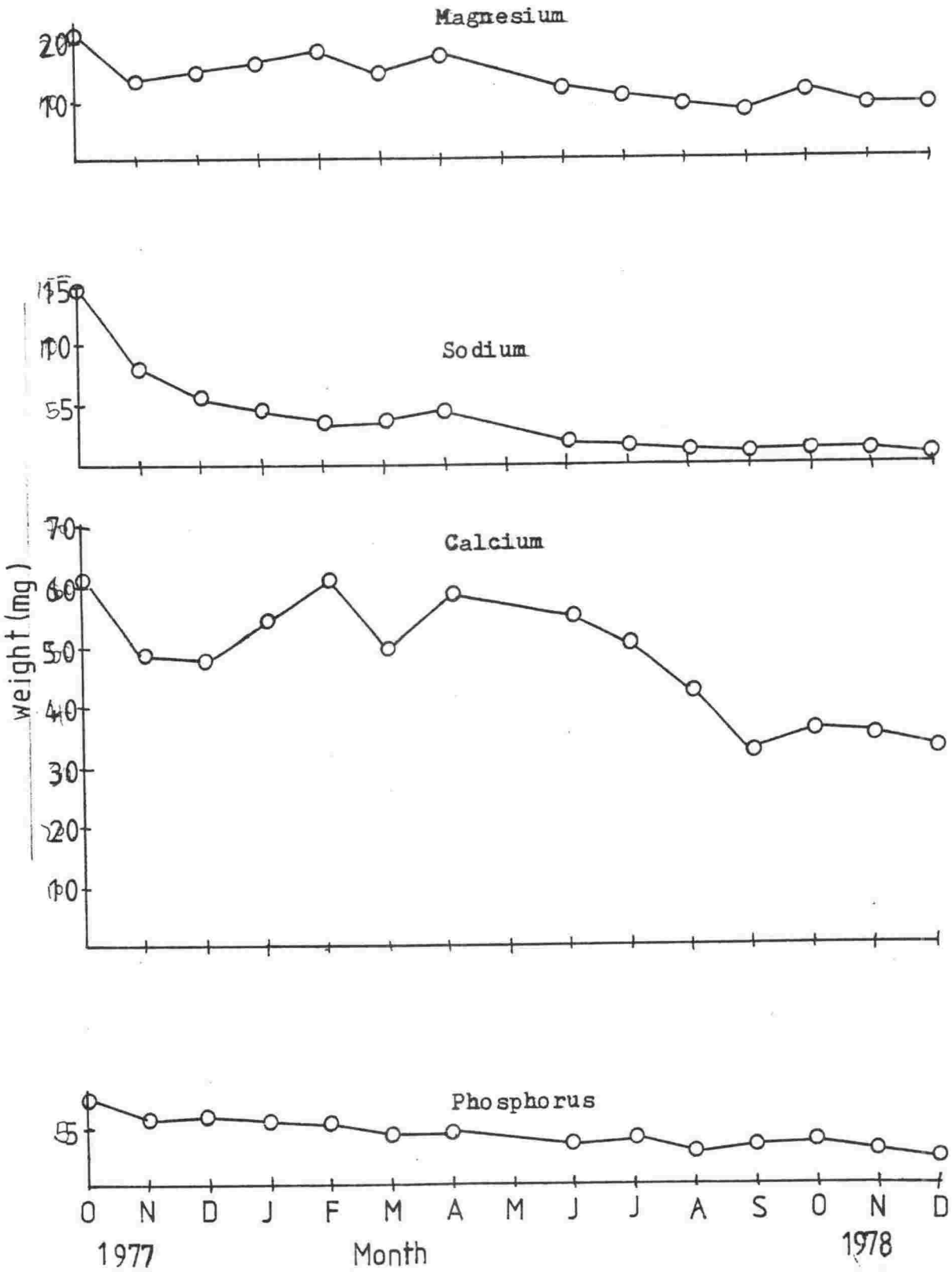


Figure 6:6b Monthly fluxes in weight and nutrient content of decomposing Coriaria-Aristotelia leaf litter.

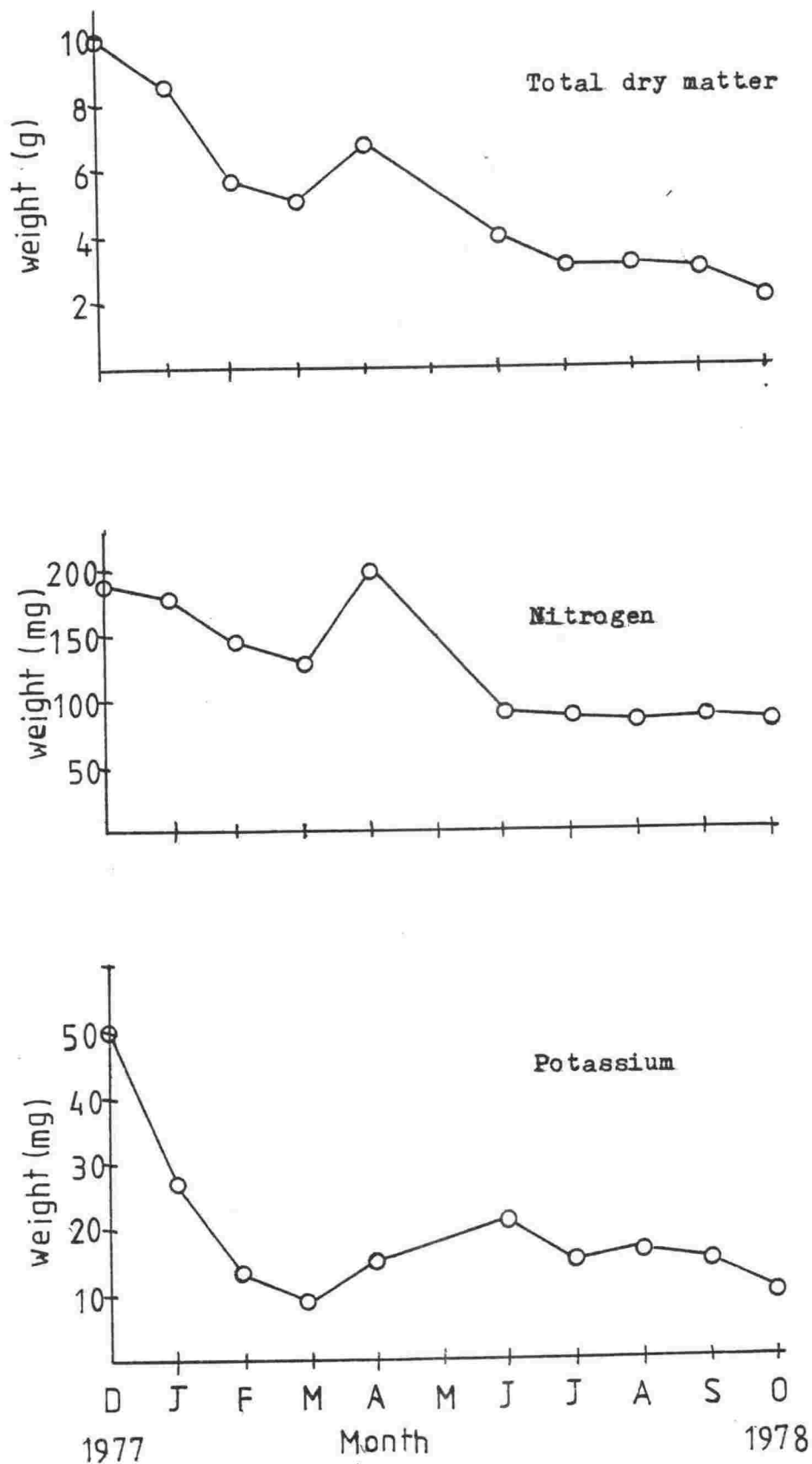
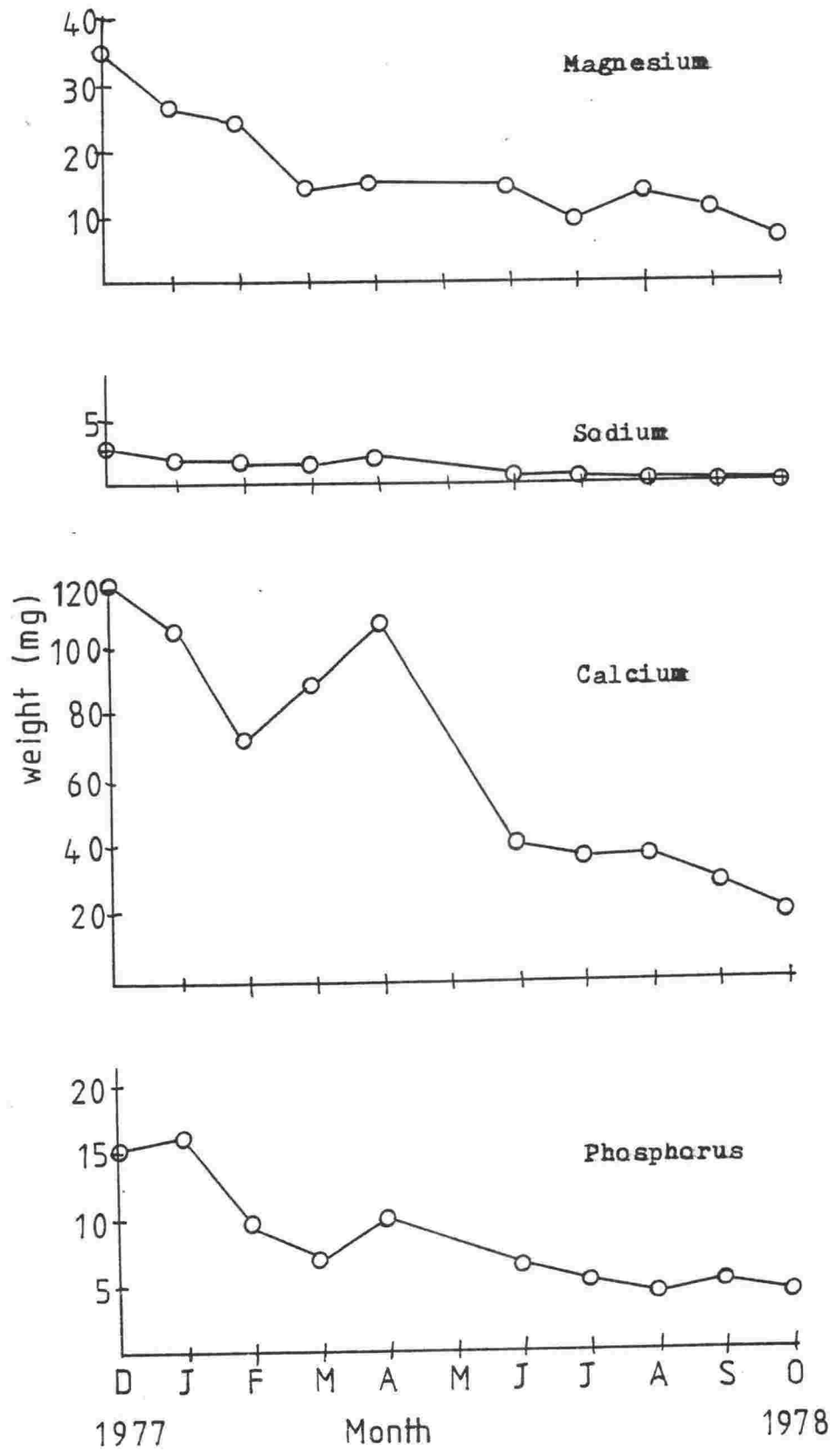




Figure 6:6b Monthly fluxes in weight and nutrient content of decomposing Coriaria-Aristotelia leaf litter.



6:9 The Relative Mobility of Elements in Litter and Forest Floor Material

Three aspects of the relative mobility of nutrients in the two adjacent successional communities were investigated:

- (1) the L. spp./C.-A. ratios of biomass parameters, the dry weight concentrations and weight of nutrients in the litter fall and forest floor, and the fluxes in decomposing leaf litter after 10 months on the forest floor were calculated (Figure 6:7),
- (2) the turnover times of the biomass and nutrient weights of the litter fall arriving on the forest floor were calculated using the annual decomposition constant k (Table 6:11), (the values of k reported are not intended to indicate that the forest floors of the two stands are in a steady-state condition but are employed as an aid in interpreting the nutrient flux behaviour of the two stands at one period in the early stage of their successional development),
- (3) the half life and time of total loss of the dry weights and element weights in decomposing leaf litter were calculated (Tables 6:12 and 6:13).

Table 6:11. Values of k and Turn-over Times for Biomass and Nutrients in the Forest Floor.

	<u>k</u>		<u>Turn over time</u> (years)		<u>Turn over time</u> ( <u>nutrient</u> <u>ratio</u> <u>biomass</u> )	
	<i>Leptospermum</i>	<i>Coriaria-Aristotelia</i>	<i>Leptospermum</i>	<i>Coriaria-Aristotelia</i>	<i>Leptospermum</i>	<i>Coriaria-Aristotelia</i>
Biomass	0.30	0.59	3.3	1.7	1.00	1.00
Nitrogen	0.26	0.59	3.9	1.7	1.18	1.00
Potassium	0.33	0.58	3.0	1.7	0.91	1.00
Magnesium	0.28	0.54	3.6	1.9	1.09	1.12
Sodium	0.52	0.52	1.9	1.9	0.58	1.12
Calcium	0.29	0.56	3.5	1.8	1.06	1.06
Phosphorus	0.32	0.60	3.1	1.7	0.94	1.00

Order of mobility:

*Leptospermum ericoides*-*L. scoparium*

Na > K > P > Biomass > Ca > Mg > N

*Coriaria arborea*-*Aristotelia serrata*

P > Biomass = N > K > Ca > Mg > Na

Table 6:12. Loss in 10 Months and Derived Time of Total Loss of Biomass and Elements in Decomposing Leaf Litter.

	% loss in 1st 10 months		Time for total loss (years)		Turn over times ( <u>nutrient</u> ) ratio biomass	
	<i>Leptospermum</i>	<i>Coriaria- Aristotelia</i>	<i>Leptospermum</i>	<i>Coriaria- Aristotelia</i>	<i>Leptospermum</i>	<i>Coriaria- Aristotelia</i>
Biomass	43	77	1.94	1.08	1.00	1.00
Nitrogen	12	57	6.94	1.46	3.58	1.35
Potassium	70	78	1.19	1.07	0.61	0.99
Magnesium	57	82	1.46	1.02	0.75	0.94
Sodium	91	93	0.92	0.90	0.47	0.83
Calcium	30	83	2.78	1.00	1.43	0.93
Phosphorus	46	54	1.81	1.54	0.93	1.43

Order of mobility:

*Leptospermum ericoides*-*L. scoparium*

Na > K > Mg > P > Biomass > Ca > N

*Coriaria arborea*-*Aristotelia serrata*

Na > Ca > Mg > K > Biomass > N > P

Table 6:13. Half Lives of Biomass and Elements in Decomposing Leaf Litter.

	Half life (weeks)		Half life ( $\frac{\text{nutrient}}{\text{total}}$ ) ratio	
	<i>Leptospermum</i>	<i>Coriaria- Aristotelia</i>	<i>Leptospermum</i>	<i>Coriaria- Aristotelia</i>
Biomass	44	12	1.00	1.00
Nitrogen	>56	24	>1.3	2.00
Potassium	3	5	0.07	0.42
Magnesium	37	10	0.84	0.83
Sodium	5	12	0.11	1.00
Calcium	>56	22	>1.3	1.83
Phosphorus	32	11	0.73	0.92

Order of mobility:

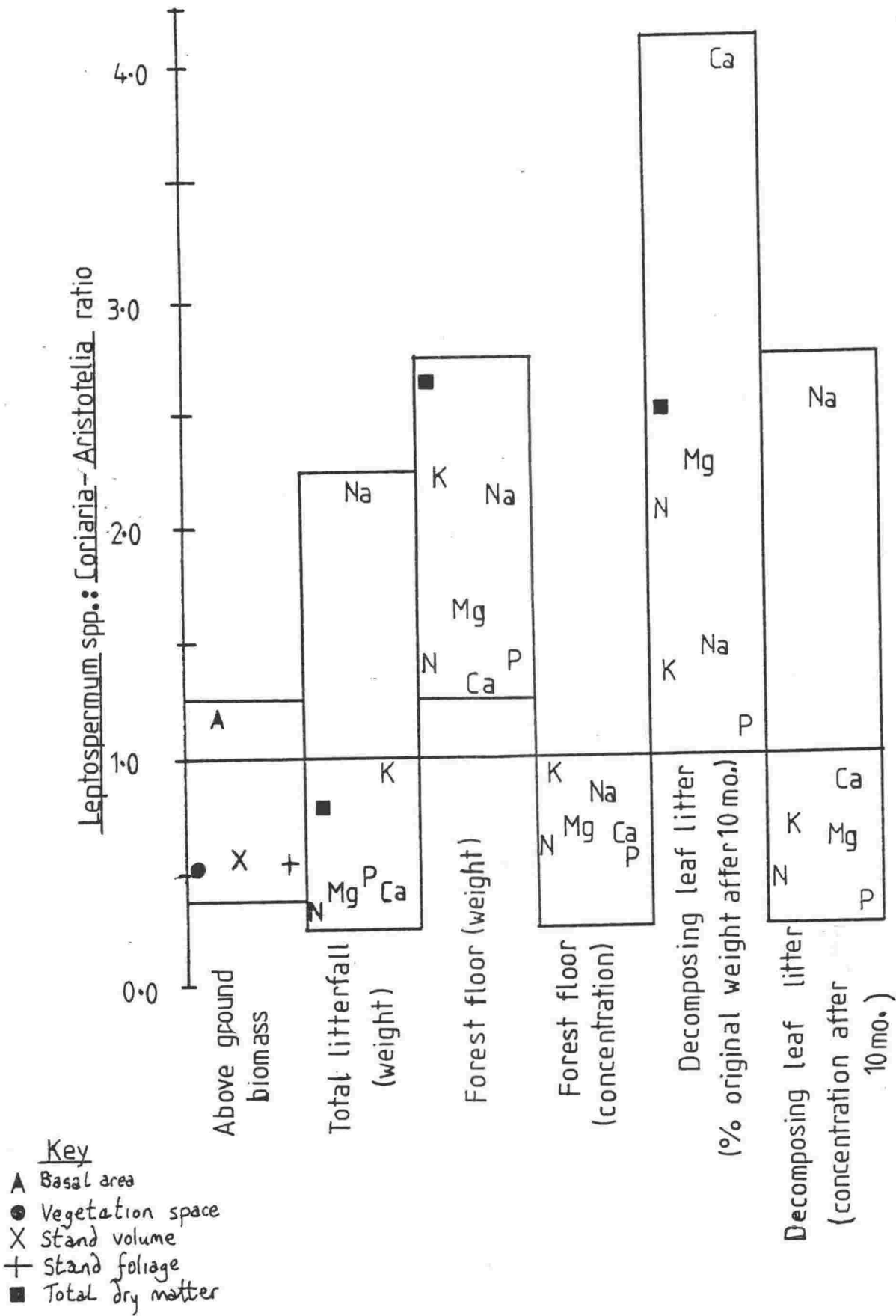
*Leptospermum ericoides*-*L. scoparium*

K > Na > P > Mg > Biomass > Ca > N

*Coriaria arborea*-*Aristotelia serrata*

K > Mg > P > Biomass = Na > Ca > N

Figure 6:7 Leptospermum spp. : Coriaria - Aristotelia ratios in above ground biomass, forest floor and decomposing leaf litter.



There is a marked difference in mobility of the elements (with the exception of Na) in decomposing leaf litter and in the forest floor between the two stands. The ratios of the element weights remaining in the *Leptospermum* leaf litter (expressed as a percentage of original leaf litter weight) compared to the weight of elements remaining in the *Coriaria-Aristotelia* leaf litter (also expressed as a percentage of original leaf litter weight) after 10 months on the forest floor are presented in Figure 6:7.

The mobility of Ca out of the *Coriaria-Aristotelia* leaf litter is especially notable. Calcium is four times more mobile in the *Coriaria-Aristotelia* leaf litter than in the *Leptospermum* leaf litter. *Coriaria-Aristotelia* leaf litter turn over is nearly two and a half times more rapid than that of *Leptospermum* leaf litter.

Similarly, the value of k for the biomass of the *Coriaria-Aristotelia* forest floor is nearly twice the value of the *Leptospermum* stand (Table 6:11) indicating that biomass turn over of the forest floors is twice as rapid under the *Coriaria-Aristotelia* stand than under the *Leptospermum* spp. stand.

The k values for the elements (again with the exception of Na) in the *Coriaria-Aristotelia* forest floor are also approximately twice the values for the corresponding elements in the *Leptospermum* forest floor. Thus, the turn over rates of the elements in the forest floor under the *Coriaria-Aristotelia* stand are approximately twice that in the forest floor under the *Leptospermum* species and it appears that the flux of elements from both forest floor types is directly related to the biomass decomposition.

The flux of Na out of leaf litter and the forest floor is the same in both vegetation types. Sodium is rapidly lost from *Leptospermum* leaf litter and forest floor material and *Coriaria-Aristotelia* forest floor material. Although it is lost at identical rates from *Leptospermum* and *Coriaria-Aristotelia* leaf litter Na is the least mobile element in the *Coriaria-Aristotelia* leaf litter (Table 6:11).

The order of mobility of the elements in the *Leptospermum* leaf litter is nearly identical with that in the forest floor of the *Leptospermum* stand. Magnesium, although rapidly lost from the leaf litter would appear to be retained in the F and H components of the forest floor to a greater extent than P or Ca.

The order of mobility of the elements in the *Coriaria-Aristotelia* leaf litter is reversed in the forest floor under the *Coriaria-Aristotelia* stand. However the elemental k values are similar and the differences in mobility are hardly significant, although it would seem that the elements that are rapidly leached from the *Coriaria-Aristotelia* leaf litter (Na, Ca, Mg and K) are held in the forest floor and are turned over at a similar rate to the less mobile elements in the leaf litter.

There is a rapid integration of *Coriaria-Aristotelia* leaf litter in the mineral soil. The leaf litter disappeared in just over one year and all small forest floor (L + F + H) material had turned over some six months later. There is a comparable rapid turn over of all elements from the litter and the forest floor under the *Coriaria-Aristotelia* stand.

In contrast the *Leptospermum* leaf litter takes approximately two years to break down and then resides in the forest floor fermentation and humic material for at least another year before complete decomposition occurs. The elements in the *Leptospermum* leaf litter (with the exception of N) are held for up to one year in the F and H layer of the forest floor. Nitrogen is only slowly released from *Leptospermum* leaf litter, the other elements are released from the *Leptospermum* leaf litter some 2.5-7 times more rapidly than N. Nitrogen, once released in to the F and H material, is turned over at a comparable rate to the other elements in the forest floor.

## 6:10 Comparison With Other Leaf Decomposition Studies

No studies of litter decomposition have been undertaken in mature, indigenous forests in New Zealand. Will conducted a study into *Pinus radiata* decomposition in an exotic plantation on the central volcanic plateau of the North Island and reported a 50.6% weight loss of pine needles after 2 years on the forest floor. This rate of leaf litter decomposition is some 2.3 times slower than that recorded with the *Leptospermum* leaf litter and 8.6 times slower than the rate of *Coriaria-Aristotelia* leaf decomposition (Will 1967).

A table of plant litter decomposition rates from a wide variety of vegetation types was presented by Singh and Gupta (1977). The rate of decomposition of leaf litters from:

- tropical forests range from 0.107-1.50% per day (average value - 0.63% per day).
- temperate broadleaf forests range from 0.016-0.30% per day (average value - 0.15% per day).
- coniferous forests range from 0.0027-0.12% per day (average value - 0.05% per day).

Percent decomposition rates for the present study (based on % weight loss during a 10 month period) were:

*Leptospermum* leaf litter - 0.14% per day

*Coriaria-Aristotelia* leaf litter - 0.26% per day.

Both values fall within the range of temperate forest litters, the *Leptospermum* leaf litter decay rate is similar to the average range of decomposition of temperate forest litters and the *Coriaria-Aristotelia* leaf litter decay rate is near the maximum rate recorded for temperate forest litters.

## 6:11 Discussion

The aim in this chapter has been to present data that focuses attention upon some aspects of nutrient cycling in two adjacent successional communities.

The investigation has been limited to a study of the effect different species have in restoring and maintaining nutrient levels in the forest floor and surface soil horizons after major disruption of the nutrient cycle by forest removal.

Large differences in function have been revealed between the two stands. The relationship between functional and structural differences of the two stands can be explored by comparing the ratios of individual nutrients and biomass between the two stands in litter fall and decomposition processes with the ratios of basal area and vegetation structural parameters for the two stands (Figure 6:7).

Contrary to the finding of Reiners and Reiners (1970) there was no marked convergence between the basal area of the two stands and their annual litter fall weights (Table 6:1). The basal area of the two stands was a poor predictor of the annual litter fall weight. The vegetation space parameters (vegetation space, stand volume, stand foliage) bore a closer relationship to the litter fall weights of the two stands. This would indicate that vegetation space parameters are better predictors of annual litter fall than is a stand's basal area. Park (1975), has also reported a close relationship between litter fall weight and vegetation space of two sub-alpine successional eucalypt ecosystems (*Eucalyptus pauciflora* and *E. delegatensis*) in the Brindabella Range, N.S.W., Australia.

It is only annual litter fall that bears any relationship to the vegetation structure of the two stands. There is a marked divergence in the ratios of the standing states of the forest floor and decomposition rates of the two stands when compared with structural parameters.

The ratios of the standing state of biomass and elements on the forest floor and their flux from decomposing leaf litter range from 1.5 x to 5 x the litter fall ratio. Hence, although more litter and nutrients reach the *Coriaria-Aristotelia* forest floor there is a greater build up of the forest floor and a locking up of nutrients on the *Leptospermum* forest floor as decomposition proceeds at a slower rate in the *Leptospermum* forest floor than in the *Coriaria-Aristotelia* forest floor.



The *Coriaria-Aristotelia* stands are restricted to fertile sites; valley floors and colluvial slope deposits. The *Leptospermum* spp. sites are found on less fertile sites; hill slopes and ridges. Thus, the flux of nutrients from the litter and into the mineral soil of the two stands reinforces the soil nutrient differences between the two sites.

In comparison to temperate forests the secondary *Leptospermum* shrubland and *Coriaria-Aristotelia* forestland return large quantities of dry matter and nutrients to the forest floor where they are fairly rapidly incorporated into the mineral soil horizon. The present study confirms the findings of overseas workers (Marks 1974, Marks and Bormann 1972 and Park 1975) that seral vegetation plays an important role in the recovery and maintenance of nutrient cycles in forest ecosystems.

## CHAPTER SEVEN

### Land Use Planning and Dynamic Ecosystems in the Marlborough Sounds

"The concept of secondary succession as a process of systems repair is central to ecological theory. Through the course of succession attributes of mature ecosystems are restored".

- Bazzaz 1975

"A conservation reserve of undisturbed old-age vegetation may be ultimately lethal for some species and dangerous to preservation of the system as a whole. Without a patchwork containing various seral species, recovery from disturbances could be slow and difficult".

- Reiners and Lang 1976

#### 7:1 Introduction

One of the original aims of this study was to relate findings of the work to land management problems of the Marlborough Sounds Maritime Park. Although the study was not designed to address specific problems encountered by the Park Board it was the author's belief that wise land use planning in the Maritime Park must be based on an intimate knowledge of the composition and dynamics of the ecosystems in the reserves of the Park.

As outlined in Chapter One there have been a number of objections to classical and contemporary ideas of succession. It is necessary to consider the relevance of the different views of succession to the Marlborough Sounds. The questions a land manager seeks answers for, when considering management options for young successional stands of vegetation, are:

- what is the expected direction of the plant succession and how will individual species respond during the succession?
- what are the consequences of further disturbance to the seral stand?
- what is the expected time for recovery?
- what will be the nature of the steady-state (climax) community?

These are questions that could reasonably be expected to be answered by invoking the classical and contemporary theories of succession. The classical theory of succession holds that vegetation development will be directional and predictable and will lead to the re-establishment of a climax community. The contemporary theory of succession, whilst not placing as much emphasis upon the identity of the successional stages or the climax community, also holds that the process of succession is predictable and directional. If the classical and contemporary theories are not valid for the successions occurring in the Marlborough Sounds then it is essential that alternative models are considered and the implications for management are understood by planners and other people involved with land use in the Sounds.

This study has not been designed in such a manner that permits a clear choice between alternative theories. In fact most successional studies fail to offer unequivocal evidence in any one direction, but rather leave the researcher with questions that cannot be conveniently answered or understood in terms of the available models (Anderson and Holte 1981).

## 7:2 Relevance of Successional Theories to the Marlborough Sounds

In a sense the classical approach has been invoked in the present study when it was shown that there are three broad pathways of succession represented at the study sites, namely: successions toward a kamahi-dominated forest, toward a mixed broadleaved species forest and toward a coastal kohekohe forest. The proposed pathways are based upon a knowledge of the vegetation structure of the stands, the life histories of species in the stands and the environment of the study areas. However the study has not elucidated whether the kamahi forests, mixed broadleaved forests or the kohekohe coastal forest will be the final 'climax' forests of the study sites.

The classical theory of succession would lead one to predict that the final composition of the forests on the study sites should be basically similar in structure and composition to that of the undisturbed lowland forests of the Marlborough Sounds on comparable sites, namely:

hard beech-(black beech) forest on ridges and spurs,  
(podocarp)/tawa mixed broadleaf forest on slopes and in valleys and  
kohekohe forest on fertile coastal sites.

There is as yet no evidence that beech species, podocarps or tawa will be represented in significant numbers at the study sites. It is more an act of faith than of science to invoke the classical theory of succession to predict the final composition of the successions; for this reason the classical theory of succession must be rejected as being of any predictive value in this study.

The contemporary theory of succession places more emphasis upon structural and functional aspects of vegetation change than upon the composition of seral and steady state stands. The contemporary theory holds that succession is an orderly process of community development that is reasonably directional and predictable, that it results from modification of the physical environment by the community and that it culminates in a stabilized ecosystem in which maximum biomass and symbiotic function between organisms are maintained per unit of energy flow (Odum 1969).

Similar difficulties are faced with the contemporary theory of succession as were experienced with the classical theory of succession. It was not possible to predict at what stage a stabilized ecosystem will develop at the study sites, in fact it is evident that different parameters of vegetation structure and function recover at different rates and also show different patterns of recovery that preclude an extrapolation to a period when all parameters become stabilized.

The following table is a summary of those structural parameters that showed recovery to levels comparable to those of adjacent undisturbed communities at the following times after disturbance.

Table 7:1. Structural Parameters and Times after Disturbance at which Steady-States are Achieved and Maintained.

Structural Parameter	Time after Disturbance (Years)
Basal area	60-70
Stem density (stems > 2 cm d.b.h.)	60-70
Crown cover	12
Crown space	20
Species diversity indices	40 (some wide variation)

The other structural parameters that were measured at the successional stands failed to attain comparable values to those of the virgin forests some 80 years after disturbance.

It would be most unwise to try and extrapolate the structural data to a time after disturbance at which the steady state of these parameters might be attained. The plot of the mean height of the successional stands along a time axis (Figure 4:4a) reveals that a mean height of 8 m is attained by 50-70 year old vegetation. This is less than the mean height of the virgin forests which range from 10-22 m. There is no indication from this study of whether the mean height of 8 m is the maximum that will be reached by successional stands or whether this is just a plateau in the lowland forest growth and at a later stage taller trees will come to dominate the vegetation.

The plots of biomass and nutrient content of forest floor (Figures 5:1 a-h ) exhibit a curvilinear relationship between the measured parameters and the time since disturbance. As the successions proceeded high concentrations of biomass were stored in the forest floor, then the forest floor biomass and nutrient content declined in the stands older than 50 years. There is no indication of the ultimate fate of the forest floors of the study sites and again it would be an act of faith to accept that the forest floors will recover to levels comparable to the levels prior to disturbance. The associated study of rates of decomposition of litter on the forest floor revealed that there are gross functional differences between stands of different species composition and it would appear that the behaviour of the forest floor in later successional stands can only be predicted when the composition of the stands is known.

The contemporary theory of succession fails to provide a constructive framework for the land manager in the Marlborough Sounds. The approach that offers most promise, I believe, is to be found in the ideas of the scientists who have presented the challenge to the classical and contemporary theories of succession. These ideas, although dating from the early writings of Gleason (1926, 1939, 1975) and later Egler (1954, 1976), can be summarised as the Modern Synthesis of successional theory. The basic tenet of the Modern Synthesis is that vegetation succession is best understood as a consequence of individual plant by plant replacement processes. The key to the prediction of the course and rate of succession is a knowledge of the life histories of the species involved in the succession.

A constructive approach for undertaking predictive studies of succession based on life histories is that proposed by Noble and Slatyer (1977, 1978). Their approach has been adopted in an abbreviated form and applied to key species involved in successions in the lowland forests of the Marlborough Sounds. As there is a lack of information about critical features of the life history of some of the species involved in the successions it has not been possible to develop the Noble and Slatyer model to the degree that has been achieved by some overseas workers (for example Cattellino *et al.* 1979, Van der Valk 1981).

### 7:3 Life History Models of Succession in the Lowland Forest Ecosystems of the Marlborough Sounds

The lowland area of the Marlborough Sounds contains different environments that are characterized by different steady-state forests. The three types of forest and environment considered in this study are:

- the hard beech forest of dry, infertile ridges,
- the lowland (podocarp)/tawa forest of relatively moist slopes, valleys and terraces and
- the coastal kohekohe forest of exposed fertile slopes and terraces.

The seral species encountered in this study were either associated with a specific environment and steady-state forest (for example tree tutu-wineberry communities were confined to fertile moist valleys that had formerly carried lowland (podocarp)/tawa forest) or with a range of environments and different steady-state forests (for example manuka communities on dry ridges that had supported *Nothofagus* forest or on slopes that had carried (podocarp)/tawa forests or on wet terraces which formerly supported kahikatea (*Podocarpus dacrydioides*) forest). The Noble and Slatyer approach to modelling succession is specific for a particular site and replacement sequences that involve species of wide environmental tolerances may be unique for specific sites and disturbance regimes.

Key features of the life history of common seral and steady-state species encountered in the lowland forest ecosystem of the Marlborough Sounds are presented in Table 7:2. Using this information it is possible to predict replacement sequences for the studied stands under various types of disturbance.

The following examples serve to illustrate the value the life history approach to understanding succession can have for the land managers of the reserves in the Maritime Park.

Repeated burning of bracken stands during mid-summer and early autumn, when rhizome reserves are least, will lead to replacement of bracken fern-land by the two *Leptospermum* species. It would appear that this replacement sequence has occurred at many sites across the Marlborough Sounds as evident by the number of *Leptospermum* stands which contained live bracken rhizomes in their soil profile.

TABLE 7:2. Selected Life History Characteristics of Species Involved in Successions in the Lowland Forests of the Marlborough Sounds.

Species	Method of Persistence	• Conditions for Establishment	Life Span Features
<i>Leptospermum scoparium</i>	<ul style="list-style-type: none"> <li>- wind dispersed seed</li> <li>- capsules with seed persist on plants for up to three years, a percentage open each year</li> <li>- capsules relatively fire resistant and open a few days after fire</li> <li>- seed shed throughout the year, but mainly in spring (Mark, no date)</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- seeds 3-6 years after establishment</li> <li>- becomes degenerate 40-50 years</li> <li>- maximum height c. 8 m</li> </ul>
<i>Leptospermum ericoides</i>	<ul style="list-style-type: none"> <li>- wind dispersed seeds</li> <li>- seed shed annually</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- seeds 6 years after establishment</li> <li>- becomes degenerate 50-80 years</li> <li>- maximum height c. 15-20 m</li> </ul>
<i>Erica lusitanica</i>	<ul style="list-style-type: none"> <li>- wind dispersed seeds</li> <li>- resprouts after cutting, spraying and fire</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- becomes degenerate 30-40 years</li> <li>- maximum height c. 3 m</li> </ul>
<i>Ulex europaeus</i>	<ul style="list-style-type: none"> <li>- seed dispersed by man (first arrival at a site)</li> <li>- exploding capsules, limited seed spread</li> <li>- large viable soil seed populations</li> <li>- seed can remain dormant for 30 years (or longer?) (Moss 1960)</li> <li>- resprouts after cutting, spraying and fire</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- two crops of seed/year (winter and summer) (Miller 1970)</li> <li>- becomes degenerate 15-25 years</li> <li>- maximum height c. 2 m</li> </ul>



TABLE 7:2 Continued.

Species	Method of Persistence	Conditions for Establishment	Life Span Features
<i>Pteridium esculentum</i>	<ul style="list-style-type: none"> <li>- tiny spores (little information about efficiency of spread by this method)</li> <li>- stout, far creeping rhizome can survive for many years under scrub</li> <li>- new fronds can arise after cutting or burning if soil moisture and temperature are suitable.</li> </ul>	<ul style="list-style-type: none"> <li>- moist environment required for spore germination</li> <li>- fronds shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- long dormant season (autumn late spring (Cockayne 1916))</li> <li>- dominant cover can develop within 2 years</li> <li>- maximum height c. 2 m</li> </ul>
<i>Cassinia leptophylla</i>	<ul style="list-style-type: none"> <li>- wind dispersed seeds</li> <li>- can establish from buried seed (Beggs 1971)</li> <li>- resprouts after cutting</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- becomes degenerate 10 years</li> <li>- maximum height c. 2 m</li> </ul>
<i>Pinus</i> spp. ( <i>radiata</i> and <i>pinaster</i> )	<ul style="list-style-type: none"> <li>- widely dispersed seeds (across the Marlborough Sounds from established plantations)</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- fertile cones on <i>P. radiata</i> in 12 years and on <i>P. pinaster</i> in 5 years</li> <li>- maximum height c. 30 m</li> </ul>
<i>Aristotelia serrata</i>	<ul style="list-style-type: none"> <li>- fruits dispersed by birds</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- unknown life span</li> <li>- maximum height c. 10 m</li> </ul>
<i>Coriaria arborea</i>	<ul style="list-style-type: none"> <li>- fruits dispersed by birds</li> </ul>	<ul style="list-style-type: none"> <li>- shade intolerant</li> </ul>	<ul style="list-style-type: none"> <li>- unknown life span</li> <li>- maximum height c. 10 m</li> </ul>
<i>Pseudopanax arboreus</i>	<ul style="list-style-type: none"> <li>- fruits dispersed by birds</li> <li>- will survive cutting</li> </ul>	<ul style="list-style-type: none"> <li>- requires shelter of established vegetation</li> </ul>	<ul style="list-style-type: none"> <li>- unknown life span</li> <li>(?70 yrs - Wassilieff 1980)</li> <li>- maximum height c. 8 m</li> </ul>
<i>Melicactus ramiflorus</i>	<ul style="list-style-type: none"> <li>- fruits dispersed by birds</li> <li>- will survive cutting</li> </ul>	<ul style="list-style-type: none"> <li>- requires shelter of established vegetation</li> </ul>	<ul style="list-style-type: none"> <li>- unknown life span</li> <li>- maximum height c. 10 m</li> </ul>
<i>Weinmannia racemosa</i>	<ul style="list-style-type: none"> <li>- wind dispersed seed</li> <li>- resprouts after cutting and fire</li> </ul>	<ul style="list-style-type: none"> <li>- requires shelter of established vegetation</li> </ul>	<ul style="list-style-type: none"> <li>- life span up to 250 years</li> <li>- maximum height c. 25 m</li> </ul>

TABLE 7:2 Continued.

Species	Method of Persistence	Conditions for Establishment	Life Span Features
<i>Nothofagus truncata</i>	- poorly dispersed wind-borne seed - mast seed years	- shade intolerant, will establish in open communities - ? need for specific mycorrhizal fungi (Baylis 1980)	- life span unknown (> 200 years) - maximum height c. 30 m
<i>Beilschmiedia tawa</i>	- large fruit, dispersed by tui and pigeon	- requires shelter of established vegetation	- life span unknown* - maximum height c. 25 m
<i>Dysoxylum spectabile</i>	- large fruit	- requires shelter of established vegetation	- life span unknown - maximum height c. 18 m
Podocarp species ( <i>Dacrydium cupressinum</i> <i>Podocarpus ferrugineus</i> <i>P. dacrydioides</i> , <i>P. spicatus</i> )	- bird distributed seed	- require shelter of established vegetation	- life span > 400 years - maximum height 25-35+ m
Tree fern species <i>Cyathea dealbata</i> <i>C. medullaris</i> <i>Dicksonia squarrosa</i>	- wind dispersed spores - resprouts after fire - will survive in open	- require shelter of established vegetation for germination	- life span unknown - maximum height 8-15 m

\* Estimated to be  $\approx$  400 yrs in Taupo forests, North Island (Ogden and West, 1981).

The consequence of repeated fires at a site dominated by both manuka and kanuka will be the loss of kanuka from the site. Kanuka has no effective strategy for recovery from fires in the late summer, autumn and winter months. If fires occur during those months the site will come to be dominated by manuka seedlings which germinate from the fire resistant capsules.

An explanation for the lack of hard beech regeneration at many suitable sites in the Marlborough Sounds can be understood in terms of the species shade intolerance and poor seed dispersal mechanisms. If an area of hard beech is burnt in a year when surviving trees or nearby trees fail to set seed the site will be colonised by other species who form a dense cover under which hard beech seed fails to establish in the following years when there is a mast fall of beech seed.

The observation of hard beech poles in a *Leptospermum* shrubland can be understood in terms of both *Leptospermum* seed and hard beech seed arriving together at an open site. Hard beech will come to dominate such a site by virtue of its rapid and greater height growth and longer life span.

The consequence of fire destroying a mixed broadleaved shrubland or forestland are not directly predictable. The replacement sequence possible are dependent upon the species composition of the burnt stand as well as upon chance events. If the mixed broadleaved stand had developed through a bracken-dominated sere then the surviving bracken rhizomes could serve to re-establish bracken at the site. If the stand contained a number of tree ferns they could resprout and dominate the site if the fire was relatively mild. The arrival of broadleaved shrubs and trees onto the burnt site would be very dependent upon the presence of birds carrying in the seeds.

A strength of the life history approach to understanding succession is that the consequences of introducing a new species into an area can be predicted. The classical and contemporary theories of succession do not allow for any interpretation of the role of new species in a succession.

Gorse is a species that has the potential to dominate much of the Marlborough Sounds which is presently covered supporting shrubland or fernland. This adventive shrub has had a restricted distribution in the Marlborough Sounds until recent times. Vegetation dominated by gorse was limited to areas adjacent to settlements, such as: the slopes behind Waikawa Bay, the Snout, the slope behind "The Pines", Endeavour Inlet, and

to areas of recently reverted pasture land, as on the slopes of Onahau Bay and the slopes between Punga Cove, Endeavour Inlet and Kenepuru Saddle.

The seeds of gorse are now throughout the Marlborough Sounds. Tracks that were cleared through indigenous scrub and forest in 1974-1975, during the process of providing an electricity reticulation service across the Marlborough Sounds, are now regenerating with gorse in many places. Each fire increases the hold of gorse on disturbed land. Gorse has a competitive advantage over manuka and kanuka as it is capable of resprouting after fires. Young *Leptospermum* seedlings have reduced space in which to establish if the gorse resprouts after a fire and are forced to compete for water and nutrients with established root systems of the gorse plants.

Gorse is also capable of establishing throughout most of the year once a seed supply is available. Gorse seed can lie dormant on the soil and in litter layers and germinate after a fire. The viability of *Leptospermum* seed, by contrast, is short (Mark, no date).

The process of gorse gaining dominance over the secondary indigenous communities on the Eastern Hutt Hills, Wellington has been reported by Druce (1957). Conditions would now appear to be suitable for a similar spread of gorse-dominated communities throughout much of the lowland area of the Marlborough Sounds if firing and clearing of established vegetation continues.

Two *Pinus* species (*P. radiata* and *P. pinaster*) are becoming prominent in shrublands throughout the Marlborough Sounds. Pines are now established in woodlots and plantations throughout the Sounds and these plantings serve as a seed source of the species into open ground. Because of the species' rapid growth and great height pines quickly overtop shrub, seral shrub and forestland species and become a conspicuous entity in these communities. The future of the pine species in the successions is unknown but because of the great height of the plants they are unlikely to be overtopped by broad-leaved forest species. When the pines degenerate and die they will not establish beneath a forest cover and so could be lost from a site. However there will always be open sites available within the Marlborough Sounds that are suitable for pine establishment (especially eroding coastal slopes) and it would seem that pines are assured of a continued presence in seral communities in the Marlborough Sounds.

Whilst the life history approach is of value to the land manager for predicting species compositional change after disturbance it is of little use to him for predicting the course of ecosystem function following disturbance. Whereas species replacement changes during succession may be understood in terms of an individual species life history the changes in function of an ecosystem during succession are dependent upon a complex of interactions between all the living and non-living components of the ecosystem (Auerbach 1978).

#### 7:4 Land Use Planning in the Marlborough Sounds

During the years in which the present study was undertaken a number of planning studies relating to land use in the Marlborough Sounds were published.

The studies are:

- "Strategy for the Conservation and Development of the Marlborough Sounds" (Marlborough Sounds Crown Planning Study - 1976)\*
- "Forestry in Marlborough" (Gabites, Alington and Edmonson 1978)
- "Outdoor-Recreation Planning - Marlborough Pilot Study" (Robertson *et al.* 1977)
- "Marlborough - A Survey of Present Resources and Future Potential" (Duckworth *et al.* 1976)
- "Open Space, Resource Use and Management in the Marlborough Sound" (Clifton *et al.* 1980).

The general attitude advanced in the above documents is that land use in the Marlborough Sounds should be based on a multiple-use design and there should be a balance between development and conservation.

The Marlborough Sounds Maritime Park is recognized as an integral part of the Marlborough Sounds and since management of reserves cannot be divorced from adjoining land uses (White and Bratton 1980) it is appropriate to consider the relevance of the present study for planning in the whole of the Marlborough Sounds as well as in the reserves of the Maritime Park.

The planning problem in the Marlborough Sounds is recognized as the

"accommodation of the different land and water uses (*namely; pastoral farming, exotic forestry, mussel farming, recreation*)\*\* ensuring that natural, cultural, landscape and recreational values are enhanced and the welfare of the population provided for in proper recognition of national, regional and local needs".

(Crown Planning Study 1976)

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\* Henceforth referred to as the Crown Planning Study.

\*\* My insert.

Whilst a solution to this problem is unlikely to be achieved in a form that is acceptable to all land users in the Marlborough Sounds the authors of the planning studies have sought to provide a framework around which planning decisions can be shaped.

Two achievements of the studies are: the recognition of areas in the Marlborough Sounds that are suitable for a selective land use and the formulation of guidelines that could be adopted in the planning of land use in the Marlborough Sounds.

Whilst the author has considerable sympathy with the approach adopted in these studies she is forced to reject some conclusions and recommendations of the documents because there has been no recognition of the dynamic nature of the ecosystems of the Marlborough Sounds in any of the listed documents.

There is one point in particular, that has been stressed in the Crown Planning Study and has been echoed at Town and Country Planning hearings concerning land uses in the Marlborough Sounds.

The policy that "substantially regenerated second growth indigenous vegetation shall be retained" in the Marlborough Sounds is a policy that warrants close examination.

There are two references to this policy in the Crown Planning Study. Planning Objective 5.3.4. states "Preserve valuable flora and fauna and protect their habitats. Achieve by: prohibiting conversion to exotic vegetation of indigenous forest or of substantially regenerated second growth indigenous vegetation".

Areas mapped as suitable for commercial forestry were chosen by ensuring that a number of criteria were satisfied; one being that there must be "no clearfelling, burning or logging of existing indigenous forests or of advanced regeneration".

The policy has been stated in a similar form in a Town and Country Planning Appeal held in 1979. At the hearing the Marlborough Forest Owners Association Inc. sought a provision in the Marlborough County District Scheme that commercial forestry should be a predominant land use in the Rural A Zone of the Marlborough Sounds "provided that commercial forestry shall be neither a predominant nor a conditional use on any piece of land:

- (a) presently covered in standing indigenous high forest; or
- (b) substantially reverted to indigenous tree species (excepting early successional *Leptospermum* species)."

Planning Tribunal Decision C 55/80.

The above examples illustrate a current belief that it is wise or good land use to retain substantially regenerated indigenous vegetation (with the possible exclusion of *Leptospermum* dominated communities) in the Marlborough Sounds. The corollary of this belief, that it is the wise or good land use to remove and develop areas that are clothed in unsubstantially regenerated vegetation is implicit in each example.

The failure to recognize the value of young regenerating vegetation is a major omission of the published documents relating to land use in the Marlborough Sounds.

There is no clear definition as to what is substantially reverted vegetation. The Crown Planning Study defines substantially reverted vegetation as vegetation where "broadleaves penetrate the scrub canopy". This definition differs quite considerably from the one offered at the 1979 Town and Country Planning Appeal by the Marlborough Forest Owners Association Inc. Similarly, there is no unanimity as to what is indigenous forest. The definition followed in Duckworth *et al.* (1976) is that indigenous forests are "areas containing indigenous tree species 10 m or taller".

The definition of indigenous forest that has been adopted in this thesis is one that has been accepted by New Zealand ecologists and is defined by Atkinson (1962) as an "area composed of *indigenous*\* plants with erect stems greater than 10 cm d.b.h. and with greater than 81% of the trees in the canopy".

Some of the conflicts that could arise when trying to decide whether or not an area carries substantially reverted vegetation or indigenous forest are illustrated by the following examples taken from the study sites of this thesis. If we employ Atkinson's definition, then the successional stands N.B.2, E.I.7, D'Urv.1, D'Urv.2, E.I.4 and G.B.1 are classified as indigenous forests, but stands G.B.1, D'Urv.1 and N.B.2 do not satisfy the Crown Planning Study definition of substantially reverted vegetation since broadleaves do not penetrate the canopy.

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\* My insert.



If the definition of indigenous forest put forward by Duckworth *et al.* (1976) is accepted then it is possible that the virgin coastal kohekohe forest in stand C.C.4 fails to satisfy the definition since the mean height of the canopy is less than 10 m and only a few trees in the stand reach a height of 10 m. There are other areas of exposed low coastal forest in the Marlborough Sounds that would definitely fail to satisfy the criterion of containing trees 10 m or higher.

The question still remains; what is "substantially regenerated vegetation"? The answer can only be subjective; e.g. tall scrub, treeland or any vegetation that is over midway (in a time sense) along the scale to the forest condition. Rather than answer this question it is pertinent to consider the dangers in applying a blanket approach to the problem of finding a suitable land use for areas of young regenerating vegetation. There are a number of values that can be associated with young regenerating ecosystems that are not considered in the policy to retain only substantially regenerated vegetation.

One of the forest types present in the Marlborough Sounds is the kohekohe-dominant coastal forest which is now a very uncommon forest association of limited distribution in the North Island and which reaches its southern limit in the Marlborough Sounds. Most areas of kohekohe-dominant forest were cleared early in New Zealand's agricultural history. The largest remnants of this forest association are now confined to islands in Cook Strait, e.g. Kapiti Island (Esler 1967), parts of D'Urville Island and the northern end of Arapawa Island (Park and Walls 1976a). The smaller islands of Cook Strait and the Marlborough Sounds also possess small remnants of formerly more extensive kohekohe forest. There are also patches of kohekohe forest on mainland North Island and mainland Marlborough Sounds. The kohekohe forests of Kapiti Island and the mainland areas are highly susceptible to possum attack and the future of the forests with the continued presence of possum is far from secure. It is only on D'Urville Island and Arapawa Island, areas that are possum free, that the future of the kohekohe forest appears to be secure.

At suitable sites on Arapawa and D'Urville Islands (colluvial coastal slopes and fertile coastal valleys) secondary succession proceeds rapidly toward a coastal kohekohe forest. The kohekohe forest develops via a *Leptospermum* dominated shrub and treeland stage (e.g. sites D'Urv.1 and N.B.4). Thus the young successional stages at suitable sites on the possum-free islands of the Marlborough Sounds fulfil an important role as the nursery for an uncommon forest association.

The ultramafic belt of D'Urville Island supports a low secondary scrubland dominated by *Leptospermum scoparium* - *Dracophyllum longifolium* *Pimelea* spp. - *Hebe* spp. A rich flora is associated with the scrubland; it possesses endemic species restricted to D'Urville Island, species of local distribution, species of disjunct distribution not found elsewhere in the Marlborough Sounds and species typically restricted to ultramafic soils (Druce A.P. 1981). The scrubland appears to have been derived from a forest originally dominated by southern rata (*Metrosideros umbellata*), kamahi and hard beech. Pockets of southern rata survive in sheltered gullies at the southern end of the island and small saplings and seedlings are present in the secondary scrubland.

Although it would seem doubtful that the ultramafic areas of D'Urville Island could be used for agricultural or forestry production it is possible that other uses for this land could be realised (for instance, serpentine mining). The scrublands of the mineral belt of D'Urville Island would hardly qualify as areas of advanced regeneration. It would be wrong to consider that the vegetation of the ultramafic zone is typical of other areas of young regenerating shrubland in the Marlborough Sounds. The secondary scrubland of the ultramafic rocks of D'Urville Island is an unique plant association not represented elsewhere. It forms a fascinating link between the ultramafic vegetation of Kerr Point Scientific Reserve, Northland, which is rich in endemic plant species and varieties and the ultramafic vegetation of Red Hill, Westland which does not appear to contain any ultramafic-endemic plant species.

A number of plant species are associated with young successional vegetation and are not common in maturing forestlands. In particular, the terrestrial orchids: *Acianthus formicatus* var. *sinclairii*, *Caladenia carnea*, *Chiloglottis cornuta*, *Corybas oblongus*, *C. trilobus*, *Microtis unifolia*, *Orthoceros strictum*, *Prasophyllum colensoi*, *Pterostylis graminea*, *P. alobula* were only found, or were most common, in very open shrub/grassland or closed *Leptospermum* dominated vegetation.

Apart from being a favoured habitat of some vascular plants the young secondary *Leptospermum* shrublands are just one of a number of indigenous vegetation associations that are rapidly disappearing from the New Zealand landscape. Secondary *Leptospermum* communities are favoured areas for conversion to pasture land or to exotic forestry.

In the study "Open Space, Resource Use and Management in the Marlborough Sounds" it is noted that "there is no real pressure on users to be concerned with the indirect effects of their use" and the study recommends that if multiple uses in the Sounds are to be accommodated then each user must recognise:

- (a) the character and condition of the environment
- and (b) the direct and indirect effects of their activity on the environment and on each other (Clifton *et al.*, 1980).

It is one of the tragedies of the New Zealand Reserves system that there has been no recognition of the need for natural buffer zones between a reserve and adjacent land. Throughout the Marlborough Sounds there are instances of land being burnt and cleared right up to the boundary of an existing reserve and there are numerous cases where fires have burnt into the reserve.

Ngaruru Bay Scenic Reserve, on Arapawa Island, is a particularly tragic example of a reserve that has suffered a history of fire abuse. The reserve was purchased in 1920 from its Maori owners and was at that time clothed with original forest which was described as "beautiful bush". Between one third and one half of the reserve has since been subjected to repeated fires. Fires were reported burning in the reserve in January 1939, February 1946, January 1960 and February 1963. The 1939, 1946 and 1963 fires appeared to have started in an adjoining farmed property to the north-east of the reserve and burnt a total of 46 ha. The 1960 fire started in an adjoining property to the south of the reserve and burnt for over 3 days destroying some 26 ha of forest.

If buffer zones do not exist between a mature forest reserve and adjoining cleared land then there is a danger that the forest will deteriorate as trees on the margin become wind pruned and subject to wind throw. The understorey vegetation suffers from desiccation and adventive weed species establish along the forest margins.

Young regenerating vegetation can fulfil an important role by providing a buffer zone in which mature forest species can establish; which helps prevent the desiccation of the mature forest understorey vegetation; which acts as a barrier to strong winds and which can act as a partial stock barrier. The young regenerating shrublands of the Marlborough Sounds can be easily fired in dry seasons so it is essential that no fires are permitted near reserve boundaries or buffer zones.

A feature of the concept of retaining only substantially reverted vegetation is that the future land use of an area can be pre-determined. The Crown Study recognizes that some key landscape elements of the Marlborough Sounds; peaks, headlands, peninsulas, prominent faces, necks enclosing important reaches, ridgelines and skylines, should be protected from development but there is no guarantee that these recommendations will be followed by authorities involved in development in the Marlborough Sounds.

Mahakipawa Arm and the slopes above Moutapu Bay are two visually prominent areas in the Marlborough Sounds that are currently covered in young regenerating vegetation and are being considered for exotic forestry.

Two studies have investigated the suitability of areas in the Marlborough Sounds for exotic forestry (Field 1976, Gabites, Allington and Edmonson 197\_). It is evident from these two studies that much of the lowlands of the Marlborough Sounds would appear to be suitable for the establishment of exotic forestry (with *Pinus radiata* being the preferred tree species). It would appear that if an exotic forestry industry is to be developed for the Marlborough Sounds region large areas of the lowlands would have to be planted. Areas identified as being suitable for exotic forestry include Nature Reserves (Maud Island), Scenic Reserves (Blumine Island), prominent landscape areas, areas of advanced regeneration and areas of young regeneration adjacent to virgin forest.

Even if the land in reserve remains in indigenous vegetation it is evident that large areas of young regenerating land in the lowlands of the Marlborough Sound would be required for exotic planting if an economic exotic forest industry is to be established around the Marlborough Sounds plantations.

#### Conclusion: Land Use Planning in the Marlborough Sounds

A blanket approach to land use planning in the Marlborough Sounds is not ecologically acceptable.

I have presented a number of examples from the Marlborough Sounds that illustrate the ecological value of young regenerating scrubland. My data on succession in the Sounds are confirmation that the process of vegetation recovery is unique to each site.

Whilst it is appropriate to have a strategy or formula upon which to base planning proposals for the Marlborough Sounds it is also necessary to ensure that planning objectives are appropriate for the areas under consideration. To satisfy this requirement it is essential that each area should be considered individually with regard to its own set of environmental conditions in any planning proposal.

## 7:5 Planning and the Scenic Reserves of the Marlborough Sounds Maritime Park

Four types of reserve are represented in the Marlborough Sounds Maritime Park, namely: Nature Reserves, Historic Reserves, Recreation Reserves and Scenic Reserves.

Management aims in the first three types of reserve are usually fairly obvious. Nature and Historic Reserves are managed in such a way as to provide maximum long-term protection to the unique floral, faunal and historic values they possess. Recreation Reserves are areas that are managed for the public enjoyment of picnicking, camping and other out-door leisure-time pursuits. The management aims for Scenic Reserves are not so clear-cut. Under the Reserves Act (1977) Scenic Reserves are:

"(a) for the purpose of protecting and preserving in perpetuity for their intrinsic worth and for the benefit, enjoyment, and use of the public, suitable areas possessing such qualities of scenic interest, beauty or natural features or landscape that their protection and preservation are desirable in the public interest.

or

(b) for the purpose of providing, in appropriate circumstances, suitable areas which by development and the introduction of flora, whether indigenous or exotic, will become of such scenic interest or beauty that their development, protection and preservation are desirable in the public interest".

Under the terms of the Reserve Act (1977) the Marlborough Sounds Maritime Park Board is obliged to provide a management plan for each reserve under its jurisdiction. I believe a dilemma is posed for the manager of Scenic Reserves. By definition the management of a Scenic Reserve could be directed toward a primary aim of the preservation and protection of the aesthetic qualities of a reserve or toward a primary aim of preserving and protecting the natural qualities of a reserve. In some circumstances management options for the distinct and different purposes of a Scenic Reserve may not be compatible.

In the Crown Study of the Marlborough Sounds a landscape study was undertaken which arrived at the conclusion that much of the Marlborough Sounds was scenically unattractive and this was due, in a large part, to the existence of large tracts of visually unattractive scrub and fern. Mature forest was recognized as being scenically attractive and held to be the ideal. Areas that were regenerating rapidly toward mature forest were held to be better

(from a visual perspective) than areas which were less advanced in regeneration. Although these conclusions on the aesthetic properties of the Marlborough Sounds vegetation may not be accepted by all people, they are, I believe, a fair representation of the views held by the public at large (and confirm many comments I heard whilst working in the Marlborough Sounds).

Recommendations in the Crown Study to upgrade the landscape visually include the use of "managed afforestation to enhance currently reverting scrubland" and the minimum modification of land in areas of high scenic quality. A number of sites are identified as fulfilling the landscape study's criteria of spectacular, outstanding or distinguished scenic quality. No recommendation is made that there should be minimum modification of land of lesser scenic quality which encompass most of the Marlborough Sounds.

The great ecological value of the Scenic Reserves of the Maritime Park is that in its entirety the Park preserves and protects the best representation of lowland forest communities in the Central Botanical Region of New Zealand. Although some 16% of the land area of New Zealand is afforded a high degree of nature protection in the New Zealand Reserve System the system is not representative of the natural communities present throughout New Zealand. The reserve system is heavily biased towards the alpine and sub-alpine communities and greatly under-represents the lowland and coastal communities (Dingwall and Wassilieff 1981, Register of Protected Natural Areas in New Zealand 1981).

The Marlborough Sounds is one of the few areas in New Zealand that preserves a near complete representation of the natural communities that were typical of the area prior to the arrival of European Man. Most of these areas are represented in the Scenic Reserves of the Maritime Park.

Disturbance and succession are natural features of any landscape. From an ecological perspective there is no virtue in upholding the belief that the virgin or steady-state forest is the ideal (or best) state of vegetation. Many studies from overseas have confirmed the dynamic nature of mature forests and have shown that species in the mature forests are adapted to external disturbance regimes (Raup 1941, Webb 1958, Heinselman and Wright 1973, Henry and Swan 1974, Sprugel 1976) or to disturbance which is intrinsic to forests (Bray 1956, Forcier 1975).



The field of research into the role of disturbance in New Zealand is poorly developed; there is little information available on the size and temporal frequency of disturbance in any type of forest. However there is ample evidence of external disturbances (fire, wind-throw, landslide, flood) disrupting mature forests in New Zealand. Three different types of forest regeneration are commonly recognized (Veblen and Stewart 1980) and appear to be applicable to the forests of the Marlborough Sounds. Catastrophic regeneration occurs with the establishment of tree species on a site following the destruction of the previous vegetation. Such a mode of regeneration is exhibited in the lowland forests of the Marlborough Sounds by the pioneering tree species, *Leptospermum ericoides*, *L. scoparium*, *Nothofagus truncata*, *N. solandri* var. *solandri*, *Coriaria arborea* and *Aristotelia serrata*. Disturbance which is intrinsic to a forest results from the death of individual tree species. Gap-phase replacement refers to the establishment of a species beneath small-to-intermediate sized canopy gaps which result from the death of one or a few trees. In New Zealand such a mode of forest regeneration has been reported for *Nothofagus* species (Cockayne 1926, June and Ogden 1978) and postulated for *Weinmannia racemosa* (Veblen and Stewart 1980) and would be expected for light-demanding canopy such as the podocarp species. The third type of forest regeneration is continuous regeneration which is exhibited by shade-tolerant species which establish and grow under closed canopies. *Dysoxylum spectabile* exhibits this type of regeneration.

Species which regenerate by gap-phase replacement or show continuous regeneration can only enter a seral sequence sometime after the establishment and consolidation of the pioneer phase. Such species are dependent upon the presence of regenerating stands of vegetation for their survival if the mature forests are destroyed.

To attach only an aesthetic value to regenerating vegetation is to deny the important role seral communities have in maintaining the compositional and functional integrity of the forest ecosystem. The preservation and protection of the forests of the Marlborough Sounds will only be achieved if areas of regenerating vegetation are permitted to exist. It is essential that all types and stages of forest regeneration are represented in the reserves of the Maritime Park if the ecological diversity and the aesthetic value of the lowland forests in the Marlborough Sounds to be preserved in perpetuity.



## ADDENDUM

A discussion paper on the difficulty in determining "advanced indigenous regeneration" in the Marlborough Sounds has been prepared (Campbell, D.J. 1982)\*. Campbell suggests that a more precise term for determining stages of succession which could be exempted from conversion to exotic forestry is "advanced succession to native forest." He also advances the idea that such vegetation could be determined on the basis of the structure of the vegetation.

Campbell proposes that, in the Marlborough Sounds, advanced succession to native forest would include:

1. Vegetation with trees more than 5m tall, comprising 20% or more of the canopy cover, regardless of the composition of the remainder of the canopy;

or

2. Vegetation composed of scrub, 2-5m tall, with at least 30% canopy cover, and with juvenile tree species 2m or more high present in at least 20% of the samples as determined by P.H.I. sampling.

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\* Campbell, D.J. (1982) "Advanced succession to native forest". A discussion paper. Ecology Division File Report, May 1982, D.S.I.R., New Zealand.

## CONCLUSION

This study of structural and functional recovery of lowland forest ecosystems in the Marlborough Sounds Maritime Park was undertaken with the primary aim of providing information to the land planners of the Maritime Park. It was the author's belief that the existing store of knowledge of seral processes in the Marlborough Sounds Maritime Park was inadequate for the wise management of the Scenic Reserves of the Park.

The study has documented and described the most common types and stages of secondary succession in the lowland forests of the Marlborough Sounds. Processes of structural, compositional and functional change during succession have been investigated by arranging data from 39 seral sites into a chronological sequence. Although the processes of structural and compositional change were unique to each study site three broad patterns of vegetation development were recognised. The vegetation development sequences were related primarily to the topographical position of each stand.

An hypothesis adopted at the beginning of this study, that types and rates of vegetation regeneration were related to site fertility, was unable to be verified. Whilst there is a relationship between soil fertility and pattern of vegetation development the relationship does not appear to be a direct one. Rates of regeneration were unrelated to measured soil fertility parameters. A more acceptable hypothesis which was adopted was that rates of vegetation regeneration were dependent upon life cycle characteristics of important seral species at each site.

Aspects of site fertility changes during succession were further investigated by sampling the weight and nutrient content of the forest floor and soil horizons in the 39 seral stands. The sampling design was inadequate for accurately estimating weights of biomass and nutrients but it was possible to recognise broad trends of forest floor development which were related to the vegetation composition of the stands.

The importance of pioneering species to the recovery of nutrient cycling ability of disrupted forest ecosystems was shown in the large quantities

of litter and nutrients returned to the forest floor by young seral vegetation. Processes of litter decomposition differed markedly between two types of common seral vegetation.

Classical and contemporary theories of succession appear to be of little predictive value to the land manager of the reserves of the Maritime Park. Ideas on vegetation replacement sequences that involve knowledge of the life histories of plant species offer the best theoretical framework for modelling processes of succession in the lowland forests of New Zealand.

There is a need for more detailed knowledge of the life cycle characteristics of common species in the lowland forests and seral communities in New Zealand. The field of research into ecosystem function in New Zealand's lowland forests has been neglected and our understanding of seral communities must necessarily be limited because of this neglect. Knowledge of ecosystem function is a pre-requisite for wise management of reserves and New Zealand ecologists must seek to overcome this defect so that land planners can make sound decisions about land use.

The reserves of the Marlborough Sounds Maritime Park are a natural laboratory that offer great scope for the study of secondary successional processes in forests. In the final analysis verification of successional models requires the repeated observation of change <sup>in</sup> permanent quadrats and it is the author's hope that this present study will serve as a suitable base for further studies on processes of secondary succession in the lowland forests of the Marlborough Sounds.

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APPENDIX I (cont'd)

B. procerum (Forst. f.) Swartz

Ctenitis glabella (A. Cunn.) Cop. (Lastreopsis glabella (A. Cunn.) Tindale)

C. velutina (A. Rich.) Cop. (L. velutina (A. Rich.) Tindale)

Cyathea dealbata (Forst. f.) Swartz

C. medullaris (Forst. f.) Swartz

C. smithii Hook. f.

Dicksonia squarrosa (Forst. f.) Swartz

Grammitis billardieri Willd.

Hymenophyllum demissum (Forst. f.) Swartz

H. dilatatum (Forst. f.) Swartz

H. multifidum (Forst. f.) Swartz

H. rarum R.Br.

H. revolutum Col.

Lindsaea trichomanoides Dryand.

Paesia scaberula (A. Rich ) Kuhn

Pellaea rotundifolia (Forst. f.) Hook

Phymatosorus diversifolius (Willd.) Pic. Ser.

Phymatosorus scandens (Forst. f.) Pic. Ser.

Pneumatopteris pennigera (Forst. f.) Holttum

ponga

mamaku

wheki

filmy fern

" "

" "

" "

" "

ring fern

hounds tongue fern

APPENDIX I (cont'd)

Polystichum richardii (Hook.) J. Smith

Pteridium esculentum (Forst. f.) Diels

bracken

Pteris macilenta A. Rich.

P. tremula R. Br.

Pyrrosia serpens (Forst. f.) Ching

Rumohra hispida (Swartz) Cop. (Lastreopsis hispida (Swartz) Tindale).

GYMNOSPERMS

Dacrydium cupressinum Lamb.

rimu

D. laxifolium Hook. f.

Phyllocladus alpinus Hook. f.

toatoa

(a) Picea engelmannii (Parry) Engelm.

Engleman spruce

(a) Pinus banksiana Lamb.

jack pine

(a) P. nigra (Arnold)

\* P. pinaster Ait.

maritime pine

\* P. radiata D. Don

radiata pine

Podocarpus dacrydioides A. Rich

kahikatea

P. ferrugineus G. Benn. ex D. Don

miro

P. hallii Kirk

Hall's totara

P. spicatus R. Br. ex Mirbel

matai

P. totara G. Benn. ex D. Don.

totara

APPENDIX I (cont'd)

MONOCOTYLEDONS

Acianthus fornicatus R. Br. var. sinclairii (Hook f.) Hatch

\* Agrostis tenuis

\* Anthoxanthum odoratum L.

Astelia solandri A. Cunn.

Baumea huttonii (Kirk) Blake

Bulbophyllum pygmaeum (Smith) Lindl.

\* Caladenia carnea

Carex secta Boott in Hook. f.

C. virgata Sol. ex Hook. f.

Chiloglottis cornuta Hook. f.

Chionochoa taxon Chionochoa flavescens x C. pallens var. pallens

(Williams et. al. 1980)

Collosporum hastatum (col.) Skottsb.

Cordyline australis (Forst. f.) Endl.

C. oblongus (Hook.f.) Reichb.f.

C. trilobus (Hook.f.) Reichb.f.

Cyperus ustulatus A. Rich.

Dendrobium cunninghamii Lindl.

Dianella nigra Col.

brown top  
sweet vernal  
perching lily

niggerhead

perching lily  
cabbage tree

N.Z. bluebell

## APPENDIX I (cont'd)

<u>Farina autumnalis</u> (Forst.f.) Hook.f.	kiekie
<u>E. mucronata</u> Lindl.	
<u>Freycinetia baueriana</u> Endl. subsp. <u>banksii</u> (A. Cunn.) Stone	
<u>Gahnia pauciflora</u> Kirk	yorkshire fog
* <u>Holcus lanatus</u> L.	sea rush
<u>Juncus maritimus</u> Lam. var. <u>australiensis</u> Buch.	
<u>Lepidosperma australe</u> (A. Rich.) Hook. f.	jointed rush
<u>Leptocarpus similis</u> Edgar	bush rice grass
<u>Microlaena avenacea</u> (Raoul) Hook. f.	
<u>Microtis unifolia</u> (Forst. f.) Reichb. f.	
<u>Orthoceras strictum</u> R. Br.	
<u>Phormium cookianum</u> Le Jolis	coastal flax
<u>Poa laevis</u> R. Br.	silver tussock
<u>Prasophyllum colensoi</u> Hook. f.	
<u>pterostylis alobula</u> (Hatch) L.B. Moore	green hood orchid
<u>P. banksii</u> A. Cunn. in Hook.	green hood orchid
<u>P. graminea</u> Hook. f.	
<u>Rhopalostylis sapida</u> Wendl. et Drude	nikau palm
<u>Ripogonum scandens</u> J.R. et G. Forst.	supplejack
<u>Scirpus</u> L. spp.	



## APPENDIX I (cont'd)

Thelymitra longifolia J.R. et G. Forst.

sun orchid

Typha orientalis C.B. Presl.

raupo

Uncinia uncinata (Linn. f.) Kük

hook grass

Zostera muelleri Aschers

eel grass

DICOTYLEDONSAciphylla squarrosa J.R. et G. Forst.

coastal spaniard

Alectryon excelsus Gaertn.

titoki

(a) Angophora costataAristotelia fruticosa Hook. f. var.Aristotelia serrata (J.R. et G. Forst.) W.R.B. Oliver

wineberry

Beilschmiedia tawa (A.Cunn.) Benth. et Hook.

tawa

\* Berberis glaucocarpa Stapf. = (B. vulgaris L.)

barberry

Brachyglottis repanda J.R. et G. Forst.

rangiora

Carpodetus serratus J.R. et G. Forst.

putaputaweta

Cassinia leptophylla (Forst. f.) R.Br.

tauhinu

C. vauvilliersii (Homb. et. Jacq.) Hook. f.Celmisia gracilentia Hook. f.Clematis australis KirkC. forsteri Gmel.

## APPENDIX I (cont'd)

<u>C. paniculata</u> Gmel.	
<u>Coprosma australis</u> (A. Rich.) Robinson = ( <u>C. grandifolia</u> Hook. f.)	kanono
<u>C. foetidissima</u> J.R. et G. Forst.	stinkwood
<u>C. lucida</u> J.R. et G. Forst.	
<u>C. propinqua</u> A. Cunn.	taupata
<u>C. repens</u> A. Rich.	
<u>C. rhamnoides</u> A. Cunn.	karamu
<u>C. robusta</u> Raoul	
<u>C. spp.</u> (unamed, included under <u>C. parviflora</u> descriptions)	tree tutu
<u>Coriaria arborea</u> Lindsay	korokia
<u>Corokia cotoneaster</u> Raoul	karaka
<u>Corynocarpus laevigatus</u> J.R. et G. Forst.	
<u>Craspedia</u> Forst. f. sp. (unnamed)	mingimingi
<u>Cyathodes fasciculata</u> (Forst. f.) Allan	patotara
<u>Cyathodes fraseri</u> (A. Cunn.) Allan	mingimingi
<u>C. juniperina</u> J.R. et G. Forst.	Scotch broom
* <u>Cytisus scoparius</u> L.	akeake
<u>Dodonaea viscosa</u> Jacquin	
<u>Donatia novae-zelandiae</u> Hook. f.	inanga
<u>Dracophyllum longifolium</u> J.R. et G. Forst. (inc. <u>D. filifolium</u> Hook. f., and	
<u>D. filifolium</u> var. <u>collinum</u> )	

APPENDIX I (cont'd)

<u>D. uniflorum</u> Hook. f.	kohekohe
<u>Dysoxylum spectabile</u> (Forst. f.) Hook. f.	
<u>Elaeocarpus dentatus</u> (J.R. et G. Forst.) Vahl	hinau
<u>Entelea arborescens</u> R. Br.	whau
<u>Erica lusitanica</u> Rud.	Spanish heath
(a) <u>Eucalyptus delegatensis</u> R.T. Baker	alpine ash
(a) <u>E. pauciflora</u> Sieb. ex Spreng.	snow gum
(a) <u>E. pilularis</u>	
<u>Euphrasia cuneata</u> Forst. f.	eyebright
<u>Fuchsia excorticata</u> (J.R. et G. Forst.) Linn. f.	tree fuchsia
<u>Gaultheria antipoda</u> Forst. f.	
<u>Geniostoma ligustrifolium</u> A. Cunn.	
<u>Gentiana</u> L. sp. (unnamed)	gentian
<u>Gnaphalium audax</u> Drury sub.sp. <u>audax</u>	coastal broadleaf
<u>Griselinea littoralis</u> Raoul	shining broadleaf, puka
<u>G. lucida</u> Forst. f.	
<u>Hebe stricta</u> (Benth.) L.B. Moore var. <u>atkinsonii</u> (ckn.) L.B. Moore	koromiko
<u>Hedycarya arborea</u> J.R. et G. Forst.	pigeonwood
<u>Helichrysum filicaule</u> Hook.	

## APPENDIX I (cont'd)

<u>Nightia excelsa</u> R. Br.	rewarewa
<u>Laurelia novae-zelandiae</u> A. Cunn.	pukatea
<u>Leptospermum ericoides</u> A. Rich.	kanuka
<u>L. scoparium</u> J.R. et G. Forst.	manuka
<u>Lophomyrtus bullata</u> (Sol. ex A. Cunn.) Burret	ramarama
* <u>Lotus pedunculatus</u> Cav.	lotus major
<u>Macropiper excelsum</u> (Forst. f.) Miq	kawakawa
<u>Melicope ternata</u> J.R. et G. Forst.	wharangi
<u>Melicytus ramiflorus</u> J.R. et G. Forst.	mahoe
<u>Metrosideros diffusa</u> (Forst. f.) Smith	climbing rata
<u>M. fulgens</u> Sol. ex Gaertn.	" "
<u>M. perforata</u> (J.R. et G. Forst.) A. Rich	" "
(a) <u>M. robusta</u> A. Cunn.	northern rata
<u>M. umbellata</u> Cav.	southern rata
<u>Muehlenbeckia australis</u> (Forst. f.) Meissn.	pohuehue
<u>Myoporum laetum</u> Forst. f.	ngaio
<u>Myrsine australis</u> (A. Rich.) Allan	mapou, red matipo
<u>M. divaricata</u> A. Cunn.	
<u>M. salicina</u> Hew. ex Hook. f.	toro

## APPENDIX I (cont'd)

<u>Nothofagus fusca</u> (Hook. f.) Oerst.	red beech
<u>N. menziesii</u> (Hook. f.) Oerst.	silver beech
<u>N. solandri</u> (Hook. f.) Oerst. var. <u>solandri</u>	black beech
<u>N. truncata</u> (Col.) Ckn.	hard beech
<u>Olearia colensoi</u> Hook. f.	leatherwood
<u>O. paniculata</u> (J.R. et G. Forst.) Druce	akiraho
<u>O. rani</u> (A. Cunn.) Druce	heketara
<u>O. serpentina</u> Simpson	
<u>Olearia solandri</u> Hook. f.	milktree
<u>Paratrophis banksii</u> Cheesm.	N.Z. jasmine
<u>Parsonsia capsularis</u> (Forst. f.) R.Br.	" "
<u>P. heterophylla</u> A. Cunn.	N.Z. passionf.
<u>Passiflora tetrandra</u> Sol. ex DC.	kaikomako
<u>Pennantia corymbosa</u> J.R. et G. Forst.	
<u>Pimelia longifolia</u> Sol. ex Wiks	lemonwood
<u>Pittosporum eugenoides</u> A. Cunn.	
<u>P. rigidum</u> Hook. f.	kohuhu
<u>P. tenuifolium</u> Sol. ex Gaertn. var. <u>tenuifolium</u>	shore ribbonwood
<u>Plagianthus divaricatus</u> J.R. et G. Forst.	

APPENDIX I (cont'd)

(a) Prunus pensylvanica L.

Pseudopanax anomalus (Hook. ) Philipson

P. arboreus (Murr.) Philipson

P. crassifolius (Sol. ex A. Cunn. ) C. Koch

Pseudowintera axillaris (J.R. et G. Forst.) Dandy

P. colorata (Raoul) Dandy

(a) Quercus petraea (Mattuschka) Leiblin.

Salicornia australis Sol. ex. Benth.

Samolus repens (J.R. et G. Forst.) Pers.

Schefflera digitata J.R. et G. Forst.

Scleranthus biflorus (J.R. et G. Forst.) Hook. f.

Selliera radicans Cav.

Senecio lagopus Raoul

\* Trifolium arvense L.

\* Trifolium pratense L.

\* T. repens L.

\* T. subterraneum L.

\* Ulex europaeus L.

Weinmannia racemosa Linn. f. var. racemosa

pin cherry

five finger

lancewood

peppertree

peppertree

glasswort

shore primrose

pate

hare'sfoot trefoil

red clover

white clover

subterranean clover

gorse

kamahi

## APPENDIX II

Nomenclature of Vegetation Structural Types

The name of the vegetation community is based on the composition of the canopy layer(s) and the predominant growth form is given to the stand. Canopy layers are separated by an oblique stroke (/) and species in the same layer are linked by a dash (-).

Diagnostic criteria for vegetation structural types mentioned in text  
(modified from Atkinson 1962)

Name of Structural Type	Proportions of leading growth forms in the canopy or on the ground	Definitions
Forest	> 80% trees	(trees (or tree-ferns) are > 10 cm d.b.h.)
Treeland	trees (20-80%) exceed area covered by any other growth form or bare ground	
Scrub	> 80% shrubs (or shrubs and trees)	Shrubs* are < 10 cm d.b.h.
Shrubland	shrubs (20-80%) exceed area covered by any other growth form or bare ground	
Tussockland	tussocks present as the leading growth form and exceeding area of bare ground	Tussocks include long-lived grasses and sedges with leaves densely clumped at the base
Grassland, sedgeland, rushland, fernland	grasses, sedges, rushes or ferns are the leading growth form and exceed area of bare ground	Excluding tussock grasses and tussock sedges
Herbfield	herbs present as the leading growth form and exceeding area of bare ground	herbaceous plants not included in the above categories

\* The growth form of flax (Phormium spp.) is included with shrubs.

## APPENDIX III

## Glossary

For definition of common ecological terms refer to Atkinson I.A.E., P.F. Jenkins and A.P. Druce (1968): Definitions and discussion of some concepts and terms relating to terrestrial ecosystems. Tuatara 16: 98-110.

A horizon

Surface soil horizon with a relatively high content of organic matter mixed with mineral matter.

B horizon

Soil horizon characterized by an accumulation of clay, iron or aluminium, usually of a blocklike or prismlike structure.

Basal area

The crosssectional area of a tree trunk at breast height (1.4 m) above the ground.

Broadleaf, Broadleaved species

A tree or shrub with its leaves exceeding narrow-linear in breadth. In New Zealand, a dicotyledonous tree or shrub, excluding Nothofagus spp., with broad leaves.

C horizon

Soil horizon embracing the parent material and parent rock.

Central Mainland Province

All the North Island of New Zealand South of Latitude 38°S and the coastal and lowland regions of the north of the South Island to Latitude 42°05'S.

Climax

Vegetation considered to have reached a steady-state condition, used synonymously with mature vegetation and virgin vegetation.

Coefficient of Variation of Canopy Height. CV%.

In P.H.I. analysis coefficient variation of the mean canopy height.



Consolidating species

Seral species which enter a succession after the establishment of pioneering species.

Crown cover

Estimate of the ground surface covered by one or more layers of vegetation (or litter) when projected vertically downwards (expressed as a percentage).

Crown space

In P.H.I. analysis the space occupied by foliage intercepts divided by the space below the canopy line (or the height class line) (expressed as a percentage).

D.B.H. (d.b.h.)

Diameter at breast height (1.4 m) of a tree or shrub species.

Ecosystem

An open system comprising living organisms and abiotic materials involved in the flow of energy and elemental cycles.

Equitability

A species diversity measure of the distribution of numbers of different species in a sample.

F. layer

A forest floor layer - the fermentation layer, consisting of partly decomposed or comminuted litter. Some of the original plant structures are visible to the naked eye.

F and H layer

A combined forest floor layer - fermentation and humus material

Forest floor

All organic matter,  $< 0.2$  cm diameter, lying above the mineral soil.

H layer

A forest floor layer - the humus layer, consisting of well decomposed organic matter often mixed with mineral soil. Original plant structures can not be seen with the naked eye.

Hydrous soil

Subdivision of yellow-brown earths in a very wet climate of  
 >2000 mm/yr.

Hygrous soil

Subdivision of yellow-brown earths in a wet climate between  
 1270 - 2000 mm/yr.

Initial floristics composition

Name given to the successional process whereby the seral sequence of vegetation unfolds from an initial flora present at the disturbed site. Cf. Relay floristics.

K-selection

Selective conditions which favour longevity of individuals at the expense of reproductive capacity. Cf. r-selection.

L layer

A forest floor layer - the litter layer, comprising fresh litterfall material with little altered plant structures.

Lowland

At the latitude of the Marlborough Sounds taken as sea level to 460 m.

Monolayer

With leaves spread in a single horizontal layer (ie without overlap).

Mor

Soil organic horizon consisting of little-decomposed plant material. Characteristically it is acid and has a high - very high C/N ratio.

Mor-like mull, Moder

Soil organic horizons consisting of slightly decomposed plant material. Characteristically they are acid and have high C/N ratios. Mor-like mulls resemble mulls more than mors. Moders are closer in nature to mors.

Mull

Soil organic horizon in which the organic material is intimately combined with the mineral portion of the soil. Characterized by a low-medium C/N ratio and is less acid than mors or moders.

Multilayer

With leaves distributed vertically and with some degree of overlap.

Perturbation

Used synonymously with disturbance. See discussion on the use of this term in McIntosh, R.P. (1980).

P.H.I. analysis

Point Height Intercept Analysis - A method of point analysis, see Park, G.N. (1973).

Point Height Frequency Distribution

In P.H.I. analysis height distribution of species foliage.

r-selection

Selective conditions which favour high reproductive rates at the expense of individual vegetative longevity.

Reiteration

Development of shoots outside the normal expression of the architectural model of a tree as a specialised environmental response (see Oldeman, R.A.A., 1978).

### Relative vegetation space (R.V.S.)

In P.H.I. analysis space below the canopy line for a particular stand divided by the space below the canopy line for a stand with maximum space in a group of stands considered (taken as N.B.4 in the present study).

### Relay floristics

Process of succession whereby a group of species ameliorates the site making it unsuitable for themselves but suitable for invasion by another group of species.

### Sere

A conceptual arrangement of a series of stands according to time.

### Species diversity

An expression of the richness of numbers of species in a stand, community or ecosystem.

### Specific vegetation space

In P.H.I. analysis the space below the canopy line divided by the space below the maximum canopy height.

### Steady-state

Condition of an ecosystem where the inputs of energy and materials are balanced by the outputs and where there is an overall constancy in the identity of the ecosystem.

### Succession

The process of directional change in the composition, structure and function of an ecosystem.

Secondary succession Succession on sites that have previously carried vegetation.

### Total stand foliage (T.S.F.)

In P.H.I. analysis the total value of foliage intercepts in the whole stand.

### Total stand volume (T.S.V.)

In P.H.I. analysis the space below the maximum canopy height.

## APPENDIX IV

Study Site Descriptions

Site descriptions for the study quadrats are recorded in the following format:

Name of study site: Code:  
 Location: Grid Reference:  
 Altitude: Topographic position and shape: Slope under quadrat:  
 Exposure to prevailing winds:  
 Vegetation description:  
 Age of vegetation:  
 Miscellaneous site data:  
 Soil profile data:

---

Endeavour Inlet 1: E.I.1

Endeavour Inlet Scenic Reserve S.16 465498

80 m. lower slope, convex 20°

Exposed to the S, W and to the NW blowing down the main valley at the head of Endeavour Inlet, sheltered from E.

Dense bracken fernland with some broadleaf species just appearing above bracken fronds.

13 yrs

Area previously in pasture

Soil profile:

litter	0-5 cm	dead bracken fronds
F & H	5-7 cm	dark brown (10 YR 3/4) decomposing bracken fronds and stipes intermeshed with many bracken rhizoids, faecal pellets present.
A hor	7-22 cm	brownish black (2.5 Y 3/2) friable, loamy sand, moderate crumb structure, some large schist fragments present, indistinct boundary to
B hor	22-40+ cm	yellow brown (10 YR 5/7) friable, silty loam, moderate crumb structure, some large schist rocks, roots and rhizoids present, rhizomes at 40 cm.

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Endeavour Inlet 2: E.I.2

Endeavour Inlet Scenic Reserve S.16 467496

65 m. lower slope, convex 15-20°

Exposed to S and W sheltered from N and E

Dense bracken fernland with emergent broadleaved and manuka shrubs

14 yrs

Soil profile:

litter	0-12 cm	dense mat of bracken fronds and stipes
F & H	12-15 cm	mat of roots, rhizomes and black decomposing bracken fronds
A hor	15-38 cm	dark brown (10 YR 3/4) very friable silt loam, moderate sized crumb structure, roots and rhizoids abundant, rhizomes present at 19 cm and 36 cm, worms and insect larvae present, charcoal present, distinct boundary to
B hor	38-45+ cm	yellow brown (10 YR 5/6) very friable silt loam, small crumb structure, a few schist chips present, few roots and rhizoids present.

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Endeavour Inlet 3: E.I.3

Endeavour Inlet Scenic Reserve

S. 16 465498

70 m. lower slope, convex 20-25°

Exposed to S, W and N, sheltered from E

Kamahi and kanuka occur as scattered emergents above a dense bracken fernland

16 yrs

Stand located upslope from E.I.2. Tree stumps and old fence posts near to plot.

Soil profile:

litter	0-3 cm	dead bracken and <i>Blechnum capense</i> fronds
F & H	3-5 cm	decomposing fern fronds and stipes containing extensive network of rhizoids and roots, faecal material present
A hor	5-35 cm	dark brown (10 YR 3/4) friable silt loam, small crumb structure weathered schist fragments abundant, roots and rhizoids abundant horizon merges into
B hor	35-45+ cm	yellow brown (10 YR 5/6) friable silt loam, small crumb structure, roots present to 40 cm.

Endeavour Inlet 4: E.I.4

Endeavour Inlet Scenic Reserve

S. 16 461514

270 m. upper ridge spur, convex-concave 25°

Exposed to S, W and N, sheltered from E

Regenerating kamahi-toro/fivefinger forest

84 yrs

Hard Beech stumps and logs present. Kamahi resprouts in plot. Old mining bench tracks above and below plot. Pig rootings.

Soil profile:

litter	0-2 cm	dry leaves and twigs of kamahi and toro
F & H	2-3 cm	decomposed leaf material, isopods present
A hor	3-12 cm	dark brown (10 YR 3/3) friable loamy sand, well developed nut structure breaking to small crumbs, weathered schist stones present, roots abundant, charcoal at 6 cm, distinct boundary to
B hor	12-40+ cm	bright yellow brown (10 YR 6/8) firm silt loam, moderately developed nut structure breaking to small crumbs, small weathered chips (6 x 5 x 2 cm) present throughout, roots to 25 cm.

Endeavour Inlet 5: E.I.5

Endeavour Inlet Scenic Reserve

S. 16 462507

80 m. lower slope, concave 10°

Exposed to S, W and N, sheltered from E

Decaying tauhinu/bracken shrubland

13 yrs

Burnt hard beech stumps present

Soil profile:

litter	0-2 cm	tauhinu leaves and twigs with some bracken fronds
F & H	2-3 cm	decomposing material, many roots present
A hor	3-21 cm	dark brown (10 YR 3/4) firm loamy sand, good nut structure breaking to fine crumbs, roots abundant, rhizomes at 20 cm, insect larvae present, distinct boundary to
B hor	21-40+ cm	yellow brown (10 YR 5/7) firm sandy loam, moderate nut structure breaking to fine crumbs, weathered schist chips present, roots and rhizoids present to 25 cm.

Endeavour Inlet 6: E.I.6

Endeavour Inlet Scenic Reserve

S.16 461505

60 m. lower slope, convex 12°

Exposed to S and W, sheltered from N and E

Decaying tauhinu/bracken shrubland

13 yrs

Pigs, goat and sheep present

Soil profile:

litter	0-1 cm	dry bracken fronds and tauhinu leaves and twigs
F & H	1-2 cm	decomposing bracken fronds and tauhinu material, roots and rhizoids abundant
A hor	2-22 cm	dark brown (10 YR 3/4) friable sand, medium nut structure breaking to fine crumbs, small schist chips (2 x 0.5 cm) present, roots and rhizoids abundant, distinct boundary to
B hor	22-40+ cm	yellow brown (10 YR 5/6) firm sandy loam, moderately developed nut structure breaking to fine crumbs and powder, bracken rhizomes at 25 and 40 cm, roots infrequent to 35 cm.

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Endeavour Inlet 7: E.I.7

Endeavour Inlet Scenic Reserve

S.16 464507

150 m. midslope, concave 25-30°

Exposed to S, W and NW, sheltered from E

Regenerating kamahi/silver tree fern forestland

70 yrs

One old kamahi stump with resprouts. Sheep present

Soil profile:

litter	0-1 cm	kamahi and tree fern leaves and fronds
F & H	1-2 cm	decomposing leaf material intermixed with fine roots and rhizoids
A hor	2-6 cm	brown (10 YR 4/4) friable loamy sand, medium sized crumb structure small schist rocks present throughout, roots abundant, distinct horizon to
B hor	6-35+ cm	yellow brown (10 YR 5/6) friable loamy sand, medium size crumb structure, schist rock fragments present, roots to 35 cm.

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Tawa Bay 1: T.B.1

Tawa Bay Scenic Reserve, Endeavour Inlet

S16: 467457

100 m. midslope, convex-concave 30-35°

Exposed to W and S, sheltered from E and N

Low manuka-kamahi shrubland

23 yrs

Soil Profile:

litter	0-1 cm	manuka and kamahi leaves and twigs
F & H	<1 cm	decomposing organic material
A hor	2-17 cm	brown (10 YR 4/4) friable silty loam, medium sized crumb structure, some orange mottling, rhizoids present, roots frequent, indistinct horizon to
B hor	17-40+ cm	yellow brown (10 YR 5/6) friable silty clay loam, medium crumb structure, roots present to 40 cm, rhizomes at 20 cm. No stones in profile.

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Tawa Bay 2: T.B.2

Tawa Bay Scenic Reserve, Endeavour Inlet S16: 467469  
 130 m. midslope, concave 28°  
 Exposed to W and N, sheltered from E and N  
 Manuka shrubland

24 yrs

Soil Profile:

litter	0-2 cm	manuka leaves, bark and twigs
F & H	2-3 cm	decomposing organic material
A hor	3-23 cm	dark brown (10 YR 3/3) friable silty loam, small crumb structure, many weathered friable schist chips present, roots abundant, worms present, indistinct boundary to
B hor	23-40+ cm	yellow brown (10 YR 5/6) friable silty loam, small crumb structure, some incorporation of A hor. Few schist chips present, roots present to 40 cm.

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Tawa Bay 3: T.B.3

Tawa Bay Scenic Reserve, Endeavour Inlet S16: 468460  
 125 m. gully, concave 22°  
 Exposed to W, sheltered from E, N and S  
 Wineberry-Tree tutu forestland

Age unknown

Soil Profile:

litter	0-1 cm	wineberry, rangiora, tree tutu leaves and twigs
F & H	<1 cm	decomposing leaf material
A hor	1-7 cm	dark brown (10 YR 3/3) firm loamy sand, well developed crumb structure, roots abundant, indistinct horizon to
B hor	7-21 cm	olive brown (2.5 Y 4/4) firm loamy sand, well developed crumb structure, roots abundant, schist rocks frequent, indistinct boundary to
C hor	21+ cm	large schist rocks

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Tawa Bay 4: T.B.4

Tawa Bay Scenic Reserve, Endeavour Inlet S16: 469464  
 230 m. ridge top, convex 29°  
 Exposed to N and W, sheltered from E and S  
 Manuka-kanuka forestland  
 35 yrs

Soil Profile:

L + F + H	<1 cm	thin litter of manuka and kanuka leaves overlying a matted network of decomposing leaves, roots and fungal hyphae
A hor	1-21 cm	brown (10 YR 4/4) friable loamy sand, small crumb structure, roots present, some dark orange mottling, worms present, small schist chips present, indistinct horizon to
B hor	21-40 cm	yellow brown (10 YR 5/6) firm silt loam, small crumb structure, roots present throughout, large schist rocks throughout.

Another pit had no schist rocks in B hor.

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Tawa Bay 5: T.B.5

Tawa Bay Scenic Reserve, Endeavour Inlet

Sl6: 466458

70 m. gully, concave 23°

Exposed to W, sheltered from E, N and S

Kanuka/mahoe-treefern forestland

70 yrs

Soil Profile:

L + F + H	0-1 cm	kanuka, manuka leaves and twigs, silver treefern fronds
A hor	1-11 cm	dark brown (10 YR 3/4) friable loamy sand, small crumb structure, small stones present, roots abundant especially in top 2 cm. Worms, millipedes and insect larvae present, indistinct boundary to
B hor	11-21 cm	dull yellow brown (10 YR 5/4) friable silty loam, small crumb structure, large and small stones present, roots present throughout, indistinct boundary to
C hor	21+ cm	large schist rocks.

Tawa Bay 6: T.B.6

Tawa Bay Scenic Reserve

Sl6: 482455

290 m. Axial ridge top, convex 18°

Exposed to W, S and N, sheltered from E

Manuka-gorse shrubland

25 yrs

Soil Profile:

litter	0-4 cm	manuka and gorse leaves and twigs, bracken fronds and petioles
F & H	4-6 cm	decomposing organic material, gorse seed germinating
A hor	6-26 cm	brown (10 YR 4/4) v. friable silt loam, small crumb structure, roots present throughout, rhizomes at 20 cm, worms and insect larvae present, indistinct boundary to
B hor	26-40+ cm	bright yellow brown (10 YR 6/6) friable silty clay loam, small crumb structure, roots present to 30 cm, no stones present.

Another pit contained schist rocks in A and B horizons.

Tawa Bay 7: T.B.7

Tawa Bay Scenic Reserve

Sl6: 459475

110 m. Gully, concave 25°

Exposed to SW, sheltered from E and N

Tree tutu-wineberry/mahoe forestland

Age unknown

Soil Profile:

litter	0-1 cm	wineberry and tree tutu leaves and twigs, <i>Cyathea medullaris</i> fronds, some decomposing litter, large stones at surface.
A hor	1-12 cm	dull yellow brown (10 YR 4/3) v. friable loamy sand, small crumb structure, roots present throughout, worms and insect larvae present, small rocks present, indistinct boundary to
B hor	12-36 cm	yellow brown (10 YR 5/6) v. friable loamy sand, small crumb structure, roots present throughout, bracken rhizomes present at 22 cm, schist rocks present, indistinct boundary to
C hor	36+ cm	large schist rocks - colluvium soil parent material

One pit had an A hor (36 cm deep) black-brown ( ) friable loamy sand overlying C hor.

Tawa Bay 8: T.B.8

Tawa Bay Scenic Reserve

S16: 472465

300 m. upper slope, convex 7-10°

Exposed to S.W. and E, sheltered from N

Manuka shrubland

21 yrs

Soil Profile:

litter	0-1 cm	manuka and broom leaves and twigs
F & H	1-2 cm	decomposing manuka leaves, mycelia present
A hor	2-24 cm	dark brown (10 YR 3/4) firm silt loam, well developed medium sized nut structure, roots abundant, bracken rhizomes present at 16 cm, worms present, medium sized rocks (7 x 4 x 2 cm <sup>3</sup> ) present, distinct boundary to
C hor	24+ cm	large schist rocks 20 x 10 x 4 cm <sup>3</sup> present.

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Tawa Bay 9: T.B.9

Tawa Bay Scenic Reserve

S16: 469465

230 m. midslope, convex 25°

Exposed to S.W. and E, sheltered from N

Manuka-kanuka shrubland

40 yrs

Soil Profile:

litter	0-1 cm	manuka and kanuka leaves and twigs
A hor	1-16 cm	dark brown (10 YR 3/4) firm sand of medium crumb structure, roots present, large schist rocks (9 x 4 x 3 cm) present, indistinct horizon to
B hor	16-26 cm	yellow brown (10 YR 5/6) firm silt loam of medium nut structure, very few roots, large schist rocks present, distinct horizon to
C hor	26+ cm	schist rocks.

Another pit had a deeper B horizon → to 34 cm before colluvial bedrock was encountered.

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Howden's Reserve 1: H.R.1

Howden's Scenic Reserve, Endeavour Inlet

S.16 473488

70 m. lower spur, convex 15°

Exposed to W, N and S, sheltered from E

Virgin hard-beech/kamahi forest

A few hard beech stumps nearby indicate that some logs were cut from this reserve some time in the past.

Soil Profile:

litter	0-1 cm	hard beech leaves and twigs
F & H	1-3 cm	tight network of roots and mycelia and decomposing organic matter, distinct horizon to
A-B hor	3-16 cm	dull yellow orange (10 YR 6/4) very friable silt loam, small crumb structure, roots abundant to 5 cm, below this they are infrequent, charcoal present at 4 cm, indistinct horizon to
B hor	16-40+ cm	yellow brown (10 YR 5/6) firm silt loam, small crumb structure. No stones present, roots to 20 cm.

In one pit no A-B horizon was present, there was a distinct horizon between the mor F & H layer and the yellow brown mineral soil.

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Howden's Reserve 2: H.R.2

Howden's Scenic Reserve, Endeavour Inlet S.16 471502  
 30 m. valley bottom, flat-gently sloping 2-5°  
 Exposed to S, W and NW, sheltered from E  
 Virgin rimu/tawa/kohekohe-silver tree fern forest  
Soil Profile:

litter	0-1 cm	tawa, hinau and kohekohe leaves and twigs intermixed with a network of <i>Hymenophyllum demissum</i> rhizoids
F & H	<0.5 cm	decomposing leaves intermixed with worm casts
A hor	1-20 cm	dark brown (10 YR 3/4) friable silt loam, moderately developed nut structure breaking easily to crumbs and powder, some large schist rocks present, roots present, worms active, distinct horizon to
B hor	20-36 cm	light brown (10 YR 4/4) firm loamy sand, medium nut structure breaking to crumbs, large schist slabs at 36 cm, roots present throughout.

In one pit, B hor of a more typical colour, yellow brown (10 YR 5/6) for this area and of a silt loam texture

Howden's Reserve 3: H.R.3

Howden's Scenic Reserve, Endeavour Inlet S.16 473484  
 140 m. midslope spur, concave 20-25°  
 Exposed to N, W and S, sheltered from E  
 Virgin hard beech-(black beech)/kamahi-toro forest  
Soil Profile:

litter	0-2 cm	beech leaves and twigs
F	2-10 cm	red brown ( ) mat of roots and decomposing leaf material, distinct boundary to
H	10-15 cm	decomposing organic material, mycelia and roots throughout, distinct boundary to
A hor	15-25 cm	yellow brown (10 YR 5/6) firm silt loam, medium sub-angular blocky structure breaking to fine crumbs, small roots to 20 cm, indistinct boundary to
B hor	25-40+ cm	bright yellow brown (10 YR 6/7) firm silt loam, medium nut structure breaking easily to crumbs, no stones in profile.

An extreme rocky variant of this profile was also sampled. The mor humus was shallow (4 cm in depth) and was not able to be separated into distinct layers. Schist rocks were present in the A hor and large schist slabs were encountered at 30 cm.

Howden's Reserve 4: H.R.4

Howden's Scenic Reserve, Endeavour Inlet S.16 475492  
 50 m. lower slope, concave-convex 15°  
 Virgin rimu/tawa-mixed broadleaf forest  
Soil Profile:

litter	0-1.5 cm	leaves and twigs of rimu and tawa
F & H	<0.5 cm	decomposing organic matter in a mat of roots
A hor	2-13 cm	brown (10 YR 4/4) friable loamy sand, small crumb structure, fine roots present, worms active, indistinct boundary to
B hor	13-35+ cm	yellow brown (10 YR 5/7) friable loamy sand, medium nut structure breaking easily to fine crumbs, roots present to 35 cm.

Another soil pit investigated had a shallow A hor. (6 cm in depth) and the texture of the B hor. was a sandy loam.

Howden's Reserve 5: H.R.5

Howden's Scenic Reserve, Endeavour Inlet

S.16: 470487

40 m. lower spur, convex 5°

Exposed to S, W and E, sheltered from N

*Gahnia* sedgeland

2 yrs

Soil Profile:

no litter present

A-B hor 1-15 cm dull yellow brown (10 YR 4/3), firm silt loam of small subangular blocky structure, small schist rocks present, roots confined to top few cm, indistinct horizon to

B hor 15-30+ cm yellow brown (10 YR 5/6) v. firm silty clay loam of small subangular blocky structure, horizon very hard to penetrate with shovel, no roots present.

Sawmill Creek 1: S.C.1

Endeavour Inlet, Queen Charlotte Sound

S16: 458489

30 m. valley, concave 10°

Exposed to E and N, sheltered from W and S

Bracken fernland

16 yrs

Soil Profile:

litter 0-20 cm Bracken fronds and petioles, very moist

F & H 20-23 cm decomposing bracken fronds and petioles

A hor 23-38 cm dark brown (10 YR 3/3) friable silt loam of well developed small nut and crumb structure, worm casts present at surface of mineral horizon, rhizoids throughout, large schist rocks (10 x 6 x 3 cm<sup>3</sup>) present, distinct horizon to

B hor 38-46 cm yellow brown (10 YR 5/6) firm silty loam, well developed medium nut structure, rhizomes present at 42 cm, large schist slabs at 46 cm onwards.

Resolution Bay 1: R.B.1

Resolution Bay, Queen Charlotte Sound

S16: 484459

200 m. upper slope, concave 30-35°

Exposed to E and N, sheltered from W and S

Kamahi/bracken shrubland

20 yrs

*Nothofagus* logs and stumps in plot.Soil Profile:

litter 0-4 cm Bracken fronds and petioles, some kamahi leaves and *Lycopodium volubile* fronds.

F & H 4-6 cm Decomposing organic material, network of fine roots and rhizoids

A hor 6-26 cm bright yellow brown (10 YR 6/8) and some olive brown (2.5 Y 4/4) friable sand, small crumb structure, much mottling, rhizomes abundant, worms present, roots throughout, charcoal present throughout, diffuse boundary to

B hor 26-40 cm yellowish brown (10 YR 5/6) friable silty loam, moderately developed crumb structure, small stones occur from 30 cm onwards, charcoal at 30 cm, bracken rhizomes at 35 cm. Large schist rocks beyond 40 cm.

Olive brown soil distributed along roots and associated with worm tunnels.

Ngaruru Bay 1: N.B.1

Ngaruru Bay Scenic Reserve, Arapawa Island

S.16 485328

150 m. ridge slope, concave 31°

Exposed to N and E, sheltered from W and S

Kanuka forestland

47 yrs

Soil Profile:

litter	0-1 cm	leaves and twigs of kanuka
F & H	1-4 cm	brown black (10 YR 3/2) fibrous duff, fungal hyphae present, integrated with mineral soil of
A hor	4-20 cm	grey yellow brown (10 YR 4/2) friable loamy sand, moderately developed nut structure breaking to crumbs, roots present throughout horizon. Dead bracken rhizomes present in top few cm of horizon (hollow inside). Large weathering rocks present, distinct horizon to
B hor	20-40+ cm	bright yellow brown (10 YR 6/7) v. firm silt loam, medium crumb structure breaking to fine powder. Roots present, large weathering rocks present.

In one pit there was a v. shallow F & H ( < 0.5 cm) over a shallow A horizon of 5 cm depth.

Ngaruru Bay 2: N.B.2

Ngaruru Bay Scenic Reserve, Arapawa Island

S.16 488329

30 m. lower ridge slope, concave 5°

Exposed to E and NE, sheltered from S and W

Kanuka-manuka/fivefinger forestland

50 yrs

Dead kanuka in plot

Soil Profile:

litter	0-1 cm	kanuka and manuka leaves and twigs
A hor	1-14 cm	grey yellow brown (10 YR 4/2), firm silt loam, moderately developed nut structure breaking to fine crumbs, <i>Leptospermum</i> roots throughout, worms present, insect larvae common, indistinct boundary to
A-B hor	14-30 cm	dull yellow brown (10 YR 4/3) firm silty clay loam with well developed nut structure, charcoal present at 26 cm. <i>Leptospermum</i> roots throughout, worms present, dead bracken rhizomes at 20 cm, well defined boundary to
B hor	30-40+ cm	bright yellow brown (10 YR 6/6) v. firm silty clay loam, small nut structure breaking to fine crumbs, no stones.

One pit had an A hor. of 13 cm depth of grey yellow brown silt loam overlying a bright yellow brown B horizon.

Ngaruru Bay 3: N.B.3

Ngaruru Bay Scenic Reserve, Arapawa Island S.16 490324

50 m. low ridge crest, flat 2-3°

Exposed to N, S and E, sheltered from W

Manuka/fivefinger shrubland

43 yrs

Manuka undergoing self thinning

Soil Profile:

L + F + H	0-2 cm	manuka leaves and twigs, isopods present, slight integration of organic matter into
A hor	2-11 cm	grey yellow brown (10 YR 4/2) firm clay loam, moderately developed nut structure breaking into crumbs, roots present, worms and cicada larvae present, indistinct boundary to
B hor	11-30 cm	bright yellow brown (10 YR 6/8) v. firm silt loam, small nut structure breaking to crumbs, some A hor. material integrated due to worm action. Roots throughout, slight organic mottling.

One pit had dark brown (10 YR 3/3) A hor. of silt loam structure and a B hor. of bright yellow brown (10 YR 6/6) firm clay.

Ngaruru Bay 4: N.B.4

Ngaruru Bay Scenic Reserve, Arapawa Island S.16 489329

5 m. valley flat 3°

Exposed to E, sheltered from W, S and N

Tawa/kohekohe/mahoe-silver tree fern tall forest

Disturbance at margin of forest at seaward end where forest abuts onto an old secondary kanuka forest.

Soil Profile:

litter	0-1 cm	kohekohe, mahoe and tawa leaves and twigs with silver tree fern fronds overlying
A hor	1-20 cm	grey yellow brown (10 YR 4/2), firm loamy sand, well developed nut structure breaking to medium sized crumbs, roots present, distinct boundary to
B hor	20-30 cm	bright yellow brown (10 YR 6/6) v. firm silt loam, roots throughout.

One pit at margin under kanuka had shallow A hor. of 2 cm depth overlying a B hor. of yellow brown (10 YR 5/6) firm silt loam.

Ngaruru Bay 5: N.B.5

Ngaruru Bay Scenic Reserve, Arapawa Island S.16 492332

125 m. upper ridge slope, convex 23-27°

Exposed to S and E, sheltered from W and N

Low manuka-spanish heath shrubland

12 yrs

Soil Profile:

L + F + H	0-1 cm	manuka leaves and twigs
A hor	1-6 cm	dull yellow brown (10 YR 5/3) firm silt loam, developed crumb structure, roots and bracken rhizomes present, charcoal present, indistinct boundary to
B hor	6-30 cm	bright yellow brown (10 YR 6/6) firm silty clay loam, moderately developed nut structure breaking to fine crumbs. There is some integration of A hor. material. Schist stones present, roots present to 30 cm.

One pit had a deep F & H layer (1-5 cm) composed of decomposing material with much charcoal, distinct boundary to an A hor. of 14 cm depth of dull yellow brown firm silt loam.

Ngaruru Bay 6: N.B.6

Ngaruru Bay Scenic Reserve, Arapawa Island

S.16 492331

90 m. mid ridge, convex 24-26°

Low open manuka-bracken shrubland

Exposed to S and E, sheltered from W and N

12 yrs

Soil Profile:

litter	0-1 cm	manuka leaves and twigs and bracken fronds and petioles
A hor	1-3 cm	grey yellow brown (10 YR 4/2) firm silt loam, medium crumb structure, charcoal present, roots and bracken rhizomes present, indistinct boundary to
B hor	3-30 cm	bright yellow brown (10 YR 6/6) firm silty loam, moderately developed nut structure breaking to fine crumbs. Small schist rocks present. Bracken rhizomes at 10 cm depth, charcoal present.

One profile had no A horizon.

Ngaruru Bay 7: N.B.7

Ngaruru Bay Scenic Reserve, Arapawa Island

S.16 492330

60 m. lower spur, concave 10-12°

Exposed to S and E, sheltered from N and W

Manuka shrubland (dead and burnt *Nothofagus* trunks present)

13 yrs

Soil Profile:

litter	0-1 cm	bracken fronds and manuka leaves and twigs, charcoal present
F & H	1-3 cm	organic material - similar to F & H under <i>Nothofagus truncata</i> forests
A hor	3-13 cm	dull yellow brown (10 YR 4/3) firm sandy loam, moderate nut structure, roots present, bracken rhizomes at 12 cm, worms present, distinct horizon to
B hor	13-30+ cm	bright yellow brown (10 YR 6/6) v. firm loamy sand, moderate nut structure breaking to large and medium sized crumbs, roots present throughout, small rock fragments present.

Ngaruru Bay 8: N.B.8

Ngaruru Bay Scenic Reserve, Arapawa Island

S.16 485329

130 m. upper spur slope, concave 26° (old slip face)

Exposed to N and E, sheltered from S and W

Kanuka/fivefinger forestland

45 yrs

Soil Profile:

L + F + H	0-2 cm	kanuka, fivefinger and heketara leaves and twigs
A hor	2-18 cm	brown (10 YR 4/4) firm silt loam, well developed moderate nut structure, roots abundant, large worms present, some weathering rocks present, distinct boundary to
B hor	18-24 cm	bright yellow brown (10 YR 6/6) v. firm clay loam, small nut structure, small roots present, large weathering rocks present, indistinct boundary to
C hor	24+ cm	large weathering schist rocks.



Ngaruru Bay 9: N.B.8

Ngaruru Bay Scenic Reserve, Arapawa Island

S.16 489328

50 m. lower slope, convex 23°

Exposed to N and E, sheltered from S and W

Kanuka/fivefinger-heketara forestland

40 yrs

Soil Profile:

L + F + H	0-1 cm	kanuka leaves and twigs, distinct boundary to
A hor	1-11 cm	grey yellow brown (10 YR 5/2) firm sandy loam, well developed nut structure, roots abundant, worms present, charcoal present, distinct horizon to
B hor	11-40+ cm	dull yellow brown (10 YR 5/4) firm loamy sand, well developed moderate nut structure, small weathered stones frequent, large kanuka roots to 30 cm.

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Cockle Cove 1: C.C.1

Cockle Cove Scenic Reserve, Queen Charlotte Sound

S.16 455390

130 m. ridge convex 20-23°

Exposed to S and W, sheltered from N and E

Manuka/fivefinger shrubland

35 yrs

Rotting hard beech trunks present

Soil Profile:

litter	0-1 cm	leaves and twigs of manuka, gorse and fivefinger
F & H	1-2 cm	decomposing organic material
A hor	2-10 cm	dull yellow brown (10 YR 5/4) firm silty loam, medium nut structure breaking to small crumbs, roots abundant, mycelia present, large earthworms present (Megascolecidae) charcoal present, distinct horizon to
B hor	10-40+ cm	yellow brown (10 YR 5/8) firm silty clay loam, moderately developed nut structure breaking easily into crumbs, roots to 25 cm, some incorporation of A hor. due to worm activity, bracken rhizomes at 25 cm, no stones present.

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Cockle Cove 2: C.C.2

Cockle Cove Scenic Reserve, Queen Charlotte Sound

S.16 455388

70 m. lower ridge, convex 25-28°

Exposed to S, sheltered from W, E and N

Pole manuka/fivefinger shrubland

40 yrs

Manuka undergoing self thinning

Soil Profile:

litter	0-2 cm	leaves, twigs and bark of manuka, leaves and twigs of fivefinger
F & H	2-3 cm	mat of roots and decomposing leaf material
B hor	3-40 cm	yellow brown (10 YR 5/6) firm loamy sand, poorly developed nut structure, large schist rocks (14 x 10 x 4 cm <sup>3</sup> ) and smaller fragments throughout, charcoal present and fire reddened schist chips near surface, roots restricted to top 5 cm, mycelia throughout, large schist rocks at 40 cm, decaying bracken rhizomes at 14 cm.

Schist rocks were present at surface and it is difficult to penetrate the soil with a spade.

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Cockle Cove 3: C.C.3

Cockle Cove Scenic Reserve, Queen Charlotte Sound S.16 456387  
 40 m. head of gulley, concave 27-29°

Exposed to S and SW, sheltered from N and E

Degenerating kanuka/mixed coastal broadleaf forestland

55 yrs

Dead kanuka stems and kanuka logs on forest floor

Soil Profile:

litter	0-1 cm	leaves and twigs of kanuka, fronds of silver tree fern
F & H	1-2 cm	decomposing leaf material intermeshed with mycelia
A hor	2-30 cm	dark brown (10 YR 3/3) firm silty loam, medium nut structure, trace of charcoal in top few cms, schist fragments present, roots abundant in top 10 cm, distinct boundary to
B hor	30-40+ cm	bright yellow brown (10 YR 6/8) firm silt loam, medium nut structure, schist chips present, some incorporation of A hor. due to worm activity, kanuka roots ( 1-4 mm diam) throughout.

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Cockle Cove 4: C.C.4

Cockle Cove Scenic Reserve, Queen Charlotte Sound S.16 451385  
 30 m. lower slope, concave-convex 25-27°

Sheltered, enclosed valley

Virgin kohekohe forest

Soil Profile:

litter	0-1 cm	leaves and twigs of kohekohe and supplejack in a tangle of <i>Blechnum filiforme</i> rhizoids
A hor	1-23 cm	dark brown (10 YR 3/3) friable sand, good nut structure breaking to medium and small sized crumbs, small schist fragments present, abundant roots, distinct boundary to
B hor	23-40+ cm	yellow brown (10 YR 5/7) firm silt loam medium nut structure breaking to small crumbs, schist rocks present, roots present to 40 cm.

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Cockle Cove 5: C.C.5

Cockle Cove Scenic Reserve, Queen Charlotte Sound S.16 449389  
 160 m. ridge top, convex 15-18°

Exposed to S and W, sheltered from E and N

Manuka/fivefinger shrubland

37 yrs

Soil Profile:

litter	0-1 cm	leaves and twigs of manuka and fivefinger
A hor	1-15 cm	dark brown (10 YR 3/3) firm loamy sand, well developed nut structure, worm casts present, roots present, decaying bracken rhizome at 15 cm, charcoal throughout, distinct boundary to
B hor	15-40+ cm	yellow brown (10 YR 5/6) firm silt loam, moderately developed nut structure, worm casts present, v. weathered schist fragments throughout.

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Cockle Cove 6: C.C.6

Cockle Cove Scenic Reserve, Queen Charlotte Sound S.16 451385

30 m. ridge slope, convex 27-29°

Exposed to N, E and S, sheltered from W

Very dense manuka shrubland

27 yrs

Dead hard-beech logs on forest floor

Soil Profile:

L + F + H	0-1 cm	leaves and twigs of manuka and kamahi and fronds of <i>Blechnum capense</i>
A hor	1-15 cm	dull yellow brown (10 YR 5/3) firm silt loam, medium nut structure breaking to give fine crumbs and powder, charcoal present, roots present, worms present, distinct boundary to
B hor	15-40 cm	bright yellow brown (10 YR 6/6) soil matrix with worm casts of grey yellow brown (10 YR 5/2), v. firm, dry silt loam, medium nut structure, roots infrequent, no stones present.

Very hard, dry soil; the B hor. was v. difficult to penetrate with the spade.

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Cockle Cove 7: C.C.7

Cockle Cove Scenic Reserve, Queen Charlotte Sound S.16 449384

75 m. mid slope, convex-concave 27-29°

Exposed to S and E, sheltered from N and W

Kanuka forestland

45 yrs

Soil Profile:

litter	<1 cm	kanuka leaves and twigs
A-B hor	1-40 cm	brown (7.5 YR 4/6) firm clay loam, medium nut structure breaking to fine crumbs and powder, schist fragments present throughout, roots present to 30 cm, charcoal distributed throughout to 25 cm in depth, worms present.

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Cockle Cove 8: C.C.8

Cockle Cove Scenic Reserve, Queen Charlotte Sound S.16 447385

80 m. midslope, convex 23-25°

Exposed to S, E and SW, sheltered from N

Kanuka/fivefinger forestland

48 yrs

Soil Profile:

litter	0-1 cm	leaves and twigs of manuka, kanuka and fivefinger
A hor	1-25 cm	dull yellow brown (10 YR 5/4) firm silt loam, well developed medium nut structure breaking to small nuts and crumbs, charcoal in top 5 cm, roots abundant, worms numerous,
A-B	25-27 cm	transition boundary to
B hor	27-40+ cm	yellow brown (10 YR 5/6) v. firm silt loam, medium nut structure breaking to fine crumbs and powder, roots present to 30 cm.

B hor. v. dry and v. difficult to penetrate with a spade.

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Goulter Bay 1: G.B.1

Ridge boundary of Goulter Bay Scenic Reserve, Kenepuru Sound S.16 301394  
 30 m. ridge top, gently undulating 5-7°

Exposed to S, E and N, sheltered from W

Degenerating tall kanuka/mixed broadleaf forest

70 yrs

Decaying hard beech logs near plot

Soil Profile:

litter	0-1 cm	kanuka and heketara leaves and twigs
F & H	1-3 cm	decomposing material intermixed with roots
A hor	3-13 cm	brown (10 YR 4/4) friable loamy sand, medium nut structure breaking to fine crumbs, worms present, roots throughout, schist fragments frequent, charcoal in top 3 cm, indistinct boundary grading into
B hor	13-40+ cm	dull yellow brown (10 YR 5/5) firm silt loam, coarse nut structure breaking to fine nuts and crumbs, schist chips throughout, roots to 40 cm.

Ants in top 10 cm of one soil profile.

Blumine Island 1: B.M.1

Blumine Island Scenic Reserve, Queen Charlotte Sound S.16 511395

110 m. ridge slope, convex 22°

Exposed to W and S, sheltered from E and N

Manuka shrubland

30 yrs

Soil Profile:

litter	0-0.5 cm	manuka leaves and twigs
F & H	0.5-1 cm	decomposing manuka leaves, distinct boundary to
A hor	1-14 cm	brownish black (10 YR 3/2) firm silt loam, medium crumb structure large schist stones present, worms and roots present, distinct boundary to
B hor	14-30+ cm	yellowish brown (10 YR 5/8) v. firm clay loam, medium-small crumb structure, no stones present, roots throughout.

Another pit had an A hor. 20 cm deep of greyish-yellow brown (10 YR 4/2) silty clay loam, with many weathered schist stones in the B hor.

Blumine Island 2: B.M.2

Blumine Island Scenic Reserve, Queen Charlotte Sound S.16 511394

120 m. upper slope, convex 24°

Exposed to S and W, sheltered from N and E

Manuka shrubland

25 yrs

Soil Profile:

L + F + H	0-1.5 cm	manuka leaves and twigs, <i>Lycopodium volubile</i> fronds overlying
A hor	1.5-23 cm	greyish yellow brown (10 YR 4/2) firm clay loam, medium-fine crumb structure, no stones, roots frequent throughout, worms present, distinct horizon to
B hor	23-30+ cm	yellowish brown (10 YR 5/6) firm silty loam, medium crumb structure, no stones, roots present.

Another pit had an A hor. of 16 cm depth.

Blumine Island 3: B.M.3

Blumine Island Scenic Reserve, Queen Charlotte Sound

S.16 507393

60 m. ridge slope, convex 25°

Exposed to N, W and S, sheltered from E

Kanuka-manuka shrubland

32 yrs

Soil Profile:

L + F + H	0-1 cm	manuka and kanuka leaves and twigs
A hor	1-28 cm	brownish black (10 YR 3/1) firm silt loam, medium nut structure, no stones present, charcoal in top few cm, roots present throughout, worms present, indistinct horizon to
B hor	28-30+ cm	yellowish brown (10 YR 5/7) firm silty loam, medium nut structure, stones at 40 cm, roots throughout.

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D'Urville Island 1: D'Urv.1

D'Urville Island Scenic Reserve, Lucky Bay, Catherine Cove

S.10 171745

30 m. lower valley slope, concave 35-40°

Exposed to E and N, sheltered from W and S

Kanuka/kohekohe forestland

58 yrs

Soil Profile:

litter	0-0.5 cm	kanuka leaves and twigs
F & H	0.5-1 cm	black decomposing material
A Hor	1-40+ cm	brown black (10 YR 3/2) firm loamy sand, medium and small subangular blocky structure breaking to medium and small nuts, charcoal present in top 5 cm, roots present throughout, rock fragments present, ants located in top portion of horizon.

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D'Urville Island 2: D'Urv.2

D'Urville Island Scenic Reserve, Lucky Bay, Catherine Cove

S.10 172750

125 m. mid slope, convex-concave 23-25°

Exposed to E and N, sheltered from W and S

Kanuka/kamahi-fivefinger forestland

58 yrs

Soil Profile:

litter	0-1 cm	kanuka and kamahi leaves and twigs
F & H	1-4 cm	tightly matted network of decomposing organic material, roots of kanuka and mycelia, indistinct transition to
A hor	4-6 cm	grey yellow brown (10 YR 5/2) friable sandy clay, small crumbs, distinct boundary to
B hor	6-40+ cm	yellow brown (10 YR 5/6) v. firm silt loam, medium nut structure breaking to small crumbs, kanuka roots throughout, rocks present.

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