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Coexistence, dynamics and disturbance history of
mixed conifer, beech, and hardwood forest,
north Westland

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Mixed conifer, beech and hardwood forests are relatively common in Aotearoa/ New Zealand, but are not well studied. This thesis investigates the coexistence, regeneration dynamics and disturbance history of a mixed species forest across an environmental gradient of drainage and soil development in north Westland.

The aim was to investigate whether conifers, beech and non-beech hardwood species were able to coexist on surfaces that differed in their underlying edaphic conditions, and if so to understand the mechanisms that influenced their regeneration on both poorly drained and well drained soils. The site selected was an area of high tree species diversity on a lowland 0.8 km² post-glacial terrace at the base of Mount Harata in the Grey River Valley.

My approach was to use forest stand history reconstruction at two spatial scales: an intensive *within-plot* study of stand dynamics (chapter 1) and a *whole-landform* approach (chapter 2) that examined whether the dynamics identified at the smaller within-plot scale reflected larger patterns across the terrace.

In **chapter 1**, three large permanent plots (0.3-0.7 ha) were placed at different points along the drainage gradient, one plot situated in each of the mainly well-drained, poorly drained and very poorly drained areas along the terrace. Information was gathered on species age and size structures, spatial distributions of tree ages, species interactions, microsite establishment preferences, patterns of stand mortality, and disturbance history in each plot.

There were differences in stand structure, composition and relative abundance of species found between the well drained plot and the two poorer drained plots. On the well drained site conifers were scarce, the beeches *Nothofagus fusca* and *N. menziesii* dominated the canopy, and in the subcanopy the hardwood species *Weinmannia racemosa* and *Quintinia acutifolia* were abundant. As drainage became progressively poorer, the conifers *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* became more abundant and

occupied the emergent tier over a beech canopy. The hardwoods *W. racemosa* and *Q. acutifolia* became gradually less abundant in the subcanopy, whereas the hardwood *Elaeocarpus hookerianus* became more so.

In the well drained plot, gap partitioning for light between beeches and hardwoods enabled coexistence in response to a range of different sized openings resulting from disturbances of different extent. In the two more poorly drained plots, species also coexisted by partitioning microsite establishment sites according to drainage.

There were several distinct periods where synchronous establishment of different species occurred in different plots, suggesting there were large disturbances: c. 100 yrs, 190-200 yrs, 275-300 yrs and 375-425 yrs ago. Generally after the same disturbance, different species regenerated in different plots reflecting the underlying drainage gradient. However, at the same site after different disturbances, different sets of species regenerated, suggesting the type and extent of disturbances and the conditions left behind influenced species regeneration at some times but not others. The regeneration of some species (e.g., *N. fusca* in the well-drained plot, and *Dacrydium* in the poorer drained plots) was periodic and appeared to be closely linked to these events. In the intervals between these disturbances, less extensive disturbances resulted in the more frequent *N. menziesii* and especially hardwood regeneration. The type of tree death caused by different disturbances favoured different species, with dead standing tree death favouring the more shade-tolerant *N. menziesii* and hardwoods, whereas uprooting created a mosaic of microsite conditions and larger gap sizes that enabled *Dacrycarpus*, *N. fusca* and *E. hookerianus* to maintain themselves in the poorly drained areas.

In **chapter 2**, 10 circular plots (c. 0.12 ha) were placed in well drained areas and 10 circular plots (c. 0.2 ha) in poorly drained plots to collect information on species population structures and microsite preferences. The aims were to reconstruct species' regeneration responses to a range of disturbances of different type and extent across the whole terrace, and to examine whether there were important differences in the effects of these disturbances.

At this landform scale, the composition and relative abundances of species across the drainage gradient reflected those found in chapter 1. There were few scattered conifers in

well drained areas, despite many potential regeneration opportunities created from a range of different stand destroying and smaller scale disturbances.

Three of the four periods identified in chapter 1 reflected distinct terrace-wide periods of regeneration 75-100 yrs, 200-275 yrs and 350-450 yrs ago, providing strong evidence of periodic large, infrequent disturbances that occurred at intervals of 100-200 yrs. These large, infrequent disturbances have had a substantial influence in determining forest history, and have had long term effects on forest structure and successional processes. Different large, infrequent disturbances had different effects across the terrace, with the variability in conditions that resulted enabling different species to regenerate at different times. For example, the regeneration of distinct even-aged *Dacrydium* cohorts in poorly drained areas was linked to historical Alpine Fault earthquakes, but not to more recent storms. The variation in the intensity of different large, infrequent disturbances at different points along the environmental drainage gradient, was a key factor influencing the scale of impacts. In effect, the underlying edaphic conditions influenced species composition along the drainage gradient and disturbance history regulated the relative abundances of species.

The results presented here further emphasise the importance of large scale disturbances as a mechanism that allows coexistence of different tree species in mixed forest, in particular for the conifers *Dacrydium*, *Dacrycarpus* and the beech *N. fusca*, by creating much of the environmental variation to which these species responded. This study adds to our understanding of the effects of historical earthquakes in the relatively complex forests of north Westland, and further illustrates their importance in the Westland forest landscape as the major influential disturbance on forest pattern and history.

These results also further develop the 'two-component' model used to describe conifer/angiosperm dynamics, by identifying qualitative differences in the impacts of different large, infrequent disturbances across an environmental gradient that allowed for coexistence of different species. In poorer drained areas, these forests may even be thought of as 'three-component' systems with conifers, beeches and hardwoods exhibiting key differences in their regeneration patterns after disturbances of different type and extent, and in their microsite preferences.

Keywords: forest disturbance, Alpine Fault, earthquakes, storms, coexistence, regeneration dynamics, conifer, beech, hardwood, north Westland, Aotearoa/ New Zealand.

CONTENTS

| | Page |
|--|--------------|
| ABSTRACT | ii |
| List of Tables | vii |
| List of Figures | viii |
| List of Plates | ix |
| CHAPTER ONE | 1 |
| Dynamics of mixed conifer/ beech/ hardwood forest, north Westland, Aotearoa/ New Zealand. | |
| Abstract | 1 |
| 1. Introduction | 4 |
| 1.1 Succession or coexistence? | 5 |
| 1.2 Gaps and regeneration | 6 |
| 1.3 Landscape and soils | 8 |
| 1.4 Disturbance and gradients | 9 |
| 1.5 Study aims | 10 |
| 2. Methods | 12 |
| 2.1 Study site | 12 |
| 2.2 Plot selection | 14 |
| 2.3 Stand structure | 15 |
| 2.4 Stand history | 16 |
| 2.5 Spatial analysis of tree age distributions | 17 |
| 2.6 Spatial patterns of tree dispersion | 18 |
| 2.7 Spatial interactions between species | 19 |
| 2.8 Patterns of microsite establishment | 19 |
| 2.9 Spatial patterns of mortality | 20 |
| 2.10 Soil and drainage patterns | 21 |
| 3. Results | 22 |
| 3.1 Very Poorly Drained Stand - PLOT A | 22 |
| 3.1.1 Stand composition, structure and soils | 22 |
| 3.1.2 Stand size and age structure | 23 |
| 3.1.3 Spatial distribution of tree ages | 26 |
| 3.1.4 Microsite differences within each group | 37 |
| 3.1.5 Patterns of tree ring release and species recruitment | 40 |
| 3.1.6 Current regeneration patterns | 43 |
| 3.2 Poorly Drained Stand - PLOT B | 44 |
| 3.2.1 Stand composition, structure and soils | 44 |
| 3.2.2 Stand size and age structure | 45 |
| 3.2.3 Spatial distribution of tree ages | 47 |
| 3.2.4 Spatial patterns and species interactions | 58 |
| 3.2.5 Spatial patterns of tree mortality | 60 |
| 3.2.6 Patterns of tree ring release and disturbance history | 63 |
| 3.2.7 Soil variability and microsite establishment | 64 |
| 3.2.8 Mode of tree death and current regeneration patterns | 65 |

| | | |
|--|---|-----|
| 3.3 | Well Drained Stand - PLOT C | 70 |
| 3.3.1 | Stand composition, structure and soils | 70 |
| 3.3.2 | Stand size and age structure | 71 |
| 3.3.3 | Spatial distribution of tree ages | 74 |
| 3.3.4 | Overhead cover and microsite preferences | 79 |
| 3.3.5 | Patterns of tree ring release and disturbance history | 80 |
| 3.3.6 | Current regeneration patterns | 84 |
| 3.4 | Synthesis Of Forest History In The Three Plots | 87 |
| 4. | Discussion | 90 |
| 4.1 | Species recruitment patterns | 90 |
| 4.2 | Disturbances and microsite heterogeneity | 96 |
| 4.3 | Drainage and conifer distributions | 99 |
| 4.4 | Patterns of stand development | 102 |
| 4.5 | Summary | 106 |
| CHAPTER TWO | | 107 |
| Effects of different large, infrequent disturbances on coexistence in mixed conifer/ beech/ hardwood forest, north Westland, Aotearoa/New Zealand. | | |
| Abstract | | 107 |
| 1. Introduction | | 109 |
| 1.1 | Landscape disturbance dynamics - coexistence and succession | 109 |
| 1.2 | Large, infrequent disturbances and vegetation dynamics in mixed species forests in Aotearoa | 110 |
| 1.3 | Background to mixed forest regeneration in north Westland | 112 |
| 1.4 | Study aims | 113 |
| 2. Methods | | 114 |
| 2.1 | Site selection | 114 |
| 2.2 | Plot selection | 114 |
| 2.3 | Stand dynamics | 116 |
| 2.4 | Microsite patterns and soil drainage | 117 |
| 2.5 | Plot classification | 117 |
| 3. Results | | 118 |
| 3.1 | Combined age structures across the terrace | 118 |
| 3.2 | Microsite establishment patterns | 126 |
| 3.3 | Probable causes of the large infrequent disturbance events | 127 |
| 4. Discussion | | 128 |
| 4.1 | Identifying the nature of past disturbance events | 128 |
| 4.2 | Differentiating earthquake and storm effects | 130 |
| 4.3 | Drainage and microsite influences | 133 |
| 4.4 | Regeneration patterns in well-drained plots | 134 |
| 4.5 | Regeneration patterns in poorly-drained plots | 135 |
| 4.6 | Coexistence between conifers, beeches and hardwoods | 137 |
| CONCLUDING SUMMARY | | 141 |
| Acknowledgments | | 144 |
| References | | 145 |
| Appendix | | 162 |

LIST OF TABLES

CHAPTER ONE

| Table | Page |
|---|------|
| 1 No. trees in different height tiers, basal area and no. identified dead stems in plot A. | 22 |
| 2 No. trees and age range of different groups in plot A identified after spatial analysis. | 30 |
| 3 Patterns of association between different age groups derived from the function $K12(t)$. | 36 |
| 4 No. trees of each species that established on different microsites in plot A. | 37 |
| 5 Analysis of organic matter content of 4 soil pits across a transect in plot A. | 39 |
| 6 Comparison of no. saplings and seedlings of different species on different microsites. | 43 |
| 7 No. trees in different height tiers, species basal area, and identified dead stems in plot B. | 44 |
| 8 No. trees and age range of different groups in plot B identified after spatial analysis. | 56 |
| 9 No. trees for each of the most abundant species in overhead cover classes in plot B. | 58 |
| 10 Patterns of spatial dispersion for trees and saplings (>30 individuals). | 59 |
| 11 Patterns of association between different species derived from the function $K12(t)$. | 60 |
| 12 Spatial relationships of trees and saplings with different modes of tree death in plot B. | 61 |
| 13 Comparison of no. trees of species on different elevated and non-elevated microsites. | 65 |
| 14 Comparison of no. saplings and seedlings of different species on different microsites. | 66 |
| 15 No. trees in different height tiers, species basal area, and identified dead stems in plot C | 70 |
| 16 No. trees and age range of different groups in plot C identified after spatial analysis. | 79 |
| 17 No. trees of each species that established on different microsites in plot C. | 79 |
| 18 No. trees for each of the most abundant species in overhead cover classes in plot C. | 80 |
| 19 Comparison of no. saplings and seedlings of different species on different microsites. | 85 |
| 20 Approximate timing of disturbances that occurred in more than one plot that initiated widespread establishment of the main tree species on differently drained surfaces. | 88 |

CHAPTER TWO

| | |
|--|-----|
| 1 Basal area (m^2/ha) and stem density per ha (≥ 5 cm dbh) in the 4 groups of plots. | 125 |
| 2 Comparison of no. trees (≥ 5 cm dbh) of species on different microsites in the 4 groups. | 127 |

APPENDIX

| | |
|---|-----|
| A1 Best fit regressions for estimating age (y) from diameter at breast height for dominant overstorey species in plot A. | 169 |
| A2 Patterns of spatial dispersion for trees and saplings in plot A. | 170 |
| B1 Best fit regressions for estimating age (y) from diameter at breast height for dominant overstorey species in plot B. | 170 |
| B2 Seedlings on logs at different stages of breakdown by decay class in plot B. | 171 |
| C1 Best fit regressions for estimating age (y) from diameter at breast height for dominant overstorey species in plot C. | 171 |
| D1 Mean annual ring width increment rates (cm/yr) for canopy and emergent species across the terrace (Table 5 from Ulrich <i>et al.</i> 1999) | 172 |
| E1 Horizonation description and classification (after Stewart <i>et al.</i> 1993), overall depth of soils in 20 circular plots across the terrace. | 173 |
| E2 Basal area (m^2/ha) and stem density per ha (≥ 5 cm dbh) in the 20 individual plots. | 174 |
| E3 No. trees that established on logs in all poorly drained plots. | 174 |

LIST OF FIGURES

CHAPTER ONE

| Figure | Page |
|--|------|
| 1 Location map of Mount Harata study area, north Westland, South Island, with the spatial extent of forest types across different landforms identified by Stewart <i>et al</i> (1993). | 13 |
| 2 Relative frequency (%) of cores in distance classes representing distance from pith. | 16 |
| 3 Age and diameter- class frequency distributions for the overstorey species in plot A. | 25 |
| 4 Age-class frequency distribution for all tree ages combined in plot A. | 26 |
| 5 Spatial correlograms of tree ages for overstorey species in plot A. | 27 |
| 6 Stem maps and age-class frequency distributions for different <i>Dacrydium</i> age groups. | 31 |
| 7 Stem maps and age-class frequency distributions for different <i>Dacrycarpus</i> age groups. | 32 |
| 8 Stem maps and age-class frequency distributions for different <i>N. menziesii</i> age groups. | 33 |
| 9 Stem maps and age-class frequency distributions for different <i>N. fusca</i> age groups. | 34 |
| 10 Stem maps and age-class frequency distributions for different <i>E. hookerianus</i> age groups. | 35 |
| 11 Stem map of live and dead <i>L. bidwillii</i> and <i>P. hallii</i> . | 36 |
| 12 Temporal distribution of growth releases in each decade over last 220 yrs. | 41 |
| 13 <i>N. menziesii</i> cores in plot A showing substantial synchronous growth releases | 42 |
| 14 Age and diameter- class frequency distributions for the main overstorey species in plot B. | 48 |
| 15 (a) Age-class frequency distribution, & (b) spatial correlogram, for all tree ages combined | 49 |
| 16 Spatial correlograms of tree ages for <i>Dacrydium</i> , <i>Dacrycarpus</i> and <i>N. menziesii</i> . | 50 |
| 17 Stem maps and age-class frequency distributions for different <i>Dacrydium</i> age groups. | 53 |
| 18 Stem maps and age-class frequency distributions for different <i>Dacrycarpus</i> age groups. | 54 |
| 19 Stem maps for different <i>N. menziesii</i> age groups. | 55 |
| 20 Stem map for <i>N. fusca</i> in plot B. | 56 |
| 21 Stem maps for <i>W. racemosa</i> , <i>Q. acutifolia</i> , <i>E. hookerianus</i> and <i>P. ferruginea</i> . | 57 |
| 22 Distribution of tree death by mode throughout plot B. | 62 |
| 23 Temporal distribution of growth releases in each decade over last 280 yrs. | 64 |
| 24 Sapling maps of different species. | 68 |
| 25 Age and diameter- class frequency distributions for the main overstorey species in plot C. | 73 |
| 26 Age-class frequency distribution for all tree ages combined in plot C. | 74 |
| 27 Spatial correlograms of tree ages for all species combined, <i>N. fusca</i> , <i>N. menziesii</i> and <i>W. racemosa</i> . | 76 |
| 28 Stem maps and age-class frequency distributions for different <i>N. fusca</i> age groups. | 77 |
| 29 Stem maps and age-class frequency distributions for different <i>N. menziesii</i> age groups. | 77 |
| 30 Stem maps and age-class frequency distributions for different <i>W. racemosa</i> age groups. | 78 |
| 31 Stem maps and age-class frequency distributions for different age <i>Q. acutifolia</i> groups. | 78 |
| 32 Temporal distribution of growth releases in each decade in the last 240 yrs. | 81 |
| 33 Spatial distribution of uproots and dead standing tree death > 35 cm dbh. | 83 |
| 34 Size-class frequency distribution of uprooted <i>N. fusca</i> and other species c. 90 yrs ago. | 84 |
| 35 Map of beech and hardwood saplings in plot C. | 86 |

LIST OF FIGURES (Continued)

CHAPTER TWO

| Figure | Page |
|--|------|
| 1 Age-class frequency distributions for overstorey species for all terrace plots combined. | 119 |
| 2 Ordination diagram of plots, with plots grouped together that were similar in their age structures and spatial location. | 120 |
| 3 Age-class frequency distributions of combined tree ages for each of the 4 Plot Groups identified from Fig. 2. | 123 |
| 4 Map of the 4 Groups of plots identified from Fig. 2 showing the extent of the disturbance events. | 124 |

APPENDIX

| Figure | Page |
|--|--------|
| B1 Stem maps and age-class distributions for <i>N. menziesii</i> in plot B from cluster analysis. | 170 |
| C1 <i>N. menziesii</i> cores in plot C showing substantial synchronous growth releases | 171 |
| C2 Cores able to be cross-matched from plot C with releases and chronology produced by Vittoz (unpubl data) as part of a wider study into earthquake impacts this century in north Westland. | 172 |
| E1 Age-class frequency distributions for overstorey species on well drained plots. | 175-76 |
| E2 Size class distributions of overstorey species in the well drained terrace plots. | 177-78 |
| E3 Age-class frequency distributions for overstorey species on poorly drained plots. | 179-80 |
| E4 Size class distributions of overstorey species in the poorly drained terrace plots. | 180-81 |

LIST OF PLATES

CHAPTER ONE

| Plate | Page |
|---|------|
| 1 Stand structure in a poorly drained area with <i>Dacrycarpus</i> and <i>Dacrydium</i> emergent over a <i>N. fusca</i> and <i>N. menziesii</i> canopy. | 11 |
| 2 Residue after ignition of peats from different soil pits along a transect in plot A. | 39 |
| 3 <i>Dacrycarpus</i> and <i>Dacrydium</i> saplings on wet forest floor sites in plot B. | 69 |
| 4 <i>N. fusca</i> saplings and small trees on a recent uproot mound in plot B. | 69 |

APPENDIX

| Plate | Page |
|---|------|
| 5 Pit 1 - plot C Soil Pit - Ahaura series. | 162 |
| 6 Pit 2 - plot C Soil Pit - Ahaura series. | 163 |
| 7 Pit 1 - plot B Soil Pit - Rotokuhu series. | 164 |
| 8 Pit 2 - plot B Soil Pit - Peaty Gley. | 165 |
| 9 Pit 3 - plot A Soil Pit - Kini series. | 166 |
| 10 Pit 4 - plot A Soil Pit - Rotokuhu series. | 167 |

CHAPTER ONE

Dynamics of mixed conifer/ beech/ hardwood forest, north Westland, Aotearoa/ New Zealand.

Abstract

I investigated the dynamics of conifers, beeches and hardwoods to see whether they were stably coexisting in an old-growth temperate rainforest in north Westland, Aotearoa/ New Zealand. I reconstructed the stand history of three mixed species stands across a soil drainage gradient by examining tree population structures, spatial analyses of tree age distributions, microsite preferences, species interactions and disturbance history on an 0.8 km² post-glacial terrace, from well drained soils on the terrace edge, to poorly and very poorly drained soils towards the terrace centre. The aims were to examine the role of disturbances in influencing underlying species distribution patterns along the drainage gradient, and to determine whether the main overstorey species (the emergent conifers *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, canopy beech *Nothofagus fusca*, *N. menziesii* and subcanopy non-beech hardwoods *Weinmannia racemosa*, *Quintinia acutifolia* and *Elaeocarpus hookerianus*) were successfully able to replace themselves.

I found species distributions were influenced by the underlying drainage gradient, and there were differences in stand structure and composition between well- and poorly-drained surfaces. On the well drained site, *N. fusca* and *N. menziesii* were dominant in the canopy, *W. racemosa* and *Q. acutifolia* were abundant in the subcanopy, and conifers were scarce and scattered. On poorer drained sites, *Dacrydium* and *Dacrycarpus* were abundant and typically emergent over a beech dominated canopy with hardwoods prevalent in the subcanopy. Hardwood composition also changed as drainage deteriorated with *E. hookerianus* becoming more abundant with *W. racemosa* and *Q. acutifolia* less so.

Where they were locally abundant, all the main overstorey species showed population structures suggesting they successfully regenerated at different times over the last 400 yrs. However, individual species had different sets of regeneration requirements, and were able to coexist by differential establishment after disturbances of different extent across the drainage gradient.

In the poorer drained areas, the long-lived *Dacrydium* was mostly found in discrete, relatively even-aged patches (often $> 1000 \text{ m}^2$) in response to large disturbances. There have been relatively few *Dacrydium* trees recruited into the canopy in the last 200 yrs. The shorter-lived *Dacrycarpus* had more frequent and recent establishment than *Dacrydium*, trees were recruited into the canopy after large disturbances and in a gap-phase manner after smaller and more frequent disturbances. On well-drained sites, the scattered trees and saplings of both conifer species were restricted to wet forest floor depressions.

Nothofagus fusca also had discontinuous age structures in poorer drained areas and groups of similarly-aged trees were found on elevated sites. Intermittent *N. fusca* regeneration occurred after extensive uprooting in the poorly drained plot, and, in the absence of competing hardwoods in the very poorly drained plot, more frequent regeneration occurred in smaller canopy openings. On the well drained site, the *N. fusca* population comprised two even-aged patches of different age; the population was dominated by an extensive even-aged patch that established following blowdown c. 100 yrs ago. *Nothofagus menziesii* had more all-aged population structures than *N. fusca* across the drainage gradient. Regeneration occurred in a range of patch sizes in response to disturbances of different extent and type.

The subcanopy hardwood *W. racemosa* had all-aged populations in both the well drained and the poorly drained plot indicating continual patterns of stem recruitment, particularly during periods of less extensive disturbances at times when *N. fusca* and conifer recruitment was comparatively low. *Quintinia acutifolia* trees were recruited after a range of disturbances on the well-drained site particularly on rotting stumps, and in the poorly drained plot establishment occurred in small gaps formed by the death of single trees. In both poorer drained plots, *E. hookerianus* trees established on forest floor sites and were periodically recruited into the overstorey in response to canopy openings along with *Dacrycarpus*.

Evidence from tree population structures, annual growth-ring releases and the spatial distribution of tree ages indicated three major periods of synchronous establishment following disturbances that occurred in more than one plot: 275-300 yrs, 190-200 yrs and 100-125 yrs ago. An older pulse of establishment 375-425 yrs ago was identified from population age structures and the spatial distribution of tree ages. Species regeneration patterns differed after these different events in the following ways:

1. There was differential species establishment in response to the same disturbance across the plots. This reflects the strong gradient in drainage and soil development across the terrace. Following a large disturbance c. 275-300 yrs ago, *N. fusca*, *N. menziesii*, *Q. acutifolia* and *W. racemosa* regenerated on the well drained site, and regeneration of conifer species, *Dacrydium*, *Dacrycarpus*, *Liboced. Podocarpus hallii*, occurred in the very poorly drained plot.

2. Different suites of species established after different disturbances on the same site. On the very poorly drained surface following the extensive pulse of conifer regeneration 275-300 yrs ago, subsequent and less extensive disturbances resulted in mainly *N. menziesii* and *N. fusca* regeneration, as better drained microsites became available, along with the hardwood *Elaeocarpus hookerianus*.

3. The type of tree death and the resulting microsite conditions influenced the establishment of different sets of species at different times. Following standing tree death in the poorly drained plot, the relatively shade-tolerant species *N. menziesii*, *W. racemosa* and *Q. acutifolia* established together during a period of less extensive disturbances 100-300 yrs ago. After more extensive uprooting at the same site in the last 100 yrs, *Dacrycarpus*, *E. hookerianus*, *N. fusca* and *N. menziesii* were recruited into the overstorey in abundance, suggesting species partitioned establishment sites with respect to the amount of overhead cover.

4. After the same disturbance, species partitioned establishment sites according to substrate drainage characteristics (e.g, logs and mounds versus forest floor, and within forest floor microsites possibly along a gradient of peat texture) with conifers and *E. hookerianus* confined to forest floor sites often around uproot pits, and the beeches and other hardwoods on elevated sites.

These results suggest that species coexist by: (1) differential response to disturbances of varying extent, (2) fine-scale differences in the regeneration niche with conifers on poorly drained sites (forest floor, pit edges) and beeches and hardwoods on better drained sites (logs, mounds, and stumps), and (3) the availability of suitable microsites resulting from different forms of tree death.

Keywords:

Disturbance, coexistence, drainage gradient, regeneration niche, beech, conifer, hardwoods, mixed species forest, spatial patterns, microsites, north Westland, Aotearoa/ New Zealand.

Nomenclature:

Allan (1961) with changes suggested by Connor and Edgar (1987) and Hill and Jordan (1993).

1. INTRODUCTION

One of the interesting questions in Southern Hemisphere forests surrounds the dynamics between the broad groups of conifers and angiosperms; specifically, are the southern conifers being replaced by angiosperms and whether it is possible to determine if replacement processes are happening fast enough to be detectable (Enright *et al.* 1995).

In Aotearoa/New Zealand, angiosperms have typically been divided into two different forest types, the beech (*Nothofagus*) species and broadleaved non-beech hardwoods (Wardle, 1991). This is due to the distinct set of morphological, biological and ecological attributes that set beech apart from other angiosperms, such as differences in growth form, canopy position, longevity, pollination vectors, seed type and dispersal mechanisms (Wardle, 1991; McGlone *et al.* 1996) and mycorrhizal associations (Baylis, 1980; Francis and Read, 1994). Dynamics between beeches, hardwoods and conifers where they co-occur have been traditionally viewed as unstable in Aotearoa, and most research into the dynamics of these mixed stands has been addressed from an invasion/succession perspective (Cockayne, 1926; Wardle, 1980; June, 1982; Allen, 1987; Rogers, 1989; Haase, 1989). This may also be in part due to long-standing biogeographical debates over the disjunct distributions of some of these species (Cockayne, 1926; Wardle, 1963, 1980, 1991; June, 1982; McGlone, 1985; Allen, 1988; Haase, 1990; Wardle and Lee, 1990; Leathwick, 1995, 1998).

Nevertheless, the interactions between conifers, beeches and hardwoods are unclear and poorly understood (Ogden and Stewart, 1995; Ogden *et al.* 1996), despite these mixed stands covering over 1 million hectares across a range of landforms, particularly at low elevations (below 600 m) (Wardle, 1984; Newsome, 1987). Moreover, there has been a general lack of research into whether species are coexisting or whether replacement processes are occurring in these forests (*cf* Lusk and Smith, 1998). There are few studies that have extensive age and spatial information on the regeneration dynamics of these groups of species where they co-occur, especially on lowland terrace landforms and along environmental gradients (Veblen and Stewart, 1981, 1982; Stewart, 1986; Allen, 1988; Rogers, 1989), and in lowland stands where the conifers, *Dacrydium cupressinum* (rimu) and/or *Dacrycarpus dacrydioides* (kahikatea) (both Podocarpaceae), are a major component (*cf* June 1982; Duncan, 1991, 1993; Lusk and Smith, 1998).

1.1 Succession or coexistence?

Historical interpretations of observed discontinuities in conifer size structures led to ideas that conifers were being replaced by more evolutionary advanced angiosperms (Cockayne, 1928, Wormsley, 1958, Robbins, 1962). Climate change was proposed as one mechanism to account for the apparent replacement of conifers by angiosperms (Holloway, 1954; Wardle, 1963; June, 1982). However, other workers noted that size discontinuities in conifer populations were not unusual and could be explained by alternative local mechanisms, such as periodic establishment in response to increased light availability in the canopy (Whitmore, 1966; Gray 1975; Clayton-Greene, 1977).

Other workers noted the apparent variation in the distribution and abundance along environmental gradients between conifers and angiosperms, and partitioning of environmental conditions was hypothesised to promote coexistence instead of succession (Regal, 1977; Bond, 1989). Bond's classic 'tortoise and hare' analogy described the dynamics between the generally slower growing, longer-lived conifers and the faster growing angiosperms. Functional constraints on conifer growth rates restrict conifers to sites, or successional stages, which lack intense competition in the regeneration phase; therefore these groups can coexist as the angiosperm (hares) capture the more favourable sites, whilst the conifers (tortoises) are more restricted in their distributions and slowly plod away on more infertile sites. However, in Aotearoa, conifers can also regenerate on relatively fertile alluvial surfaces, landslide debris or recent ash deposits (McKelvey, 1963; Wardle, 1974; Veblen and Stewart, 1982; Stewart and Rose, 1989; Duncan, 1993), and have been described as 'long-lived pioneers' that can occupy sites for many centuries after establishment following large disturbances (Ogden and Stewart, 1995). It is not uncommon for two or three generations of angiosperms to grow up and die during the lifespan of one long-lived conifer.

An alternative explanation of coexistence has therefore been proposed that describes mixed conifer and angiosperm stands as 'two-component' systems, where groups occupy different strata of the forest and exhibit different regeneration patterns in the same stands in response to natural disturbances (Veblen and Stewart, 1982; Ogden and Stewart, 1995). Under this model, conifers and angiosperms regenerate in response to natural disturbances of different scales (Ogden, 1985; Ogden and Stewart, 1995). The emergent conifers typically have discontinuous age and size populations consistent with a light-demanding regeneration response to infrequent, large-scale disturbances, whereas the broadleaved subcanopy and canopy angiosperms usually have less size discontinuities and

all-aged structures suggesting more continual recruitment in response to more frequent disturbances (Ogden *et al.* 1996). In this respect, the 'two-component' model may not be entirely mutually exclusive from the 'tortoise and hare' hypothesis of coexistence; in that large disturbances could provide an equivalent release for conifers from intense angiosperm competition in the juvenile phase allowing them to successfully regenerate, as poor environmental conditions are predicted to do (Bond 1989).

Coexistence theory is premised around the idea of different species having a different *niche*, which is a multi-dimensional concept describing an individual species need and use of resources, its environmental tolerance, and its habitat requirements (Hutchinson, 1957, 1959). Species avoid competitive-exclusion (*sensu* Gause, 1934) and generally coexist by inhabiting different niches in the same environment. Species have a *fundamental* niche where they can potentially inhabit, and a *realised* niche where they may be restricted by competition from other species, by physiological limitations in response to environmental conditions, chance occurrences, or by biogeographical influences (Hutchinson, 1957; Crawley, 1997). Where different species can potentially occupy the same niche in the same environment, variability in disturbance regimes (frequency, intensity and type) can allow for coexistence by providing much of the variation in light and soil conditions that species respond to differentially (Connell, 1978; Huston, 1979).

The influence of natural disturbances in structuring forest communities has been a key area of research in Aotearoa, and other southern lands, in understanding processes of succession, replacement, community composition and dynamics (Foweraker, 1929; Hutchinson, 1932; Veblen and Ashton, 1978; Veblen and Stewart, 1982; Ogden, 1985; Stewart, 1986; Veblen and Lorenz, 1987; Read and Hill, 1988; Burns, 1991, 1993; Lara, 1991; Lusk and Ogden, 1992; Veblen *et al.* 1992; Duncan 1993; Ogden *et al.* 1996). The effects of disturbances that occur across different parts of the landscape at different times create a spatial mosaic of patches that are in a constant state of dynamic change. This has given rise to the patch dynamics perspective in community ecology where disturbances influence the availability of resources to plants through mortality, and affect interactions between different species, either at a fine scale (e.g., canopy gaps), a stand scale, the landscape level or at a regional scale (Pickett and Thompson; 1978; Runkle, 1982; White and Pickett, 1985; Veblen, 1992; Wells, 1998).

1.2 Gaps and regeneration

Under the patch dynamics model, species have been characterised as having a regeneration mode in response to different disturbances: *catastrophic*, *gap-phase*, and

continuous (Veblen and Stewart, 1980; Veblen, 1992). Inferences into mixed species dynamics can be gained from examination of different species regeneration modes, and close examination of different species regeneration patterns using analysis of stand age structures and the spatial distributions of tree ages (Henry and Swan, 1974; Oliver and Stephens, 1977; Duncan and Stewart, 1991). Species dependent on *catastrophic* disturbance mostly exhibit an even-aged population structure over large areas in response to the sudden release in resources caused by these events (Veblen and Stewart, 1980; Veblen, 1992). *Gap-phase* regeneration refers to species that reach the canopy in smaller canopy openings caused by the death of few trees (e.g., gaps $< 1000 \text{ m}^2$ and < 10 treefalls - Rebertus and Veblen, 1993); and this can be recognised in smaller patch sizes and less discontinuities in age structures. Species that can respond to very small openings or grow up under the canopy can be said to show a *continuous* mode of regeneration. However, these are not fixed modes as species can show different regeneration patterns in the presence and absence of other species across environmental gradients (Veblen, 1989; Veblen *et al.* 1992).

Aside from a species regeneration *mode*, at a finer scale species can be said to have a regeneration *niche* that they occupy after disturbance (*sensu* Grubb, 1977). Disturbances influence coexistence and species diversity by providing much of the environmental variation to which species respond differentially, particularly in the regeneration niche in terms of microsite type and availability (Grubb, 1977; Whittaker and Levin, 1977; Duncan, 1993). Differences in microsite establishment preferences can enable species to coexist, with elevated and non-elevated microtopography providing a mosaic of regeneration opportunities in time and space, and the availability of certain microsites can allow species to establish at the edge of their environmental tolerance ranges where ordinarily they would be excluded (Grubb, 1977; Harper, 1977; Beatty, 1984; Nakashizuka, 1989; Adams and Norton, 1991; Putz and Sharitz, 1991; Duncan, 1993; Gray and Spies, 1997).

The spatial and temporal effects of disturbances can also maintain species diversity by creating heterogenous light conditions after treefall. This has a spatial dimension in the regeneration niche in terms of light availability from gap size and within-gap position, with species coexisting by partitioning a broad gradient from gap centre (shade intolerance) to gap understorey or edge (relative shade tolerance) (Ricklefs, 1977; Hartshorn, 1978; Denslow, 1980; Orians, 1982; Brokaw, 1985; Swaine and Whitmore, 1988; Whitmore, 1989; Runkle *et al.* 1995; Runkle *et al.* 1997; but see Brown and Whitmore, 1992; Sipe and Bazzaz, 1995; Busing and White, 1997). There is also a temporal dimension with the influence of changing conditions in gaps, due to the age of gaps and the ability of species to survive periods of suppression (Poulson and Platt, 1989; Runkle *et al.* 1995).

However, other workers argue that the concept of the regeneration niche does not by itself provide a complete explanation for coexistence in mixed conifer/angiosperm stands, and differences in species life histories expressed during the adult stages need to be considered (Lusk and Smith, 1998). Species that persist due to longer life-spans may compensate for lower juvenile survivorship as sooner or later sporadic opportunities for recruitment will occur (Shmida and Ellner, 1984; Veblen, 1986), an explanation invoked by Lusk and Smith (1998) for the coexistence of scattered, long-lived conifer *Dacrydium* trees in a well-drained mixed species hillslope forest in south Westland dominated by beech and hardwoods.

1.3 Landscape and soils

At a broad regional scale, species distributions are a reflection of variation in abiotic gradients such as climate, latitude, altitude, aspect, slope, landform, parent material, soils and drainage (Whittaker, 1956; Wardle, 1984; Huston, 1994). In Westland, Aotearoa, past studies have demonstrated a close relationship between vegetation patterns with different landforms and stages of soil development (Wardle, 1977; Reif and Allen, 1988; DeVelice *et al.* 1988, Norton and Leathwick, 1990; Stewart *et al.* 1993). At a landscape level, beech and hardwood species dominate on hillslopes and better drained soils, and conifers occur more frequently on poorly drained sites, particularly on terraces (P. Wardle, 1980; J. Wardle, 1984; Smith and Lee, 1984; Stewart *et al.* 1993; Leathwick, 1995). Increasing surface age and leaching of nutrients under high rainfall regimes result in corresponding changes in vegetation observed in soil chronosequences, with conifers becoming dominant in deep peat filled depressions or gley podsol soils in south Westland (Smith and Lee, 1984; Sowden, 1986).

In Westland, drainage is a key environmental variable in influencing soil development and forest pattern (Mew, 1975; Simmons, 1982; Rogers 1995; Almond, 1997), and there appears to be a good relationship between soil drainage on terraces and the vegetation sequence, with soil fertility being less important than drainage in determining forest pattern (Mew, 1975). The general pattern of soil development with age goes from free-draining alluvial and colluvial sediments, to yellow-brown earths on recent terraces and river flats (Ross *et al.* 1977). Changes in soil permeability with increasing rainfall promote greater leaching and podsolisation as soils develop (Tonkin *et al.* 1985). Gley podsoles occur on the flat surfaces of intermediate and higher terraces, and on older terraces soils are generally leached and poorly drained in areas, often composed of gley soils, gley

podsoles and peats (Mew, 1975; Mew and Leamy, 1977). The distribution of different soils on these terrace landforms is complex, often passing from one to another in less than a metre (Campbell and Mew, 1986). The explanation for this heterogeneity is due to differences in parent material, topography, geomorphology and vegetation; disturbance also truncates soil development by retarding or redirecting soil pedogenesis after the uprooting of trees and associated soils (Campbell and Mew, 1986; Adams and Norton, 1991; Stewart *et al.* 1993).

Forest composition in relation to landforms and soil types has been described at various sites in north Westland, with changes in species composition reflecting increasing soil development and deteriorating drainage (Ross *et al.* 1977). The *Dacrycarpus* - *Nothofagus fusca* (red beech - Nothofagaceae) forest type reaches its maximum development on recent alluvial deposits of river flats, and fertile silty loams on low terraces and valley floors (Morris, 1959; Mew, 1975; Ross *et al.* 1977). *Nothofagus menziesii* (silver beech) is found on wetter, poorly drained terraces, and on the more poorly drained intermediate and high terraces *Dacrydium*, *Libocedrus bidwillii* (kaikawaka - Cupressaceae), and *Weinmannia racemosa* (kamahi - Cunionaceae) are common (Morris, 1959; Wardle, 1984).

1.4 Disturbance and gradients

Species distributions are also influenced by processes such as the dynamic impacts of disturbances at different points along environmental gradients (Romme and Knight, 1981; Harmon *et al.* 1983). Understanding how species distributions are influenced by these processes is an increasingly interesting area of ecological research, particularly with respect to coexistence between different species. Several studies have examined how successional patterns and species interactions were influenced by the effects of different types of disturbances, and their interaction with broad scale environmental gradients. For example, Romme and Knight (1981) found that the distributions of spruce, fir and pine species were influenced by the frequency of fire, and rates of secondary succession along a topographical gradient in Wyoming, US. Harmon *et al.* (1983) studied the influence of human modifications to the disturbance regime (fire frequency, logging and exotic species invasions) in the US Great Smoky Mountains, and found these influences caused shifts in species composition across broad topographic, elevation and moisture gradients. In Japan, eight canopy species coexisted due to the interaction between windfall and logging impacts across a topographic moisture gradient (Ishizuka and Sugawara, 1989). Across a broad

Trans-Andean geographical rainfall gradient, fire, earthquakes, logging and grazing influenced the dynamics between different canopy species in different places (Veblen, 1989; Veblen *et al.* 1992). These authors found the beech *N. dombeyi*, and conifer *Austrocedrus chilensis*, regenerated in different ways in response to variation in canopy openings caused by different disturbances, depending on the composition of the forest understorey at different points along the gradient, and post-disturbance conditions such as the availability of suitable microsites. In wetter species diverse lowland forests, large disturbances (e.g., fire) resulted in even-aged *N. dombeyi* and *A. chilensis* establishment, with little subsequent recruitment in the absence of further large disturbances, and smaller-scale gap-phase processes favoured the regeneration of more shade-tolerant hardwood species. In contrast, in drier upland forests with fewer broad-leaved hardwoods, stands dominated by mixed *N. dombeyi* and *A. chilensis* regenerated more frequently in small gaps (Veblen *et al.* 1992).

1.5 Study Aims

My study aimed to address questions of coexistence between conifer, beech and hardwood species, by determining whether these forests were in compositional equilibrium (*sensu* Veblen, 1992). My approach was to examine the regeneration patterns and dynamics of different species at different scales, along an environmental gradient in drainage and soil development in north Westland. I investigated the impact of different disturbances on species distributions at different points along the gradient at a *within stand* scale and at the *whole landform* scale, to understand how these groups responded to disturbances, and the subsequent availability of suitable establishment sites. Therefore, this thesis is structured in two parts reflecting examination of dynamics and disturbance history at the *within stand* plot scale (**chapter 1**) and the *whole landform* scale (**chapter 2**)

My objective was to understand the relative roles of environmental (soil drainage) conditions (Bond's 'tortoise and hare' hypothesis) and disturbance history (Ogden and Stewart's 'two-component' model) in determining species composition and abundance along the drainage gradient.

To address this, in **chapter 1** at the *within stand* scale, I conducted an intensive study of stand development patterns, recruitment dynamics and disturbance history in three large plots, situated at different points along the gradient in drainage and soil development from well drained to very poorly drained soils.

Specifically at the three positions along the soils/drainage gradient I:

1. examined patterns of stand development.
2. reconstructed and examined the nature of historical disturbances.
3. investigated the patterns of individual species recruitment, specifically to understand how each species has responded to disturbances; and
4. examined how the conditions created by disturbances of different type and extent influenced compositional variation across the drainage gradient.

In **chapter 2**, I investigated whether the patterns and processes identified in these large plots reflected processes occurring at a *whole landform* scale.



Plate 1: Stand structure in a poorly drained area of north Westland with *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* emergent over a *Nothofagus fusca* and *N. menziesii* canopy.

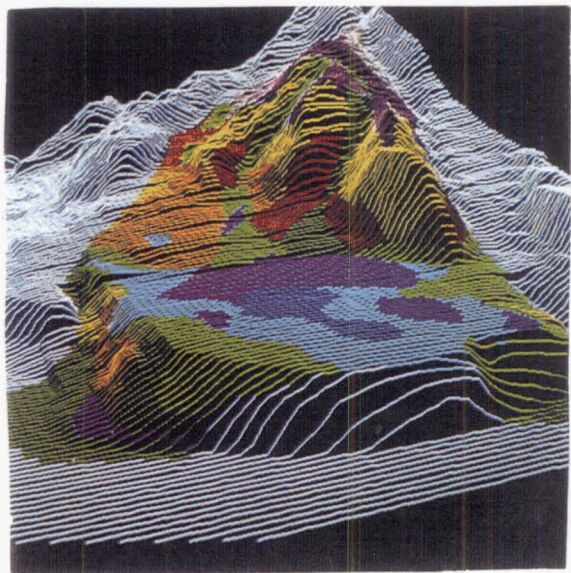
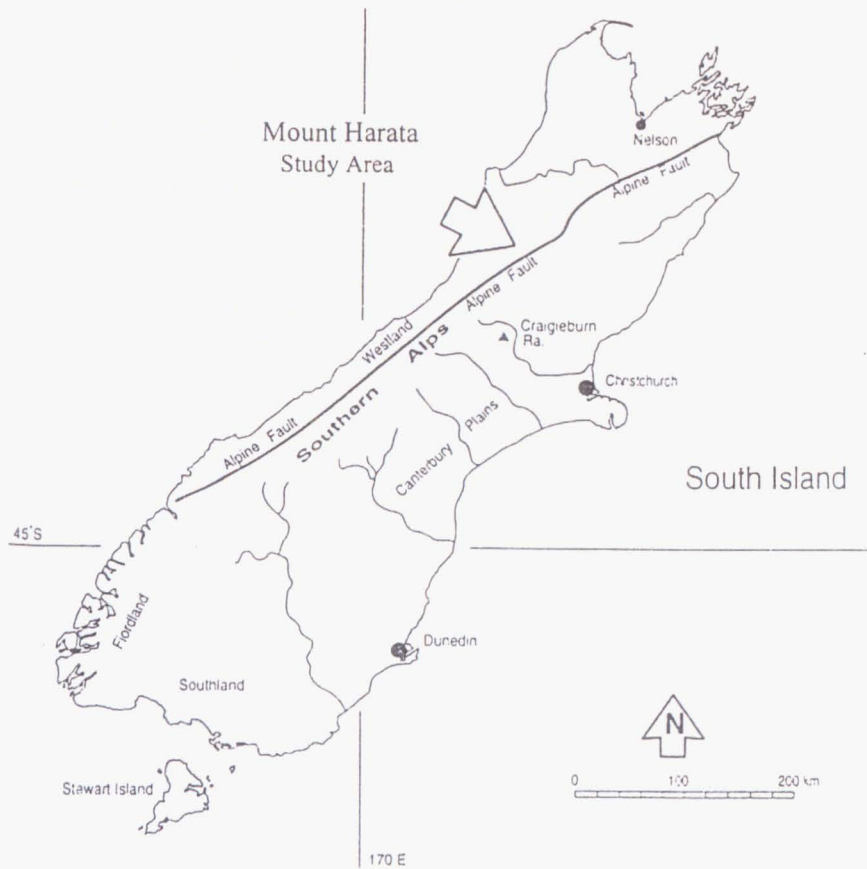
2. METHODS

2.1 Study site

Mount Harata, in the north Westland region of the South Island (42° 22' S, 171° 51' E) is a granitic dome located in the Upper Grey River Valley above the confluence of the Big Grey and Clarke Rivers, approximately 15 km from the Alpine Fault and c. 30 km south of Reefton (Stewart *et al.* 1993) (Fig. 1). Annual rainfall at the site is likely to be around 2500 mm (Stewart *et al.* 1993).

The lowland forests at the base of Mount Harata (200-300 m a.s.l.) comprise relatively high tree species diversity for Westland, and this area is where elements of distinctly different forest types from the north and south come together in the Grey Valley. To the north, extensive beech stands dominate the nearby Maruia Valley and Rahu Saddle c. 20 km away, with *Nothofagus solandri* var. *cliffortioides* (mountain beech), *N. fusca*, and *N. menziesii* abundant on a range of sites, with conifers and hardwoods less common and generally restricted in their distributions (Wardle, 1984). To the south, the conifers, especially *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*, and non-beech hardwoods, particularly *Weinmannia racemosa* and *Quintinia acutifolia* (Westland quintinia), dominate on the glacial moraines, outwash and recent alluvial terraces of central and south Westland, in the zone where beeches are absent for c. 150 km (Cockayne 1926, Wardle, 1963). To the west on the seaward side of the Paparoa range, podocarp/ hardwood and mixed podocarp/beech/hardwood stands are common on karst bedrock derived surfaces (DeVelice *et al.* 1988).

Mount Harata therefore, represents a key site for the study of mixed species dynamics and for addressing coexistence questions in the ecologically diverse north Westland region. Mount Harata was selected due to the range of conifer, beech and non-beech hardwood species found on a range of soil types (Stewart *et al.* 1993). These authors described relatively intact, unlogged vegetation sequences and associated soil variability on terraces (except for the most recent terrace which is grazed), fans, and forested hillslopes from the Grey River to mid elevations on Mount Harata. On the very well-drained hillslopes and terrace side-slopes, *N. truncata* (hard beech) dominates in association with *Metrosideros umbellata* (southern rata), *Q. acutifolia* and also *N. fusca* on the gentler slopes (Fig. 1). Conifers are uncommon and are scattered across the hillslopes.



- A1 *N. solandri* var. *cliffortioides*
- B1 *N. fusca*-*N. menziesii*
- B2 *D. cupressinum*-*N. fusca*-*N. menziesii*
- B3 *N. fusca*
- B4 *N. fusca*-*W. racemosa*
- C1 *N. truncata*-*N. fusca*
- C2 *N. truncata*-*W. racemosa*
- C3 *W. racemosa*-*Q. acutifolia*
- C4 *N. truncata*
- C5 *N. truncata*-*M. umbellata*

Figure 1: Location map of Mount Harata study area, north Westland, South Island, with the spatial extent of forest types across different landforms identified by Stewart *et al.* (1993) (used with author's permission).

A large post-glacial terrace of Otiran age (c. 14000 yrs B.P- Bowen, 1964) situated 120 m above the Grey River (300 m a.s.l) was considered suitable for study (Fig. 1). This c. 1 km long by c. 800 m wide terrace has broad variation in soil types and drainage, and at least eight conifer, three beech, and three abundant non-beech hardwood species (Stewart *et al.* 1993). Soils of the terrace edges are predominantly well-drained yellow-brown earth soils (Ahaura series) and there are some associated patches of imperfectly- and poorly drained gleyed yellow-brown earths. Moving toward the terrace centre, well-drained soils grade into poorly drained gley soils (Maimai series) and fluid mineral peats (Rotokuhu series), and eventually into very poorly drained organic peats (Kini series) close to the terrace centre.

The most abundant conifers found across the terrace are *Dacrydium* and *Dacrycarpus* with lesser numbers of *Prumnopitys ferruginea* (miro), *Podocarpus hallii* (Hall's totara) (all Podocarpaceae) and *Libocedrus bidwillii*. Other conifers are also present but were almost exclusively confined to the most extremely poorly drained deep peats near the terrace centre: *Phyllocladus aspleniifolius* var. *alpinus* (mountain toatoa), *Lagarostrobos colensoi* (silver pine) and *Halocarpus biformis* (pink pine) (all Podocarpaceae) are associated in these areas with the beech *N. solandri* var. *cliffortioides* (Fig. 1 - Forest Type A1).

Structurally, *Dacrydium* and *Dacrycarpus* are commonly emergent over a canopy of beeches and a hardwood sub-canopy across the terrace, and therefore these were the main conifer species studied (Plate 1, Fig. 1 - Forest Types B1 and B2). Beeches were very abundant with *N. fusca* and *N. menziesii* found across the terrace on a range of soils (Forest types B1, B2, B4), except in the most extremely poorest drained soils where *N. solandri* var. *cliffortioides* dominated (Fig. 1). Due to the abundance of *N. fusca* and *N. menziesii* in a range of well drained and poorly drained soils across the terrace, these were the beech species studied. The three main non-beech hardwood species studied were the abundant *W. racemosa*, *Q. acutifolia* and *Elaeocarpus hookerianus* (pokaka -Elaeocarpaceae).

2.2 Plot selection

Three rectangular permanent sample plots were established on differently drained areas in different forest types identified by Stewart *et al* (1993) (Fig. 1). Plot A (50 m x 60 m) was located in very poorly drained soils near the terrace centre in forest type B2, characterised by dominant *Dacrydium*, *Dacrycarpus*, *N. fusca* and *N. menziesii* with associated *E. hookerianus* (Figs. 1 and 3 in Stewart *et al.* 1993). Plot B (100 m x 70 m),

halfway between the centre and terrace edge, was situated in the extensive forest type B1 on poorly drained and very poorly drained soils, dominated by *N. menziesii* and *N. fusca* with associated *Dacrydium* and *Dacrycarpus*. Plot C (50 m x 60 m) was located in forest characterised by dominant *N. fusca*, *W. racemosa*, *Q. acutifolia* and *N. menziesii* trees on well drained soils near the terrace edge (forest type B4) with scattered, emergent *Dacrydium*. Data were collected over three years from 1996 to 1998. For ease of sampling each plot was sub-divided into 5 x 5 m contiguous subplots.

2.3 Stand structure

To investigate population dynamics of overstorey tree species, I measured the diameter at breast height (dbh), 1.4 m tall from the point of establishment of each tree ≥ 5 cm dbh. Where there was more than one leader I measured the dbh of the largest one. Trees were grouped into 10 cm size classes (e.g., 5-14.9 cm dbh, 15-24.9 cm dbh, etc.) to aid in interpretation of size-class frequency histograms. I recorded the spatial location of all saplings (<5 cm dbh, > 1.4 m tall) of the main overstorey species. Seedling densities were recorded in 0.2 m² quadrats in each contiguous 5 x 5 m subplot (see section 2.8).

To determine population age structures, I cored every tree > 10 cm dbh and every second tree from 5 to 10 cm dbh. Increment cores were extracted from 1 m above establishment point. For trees > 50 cm diameter, two cores were often taken for better age resolution. Cores were mounted, air dried, then progressively sanded with increasingly finer grit sandpaper until the growth rings were clear and distinguishable. Cores were aged by counting each individual ring, each ring was assumed to be annual. Other studies have either demonstrated annual ring production or assumed annual ring growth (for *Dacrydium* see Franklin, 1969, Stewart and White, 1995; *Dacrycarpus* - Duncan, 1993; *N. menziesii* - Norton, 1983a; *N. fusca* - Runkle *et al.* 1997; *L. bidwillii* - Norton *et al.* 1987), although missing and false rings have sometimes been recorded for these species (Norton *et al.* 1987). Cores were extracted from the longest radius of the trunk as this was less likely to underestimate age, especially for *Dacrydium* (Stewart and White, 1995). No correction was made for age to coring height, therefore ages will be underestimates of the true age.

For cores that missed the pith but had visible arcs, Duncan's (1989) geometric model for calculating the missing portion was used. Cores that had arcs > 50 mm from the pith were rejected. For cores that were rotten and were short of the chronological centre (27 cores), age was estimated by assuming the distance to the geometric centre also represented the distance to the chronological centre (Norton *et al.* 1987). Cores that were <

70% in length to the estimated geometric centre were rejected (48 cores) and ages were estimated from age/ diameter relationships within each plot.

To investigate the accuracy rate of cores in terms of the distance from the pith, the proximity of the pith for > 1700 trees was examined (Fig. 2). Over 84 % of cores either hit the pith or were within a radius of 10 mm with relatively few short cores (< 5%), which enabled a robust interpretation of age structures. Trees were grouped into 25 yr age classes for the beeches and podocarps up to 300 yrs old, and 50 yr age-classes thereafter. The clarity and distinction of rings varied in many *W. racemosa* cores, making it difficult to confidently place this species in 25 yr classes. Hence, to minimise possible counting errors 50 yr age classes were considered more appropriate for analysing population structures.

As a measure of canopy density, overhead canopy cover was subjectively estimated in one of three classes above each tree and sapling, and for seedlings above all quadrats in each subplot. These were *open* (<1/3 canopy cover), *intermediate* (1/3-2/3) and *closed* (>2/3). Trees were also subjectively classified within one of four height tiers: *understorey* (2-5 m), *sub-canopy* (5-15 m), *canopy* (15-25 m) and *emergent* (>25 m).

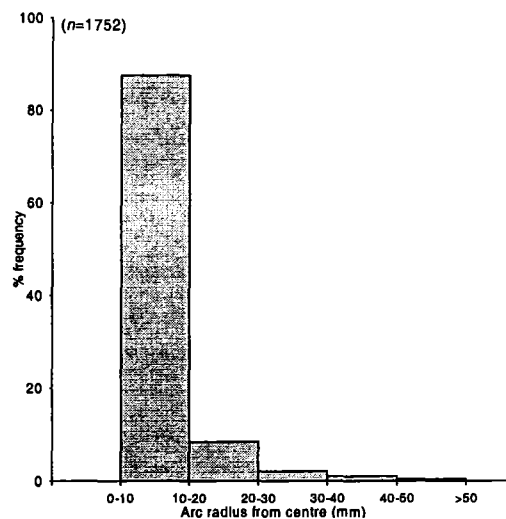


Figure 2: Relative frequency (%) of cores of all tree species in distance classes representing distance from pith (chronological centre) for cores with arcs for trees in north Westland.

2.4 Stand history

To detect and date past disturbances, I examined changes in radial growth patterns that could provide evidence of tree growth responses to disturbances (Lorimer, 1985; Lorimer and Frelich, 1989). This method enables the detection and reconstruction of the historical frequency and intensity of disturbances; for example, evidence of widespread

extensive disturbance would be preserved in a rapid increase in radial growth patterns that would be synchronous for trees that survived the disturbance.

Disturbances are defined for the purpose of this study as “*a discrete, punctuated killing, displacement of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established*” (Sousa 1984: 356). Disturbance *type* simply means the agent of disturbance (storms, earthquakes, drought etc), *extent* or *scale* refers to the spatial area disturbed; *frequency* refers to the number of disturbances in a given period; *magnitude* refers to *intensity* (strength or physical force unleashed) and *severity* is the impacts on the individual or community (White and Pickett, 1985; Romme *et al.* 1998).

For consistency across plots, I selected *N. menziesii* for the examination of tree ring releases because it was the only species that met a range of *a priori* criteria. First, this species was abundant in all three plots with a number of trees older than 200 yrs. Second, *N. menziesii* has clear annual rings with minimal false or missing rings demonstrated from previous cross-dating and chronology production (Norton, 1983a). Third, previous studies of radial growth patterns have shown *N. menziesii* to be sensitive to a range of different sized canopy openings from disturbances that differed in intensity and extent (Stewart and Rose, 1990; Runkle *et al.* 1997).

I defined a growth release as a $> 200\%$ increase in mean ring width when consecutive 5-year means were compared. These were grouped into decades as a measure of canopy disturbance frequency (see Lorimer and Frelich, 1989). This was because (with the exception of the well-drained plot) trees were not cross-dated, and errors in absolute age of about ± 0.5 yrs are therefore possible because of locally absent or false rings.

2.5 Spatial analysis of tree age distributions

The spatial position (x, y co-ordinates) of all trees (>5 cm dbh) and saplings (<5 cm dbh, > 1.4 m tall) of each canopy species were mapped. To identify even-aged patches of trees that had established in response to historical disturbances (Lorimer, 1985), I used the techniques outlined in Duncan and Stewart (1991) to examine the spatial distribution of individual species tree ages. This method has previously been successfully applied in South Island beech and conifer forests in detecting different aged patches of trees (Stewart and Rose, 1990; Duncan and Stewart, 1991; Duncan, 1991; Van Uden, 1998).

In detecting even-aged patches of trees, a measure of spatial autocorrelation in tree ages would suggest they are grouped together in a non-random manner; ie, spatial

autocorrelation tests the independence of observed values in one area against those in a neighbouring locality (Sokal and Oden, 1978). The detection of a significant spatial structure involves constructing a spatial correlogram using a coefficient (Morans I) of association to test for deviation from a random distribution (Legendre and Fortin, 1989; Upton and Fingleton, 1985; Duncan and Stewart, 1991). Spatial correlograms were constructed and the shape of the correlogram was interpreted for significant spatial structure (Legendre and Fortin, 1989). If species ages showed a deviation from the random distribution, which is in effect the null hypothesis (Upton and Fingleton, 1985), then variables are significant spatially autocorrelated. This is done by measuring distances between neighbouring points in 3 metre distance classes, or 4 metre classes if sample size was not large enough, to give at least 20 pairs of neighbouring points which is the minimum for interpretation of significant deviation from the null hypothesis (Legendre and Fortin, 1989). Negative deviation represents distance between patches of different age, whereas positive deviation represents trees of similar age that are positively associated, i.e., they are grouped together in patches (Duncan and Stewart, 1991). To determine whether correlograms were statistically significant, a global test of significance was performed using the conservative Bonferroni method (Legendre and Fortin, 1989).

If individual correlograms were significant, the methods outlined in Duncan and Stewart (1991) were followed to determine patch composition, size and location. Ordination analysis of tree ages was performed to investigate the spatial extent and distribution of even-aged patches by constructing a matrix of association (Bray-Curtis similarity measure), and non-metric multi-dimensional scaling was performed to arrange these association measures in a two-dimensional graph (analysis in PATN statistical package - Belbin, 1989). To ensure an additional measure of objectivity in grouping trees of each patch, dendrograms were constructed to cluster together trees of similar age and spatial location using agglomerative hierarchical clustering (UPMGA) in the PATN analysis programme (Belbin, 1989).

2.6 Spatial patterns of tree dispersion

The spatial distribution of trees was investigated for significant univariate spatial patterns. This was also performed for saplings. The distance between each tree was analysed using the function $K(t)$ (Ripley, 1977) to see whether trees were clumped, randomly distributed or uniformly spaced (see Duncan, 1991). The function $K(t)$ uses each tree-tree distance to provide a measure of spatial patterns at distance t for each species

within stands (Ripley, 1977, Upton and Fingleton, 1985). Duncan's spatial analysis programme (1990) was used to test whether these spatial patterns deviated from a null hypothesis of a random distribution by using Monte-Carlo simulations to generate random co-ordinates. The resulting 95 % or 99 % confidence envelopes generated were examined to see whether values of $K(t)$ were above (i.e., clumped distribution) or below (uniform or regular distribution) the confidence envelopes. This method has been used to study spatial patterns in south Westland conifer/ hardwood forests (Duncan, 1991; Rogers, 1995).

2.7 Spatial interactions between species

To investigate the spatial patterns for trees and saplings of different species relative to one another, a bivariate measure of spatial association was calculated also using Duncan's (1990) spatial analysis programme. The location of pairs of species was analysed using the function $K_{12}(t)$ which examines the spatial independence of each species at distance t (Lotwick and Silvermann, 1982; Upton and Fingleton 1985). Monte-Carlo simulations were used to generate random pairs of co-ordinates and investigate deviations from the null hypothesis of independence. Confidence intervals at either 95 % or 99 % levels generated were calculated from 19 or 99 toroidal shifts between species (Lotwick and Silvermann, 1982; Upton and Fingleton, 1985). Values of $K_{12}(t)$ which were above the confidence envelopes showed species to be positively associated with respect to each other, and below the confidence envelopes species were negatively associated.

2.8 Patterns of microsite establishment

Microsite establishment sites (*forest floor, pits, mounds, stumps, logs, and tree ferns*) for all trees and saplings were recorded by visual assessment. *Mounds* were defined as clearly elevated surfaces above the forest floor such as an uprooted soil mass, or the litter cone of a dead standing tree or stump. *Stumps* were the decaying wood of dead or snapped trees. *Log* establishment sites were defined as visible remnants of fallen boles, or where these had decayed and there was clear evidence in the tree growth form, i.e., arched, elevated roots with a gap between the trunk and the forest floor surface. *Pits* were visible depressions in the ground formed by uprooted trees. *Tree ferns* were the fibrous trunks or bases of *Dicksonia squarrosa* and *Cyathea smithii*. *Forest floor* was the surface of the forest. If the microsite establishment site was not clearly identifiable and able to be confidently determined, the microsite type was recorded as *forest floor*; for example, some

Dacrydium trees in the very poorest drained peats had extensive, spreading root plates and it was unclear on what microsite type they had originally established on.

To measure seedling densities in each plot and their microsite establishment sites, I placed a 0.2 m² (0.6 m x 0.33 m) quadrat on each microsite type in every contiguous 5 m x 5 m subplot. Where there was more than one microsite of a particular type, the microsite sampled was randomly selected by throwing the quadrat high into the air, and then moving it to the closest microsite of each type from where it landed. If a particular microsite were absent within a 5 m x 5 m quadrat, no quadrat was able to be taken for that microsite (*cf* Duncan *et al.* 1998).

For seedlings that established on logs, the decay class of each log was visually assessed in one of four classes adapted from Stewart and Burrows (1994). Decay class L1 was recent logs that were characterised by intact outer bark. Decay was more advanced in class L2, bark had detached and moss cover had advanced (<50% of the log). L3 logs had greater sapwood decay, loss of some structural integrity was apparent and abundant moss covered the log (>50%). Class L4 logs were visibly rotten and had lost their structural integrity.

2.9 Spatial patterns of mortality

In each plot, dead spars and logs were mapped along with their mode of death (dying standing, bole snap, uprooted) and identified to species where possible. Identification proved problematical for well decayed logs, so several lines of evidence were assessed to identify species: bole diameter, length and buttressing of bole, identification of remaining bark, smell and the colour of wood, and comparison with better preserved specimens of different species (Stewart and Burrows, 1994). The diameter of dead stems was recorded, or reconstructed where portions of the bole or stump were missing. It should be recognised that there are some limitations to this data. Some species decay faster than others after the same disturbance, and some boles decay faster than others depending on whether boles are lying in water or elevated above the soil surface (Stewart and Burrows, 1994). Therefore, the composition of species in coarse woody debris may not truly reflect past forest composition, and spatial patterns of mortality are limited by identification. Nevertheless, this information was gathered across the entire area of each plot so key overall spatial patterns of mortality could be detected, and any random sampling errors minimised.

2.10 Soil and drainage patterns

To obtain a measure of soil variability and drainage within each plot, augur bores were taken at the intersection of each 10 m x 10 m grid to determine depth to gravels, drainage and soil profile morphology. Soil pits were dug along at the intersection of 20 m x 20 m points to describe the soil profile morphology and variability in each plot. Soil series names were recognised according to the study of Grey Valley soil types by Mew and Ross (1980). Drainage was assessed from examination of soil profile development in three classes: *very poorly drained*, *poorly drained*, *well drained* (see appendix). Classes were assessed from those devised by Taylor and Pohlen (1970) and the Canadian Soil Science Drainage Assessment Criteria (1987) with some modifications.

To examine subsurface differences in peat texture in plot A, samples were collected from four pits across a 60 m transect at 15 m intervals. Samples were taken at different depths in each pit where there was a distinct change in soil profile morphology. The proportion of organic matter to mineral material was determined by loss of organic matter on ignition (Allen, 1974). Peat samples were placed in small crucibles and put into ovens for 48 hours at 100° C. After removal from the oven, samples were immediately placed in a desiccator to avoid moisture accumulation, then weighed (the crucibles were weighed beforehand). Samples were then placed in a blast furnace at 550° C for at least 4 hours to burn off organic matter. Samples were removed from the oven, immediately placed in a desiccator to avoid moisture accumulation then reweighed to ascertain the relative proportion of organic material to mineral material. In a number of samples, remaining mineral material was clearly identifiable as blue-grey silt, in others only ash remained with no mineral material visible.

3. RESULTS

3.1 VERY POORLY DRAINED STAND - PLOT A

3.1.1 Stand composition, structure and soils

Conifers

The conifers *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* had the largest basal areas in this plot, and occupied the canopy and emergent tiers (Table 1). Of the other conifers, there were only two live *Libocedrus bidwillii* and three *Podocarpus hallii*, although 17 dead *L. bidwillii* and 6 dead *P. hallii* stems were identified, which indicates they were more abundant in the past.

Beeches

Nothofagus fusca and *N. menziesii* were also significant components of this plot. Both species had similar stem densities and basal area, and mainly occupied the canopy and sub-canopy (Table 1).

Non-beech hardwoods

Elaeocarpus hookerianus was the only abundant non-beech hardwood present, although lower in density and basal area compared with the conifer and beech species. The other hardwood, *Weinmannia racemosa*, was scarce with only two trees and two saplings. There was a dense understorey of the tree ferns *Cyathea smithii* and *Dicksonia squarrosa*.

Table 1: No. trees (≥ 5 cm dbh) in different height tiers, basal area, and no. identified dead stems in 0.3 ha plot A, Mt Harata. All values converted to a per hectare basis.

| Species | Understorey (2-5 m) | Subcanopy (5-15 m) | Canopy (15-25 m) | Emergent (> 25 m) | Total stems / ha | Dead stems / ha | Basal area m ² / ha |
|-----------------------|------------------------|-----------------------|---------------------|----------------------|------------------------|-----------------------|--------------------------------------|
| <i>Dacrydium</i> | 3 | 27 | 50 | 57 | 137 | 40 | 17.2 |
| <i>Dacrycarpus</i> | 3 | 17 | 40 | 80 | 140 | 80 | 13.7 |
| <i>N. fusca</i> | 33 | 23 | 70 | 3 | 129 | 43 | 9.1 |
| <i>N. menziesii</i> | 57 | 50 | 63 | | 170 | 97 | 9.6 |
| <i>E. hookerianus</i> | 13 | 60 | 10 | | 83 | 3 | 3.4 |
| <i>L. bidwillii</i> | | 3 | 3 | | 6 | 57 | 0.5 |
| <i>P. hallii</i> | 3 | 3 | 3 | | 9 | 20 | 0.7 |
| Total | | | | | 674 | 340 | 54.2 |

Plot A was dominated by very poorly drained deep Kini peats and Rotokuhu peats varying in depth to underlying gravels from 50 cm to 115 cm, with a mean depth of 77 cm (soil series names after Mew and Ross, 1980). Kini peats typically had a common horizon sequence of *O* (> 50 cm) overlying a thin *Bg* horizon over gravels, Rotokuhu peats had an *O* layer (20-50 cm) overlying a *Bhr* layer comprising fluid peat with incorporated mineral material (see appendix for detailed soil profile descriptions). The abundance of Kini peats placed this plot in the very poorly drained part of the drainage sequence. It was located close to the transition to deeper extremely poorly drained basin peats near the plot centre, where forest composition and structure markedly changed.

3.1.2 Stand size and age structure

Conifers

Dacrydium cupressinum ranged in age from 95-275 yrs but had a unimodal age distribution with c. 50% of live stems aged 225-275 yrs and progressively fewer stems in younger age classes, suggesting a relatively even-aged population (Fig. 3a). The size class distribution also suggested an even-aged population with > 60 % stems in the 35-64.9 cm diameter classes and few smaller trees (Fig. 3b). The majority of dead stems (66%) were also between 35-64.9 cm dbh, most of these were scattered throughout the plot and had died from being uprooted, suggesting random mortality had occurred within the even-aged population. Only three saplings were present, and there was only one aged tree < 100 yrs old, suggesting that conditions in the plot have been unfavourable for recent *Dacrydium* establishment and recruitment.

Tree age ranges for the emergent *Dacrycarpus dacrydioides* were similar to *Dacrydium* with the ages of cored trees ranging from 93-323 yrs, with several older trees 387 yrs and 430 yrs (Fig. 3c). Unlike *Dacrydium*, the *Dacrycarpus* age distribution had several peaks evident: 300-325 yrs, 250-275 yrs and 150-200 yrs. Dead standing stems were evenly spread throughout the size classes 15-55 cm dbh (Fig. 3d), age/ diameter regressions suggest these were probably aged between 150-310 yrs making a definitive interpretation of the age structure difficult at this stage (appendix: Table A1). There were more *Dacrycarpus* trees in smaller size classes compared with *Dacrydium*, and 10 times the number of saplings that were probably < 100 yrs, suggesting more recent recruitment than *Dacrydium* (Fig. 3d).

There were few live *L. bidwillii* and *P. hallii* in the plot, the two surviving stems of each species ranged from 228 to 320 yrs. Saplings and small diameter stems were scarce,

and dead stems were of a similar diameter to live stems suggesting small, even-aged populations (Figs. 3k and 3l).

Beeches

The beech had different size and age structures from the conifers. Few beech trees were older than 250 yrs and there were more beech trees in younger age classes, and more numerous saplings than the conifers (Fig. 3). The cored *Nothofagus menziesii* trees ranged in age from 25-384 yrs, and the age distribution had a discontinuous structure with distinct peaks evident in the 300-325 yrs, 175-200 yrs and 25-50 yrs classes (Fig. 3e). Dead stems were concentrated in the 15-45 cm dbh classes; age/diameter regressions suggest these were probably aged between 125-247 yrs when mortality occurred (Fig. 3f).

Nothofagus fusca trees had a similar diameter range to *N. menziesii* (5-75 cm) with many stems in the smallest size classes (Fig. 3h). However, in contrast to *N. menziesii*, most trees were < 175 yrs old with two distinct peaks evident in the 125-175 yrs and 25-50 yrs age classes (Fig. 3g). Most dead stems were between 21-31 cm dbh, which age/ diameter regressions suggest were aged between 97-131 yrs when mortality occurred (appendix: Table A1).

Non-beech hardwoods

The cored *Elaeocarpus hookerianus* trees ranged in age from 81-270 yrs, and the age distribution resembled the *N. fusca* age distribution with a clear peak in the 125-175 yrs age range, and with few stems > 225 yrs. There were 22 saplings which age/diameter regressions suggest were aged between 65-80 yrs (Fig. 3j).

Several peaks in the age-class distributions coincided across the species. For example, *Dacrydium* and *Dacrycarpus* both have peaks c. 250-275 yrs. Likewise *Dacrycarpus* and *N. menziesii* (175-200 yrs), *N. fusca* and *E. hookerianus* (125-175 yrs) and *N. fusca* and *N. menziesii* (25-50 yrs) share similar peaks. It is possible that these coincidental peaks in the age distributions reflect episodes of establishment in response to infrequent canopy disturbance. The ages of all trees were summed to help recognise consistent periods of simultaneous establishment within the plot (Fig. 4). There were several major age peaks that suggested distinct upsurges in establishment occurred at different times in the plot: c. 300-325 yrs, 225-275 yrs, 125-200 yrs and 25-50 yrs ago.

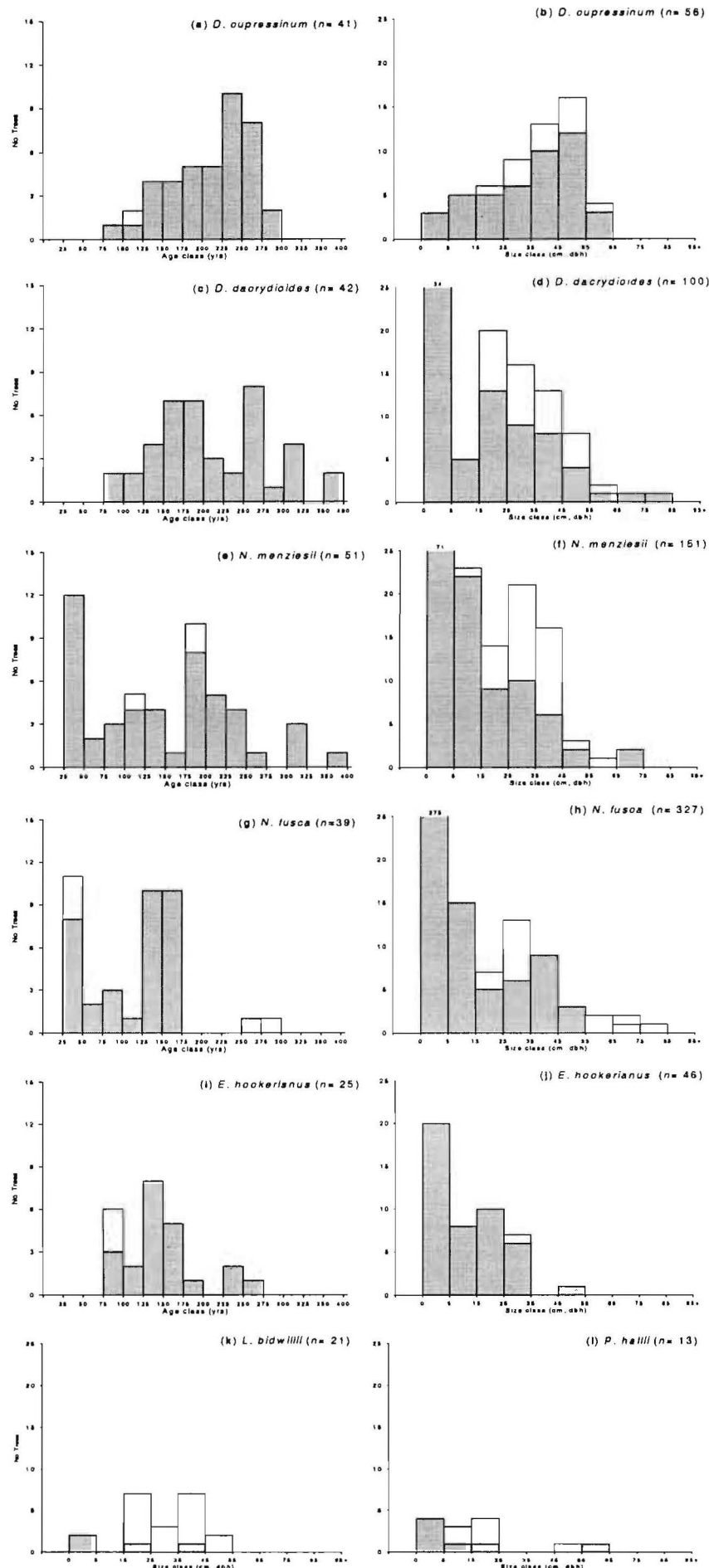


Figure 3: Age- and diameter-class frequency distributions for the main overstorey species in plot A (*L. bidwillii* and *P. hallii* diameter class only). Unfilled bars in age class diagrams represent estimated ages for unaged trees. Unfilled bars in size class diagrams represent diameter class of dead stems, 0-5 cm = saplings in the size class diagrams.

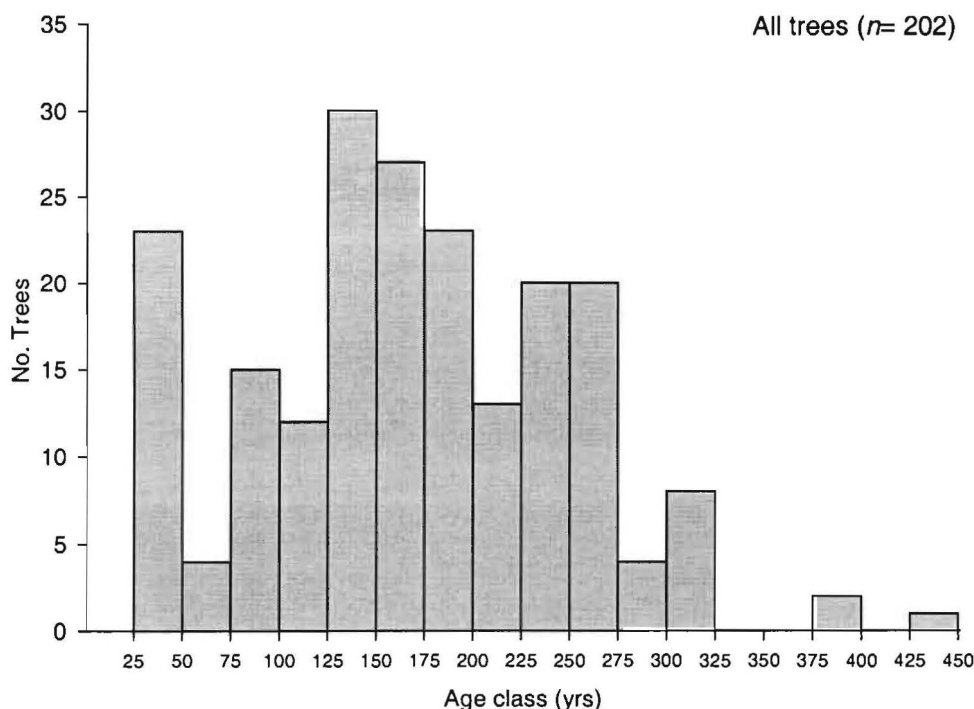


Figure 4: Grouped age-class frequency distribution for the main overstorey species in very poorly drained plot A (*Dacrydium*, *Dacrycarpus*, *N. menziesii*, *N. fusca*, *E. hookerianus*, *L. bidwillii* and *P. hallii*).

3.1.3 Spatial distribution of tree ages

I constructed spatial correlograms to look for evidence of patchiness in tree age distributions, to see whether the apparent coincidental peaks in age for different species represented spatially distinct groups of similarly aged trees. All species showed evidence of patchiness in their spatial structures although they were not globally significant (Fig. 5). Nevertheless, correlograms for *Dacrydium* (Fig. 5a), *N. menziesii* (Fig. 5c), and *N. fusca* (Fig. 5d) showed evidence of similarly-aged trees grouped together at short distances, all had significant positive values at short distances (c. 1-12 m depending on species), and negative values at larger distances indicating the distance between patches of different age (c. 24-45 m). The correlogram for *Dacrycarpus* was similar in shape to *Dacrydium* and showed a structure indicating relatively even-aged trees were grouped together at short distances, although this was not statistically significant (Fig. 5b). A correlogram was not constructed for *E. hookerianus*, as there were too few trees to test for spatial structure.

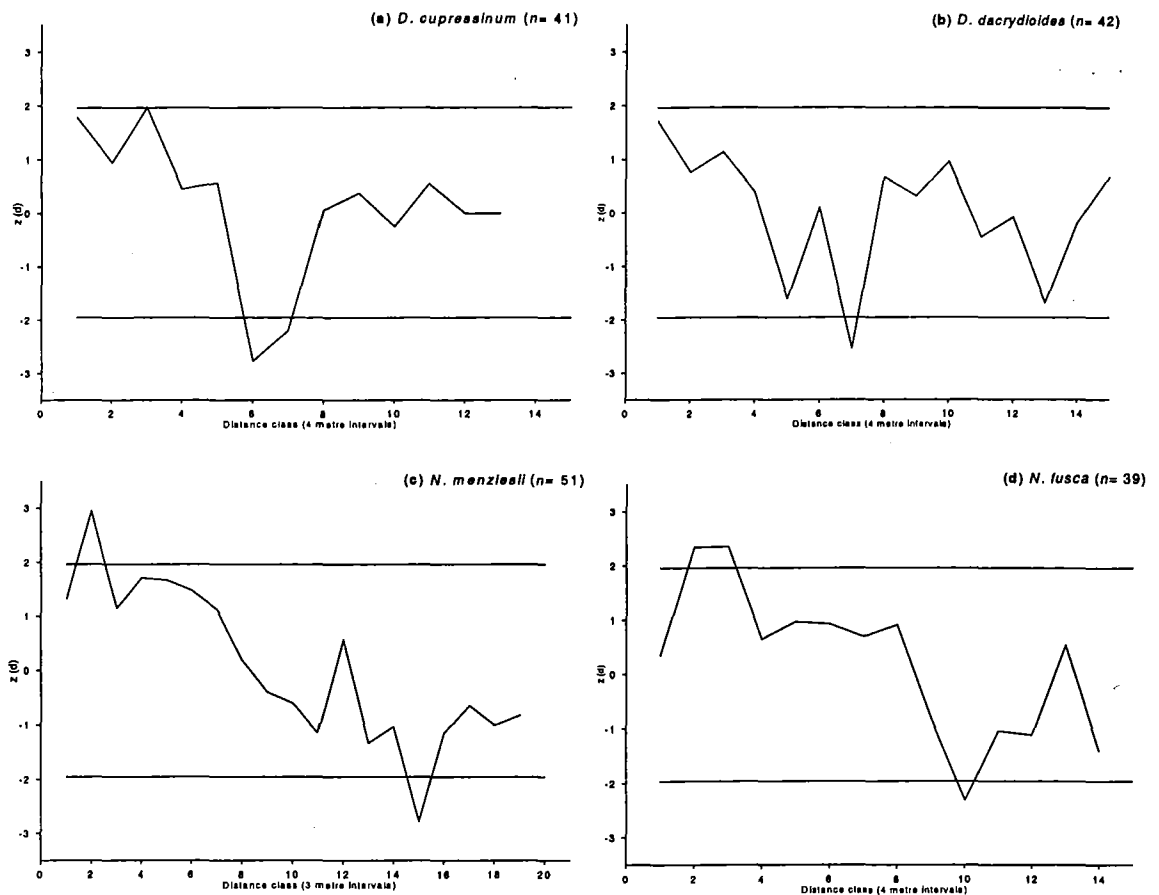


Figure 5: Spatial correlograms of tree ages for (a) *Dacrydium cupressinum* (b) *Dacrycarpus dacrydioides* (c) *N. menziesii* and (d) *N. fusca*. Horizontal lines of significance at $\alpha = 0.05$ level for individual distance classes.

Conifers

The *Dacrydium* correlogram suggested there were even-aged patches of trees (Fig. 5a). Subsequent cluster analysis identified two groups, the first aged 151-275 yrs, and the second aged 95-213 yrs (Fig. 6; Table 2). These two groups were spatially separated, the first located primarily in the centre and right of the plot (Fig. 6a), and the second found mostly in the upper left of the plot (Fig. 6b). The age distributions of the two groups overlapped but were significantly different, suggesting the groups established at different times in response to different disturbances (two-tailed Kolmogorov-Smirnov test = 0.74, $P < 0.001$).

Groups of even-aged *Dacrycarpus* trees were also evident from the correlogram (Fig. 5b). Three distinct age groups were identified from the cluster analysis: 322-430 yrs, 218-323 yrs and 93-215 yrs (Fig. 7; Table 2). The three groups were mostly separated with the oldest group comprising 3 trees located toward the top of the plot (Fig. 7a), the group 218-323 yrs occurred in clumps on either side of the plot centre (Fig. 7b), and the youngest group was concentrated in the lower left and top right of the plot (Fig. 7c). The distribution of tree ages in each group were significantly different (between groups 1 and 2 Kolmogorov-Smirnov (K-S) test = 1, $P < 0.001$; groups 2 and 3, K-S test = 0.87, $P = 0.03$).

Beeches

The *N. menziesii* correlogram suggested there were even-aged patches of trees (Fig. 5c). Four different aged groups were identified from the cluster analysis: 315-384 yrs, 174-252 yrs, 65-147 yrs and 25-80 yrs (Table 2) and these groups were spatially discrete (Fig. 8). The oldest group, comprising just four trees, was located in the top centre of the plot (Fig. 8a), the group 174-252 yrs was confined to the left of the plot with one outlier in the bottom right (Fig. 8b), the group 65-147 yrs was mostly around the centre of the plot (Fig. 8c), and the group 25-80 yrs was located in the upper centre and top right of the plot (Fig. 8d). There was some age overlap but the distribution of ages in each group was significantly different (between groups 1 and 2 two-tailed K-S test = 0.87, $P < 0.001$; between groups 2 and 3, K-S = 1, $P < 0.001$; between groups 3 and 4, K-S = 1, $P < 0.001$).

Patchiness in tree ages was also evident from the correlogram for *N. fusca* (Fig. 5d). Subsequent cluster analysis identified three discrete age groups: 251-276 yrs, 128-173 yrs, 25-122 yrs (Fig. 9, Table 2). These groups were mostly separated spatially, with the group 251-276 yrs comprising just two trees in the far left of the plot (Fig. 9a), the group 125-173 yrs located in the lower left and far right (Fig. 9b), and the youngest group (22-122 yrs) was mostly in the top right and top centre of the plot (Fig. 9c). Tree age distributions for each group did not overlap.

Non-beech hardwoods

Cluster analysis of *E. hookerianus* identified two discrete age groups, the first 237-270 yrs and the second 81-185 yrs (Table 2). These groups were spatially discrete, the oldest group was in the top centre, and the youngest group was in the centre and right of the plot (Figs. 10a and 10b). Tree age distributions for each group did not overlap.

For each species, age ranges of different groups appeared to generally reflect the age-class peaks identified in Figs. 3 and 4, further suggesting that there were distinct periods of establishment in the plot. For different species, patches with broadly corresponding age ranges were placed into four age groups (Table 2). Within these four broad groups, the spatial distribution of each patch of trees was compared to see whether trees of different species were recruited at similar times in the same part of the plot. These groups are shown on the stem maps in Figs. 6 - 10, and they appeared to overlap spatially.

Almost all trees in group 1 (aged > 300 yrs) comprising *Dacrycarpus* and *N. menziesii* were found in the close proximity in the top centre of the plot, their ages also overlapped suggesting relatively synchronous establishment (Figs. 7a and 8a).

Trees in group 2 (mostly aged between 175-275 yrs) were numerous (54), and located in different parts of the plot from group 1 suggesting a distinct pulse of establishment. *Dacrydium* trees were mostly clustered in the centre with no interspersed, older surviving trees, suggesting a pulse of establishment in a large, discrete opening in the canopy (Fig. 6a). There were several *Dacrydium* trees located close to the plot edges, outside the plot there were many similar-sized *Dacrydium* in close proximity suggesting a more extensive even-aged patch. *Dacrycarpus* were in a different part of the plot to *Dacrydium* (Fig. 7b) and were negatively spatially associated (Table 3), suggesting partitioning of establishment conditions after disturbance.

Corresponding to the establishment of trees in group 2, were aged trees of two other surviving conifer species, *P. hallii* (228 yrs and 273 yrs) and *L. bidwillii* (246 yrs and 320 yrs) indicating establishment occurred also around the same time as the other conifers. These were mapped along with the identified dead stems of each species (Fig. 11), *P. hallii* were located in the far right and *L. bidwillii* in the centre and right side only. A general lack of young stems or saplings in the last 200 yrs suggests establishment has been infrequent for these species.

The maximum *N. menziesii* age of the 174-252 yrs group was within 25 yrs of *Dacrydium* in group 2, however the peak in its age-class distribution (175-200 yrs class) was offset by c. 50 yrs compared to the conifers in group 2. Most trees (75%) were <225 yrs old. There are two possibilities to explain this offset: either there was a delay in *N. menziesii* establishment, or trees were slower growing to coring height, after whatever initiated the upsurge in conifer recruitment c. 275-300 yrs ago; or alternatively *N. menziesii* establishment and recruitment into the canopy also occurred in response to another event (s). The peak in the *N. menziesii* age-class distribution 175-200 yrs ago coincided with a peak in the *Dacrycarpus* age-class distribution (Figs. 7c and 8b), and also reflected the general upsurge in recruitment evident in the combined age-class distribution 175-200 yrs ago (Fig. 4). This suggests that whilst some *N. menziesii* establishment may have been linked to whatever initiated conifer recruitment c. 275-300 yrs ago, its subsequent pulse of recruitment into the canopy could be due to a separate occurrence around 200 yrs ago. Hence, *N. menziesii* 174-252 yrs were placed in group 3 along with *Dacrycarpus* of similar age.

Trees in group 3 (mostly aged 125-200 yrs) were also widely distributed throughout the plot, but differed in their distribution from group 2. *Dacrydium* trees were clumped in the upper left of the plot, spatially separated from most trees of other species, suggesting establishment occurred in a discrete opening in the canopy (Fig. 6b). This patch could also

be part of a larger patch outside the plot. *Dacrydium* trees in group 3 were negatively associated with *N. fusca* and *E. hookerianus* of similar age (Table 3).

In contrast, the other species in group 3 had spatial patterns more consistent with establishment in smaller canopy openings in different parts of the plot. *Dacrycarpus* were mainly situated in the bottom left and upper right of the plot mainly in groups of two or more trees (Fig. 7c). *Nothofagus menziesii* were confined to the left of the plot only (Fig. 8b). *Nothofagus fusca* and *E. hookerianus* were found mostly together in the bottom left, centre and bottom right of the plot (Fig. 9b, 10b), and although there were differences in their distributions, they were positively associated at short distances (Table 3). *Nothofagus fusca* was distributed in a series of distinct clumps of between 2 to 6 trees in the lower half of the plot, suggesting establishment in a series of similar-sized canopy openings. *Elaeocarpus hookerianus* were more widely distributed, both in small clumps close to *N. fusca*, and individually in the centre and right of the plot amongst the older *Dacrydium* and *Dacrycarpus* trees.

Trees in *N. menziesii* group 4 (65-147 yrs) had also established in similar areas to *N. fusca* and *E. hookerianus* of group 3 (Fig. 8c), and were positively associated at short distances ($P < 0.05$, $n = 32$; $P < 0.05$, $n = 34$). The age-class distribution of trees in *N. menziesii* group (4) suggested delayed and protracted establishment in small canopy openings after *N. fusca* and *E. hookerianus* (Fig. 8c).

Table 2: No. of trees and age range of different groups in plot A, mean age (\pm s.d.) and maximum distance between trees.

| Groups | Species | No. Trees | Age range (yrs) | Mean age \pm 1 s.d. (yrs) | Max. distance between trees (m) |
|--------|-----------------------|-----------|-----------------|-----------------------------|---------------------------------|
| 1 | <i>Dacrycarpus</i> | 3 | 322-430 | 380 \pm 54 | 31 |
| 1 | <i>N. menziesii</i> | 4 | 305-384 | 331 \pm 36 | 18 |
| 2 | <i>Dacrycarpus</i> | 15 | 218-323 | 267 \pm 31 | 61 |
| 2 | <i>L. bidwillii</i> | 2 | 246-320 | 283 \pm 37 | 30 |
| 2 | <i>N. fusca</i> | 2 | 251-276 | 263 \pm 18 | 10 |
| 2 | <i>P. hallii</i> | 2 | 228-273 | 251 \pm 23 | 25 |
| 2 | <i>E. hookerianus</i> | 3 | 237-270 | 250 \pm 18 | 58 |
| 2 | <i>Dacrydium</i> | 30 | 151-275 | 228 \pm 35 | 68 |
| 3 | <i>N. menziesii</i> | 21 | 174-252 | 207 \pm 22 | 55 |
| 3 | <i>Dacrycarpus</i> | 24 | 93-215 | 158 \pm 32 | 73 |
| 3 | <i>N. fusca</i> | 20 | 128-173 | 148 \pm 11 | 60 |
| 3 | <i>Dacrydium</i> | 11 | 95-213 | 144 \pm 35 | 43 |
| 3 | <i>E. hookerianus</i> | 22 | 81-185 | 128 \pm 29 | 57 |
| 4 | <i>N. menziesii</i> | 12 | 65-147 | 116 \pm 23 | 48 |
| 5 | <i>N. fusca</i> | 17 | 25-122 | 46 \pm 28 | 55 |
| 5 | <i>N. menziesii</i> | 14 | 25-80 | 37 \pm 16 | 50 |

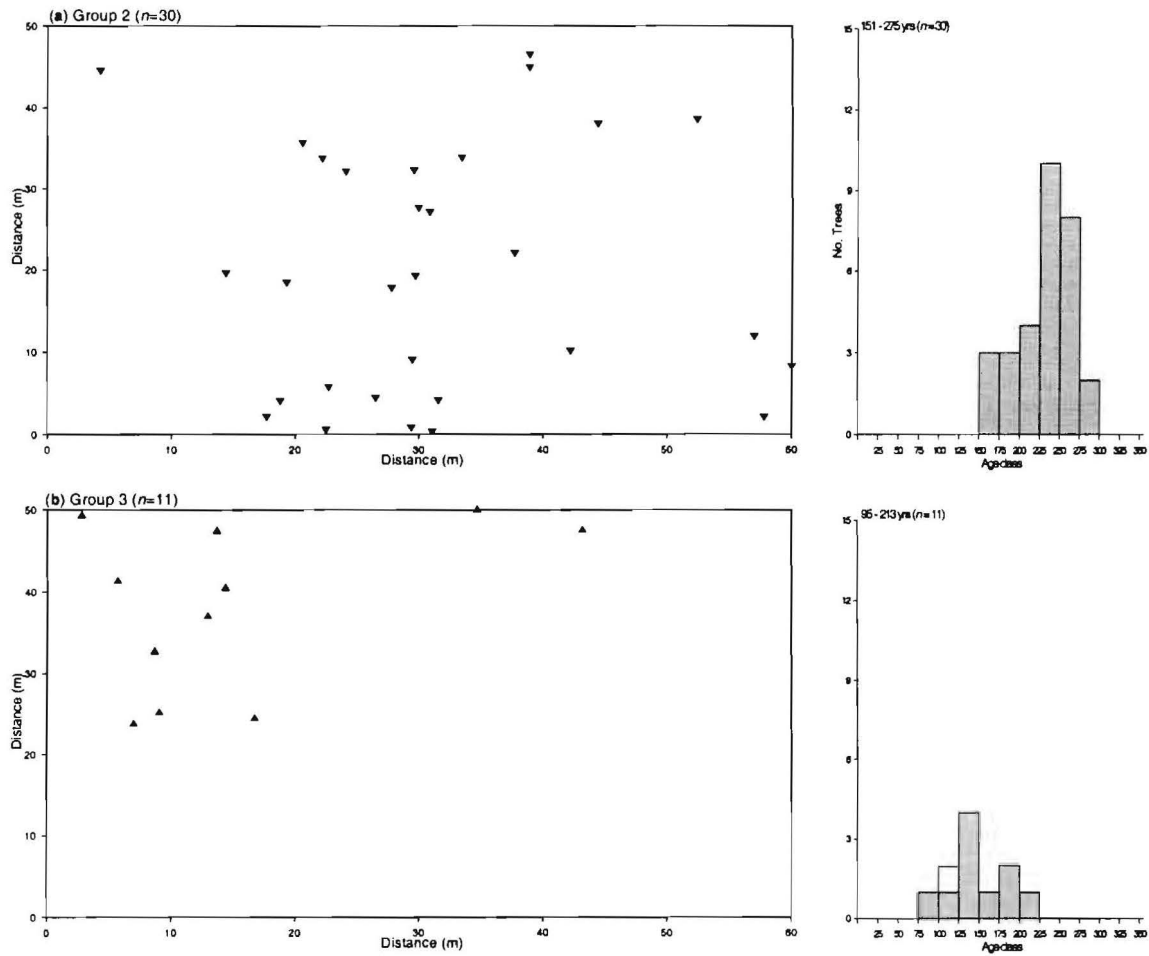


Figure 6: Stem maps and age-class frequency distributions for *Dacrydium* age groups (a) 151-275 yrs, (b) 93-213 yrs. Unfilled bars represent ages estimated from age/diameter regressions.

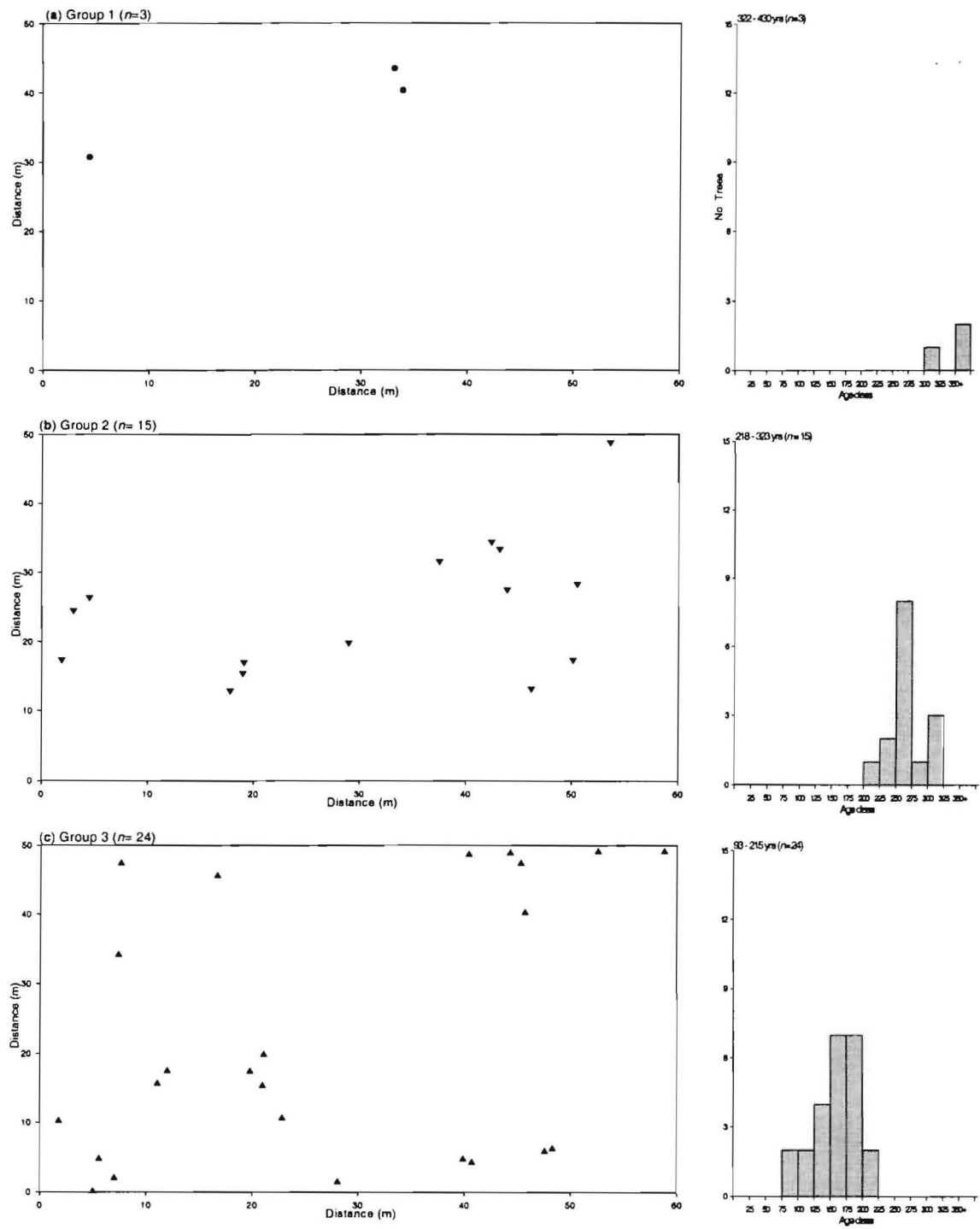


Figure 7: Stem maps and age-class frequency distributions for *Dacrycarpus* age groups (a) 322-430 yrs (b) 218-323 yrs (c) 93-215 yrs.

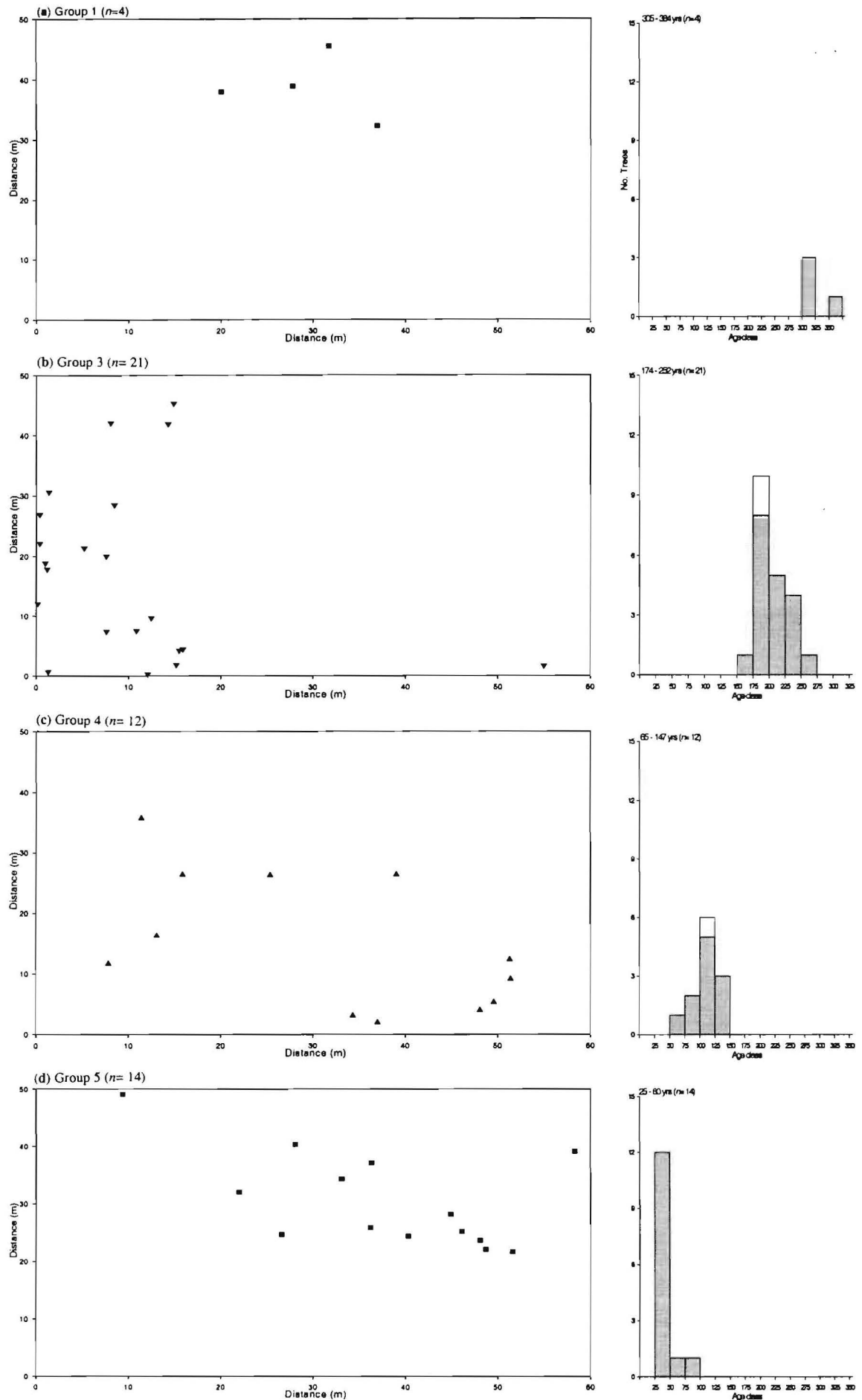


Figure 8: Stem maps and age-class frequency distributions for *N. menziesii* age groups (a) 305-384 yrs (b) 174-252 yrs (c) 65-147 yrs and (d) 25-80 yrs. Unfilled bars are estimated ages.

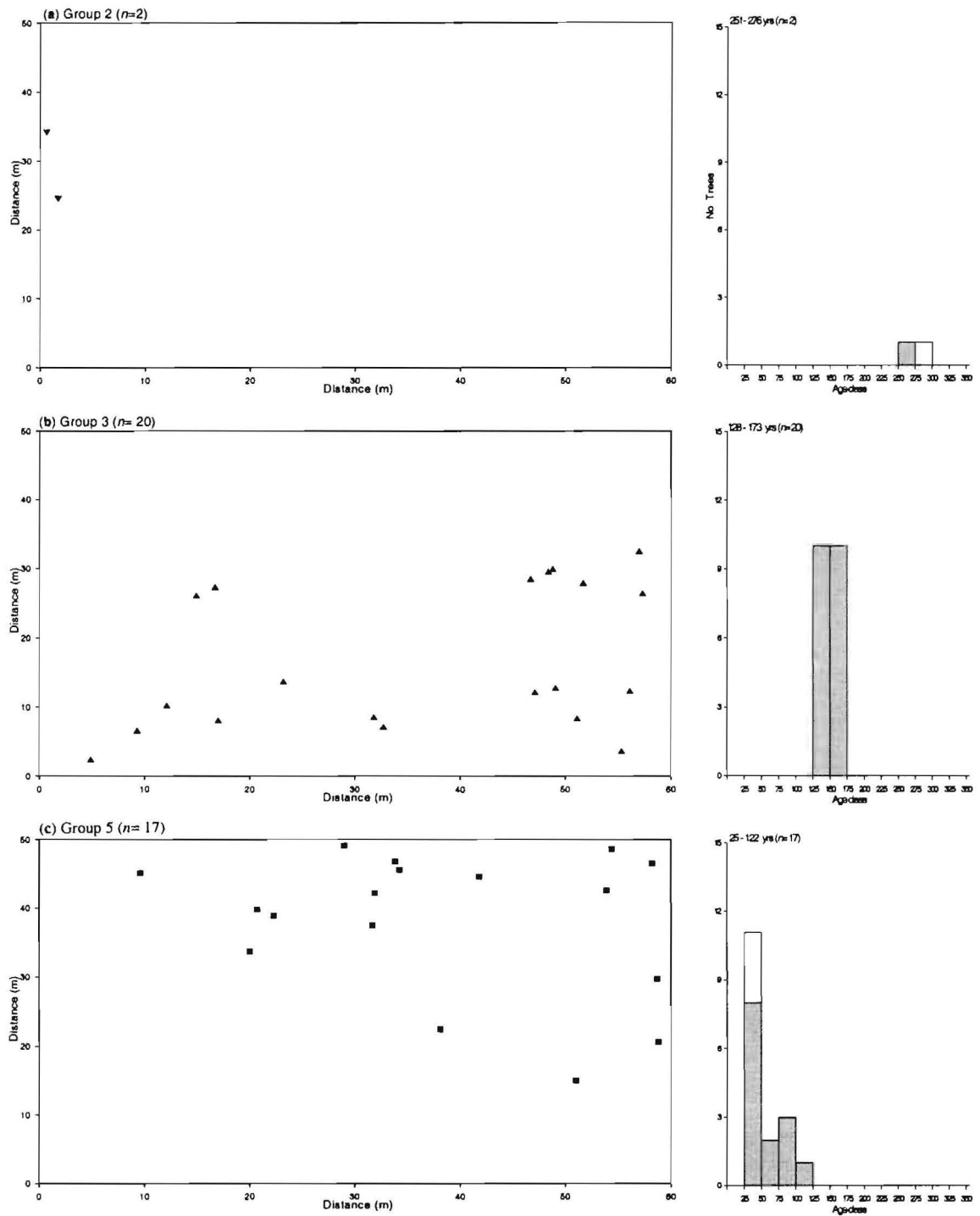


Figure 9: Stem maps and age-class frequency distributions for *N. fusca* age groups (a) 251-276 yrs (b) 128-173 yrs and (c) 25-122 yrs. Unfilled bars represent ages estimated from age/diameter regressions.

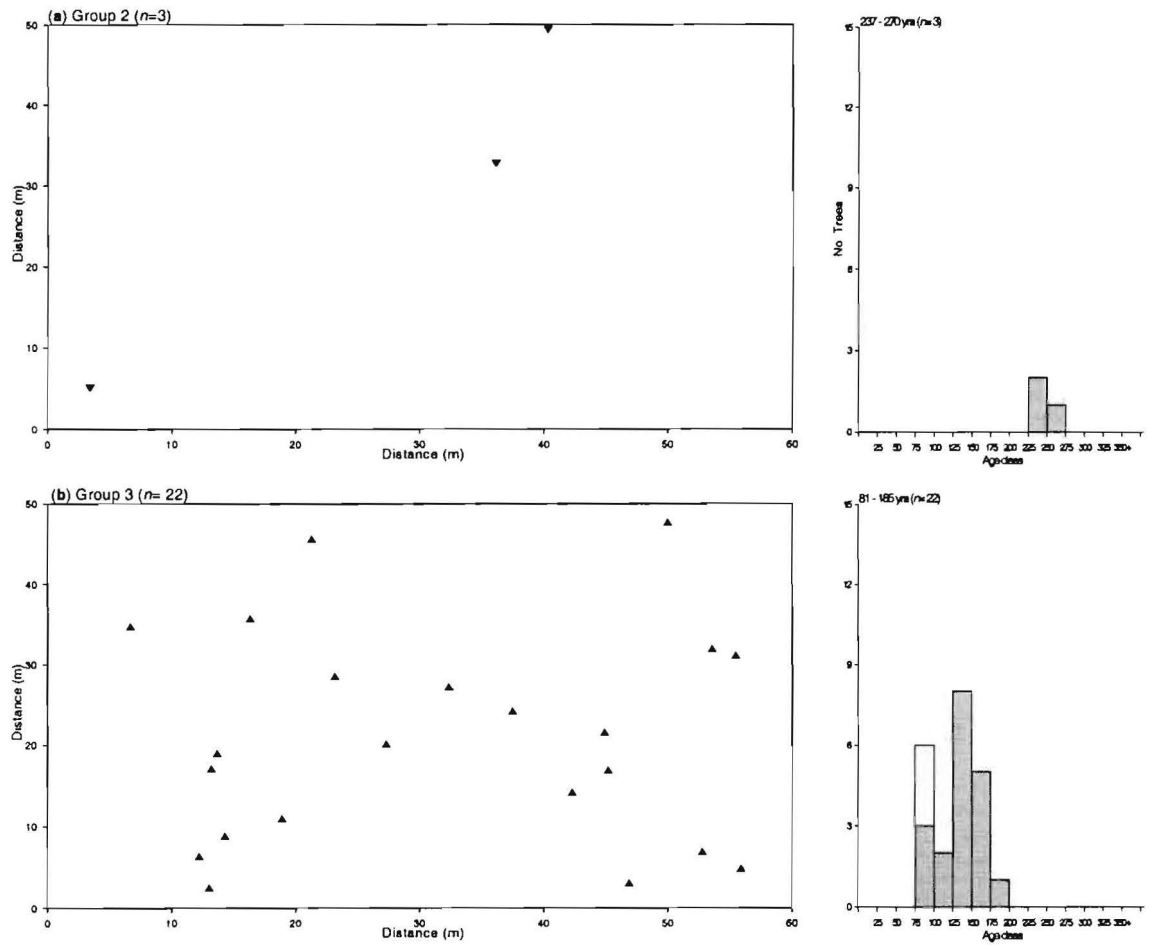


Figure 10: Stem maps and age-class frequency distributions for *E. hookerianus* age groups (a) 237-270 yrs and (b) 81-185 yrs. Unfilled bars represent ages estimated from age/diameter regressions.

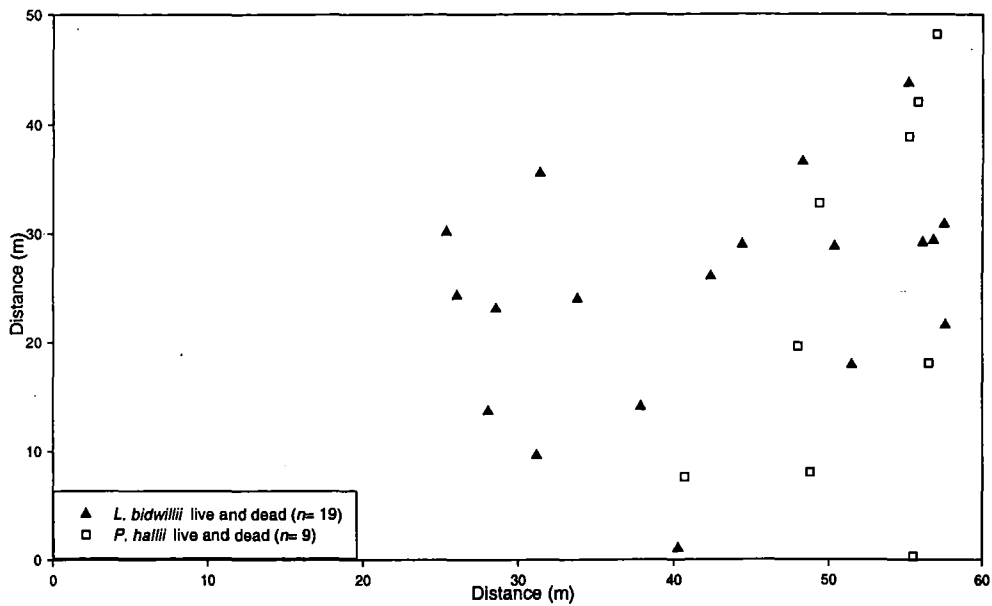


Figure 11: Stem map of live and dead *L. bidwillii* and *P. hallii* (n=28).

There were comparatively few trees < 100 yrs with only the beeches showing a number of similarly-aged trees in group 5 (Table 3). Trees of *N. menziesii* and *N. fusca* were in the upper centre and right of the plot. Most *N. menziesii* stems were either clumped among dead *L. bidwillii* stems in the right or spread out on logs and mounds underneath the older *Dacrydium* canopy in the plot centre (Fig. 8d). The *N. fusca* trees were clumped on mounds around the oldest *Dacrycarpus*/*N. menziesii* trees, and spread out amongst the dead *L. bidwillii* in the right of the plot (Fig. 9c).

Table 3: Patterns of association between groups of trees (≥5 cm dbh) of different species derived from the function K12(*t*). + and - denote significant (P<0.05) positive and negative associations for distances *t* up to 10m; dot indicates no significant association after testing between groups.

| SPECIES | Dacrycarpus Group 2 | | | |
|----------------------|----------------------|----------------------|------------------|------------------------|
| Dacrydium Group 2 | - | | | |
| | Dacrycarpus Group 3 | N. menziesii Group 3 | N. fusca Group 3 | E. hookerianus Group 3 |
| Dacrydium Group 3 | . | . | - | - |
| Dacrycarpus Group 3 | | . | . | . |
| N. menziesii Group 3 | | | . | . |
| N. fusca Group 3 | | | | + |
| | N. menziesii Group 5 | | | |
| N. fusca Group 5 | . | | | |

3.1.4 Microsite differences within each group

Dacrycarpus trees in group 1 had established on forest floor sites, whereas *N. menziesii* were all on elevated logs and mound sites (Table 4). In group 2, most *Dacrycarpus* trees were on forest floor sites along with *c.* 50 % of *Dacrydium* trees in this group, the remaining *Dacrydium* had elevated root plates (15). It was unclear whether these elevated, spreading surface root plates which extended up to 2 m from the base of each tree, indicated establishment on material that since decayed. Another possibility is these root plates were a morphological response to heavily saturated peats by offering structural support after forest floor establishment, or were a response to anaerobic conditions in the subsurface environment.

Table 4: Numbers of trees of each species established on different microsites for each approximately even-aged group identified from the spatial analysis of tree age distributions.

| Group | Species | Elevated Logs | Elevated Mounds | Non-Elevated Forest floor | Total N |
|-------|-----------------------|------------------|--------------------|------------------------------|------------|
| 1 | <i>Dacrycarpus</i> | | | 3 | 3 |
| 1 | <i>N. menziesii</i> | 1 | 3 | | 4 |
| 2 | <i>Dacrycarpus</i> | | 1 | 14 | 15 |
| 2 | <i>N. fusca</i> | 1 | 1 | | 2 |
| 2 | <i>E. hookerianus</i> | | 1 | 2 | 3 |
| 2 | <i>Dacrydium</i> | | 2 | 28 | 30 |
| 3 | <i>N. menziesii</i> | 11 | 8 | 2 | 21 |
| 3 | <i>N. fusca</i> | 10 | 8 | 2 | 20 |
| 3 | <i>Dacrycarpus</i> | | 2 | 22 | 24 |
| 3 | <i>Dacrydium</i> | 1 | | 10 | 11 |
| 3 | <i>E. hookerianus</i> | 4 | | 18 | 22 |
| 4 | <i>N. menziesii</i> | 9 | 2 | 1 | 12 |
| 5 | <i>N. fusca</i> | 3 | 14 | | 17 |
| 5 | <i>N. menziesii</i> | 3 | 10 | 1 | 14 |

There was a gradient in organic matter in soil pits across the plot with the highest concentrations of organic matter (Kini peats) in the centre of the plot (Table 5), which broadly coincided with the distribution of *Dacrydium* in group 2 (Fig. 6a). Increasing amounts of mineral material in peats in the other areas of the plot (Rotokuhu peats) broadly coincided with the distribution of *Dacrycarpus* in group 2 (Fig. 7a, Plate 2).

Soil samples were taken from within 1 metre of 10 randomly selected *Dacrydium* and *Dacrycarpus* from group 2. The proportion of organic matter to mineral material was greatest underneath *Dacrydium* (10-25 cm depth: range 72.3-96.4 %; 25-40 cm depth: 44.6-91.7

%), whereas the proportion of organic material decreased with more mineral (silt) material in the peats towards the outsides of the plot underneath *Dacrycarpus* trees (10-25 cm depth: range 46.7-84.6 %; 25-40 cm depth: 35.6-81.4 %).

Although sample size was limited, there was a significant difference between the organic matter concentration at different depths between species, with *Dacrydium* found in peats with higher organic contents (Kruskal-Wallis test of mean organic matter concentration between species: 10-25 cm depth $X^2=5.50$, $P=0.019$, 1 d.f.; 25-40 cm depth, $X^2=4.48$, $P=0.034$, 1 d.f.). This suggests that as the concentration of organic material increases *Dacrydium* becomes more abundant and *Dacrycarpus* less so. However, peat textural differences alone can not fully explain the distribution of these species within the plot, as there was some overlap, with both species occurring on peats with similar proportions of organic material. This suggests that other factors are also influencing their successful recruitment into the canopy, although textural differences may be a factor separating species in the most organic peats.

In group 3, establishment site differences were apparent between the species (Table 4). Elevated sites on these very poorly drained sites appear critical for enabling beech establishment, almost all the beeches were on elevated sites, with > 50 % of *N. menziesii* and *N. fusca* on logs. However, the conifers and hardwoods had established on forest floor sites, along with the hardwood *E. hookerianus*.

Most *N. menziesii* and *N. fusca* trees in group 5 were on elevated mounds with proportionately fewer trees on logs compared to *N. menziesii* and *N. fusca* trees in group 3, and *N. menziesii* in group 4 (Table 4). Elevated mounds were characterised by a *L*, *F* and *H* layer (litter, fermentation and humic layer) over an *O* or peat horizon, compared with forest floor and pit sites that generally have a saturated *O* layer only. The *L*, *F*, *H* layer is created by better drainage due to elevation, and are therefore not permanently saturated and are likely to be more aerated and warmer than the forest floor *O* layers.

Table 5: Analysis of organic matter content of 4 soil pits across a transect in plot A at Mt Harata. Co-ordinates along transect, depth to gravels, brief soil description and percentage organic matter taken from samples in each layer. % organic matter represents absolute minimum of organic matter content after ignition.

| Pit No. | Co-ordinates | Depth to gravels (cm) | Soil layer depth (cm) | Brief Description | % organic material |
|---------|----------------|-----------------------|-----------------------|--|--------------------|
| 1 | x =5 y =20 | 50 | 5-10 | Very strongly decomposed layer | 76.1 |
| | | | 10-25 | Very strongly decomposed dark brown with black concretions, slightly sticky | 59.6 |
| | | | 25-40 | Lighter brown in colour, fewer roots | 47.4 |
| 2 | x=20 y =24 | 80 | 5-10 | Very strongly decomposed dark brown/black material | 94.8 |
| | | | 10-25 | Weakly decomposed fine leaves, twigs, intact pieces of wood, dark brown | 96.6 |
| | | | 25-40 | Very wet fluid soil, abundant live roots down to gravels | 74.8 |
| 3 | x =35 y =20 | 80 | 5-15 | Very strongly decomposed dark brown/black material | 99.3 |
| | | | 15-40 | Weakly decomposed fine leaves, twigs, intact pieces of wood, dark brown | 99.2 |
| | | | 40-65 | Semi-decomposed material, mushed up pieces of wood, bad smell, chocolate brown | 99.2 |
| 4 | x =55 y =20 | 60 | 5-8 | Very strongly decomposed dark brown with black concretions, slightly sticky | 84.3 |
| | | | 8-30 | Weakly decomposed fine leaves, twigs, intact pieces of wood, greyish brown | 71.4 |
| | | | 30-60 | Very wet fluid soil, abundant live roots | 54.1 |

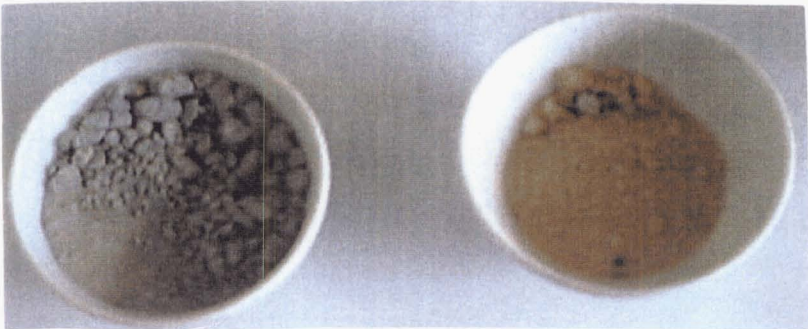


Plate 2: Residue after ignition of peats from pit 1 (left) and pit 3 (right) in plot A. Note the blue-grey material from pit 1 are fine silt grains that were incorporated into the peat. The brown colour of material in pit 3 represents ash from organic material with few silt grains visible.

3.1.5 Patterns of tree ring release and species recruitment

The episodic nature of tree recruitment that coincided for different species suggests that disturbances causing openings in the canopy are the likely causal explanation for patterns of synchronous tree recruitment evident in Figs. 3 and 4. From the distribution of the four groups in Table 2, it appears that these periodic disturbances had differential effects in different parts of the plot during the last 300 yrs.

The most extensive event in the last 300 yrs was the disturbance (s) that resulted in the plot-wide (and probably beyond) synchronous establishment of predominantly conifer species in group 2 c. 275-300 yrs ago. However, there were only three *N. menziesii* with sufficiently long ring series to accurately determine the exact timing of this event, and releases were found in two of them in the decade between 270-280 yrs ago. The oldest trees for each species in group 2 were similar in age being clustered between 252-276 yrs (Table 2), with the exception of *Dacrycarpus*, which had a maximum age of 323 yrs (Fig. 7d). However, there is > 30 yr gap from the three oldest trees to the main peak in the *Dacrycarpus* age distribution; the next oldest *Dacrycarpus* tree is 278 yrs, suggesting these three trees > 300 yrs may have represented advanced regeneration. Six of the *Dacrydium* in group 2 branched as low as 6-10 m, which was unusual for this species that typically has a tall straight bole with an emergent crown, suggesting lack of interspecific competition under open conditions.

The delay in *N. menziesii* recruitment compared to the conifers in group, may well also reflect response to a subsequent disturbance (s). I examined the patterns of annual growth ring release in *N. menziesii* to investigate whether there were major periods of tree ring growth releases that coincided with upsurges in tree recruitment, which could indicate evidence for the timing of past disturbances (Fig. 12). Periods of release were considered significant if they were present in $\geq 20\%$ of all trees measured. Most *N. menziesii* trees with sufficiently long ring series were concentrated in the left of the plot, reflecting the distribution of *N. menziesii* trees > 150 yrs old (Fig. 8b). This meant that the spatial distribution of releases could not be used in interpreting the extent of disturbances that occurred throughout the plot at different times, so individual species spatial distributions were used instead. Cores were not cross-dated so the actual timing of events was also unable to be accurately ascertained.

The largest peaks in releases were found in the periods 190-220 yrs, 140-160 yrs, 70-90 yrs, and in the last 50 yrs (Fig. 12). Several peaks in releases coincided closely with upsurges in species establishment within the plot suggesting these periods reflected the timing of past disturbances. For example, two of these periods 190-220 yrs and 20-50 yrs

corresponded with the upsurges in establishment 175-200 yrs and 20-50 yrs ago evident in the combined species age-class distribution in Fig. 4. The period 140-160 yrs ago coincides with the upsurge in the *N. fusca* and *E. hookerianus* age-class distributions in group 3. In between these periods there were releases in $\geq 10\%$ of trees suggesting periods of less extensive disturbance.

The releases 190-220 yrs closely coincided with the increase in *N. menziesii* establishment and recruitment in group 3. The seven *N. menziesii* that were older than 220 yrs were pre-existing saplings that probably established after the disturbance c. 275-300 yrs ago, but experienced a significant growth release between 190-220 yrs ago enabling their recruitment into the canopy. Evidence for this was found in the sudden and abrupt increase in ring width that was sustained for a period of time after initial slower growth (Fig. 13). The disturbance (s) also enabled an additional pulse of *D. dacrydioides* recruitment into the canopy, explaining the corresponding peak in their age-class distribution in group 3 to *N. menziesii*.

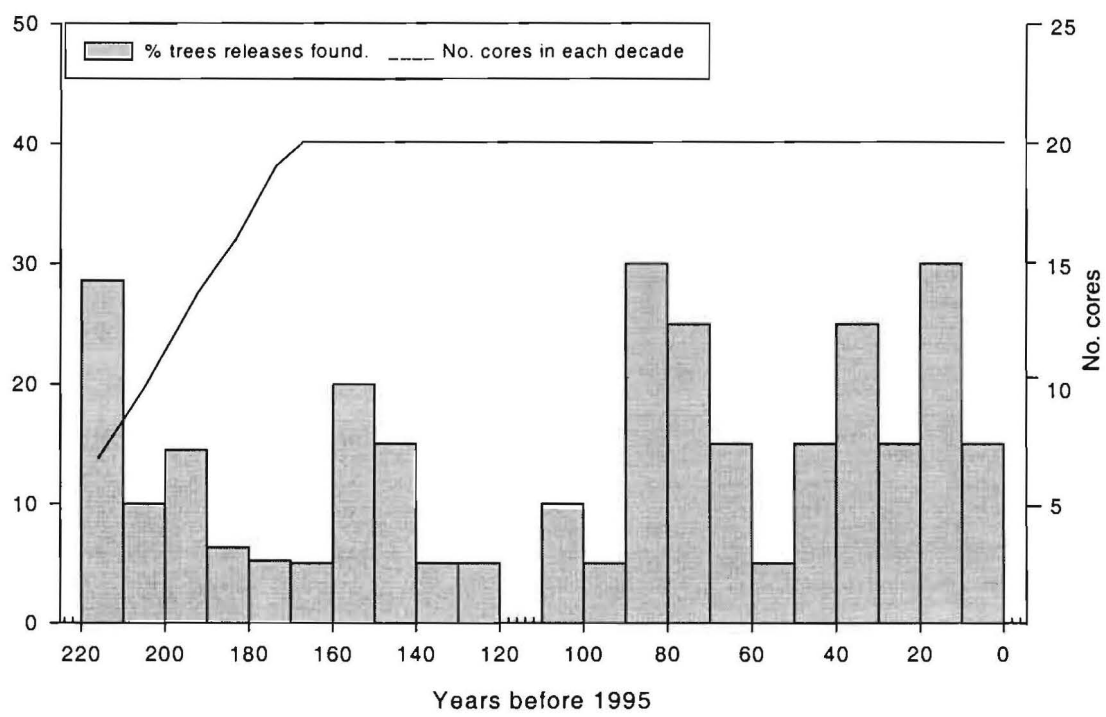


Figure 12: Temporal distribution of growth releases in each decade over last 220 yrs ($n=20$ trees). Filled bars are relative proportion of trees with releases in each decade, solid line is total no. of cores measured in each decade.

The subsequent peak in releases commencing 150-160 yrs ago coincided with the abrupt upsurge of recruitment into the overstorey of *N. fusca* and *E. hookerianus* trees in group 3. These trees had established in other parts of the plot to *N. menziesii* in group 3, and were mostly younger, suggesting the releases 140-160 yrs ago reflected a distinct disturbance event (s) to the understorey or canopy which facilitated *N. fusca* and *E. hookerianus* recruitment into the overstorey.

The periods of significant release identified in Fig. 12 represent disturbances that were less extensive in their effects on species recruitment than the disturbance c. 275-300 yrs ago. Two lines of evidence support this: first, establishment of trees in groups 3 and 5 were in separate parts of the plot, and secondly trees in groups 3, 4 and 5 had generally established in canopy gaps between and around older trees.

The releases in the last 90 yrs were found in most *N. menziesii* trees; however, the youngest groups of stems were in the top right of the plot (group 5) on mounds around the bases of dead standing conifers *Libocedrus bidwillii* and *Podocarpus hallii* (Figs. 8d, 9c and 11). Both *N. menziesii* and *N. fusca* trees in group 4 show significant positive associations with dead *L. bidwillii* and *P. hallii* at very short distances (*N. menziesii* 1 & 4 m, $P < 0.05$, $n = 37$; *N. fusca* 2-3 m, $P < 0.05$, $n = 40$). This could possibly reflect the changing establishment opportunities in the plot with increasing microsite availability around the mounds and bases (litter cones) of dead trees as the older trees die, particularly *L. bidwillii* in the same area of the plot.

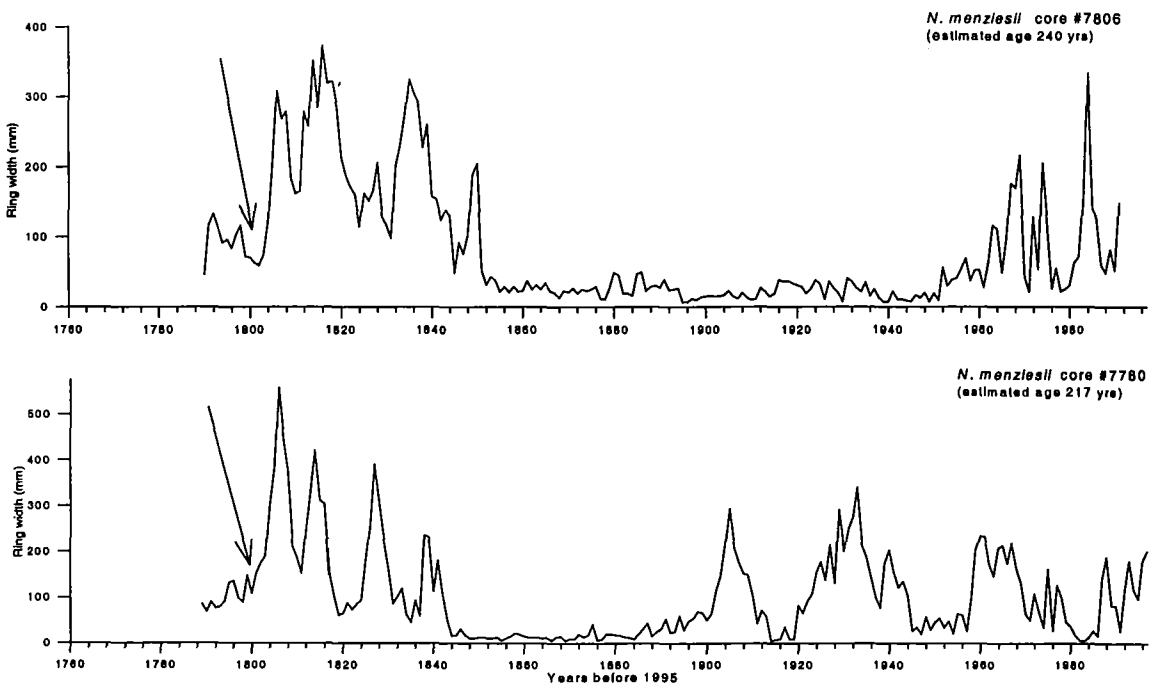


Figure 13: Examples of *N. menziesii* cores in plot A showing substantial synchronous growth increases c. 190-200 yrs ago (represented by arrows) after release from slower initial growth.

3.1.6 Current regeneration patterns

Patterns of microsite establishment for saplings of different species reflected those found for trees of different species, with the conifers and *E. hookerianus* mostly on non-elevated sites, and the beeches on elevated microsites (Table 6). Saplings of all species were clumped in their distribution (appendix: Table A2), except *Dacrydium* for which there were too few saplings to test.

In a similar pattern to the distribution of trees in group 4, saplings of both *N. fusca* and *N. menziesii* were positively associated with dead standing trees (*N. fusca* at 1m, 3-5 m, $P<0.01$, $n=341$; *N. menziesii* 2 & 5m, $P<0.01$, $n=85$). *Nothofagus fusca* saplings also have a positive association with the litter cones of live *Dacrycarpus* > 250 yrs old ($P<0.01$, $n=290$). Conditions are similar on these humic cones or mounds built up from leaf litter, twigs and sloughed bark under live *Dacrycarpus* > 250 yrs in terms of an available *L*, *F*, *H* layer. These live *Dacrycarpus* trees commonly exceed 30 m in height with a sparse open canopy, allowing light to penetrate to the humic litter cones.

In contrast to sapling establishment patterns, seedlings of all species established on a range of microsites, with the exception of *L. bidwillii* for which no seedlings were found (Table 6). Only *Dacrydium* seedlings showed a non-random positive association with any particular microsite (tree ferns $X^2 = 10.70$, $P<0.01$, 1 d.f.), although most *E. hookerianus* seedlings were found on non-elevated sites. However, *Dacrycarpus*, *N. fusca* and *N. menziesii* seedlings were abundant on different microsites. This suggests that other factors other than germination, inhibit beech species from reaching sapling size on non-elevated sites and conifers on elevated sites.

Table 6: Comparison of number of saplings (<5 cm dbh, >1.4m tall) and seedlings (<1.4m tall) \pm 1 s.d. of different species across different microsites in plot A (all values converted to a per hectare basis).

| Species | | Forest Floor | Logs | Stumps | Mounds | Tree ferns | TTL (ha^{-1}) |
|-----------------------|-------|------------------|----------------|----------------|----------------|--------------|--------------------------|
| <i>Dacrydium</i> | Sapls | 7 | 3 | | | | 10 |
| | Seedl | 95 \pm 18 | 160 \pm 8 | 287 \pm 14 | 980 \pm 49 | 370 \pm 19 | 2114 \pm 108 |
| <i>Dacrycarpus</i> | Sapls | 113 | | | | | 113 |
| | Seedl | 31816 \pm 1591 | 4733 \pm 236 | 3220 \pm 161 | 2943 \pm 147 | 30 \pm 2 | 42742 \pm 2137 |
| <i>L. bidwillii</i> | Sapls | 3 | | | 3 | | 6 |
| <i>N. fusca</i> | Sapls | 7 | 223 | 43 | 643 | | 916 |
| | Seedl | 1580 \pm 79 | 517 \pm 26 | | 360 \pm 18 | 7 \pm 1 | 2464 \pm 124 |
| <i>N. menziesii</i> | Sapls | 7 | 40 | 20 | 170 | | 237 |
| | Seedl | 6636 \pm 332 | 1273 \pm 64 | 117 \pm 6 | 2156 \pm 108 | 7 \pm 1 | 10183 \pm 511 |
| <i>E. hookerianus</i> | Sapls | 60 | 3 | | 3 | | 66 |
| | Seedl | 1580 \pm 79 | 40 \pm 2 | | 157 \pm 3 | 20 \pm 1 | 1697 \pm 85 |

3.2 POORLY DRAINED STAND - PLOT B

3.2.1 Stand composition, structure and soils

Dacrydium cupressinum had the largest basal area of any species in this plot, although there were relatively few stems (Table 7). The other conifers *Dacrycarpus dacrydioides* and *Prumnopitys ferruginea* had low basal area and stem density. No live or dead *Libocedrus bidwillii* or *Podocarpus hallii* were found in this plot.

Both *Nothofagus menziesii* and *N. fusca* stems were abundant and the beech species had the highest stem densities in this plot (Table 7). Stems of the non-beech hardwood *Weinmannia racemosa* were also abundant. Other non-beech hardwoods *Quintinia acutifolia* and *Elaeocarpus hookerianus*, were also present, but in low densities.

Structurally, *Dacrydium*, and to a lesser extent *Dacrycarpus*, were emergent over a canopy dominated by *N. fusca* and *N. menziesii* (Table 7). The subcanopy tier comprised abundant *N. fusca*, *N. menziesii* and *W. racemosa*, with associated *Dacrycarpus*, *Q. acutifolia* and *E. hookerianus*, over an understorey of young beeches, hardwoods and tree ferns (*Dicksonia squarrosa* and *Cyathea smithii*).

The most abundant identifiable dead stems were *Dacrydium* and *N. fusca*, with fewer other conifers and *N. menziesii* (Table 7). No dead hardwoods were identified although there were often dead and rotten leaders attached to live *W. racemosa*.

Table 7: No. of trees (≥ 5 cm dbh) in different height tiers, basal area of live stems, and no. identified dead stems within 0.7 ha plot B. All values converted to a per hectare basis.

| Species | Understorey (2-5 m) | Subcanopy (5-15 m) | Canopy (15-25 m) | Emergent (> 25 m) | TOTAL stems / ha | Dead Stems /ha | Live Basal Area m ² / ha |
|-----------------------|------------------------|-----------------------|---------------------|----------------------|------------------------|----------------------|---|
| <i>Dacrydium</i> | | 1 | 11 | 41 | 53 | 44 | 24.9 |
| <i>Dacrycarpus</i> | 11 | 21 | 4 | 9 | 45 | 24 | 4.0 |
| <i>P. ferruginea</i> | 7 | 7 | 9 | | 23 | 7 | 1.4 |
| <i>N. menziesii</i> | 46 | 96 | 71 | 1 | 214 | 19 | 11.1 |
| <i>N. fusca</i> | 27 | 74 | 47 | 6 | 154 | 56 | 7.1 |
| <i>W. racemosa</i> | 33 | 104 | 9 | | 146 | | 7.0 |
| <i>Q. acutifolia</i> | | 9 | 13 | | 22 | | 1.8 |
| <i>E. hookerianus</i> | | 14 | 7 | | 21 | | 0.5 |
| Total | | | | | 678 | 150 | 57.8 |

Soils in this plot were a mixture of poorly drained peaty gley soils and very poorly drained mucky, fluid Rotokuhu peats with incorporated mineral material (see appendix). Although there were both poorly and very poorly drained soils in this plot, I placed this plot in the 'poorly drained' part of the terrace drainage sequence due to the general lack of Kini peats and the presence of relatively shallower peaty-gley soils. The peaty-gley soils typically had a horizon sequence comprising an *O* layer (20-50 cm in depth), over *Ah*, *Bg* and *C* layers. From soil pits and auger bores ($n=39$) these peaty-gley soils were generally shallower in depth to gravels (mean depth 62 cm) than the deeper Rotokuhu ($n=31$) peats (mean depth 80 cm - ANOVA between depths F-ratio 62.77, $P<0.001$, $n=70$). The Rotokuhu peats were mainly found in a band in the left of the plot, whereas the less poorly drained shallower peaty gley soils mostly occupied the right side of the plot. This spatial pattern could indicate a subsurface physical feature influencing drainage, such as an old stream channel forming an underlying depression in the left of the plot. The main stream flowing across the terrace now runs c. 100 metres farther east and parallel to this peat band.

3.2.2 Stand age and size structure

Conifers

The multi-modal age distribution for *Dacrydium* had a discontinuous structure with three peaks evident in the 300-350 yrs, 600-650 yrs and 800-850 yrs classes, suggesting a population composed of relatively even-aged groups of trees (Fig. 14a). The cored trees ranged in age from 287-1052 yrs. The *Dacrydium* size-class frequency distribution also had a discontinuous structure with most trees in larger size classes (>45 cm dbh) and few smaller diameter trees (Fig. 14b). The lack of trees <300 yrs suggests conditions have been unfavourable for recruitment into the canopy during this time, although there are a number of saplings which age/diameter regressions suggest were <60 yrs old (appendix: Table B1).

Other species with shorter longevity show age patterns that could be attributable to distinct pulses of recruitment and/or mortality at more frequent intervals in the last 400 yrs. The age distribution of the emergent *Dacrycarpus* had a discontinuous structure with most (c. 90 %) trees either <100 yrs or >300 yrs old suggesting intermittent recruitment into the canopy (Fig. 14c). The cored trees ranged in age from 30-417 yrs. The *Dacrycarpus* size structure also had a discontinuous distribution with most trees <21 cm dbh and prolific saplings, and a gap to the larger trees >43 cm dbh (Fig. 14d).

There were few scattered *Prumnopitys ferruginea* (16) and the cored tree ages ranged from 35-635 yrs. Recruitment into the canopy was sporadic with one or two trees recruited into the canopy per century, only three individuals were recruited into the canopy in the last 100 yrs and there were no saplings present. Trees were scattered within the plot.

Beeches

In contrast to the conifers, beeches and non-beech hardwoods were more numerous and substantially more stems were recruited into the canopy over the last 250 yrs (Fig. 14).

The multi-modal age distribution for *N. menziesii* had a discontinuous structure with several peaks evident in the 50-100 yrs, 175-200 yrs, 250-275 yrs and 350-400 yrs age classes, suggesting either a population reflecting distinct periods of recruitment and/or mortality (Fig. 14e). The cored trees ranged in age from 25-368 yrs. The size-class frequency distribution had most trees in smaller size classes and decreasing numbers of trees in larger size classes (Fig. 14f). Over 200 saplings were found which age/ diameter regressions suggest were < 70 yrs (appendix: Table B1).

The *N. fusca* age-class frequency distribution also had a discontinuous pattern with most trees in younger age classes (Fig. 14g). The cored trees ranged in age from 25-423 yrs (Fig. 14g). There were several older trees > 300 yrs old with a gap in ages of c. 100 yrs until about 225 yrs ago when establishment of stems recommenced. Most trees (c. 90%) were < 100 yrs, which may reflect most of the population having arisen abruptly commencing c. 100 yrs ago, or it may suggest a pattern of more continuous recruitment and/or mortality. The *N. fusca* size class distribution shows a much steeper reverse 'J' shape than *N. menziesii* with decreasing numbers of trees in larger size classes (Fig. 14h), which could also reflect recent establishment of a large, relatively even-aged population, or alternatively indicate a continuous recruitment pattern with high mortality in smaller size classes. There was prolific recent sapling establishment (> 300), which age/diameter relationships suggest were < 50 yrs in age (appendix: Table B1).

Non-beech hardwoods

The cored *W. racemosa* stems ranged in age from 50-440 yrs, and the majority of the population were aged between 100-200 yrs (Fig. 14i). This could reflect a large pulse of stem recruitment commencing 200-250 yrs ago with comparatively less subsequent establishment in the last 100 yrs, although there were 34 saplings not aged that age/diameter regressions suggest were < 90 yrs. The size class distribution had a similar shape to the age distribution with a peak in the 15-24.9 cm class suggesting a distinct period of stem initiation (Fig. 14j). There were fewer saplings than the beeches and

conifers. The largest living leader of each *W. racemosa* was cored; however, this does not necessarily reflect the actual establishment age of the tree. *Weinmannia racemosa* can resprout as old leaders die and rot away, and it is not uncommon to see a main leader in an advanced state of decay with young, vigorous leaders growing from the base. New leaders can also be produced alongside older, intact stems in response to more recent canopy openings. Nevertheless, this species appears to have different age patterns to the beeches and conifers, with proportionately more stems aged between 100-200 yrs ago, when beech and conifer recruitment was comparatively low. Intriguingly, there has been significantly less new establishment of *W. racemosa* trees in the last 100 yrs than the beeches. This pattern is also reflected in the size class distribution as there were substantially less saplings and small stems (< 15 cm dbh) in this plot than the beeches and *Dacrycarpus* (Fig. 14j).

There were few stems of the other hardwoods *Q. acutifolia* and *E. hookerianus* (Table 7); these ranged in age from 50-250 yrs for both species. There were also few saplings recorded (6 and 22 respectively) indicating recent recruitment for these species has been infrequent in the plot.

Tree age distributions for several individual species suggested that there had been distinct periods of establishment within the plots over the last 900 yrs. Therefore, to investigate whether there were distinct periods of stem establishment, I combined the ages of all conifers, beeches and hardwoods together (Fig. 15a). There were five main periods where there was a distinct upsurge in stem establishment in the plot over the last 900 yrs: 50-100 yrs, 200-250 yrs, 350-450 yrs, 600-650 yrs and 800-850 yrs. Several of these periods were also evident as peaks in individual species age-class distributions, suggesting there were periods where there were pulses of establishment of different sets of species at different times. For example, coinciding with a peak in the *Dacrydium* age distribution 350-400 yrs ago, there is a peak of similarly-aged *Dacrycarpus* and *N. menziesii* trees, with several *N. fusca* (Fig. 14). Commencing c. 100 yrs ago there was a coincidental upsurge in *Dacrycarpus*, *N. menziesii*, and *N. fusca* establishment, and between 200-250 yrs there was an increase in *N. menziesii* and *W. racemosa* stems.

3.2.3 Spatial distribution of tree ages

I constructed a spatial correlogram of the tree ages for all species combined, to look for evidence of patchiness in tree age distributions, and to see whether these pulses of establishment represented spatially distinct groups of similarly-aged trees (Fig. 15b).

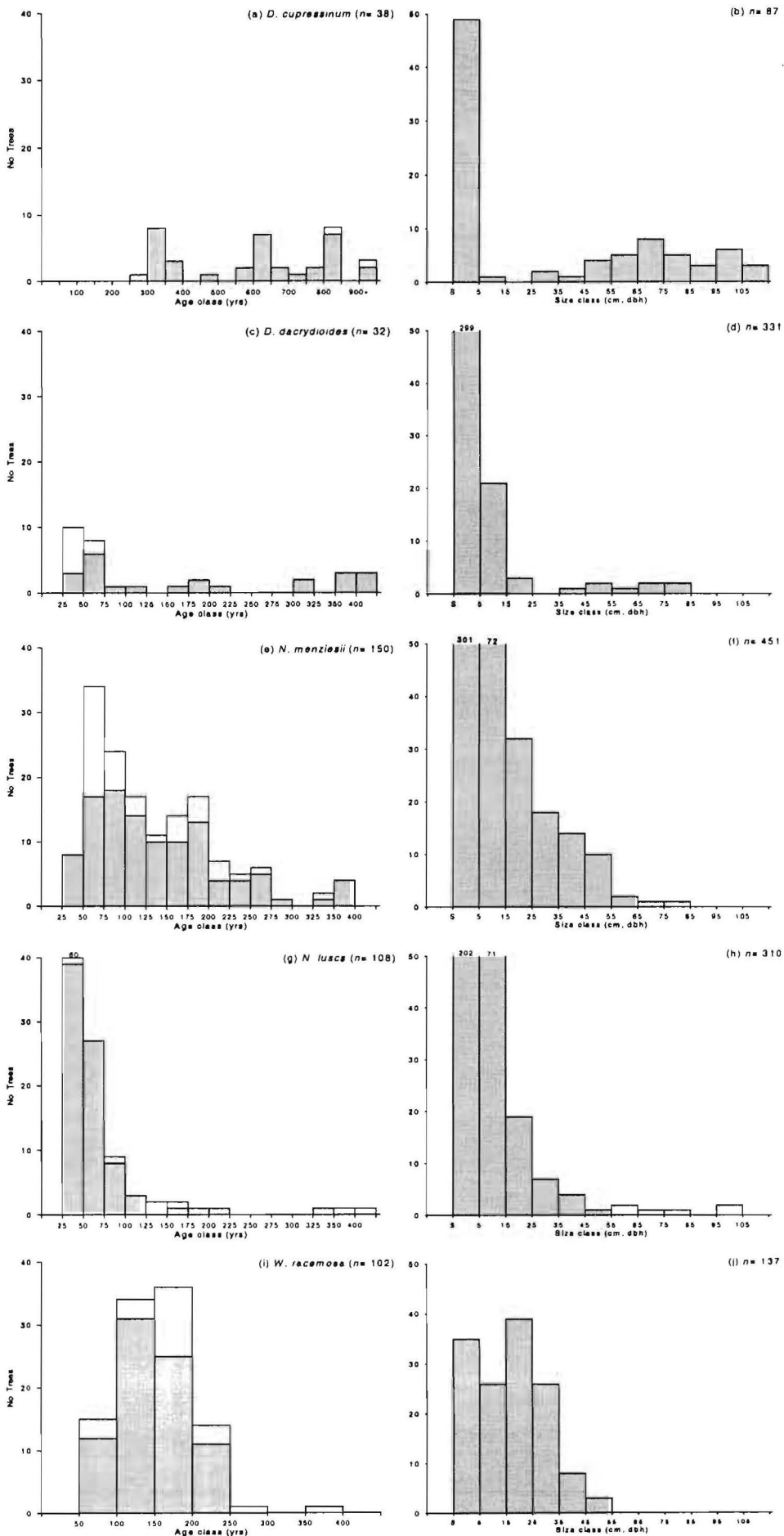


Figure 14: Age- and size- class frequency distributions for the main overstorey species (> 30 trees) found in plot B. Unfilled bars in the age diagrams represent ages estimated from age/ diameter regressions for unaged trees. S = saplings in size class diagrams. All regressions significant at $P<0.01$ (appendix: Table B1).

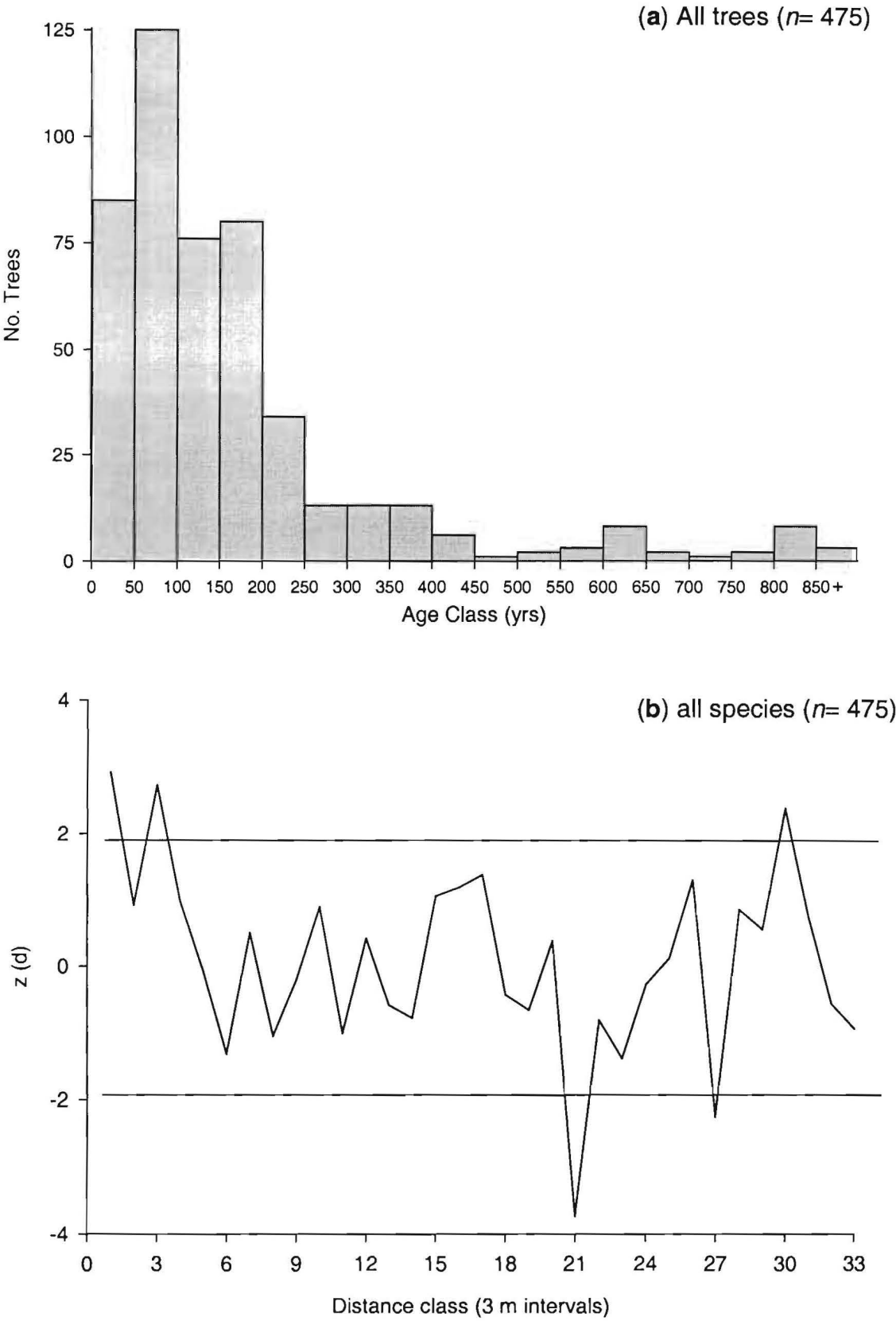


Figure 15: (a) Grouped age-class frequency distribution for all species in poorly drained plot B (*Dacrydium*, *Dacrycarpus*, *P. ferruginea*, *N. menziesii*, *N. fusca*, *W. racemosa*, *Q. acutifolia*, and *E. hookerianus*). (b) Spatial correlogram of tree ages for all combined species tree ages. Horizontal lines of significance at $\alpha = 0.05$ level for individual distance classes. Bonferroni correction test globally significant at $\alpha = 0.01$ level

The correlogram for all species combined showed patchiness in tree age distributions and was globally significant (Fig. 15b). Positive values at small distance classes indicated that trees of similar age were grouped together at short distances, and negative values at larger distances reflected the distance between patches. A further positive value at distance class 30 suggested there was some distance between patches of similar age across the plot. Correlograms for the main tree species (> 30 individuals) were then constructed for *Dacrydium*, *Dacrycarpus*, *N. fusca*, *N. menziesii* and *W. racemosa*. Only the *Dacrydium*, *Dacrycarpus* and *N. menziesii* correlograms showed evidence of significant spatial structures that suggested patchiness in tree age distributions, and these were all globally significant (Figs. 16a-c). These three correlograms all had significant positive values at small distance classes indicating that trees of similar ages were clustered together at short distances, and significant negative significant values at larger distances reflecting distances between patches of different age.

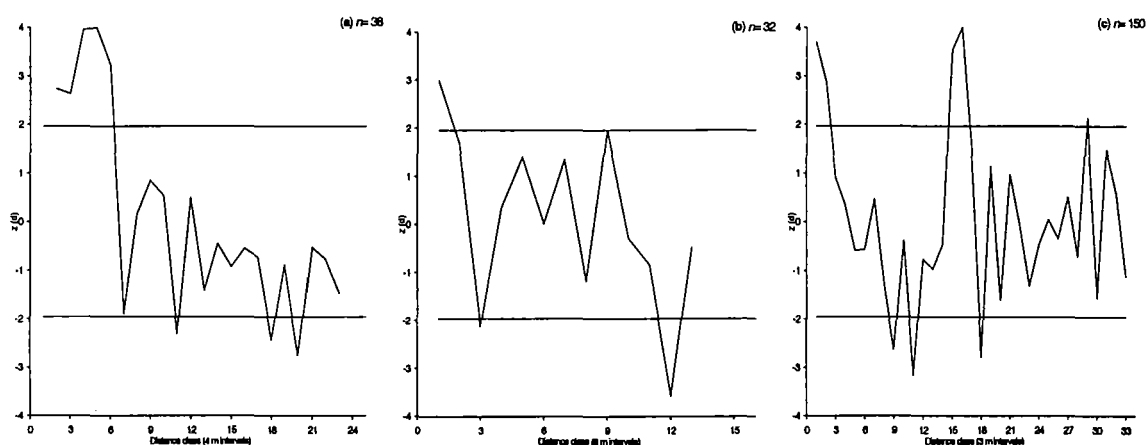


Figure 16: Spatial correlograms of tree ages for (a) *Dacrydium cupressinum* (b) *Dacrycarpus dacrydioides* and (c) *Nothofagus menziesii*. Horizontal lines of significance at $\alpha = 0.05$ level for individual distance classes. Bonferroni correction test *Dacrydium* and *Dacrycarpus* globally significant at $\alpha = 0.01$ level, *N. menziesii* significant $\alpha = 0.05$. For *Dacrydium* distance classes 23-25 (88-100 m), and for *Dacrycarpus* distance classes 13-16 (72-100 m), were excluded as there were less than 20 pairs of neighbouring points.

Conifers

The *Dacrydium* correlogram suggested there were even-aged patches of trees (Fig. 16a). I mapped the trees that comprised each modal peak as well as the age class either side, to give a maximum span of 150 yrs for each possible cohort. The three groups of different aged trees were found to be spatially separated in different parts of the plot (Fig. 17). These distinct age groups reflect relatively even-aged cohorts that were recruited into the canopy at different times.

Trees in the oldest group (784 - 1052 yrs) had a peak evident in the 800-850 yr class, and were extensively distributed in the towards the lower half of the plot except in the far right (Fig. 17a). Nine of the 13 trees were short cores with rotten centres, although two cores that hit the pith were aged 826 yrs and 840 yrs respectively.

Most trees in the second group (553-723 yrs) were aged between 600-650 yrs, and were found in two clumps, one in the top left and the other in the far right of the plot (Fig. 17b). Both these clumps adjoined more extensive stands of relatively similar-sized *Dacrydium* trees that lay outside the plot boundaries.

Trees in the youngest *Dacrydium* patch showed a bell-shape distribution peaking in the 300-350 yr class, the oldest trees were 373 yrs and 398 yrs (Fig. 17c). These trees were densely packed in a small discrete patch situated in the top right of the plot, along with an outlier of 472 yrs (denoted by the symbol ∇ - Fig. 17c).

For *Dacrycarpus*, three groups of relatively even-aged trees were identified from cluster analysis: 30-102 yrs, 153-201 yrs and 303-417 yrs (Table 8). The oldest group (303-417 yrs) were found mainly in the top right of the plot (Fig. 18a). Most of these trees were located together with the similarly-aged 300-400 yrs *Dacrydium* patch suggesting relatively synchronous establishment.

The four trees in the group (153-201 yrs) were located around the plot centre (Fig. 18b). In the youngest group (30-102 yrs), most trees were concentrated in three small clumps in the centre of the plot, with scattered individuals found in the far right and far left of the plot (Fig. 18c). Within this age grouping, there was no further separation of ages into younger and older groups, with tree ages in the three small clumps ranging from 30-82 yrs, 40-72 yrs and 39-102 yrs. The distribution of this youngest group in relatively distinct clumps may well reflect establishment in discrete canopy gaps.

Beeches

The correlogram for *N. menziesii* suggested there were even-aged patches of trees (Fig. 16c). I mapped the four modal peaks evident in the *N. menziesii* age-class distribution: 25-124 yrs, 125-199 yrs, 200-299 yrs and 325-400 yrs, that corresponded to the main peaks identified in Fig. 15a, and the age range of the distinctive age groups identified for *Dacrycarpus* in Fig. 18 (Fig. 19). A cluster analysis of *N. menziesii* ages produced four very similar groupings of similarly-aged trees that were spatially clumped, and stem maps showed them to be distributed in the same areas (appendix: Fig. B1); however, for clarity the maps of the modal peaks are presented. Trees in each of the four groups were clumped together, often in small groups, and were mainly found in different

parts of the plot, reflecting pulses of recruitment into the canopy in response to disturbances at different times (Fig. 19).

Trees in the oldest group, 330-368 yrs, were located in the centre and right of the plot (Fig. 19a). There were two trees situated close to the 300-400 yrs *Dacrydium* patch (Fig. 17c), and several were located close to *Dacrycarpus* of similar age in the lower right suggesting relatively synchronous establishment (Fig. 18a).

Trees in the group 205-281 yrs were located in three different clumps in different parts of the plot, suggesting establishment in canopy gaps commenced around the same time *c.* 280 yrs ago (Fig. 19b). Trees located in small clusters in the lower right, and in the far left of the plot, were surrounded by old-growth emergent *Dacrydium*, suggesting establishment in small canopy gaps (Figs. 17a-b). These trees had all established on log microsites in the lower right of the plot, and on mounds and logs in the far left. Trees in the upper centre were amongst the 300-400 yrs *Dacrydium* and *Dacrycarpus* patch, suggesting either delayed establishment to whatever initiated conifer establishment, or more likely establishment in response to subsequent canopy openings. All six trees were on elevated sites favouring the latter explanation.

The upsurge in establishment around 200 yrs ago for *N. menziesii* predominantly occurred in the left of the plot, and stems were in clumps amongst oldest *Dacrydium* cohort (Fig. 19c). The other distinct cluster of seven trees established in small clumps amongst the youngest *Dacrydium* cohort in the upper right of the plot, also suggesting response to small canopy openings amongst surviving trees.

There was a major upsurge in recruitment beginning around 125 yrs ago, which peaked in the 50-75 yrs class (Fig. 14e). Trees in the group 25-125 yrs mainly distributed in discrete small clumps between surviving trees throughout the plot, particularly large conifers in the centre and right of the plot (Fig. 19d).

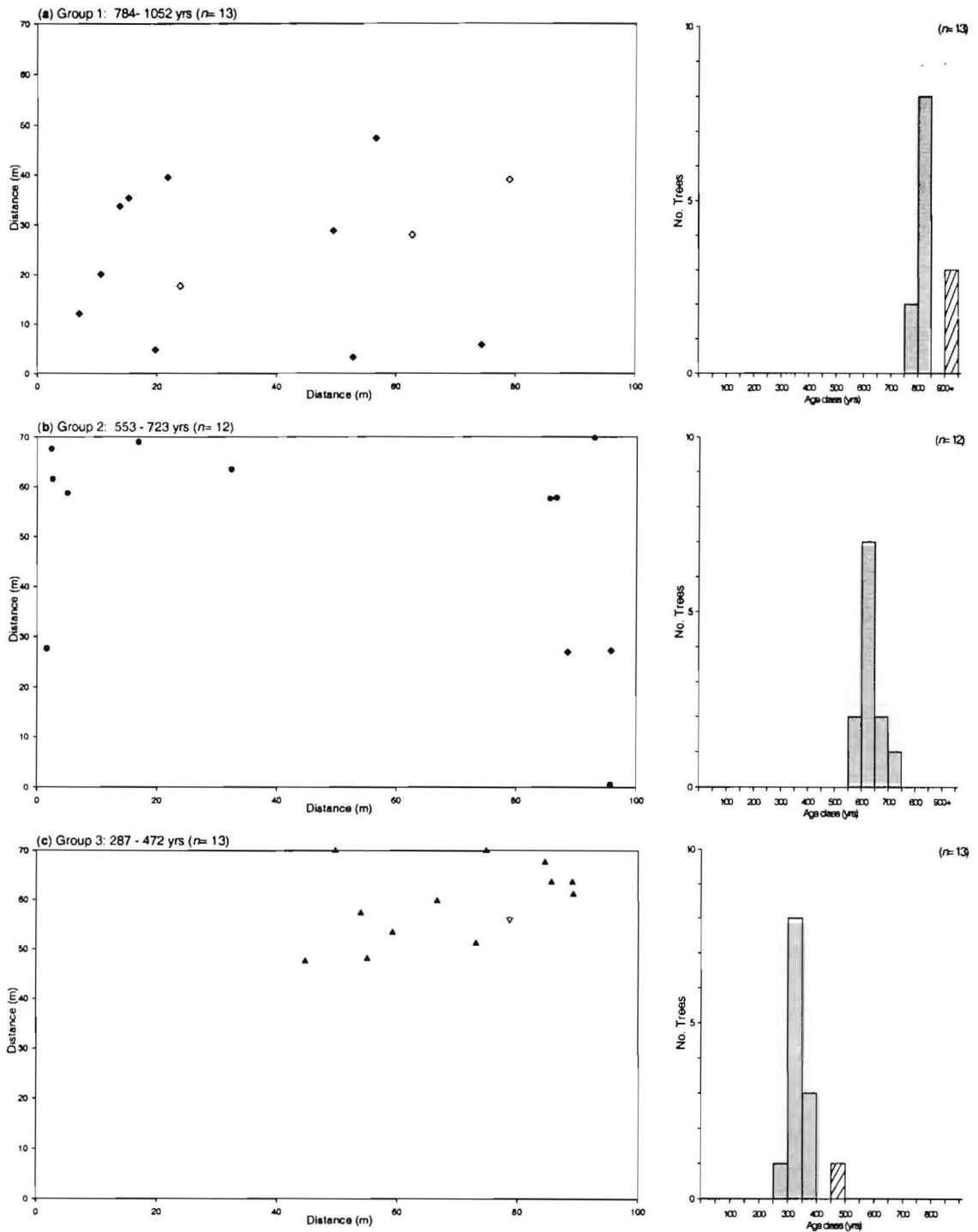


Figure 17: Stem maps and age-class frequency distributions for *Dacrydium* showing spatially separated patches of relatively even-aged trees. The hatched lines in Fig. 17a are represented by the symbol ☉. The symbol ∇ in Fig. 17c also represents an outlier of 472 yrs that did not easily fit into any groups (see text).

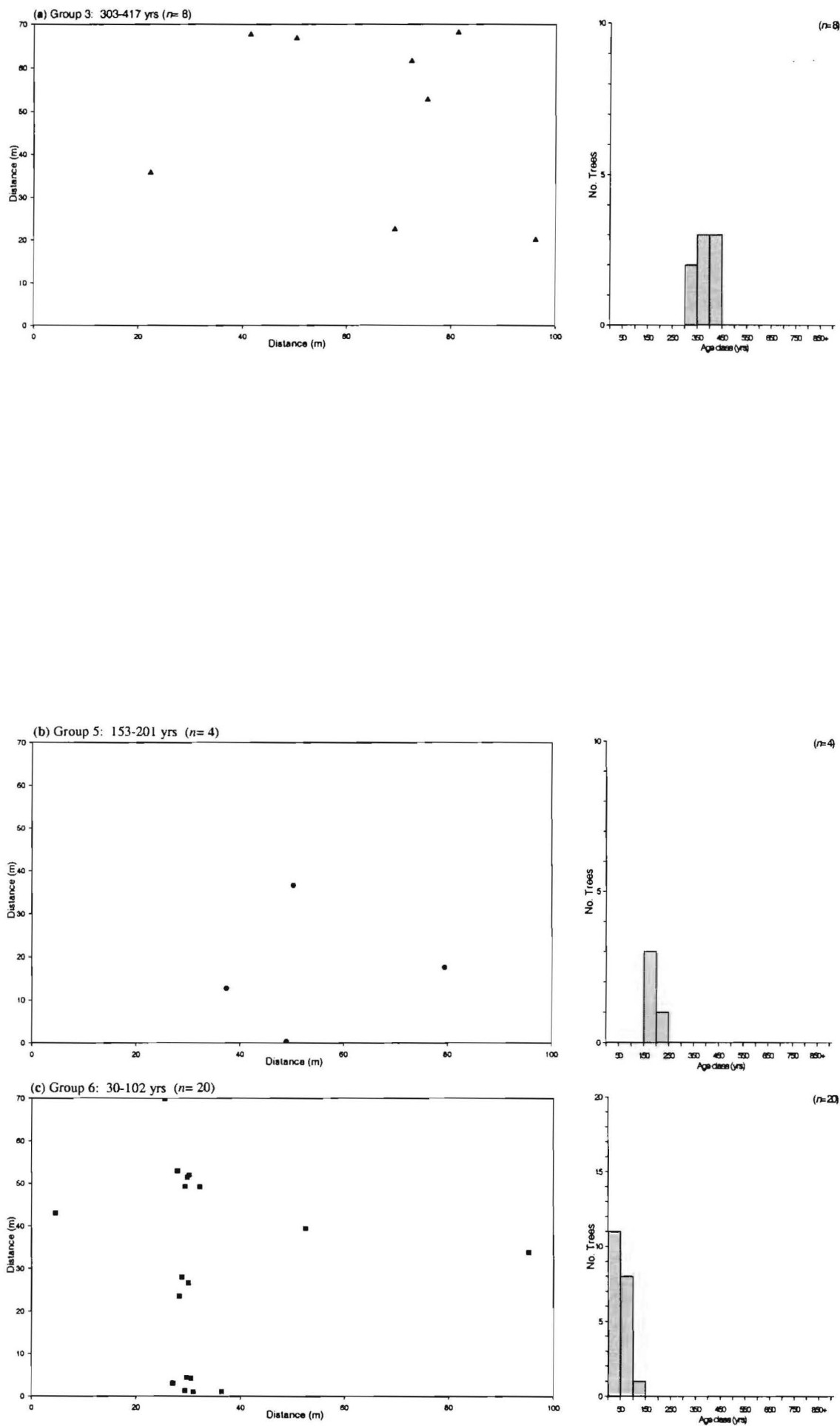


Figure 18: Stem maps and age-class frequency distributions for *Dacrycarpus* age groups.

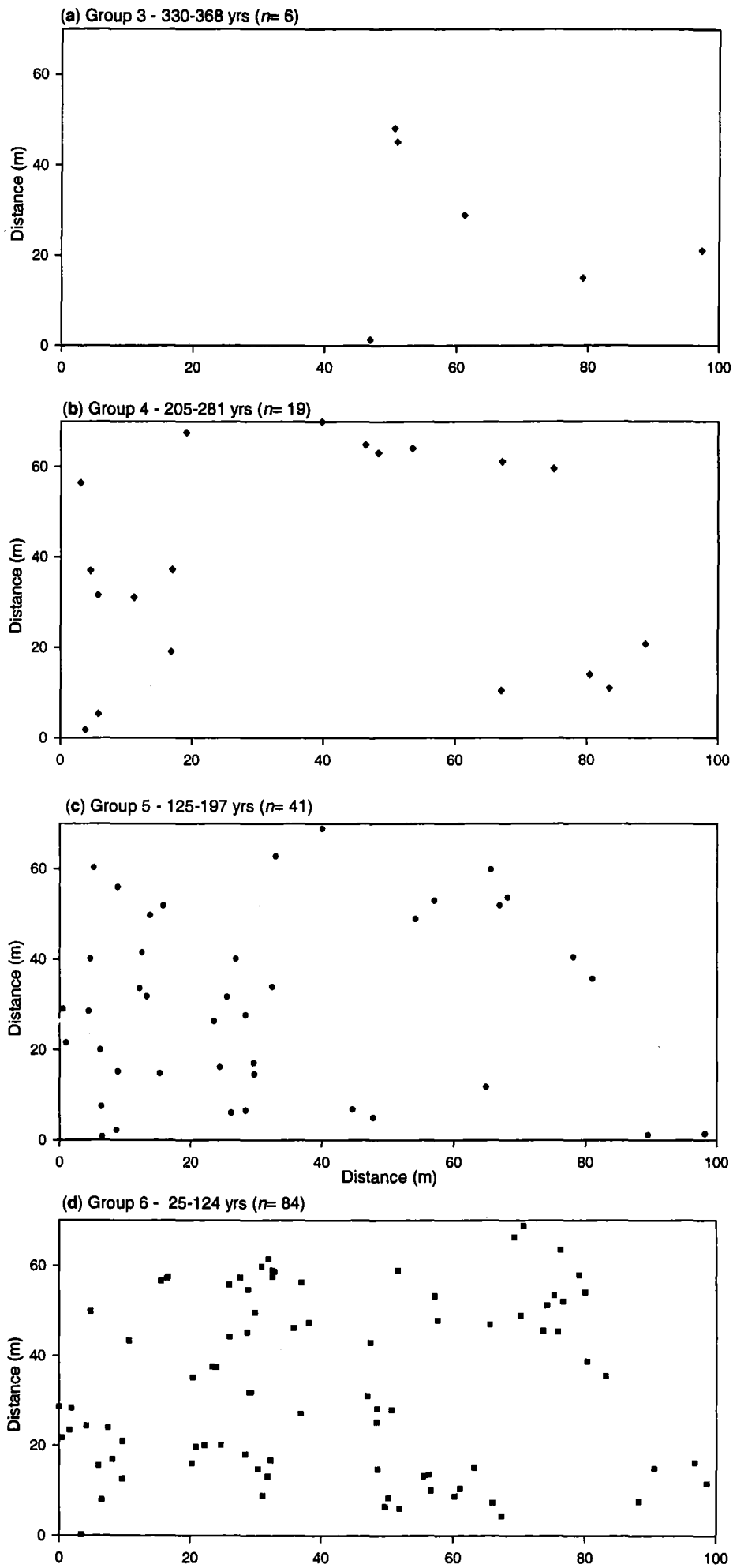


Figure 19: Stem maps for *N. menziesii* age groups mapped from their modal age peaks in Fig. 14a.

Table 8: No. of trees and age range of different groups, mean age (\pm s.d) and maximum distance between trees.

| Groups | Species | No. trees | Age range (yrs) | Mean age \pm 1 s.d (yrs) | Max. distance between trees (m) |
|--------|---------------------|-----------|-----------------|----------------------------|---------------------------------|
| 1 | <i>Dacrydium</i> | 13 | 784-1052 | 865 \pm 92 | 80 |
| 2 | <i>Dacrydium</i> | 12 | 553-723 | 633 \pm 48 | 100 |
| 3 | <i>Dacrydium</i> | 12 | 287-398 | 334 \pm 31 | 50 |
| 3 | <i>Dacrycarpus</i> | 8 | 303-417 | 373 \pm 46 | 75 |
| 3 | <i>N. menziesii</i> | 6 | 330-368 | 352 \pm 15 | 50 |
| 4 | <i>N. menziesii</i> | 19 | 205-281 | 239 \pm 23 | 25 |
| 5 | <i>N. menziesii</i> | 41 | 125-197 | 163 \pm 22 | 90 |
| 5 | <i>Dacrycarpus</i> | 4 | 153-201 | 181 \pm 20 | 45 |
| 6 | <i>N. menziesii</i> | 84 | 25-124 | 77 \pm 22 | 40 |
| 6 | <i>Dacrycarpus</i> | 20 | 30-102 | 52 \pm 19 | 95 |

Nothofagus fusca trees were distributed throughout the plot with notably few stems amongst the 300-400 yrs *Dacrydium*/ *Dacrycarpus* patch in the top right of the plot (Fig. 20). Trees are clumped together within the plot particularly trees < 125 yrs concentrated around the plot centre (Fig. 20). These trees appeared vigorous, and were clustered together along with trees of the youngest *Dacrycarpus* group in relatively recent canopy openings formed by the uprooting of large boles, particularly around the plot centre. About 80% of *N. fusca* trees had established under open conditions in canopy openings (Table 9).

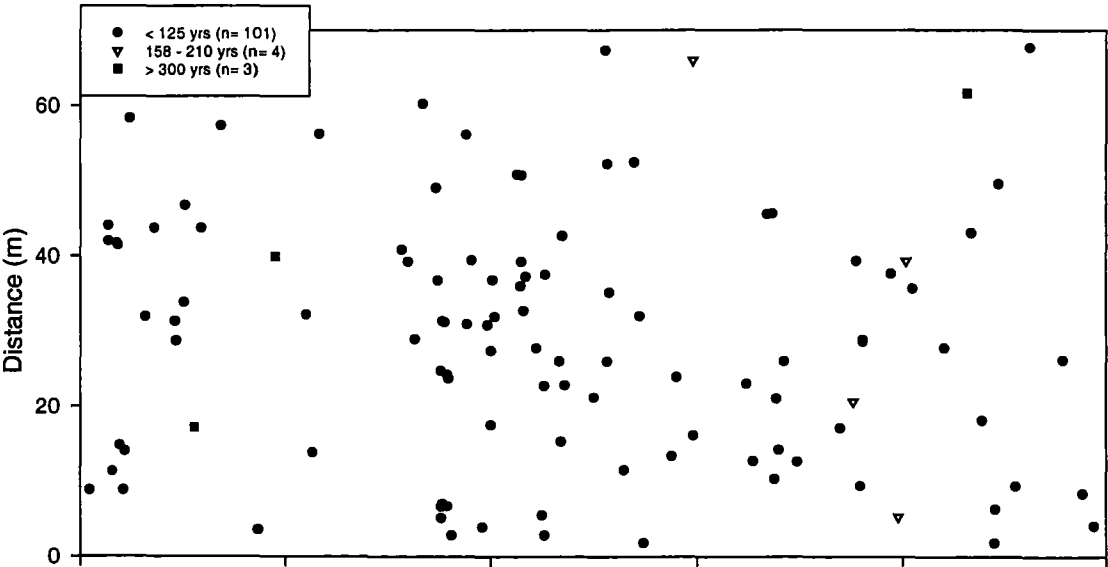


Figure 20: Stem map for *N. fusca* (n= 108).

Non-beech hardwoods

Weinmannia racemosa trees were widely distributed throughout the plot (Fig. 21a). The few *W. racemosa* stems that established in the last 125 yrs were scattered around the plot, compared with the beeches and *Dacrycarpus*, which were more densely clumped towards the plot centre, suggesting there were differences in regeneration strategies in response to canopy openings (Fig. 21a).

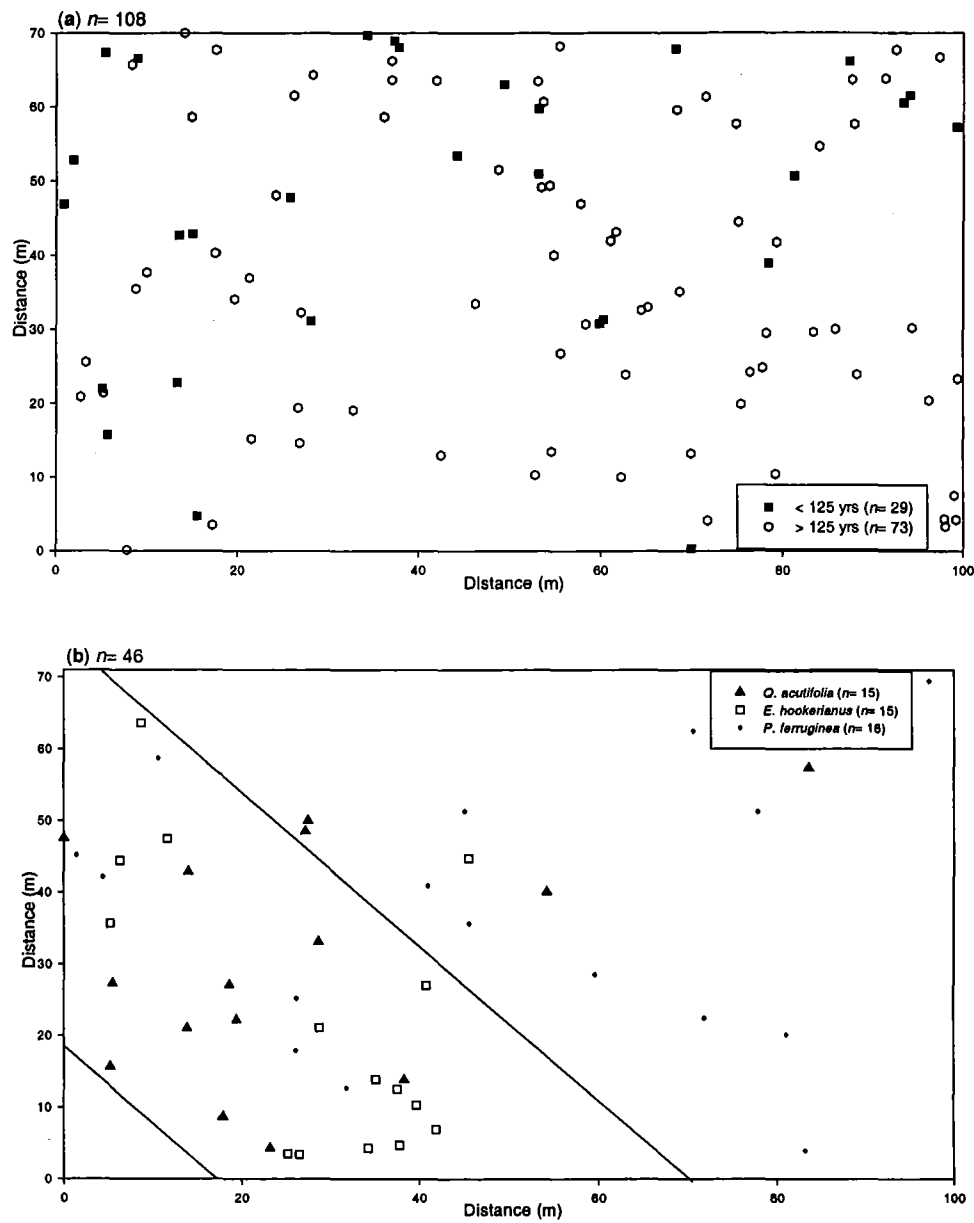


Figure 21: (a) Stem map for *W. racemosa* (n= 102). (b) Stem map of the non-beech hardwoods *Q. acutifolia* and *E. hookerianus*, and the conifer *P. ferruginea*. The area between the solid lines broadly depicts the main area of very poorly drained fluid Rotokuhu peats that run in a continuous band through the left side of the plot.

Elaeocarpus hookerianus and *Q. acutifolia* were mainly located in the left of the plot in an area dominated by the very poorly drained Rotokuhu peats (Fig. 21b). Trees of *E. hookerianus* were found in two main clumps in the lower centre and upper left of the plot. Nine of the 10 trees in the lower centre which ranged in age from 35-117 yrs were situated close to, and were of similar age, to the youngest group of *Dacrycarpus*, suggesting establishment occurred around the same time (Fig. 18c). In contrast, most *Q. acutifolia* trees (66%) in the left of the plot were aged between 128-220 yrs and were situated close to *N. menziesii* trees of similar age in group 5 (Fig. 19c).

Table 9: No. trees for each of the most abundant species in overhead cover classes in plot B.

| Species | Open | Intermediate | Closed | Total |
|---------------------|------|--------------|--------|-------|
| <i>Dacrydium</i> | 36 | 2 | | 38 |
| <i>Dacrycarpus</i> | 21 | 5 | 6 | 32 |
| <i>N. menziesii</i> | 94 | 24 | 32 | 150 |
| <i>N. fusca</i> | 82 | 16 | 10 | 108 |
| <i>W. racemosa</i> | 50 | 28 | 24 | 102 |

3.2.4 Spatial patterns and species interactions

Dacrydium cupressinum trees were distributed in clumps at mid- to large distances reflecting a population composed of large patches (Table 10). *Dacrycarpus dacrydioides*, *N. menziesii* and *N. fusca* all had similar patterns of clumping at small and large distances reflecting their patchy distribution throughout the plot and establishment in different sized canopy gaps (Table 10). Both *N. menziesii* and *Dacrycarpus* trees had also established in areas with open or intermediate overhead canopy cover (Table 9). *Weinmannia racemosa* trees were clumped at short distances but randomly distributed at mid to large distances suggesting establishment in small groups. There were less *W. racemosa* than other species in the open overhead cover class (Table 9), possibly suggesting that they were recruited into a range of canopy openings.

There appeared to be two broad groups of species recruited at different times. One group comprised a pulse of similarly-aged *Dacrycarpus*, *N. fusca*, *N. menziesii* and *E. hookerianus* that established c. 100 yrs ago. The prolific establishment of these species appeared to reflect a prevalence of canopy gaps created by ongoing canopy collapse of the oldest two *Dacrydium* cohorts in the last century. Three large (c. 100 cm) dbh *Dacrydium* trees died in early 1998 (subsequent to being tagged and cored), and 31 dead large diameter *Dacrydium* boles were also identified on the forest floor in various stages of decay.

The other group of species comprised *N. menziesii*, *W. racemosa* and similarly-aged *Q. acutifolia*, which had a corresponding upsurge in recruitment around 250 yrs ago mainly in the far left of the plot. *Nothofagus menziesii* and *W. racemosa* were positively associated at short distances, and *W. racemosa* was also positively associated with *Q. acutifolia* at short distances (Table 11).

Many *W. racemosa* stems were located amongst older, emergent *Dacrydium* trees, however, they were sparsely distributed in the areas of dense *N. fusca* and *Dacrycarpus* aged < 100 yrs particularly around the plot centre (Fig. 21). *Weinmannia racemosa* stems were found to be negatively associated with *Dacrycarpus* and *N. fusca* at short distances, and also with the other subcanopy hardwood *E. hookerianus* (Table 11).

There are also structural differences between species with *W. racemosa* mainly occupying the subcanopy and often exhibiting a characteristic twisting, angled, multi-leadered growth form, compared to *N. fusca* and *Dacrycarpus* trees which typically had one straight leader and occupied the canopy or emergent tier (Table 7). This growth form in the subcanopy may allow *W. racemosa* to take advantage of small light openings; for example, *W. racemosa* trees had a significant positive association with emergent *Dacrydium* trees (Table 11), establishing on the humic litter cones around the tree bases which have formed from centuries of litter fall, twigs, sloughed bark and moss. In contrast, *N. fusca*, *Dacrycarpus* and *E. hookerianus* trees were negatively associated with *Dacrydium* at short distances (Table 11).

Table 10: Patterns of spatial dispersion for trees (≥ 5 cm) and saplings (>1.4 m ht, <5 cm) by species. Letters indicate significant ($P<0.05$) deviation from a random distribution at distance t based on values of the function $K(t)$: C = clumped distribution; . = random distribution. Only distances up to 20 m presented. Spatial correlograms were only constructed for species with > 30 individuals.

| | | <i>t</i> (metres) | | | | | <i>n</i> |
|-------|---------------------------------|-------------------|---|----|----|----|----------|
| Type | Species | 1 | 5 | 10 | 15 | 20 | |
| trees | <i>Dacrydium cupressinum</i> | | . | . | . | . | 38 |
| sapl | <i>Dacrydium</i> | | C | C | C | C | 49 |
| trees | <i>Dacrycarpus dacrydioides</i> | | C | C | C | C | 32 |
| sapl | <i>Dacrycarpus</i> | | C | C | C | C | 299 |
| trees | <i>Nothofagus fusca</i> | | C | C | C | C | 108 |
| sapl | <i>N. fusca</i> | | C | C | C | C | 202 |
| trees | <i>Nothofagus menziesii</i> | | C | C | C | C | 150 |
| sapl | <i>N. menziesii</i> | | C | C | C | C | 301 |
| trees | <i>Weinmannia racemosa</i> | . | C | C | C | C | 102 |
| sapl | <i>W. racemosa</i> | | C | C | C | C | 35 |

Table 11: Patterns of association between groups of trees (≥ 5 cm dbh) and between saplings (< 5 cm dbh., > 1.4 m tall) of different species derived from the function $K12(t)$ + and - denote a significant association for distances t up to 15 m; dot . indicates no significant association.

| TREES | <i>Dacrydium</i> | <i>Dacrycarpus</i> | <i>N. fusca</i> | <i>N. menziesii</i> | <i>W. racemosa</i> |
|-----------------------|------------------|--------------------|-----------------|---------------------|--------------------|
| <i>Dacrydium</i> | | - | - | + | + |
| <i>Dacrycarpus</i> | | | . | . | - |
| <i>N. fusca</i> | | | | . | - |
| <i>N. menziesii</i> | | | | | + |
| <i>E. hookerianus</i> | - | + | . | . | - |
| <i>Q. acutifolia</i> | . | . | - | . | + |
| <i>P. ferruginea</i> | . | . | . | . | . |
| SAPLINGS | | <i>Dacrycarpus</i> | <i>N. fusca</i> | <i>N. menziesii</i> | <i>W. racemosa</i> |
| <i>Dacrydium</i> | | + | . | . | . |
| <i>Dacrycarpus</i> | | | . | . | . |
| <i>N. fusca</i> | | | | + | . |
| <i>N. menziesii</i> | | | | | + |

3.2.5 Spatial patterns of tree mortality

There were differences in the distribution of different types of mortality across the plot that has influenced the recruitment of different species at different times. Corresponding to the establishment of mostly *N. menziesii*, *W. racemosa* and *Q. acutifolia* over the last 250 yrs in the far left third of the plot, dead standing trees and bole snaps dominated in terms of mortality type (81%) with only few scattered uproots (Fig. 22a). *Nothofagus menziesii* trees in group 5 (125-197 yrs) and *W. racemosa* > 125 yrs were both positively associated with dead standing trees and bole snaps at short distances (Table 12). Establishment occurred between the spread out live, emergent *Dacrydium* in this area, and clumping of *N. menziesii* probably reflected establishment and/or release in small gaps after patchy mortality, as trees died standing or were bole snapped.

In contrast, there were over double the amount of uproots in the centre of the plot and fewer dead standing trees/bole snaps (Fig. 22b). There was a concentration of uproots in the centre and lower left of the plot corresponding to the distribution of the youngest *Dacrycarpus*, *E. hookerianus*, and the most dense concentration of *N. fusca* < 125 yrs. *N. fusca* < 125 yrs were positively associated with uprooted trees at short distances, and negatively associated with smaller gaps created by dead standing trees and bole snaps along with *Dacrycarpus* (Table 12). The concentration of *N. fusca* was in the part of the plot where there was a gap in the live *Dacrydium* distribution (Fig. 17a), and the relatively recent uprooting here created a series of large canopy openings covering c. 1500 m² with

few surviving canopy trees. In contrast, the *W. racemosa* of similar age (< 125 yrs) were negatively associated with uproots. This suggests there was temporal variation in the effects of disturbance with different sets of species responding to different types of tree death at different times. In general, *Dacrycarpus*, *N. fusca*, *E. hookerianus* and *N. menziesii* regenerated in gaps created by large uproots, and *N. menziesii*, *W. racemosa*, and *Q. acutifolia* were recruited in smaller gaps from individual standing tree death and bole snapping.

In the right of the plot, dead standing trees and bole snaps were prevalent in the top right around the edges of the youngest *Dacrydium* patch (Fig. 22c). This was an area dominated by bole snapped (8) and dead standing (4) large *Dacrydium*, and *N. menziesii* along with *W. racemosa* had captured the resulting light gaps caused by this type of mortality. This pattern was also found in the lower centre of the plot, where *N. menziesii* < 125 yrs were also clustered around five large *Dacrydium* bole snaps. This suggests that there was spatial variation in disturbance effects, with different species responding to canopy gaps created by different types of tree death around the same time. In general, dead standing trees and bole snaps favoured *N. menziesii* and *W. racemosa* recruitment, whereas uprooting favoured *N. fusca*, *Dacrycarpus*, *E. hookerianus* and *N. menziesii* in the last 100 yrs in different parts of the plot.

Table 12: Spatial relationships of trees and saplings of different species with different modes of tree death derived from the function K12(*t*). + ve and - ve denote significant (P<0.05) positive and negative association for distances *t* up to 10m; dot indicates no significant association.

| Species | <i>n</i> | Bole snaps and dead standing combined (<i>n</i> =69) | Uproots (<i>n</i> =31) |
|-------------------------------|----------|---|-------------------------|
| <i>Dacrycarpus</i> < 125 yrs | 20 | - ve 1 - 3, 6 m | . |
| <i>N. fusca</i> < 125 yrs | 101 | - ve 6-11 m | + ve 4 - 11 m |
| <i>N. menziesii</i> <125 yrs | 84 | . | . |
| <i>W. racemosa</i> < 125 yrs | 29 | . | - ve 1 - 4 m |
| <i>N. menziesii</i> > 125 yrs | 41 | + ve 4 m | - ve 1 - 4 m. |
| <i>W. racemosa</i> > 125 yrs | 73 | + ve 1- 20 m | - ve 1 - 4 m |
| Saplings | | | |
| <i>N. fusca</i> | 202 | + ve 2, 10 m | + ve 2 m |
| <i>N. menziesii</i> | 301 | + ve 2 - 3 m | . |
| <i>W. racemosa</i> | 35 | + ve 1 - 3, 8 m | + ve 1-5 m |
| <i>Dacrydium</i> | 49 | - ve 1 - 2, 4 - 5 m | + ve 4-5 m |
| <i>Dacrycarpus</i> | 299 | - ve 2 - 8 m | . |

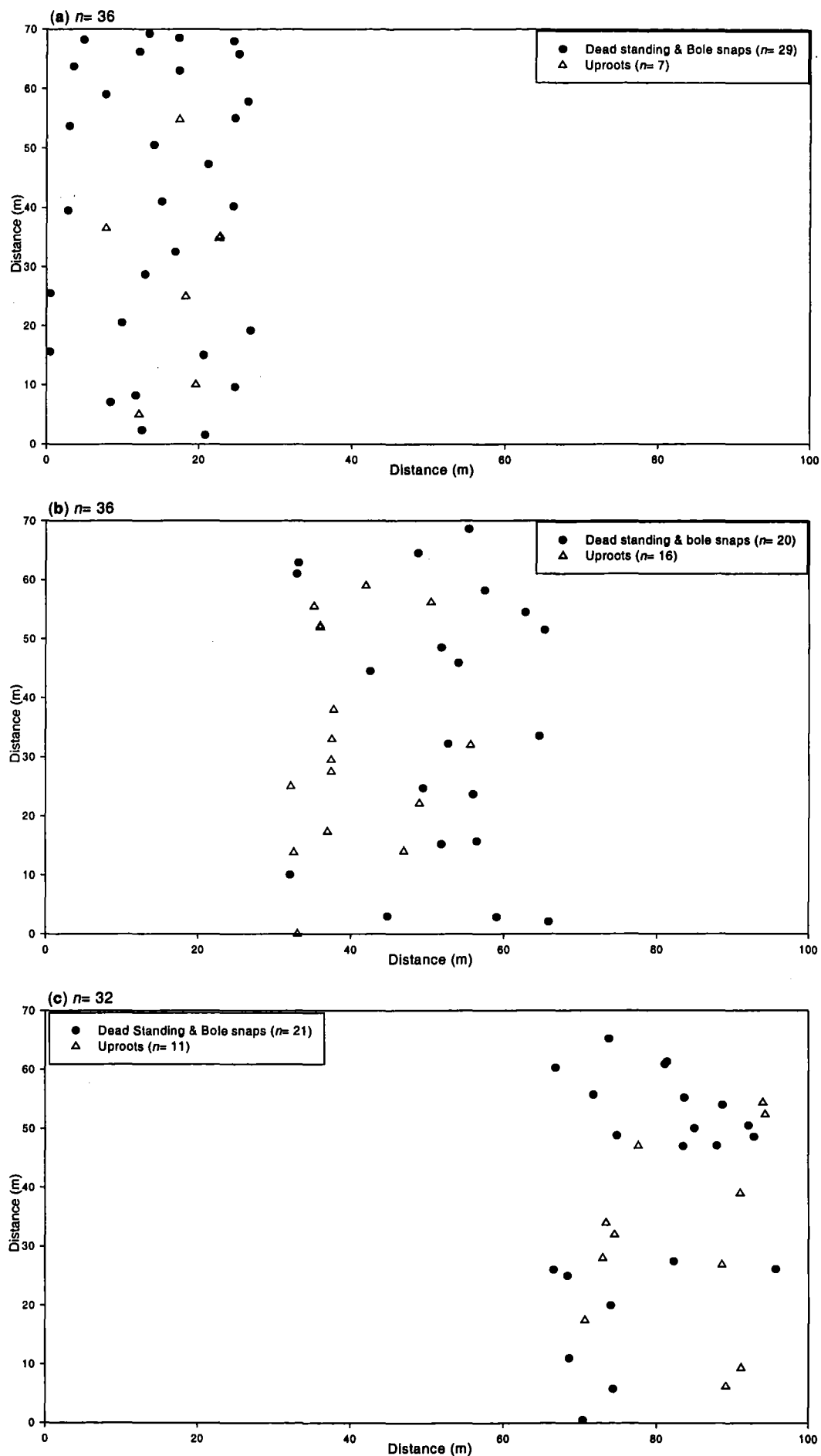


Figure 22: Distribution of tree death by mode throughout plot B

3.2.6 Patterns of tree ring release and disturbance history

Clearly, the spatial distribution of the conifers and beeches demonstrate distinct pulses of recruitment within different areas of the plot, and the most likely cause of these patterns are disturbances causing openings in the canopy. However, there are no reliable ring series that can aid in reconstructing past timing of disturbance in periods of *Dacrydium* recruitment 650-700 yrs or 800-900 yrs ago.

Similarly, ring width information from *N. menziesii* trees is not available for ascertaining the timing of whatever initiated the youngest patch of *Dacrydium* recruitment 350-400 yrs ago; however, recruitment for *Dacrycarpus* and *N. menziesii* also occurred around the same time in the same side of the plot covering at least c. 2000-3000 m² suggesting an extensive disturbance around this time (Figs. 17, 18, 19). The clustering of ages of the oldest trees 413 and 417 yrs for *Dacrycarpus*, 373 and 398 yrs for *Dacrydium* and 362 and 368 yrs for *N. menziesii* suggests the disturbance (s) likely occurred between 375-425 yrs ago. The dense packing of *Dacrydium* and, to a lesser extent, *Dacrycarpus* in the top right of the plot, indicates that this was a large discrete opening with no interspersed older surviving trees in this area. An absence of similarly-aged *Dacrydium* in the lower right of the plot, in contrast to recruitment of *Dacrycarpus* and *N. menziesii* 375-425 yrs ago interspersed between older *Dacrydium* cohorts, indicates that the impacts of disturbance (s) varied within the plot, and were less extensive in the lower right compared to the top right of the plot.

Interruptions in *N. menziesii* tree ring growth over the last 300 yrs were examined to investigate whether there were widespread synchronous periods of release that could provide further evidence for disturbances as an explanation for the age structures in this plot. Releases were considered significant if they were present in ≥ 20 % of trees measured. The largest peaks in release occurred in the last 90 yrs (Fig. 23). There were also releases found in $< 20\%$ trees in most other decades, particularly between 100-280 yrs ago, which most likely represent a history of frequent smaller scale or less extensive disturbances.

The peaks in releases over the last 90 yrs correspond to the recent widespread upsurge in beech and *Dacrycarpus* recruitment throughout the plot, and could reflect partial canopy breakdown of the older *Dacrydium* cohorts.

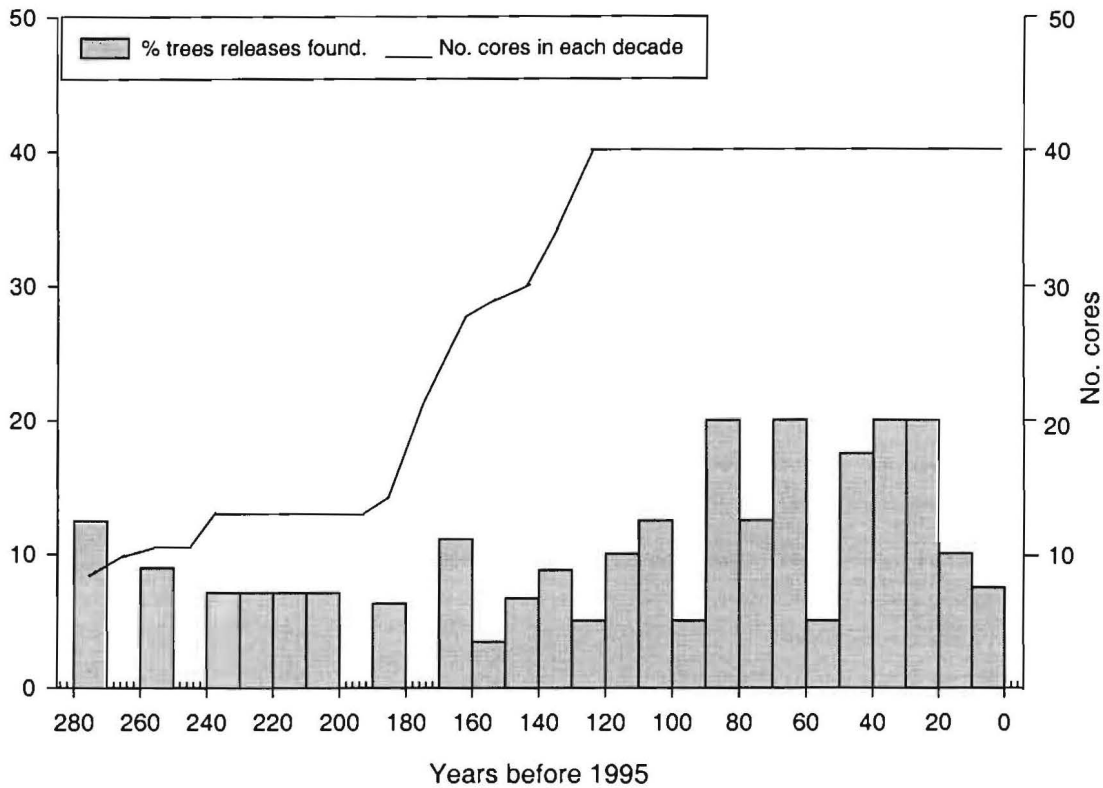


Figure 23: Temporal distribution of growth releases in each decade over last 280 yrs ($n=40$ trees). Filled bars are proportion of trees with releases in each decade, line represents no. cores measured in each decade.

3.2.7 Soil variability and microsite establishment

Although the most abundant tree species spatial distributions did not reflect the underlying soil differences, species broadly partitioned the plot according to differences in drainage on establishment sites. Beeches and hardwoods found on better drained elevated microsites (logs, stumps, mounds), and the conifers and *E. hookerianus* mainly found on poorly to very poorly drained non-elevated sites (forest floor and pits) (Table 13).

Only the non-beech hardwoods *Quintinia acutifolia* and *Elaeocarpus hookerianus* show a distribution that reflected the differences in soil and drainage patterns, with these species mostly found on very poorly drained fluid peats (Fig. 21b). However, most *Q. acutifolia* had established on better drained elevated microsites (12 of 15 trees) whereas *E. hookerianus* were mainly on the forest floor (12 of 15 trees) (Table 13). Trees of the conifer *Prumnopitys ferruginea* were scattered across the plot on a range of microsites.

Table 13: Comparison of no. trees (>5 cm dbh) of species on different elevated and non-elevated microsites.

| Species | Non-elevated | Elevated | | | | Total |
|-----------------------|--------------|----------|--------|--------|-----------|-------|
| | Forest floor | Logs | Mounds | Stumps | Tree fern | |
| <i>Dacrydium</i> | 38 | | | | | 38 |
| <i>Dacrycarpus</i> | 31 | | 1 | | | 32 |
| <i>N. menziesii</i> | 3 | 64 | 77 | 6 | | 150 |
| <i>N. fusca</i> | 5 | 36 | 66 | 1 | | 108 |
| <i>W. racemosa</i> | 6 | 12 | 74 | 5 | 5 | 102 |
| <i>Q. acutifolia</i> | 3 | | 12 | | | 15 |
| <i>E. hookerianus</i> | 12 | 3 | | | | 15 |
| <i>P. ferruginea</i> | 5 | 5 | 5 | 1 | | 16 |

3.2.8 Mode of tree death and current regeneration patterns

Saplings

Patterns of microsite establishment for saplings of different species reflected those found for trees of different species, with the conifers and *E. hookerianus* mostly on non-elevated sites, and the beeches and non-beech hardwoods on non-elevated microsites (Table 14).

Dacrydium cupressinum saplings had a marked association with non-elevated forest floor and pit sites; similarly, over 95% of *Dacrycarpus* saplings and trees were found on forest floor and pit sites (Table 14, Plate 3). Saplings of these two species were found together in highly dense patches, particularly in the upper left and centre of the plot (Fig. 24a). Saplings of these two species were positively associated, in contrast to their negative association as trees (Table 11).

On elevated sites, *N. menziesii* were abundant on logs, stumps and mounds along with *N. fusca* (Table 14). Both species were found together in dense clumps throughout the plot wherever available elevated microsites were situated, especially throughout the left and centre of the plot, which could partly explain their distributions (Fig. 24b). Saplings of *N. fusca* and *N. menziesii* were positively associated at short distances (Table 11). Beech saplings were almost absent underneath the densely packed 300-400 yrs *Dacrydium/Dacrycarpus* patch in the top right of the plot (Fig. 24b).

Weinmannia racemosa saplings also showed a preference for mounds, particularly around the litter cones of live trees and the base of large *Dicksonia* tree ferns (Table 14). There were few *W. racemosa* saplings compared with the beeches and *Dacrycarpus*, and

although scattered throughout the plot, most were in the left side (Fig. 24c). Saplings of *W. racemosa* were also positively associated with *N. menziesii* saplings (Table 11).

Table 14: Comparison of number of saplings \pm 1 s.d. (<5 cm dbh, >1.4 m tall) and seedlings (<1.4 m tall) of species on different microsites. (all values converted to a per hectare basis).

| Species | | Forest Floor | Pits | Logs | Stumps | Mounds | Tree ferns | TOTAL (ha ⁻¹) |
|-----------------------|-------|----------------|-------------|----------------|--------------|----------------|---------------|---------------------------|
| <i>Dacrydium</i> | sapls | 54 | 4 | | 4 | 7 | | 69 |
| | Seedl | 3366 \pm 168 | 57 \pm 3 | 1180 \pm 59 | 241 \pm 13 | 984 \pm 49 | 47 \pm 3 | 5875 \pm 295 |
| <i>Dacrycarpus</i> | sapls | 414 | | | 7 | 3 | 3 | 427 |
| | seedl | 9730 \pm 487 | 173 \pm 9 | 1648 \pm 83 | 241 \pm 13 | 833 \pm 41 | 7 \pm 2 | 12632 \pm 635 |
| <i>N. fusca</i> | sapls | 19 | | 127 | 26 | 117 | | 189 |
| | seedl | 792 \pm 40 | 57 \pm 3 | 896 \pm 44 | 48 \pm 3 | 606 \pm 30 | | 2399 \pm 120 |
| <i>N. menziesii</i> | sapls | 34 | | 243 | 53 | 99 | 1 | 430 |
| | seedl | 3676 \pm 184 | | 9168 \pm 459 | 241 \pm 13 | 3481 \pm 183 | 7 \pm 2 | 16573 \pm 841 |
| <i>W. racemosa</i> | sapls | | | 10 | 9 | 30 | 1 | 50 |
| | seedl | 1837 \pm 92 | | 1254 \pm 63 | 577 \pm 29 | 2648 \pm 133 | 1041 \pm 51 | 7357 \pm 368 |
| <i>Q. acutifolia</i> | sapls | | | 1 | 1 | 6 | | 18 |
| | seedl | 552 \pm 28 | | 36 \pm 3 | 914 \pm 46 | 1287 \pm 64 | 287 \pm 14 | 3076 \pm 155 |
| <i>E. hookerianus</i> | sapls | 17 | | 10 | 1 | 3 | | 31 |
| | seedl | 185 \pm 9 | | | | | | 185 \pm 9 |
| <i>P. ferruginea</i> | seedl | 1103 \pm 55 | | 430 \pm 23 | | 303 \pm 16 | 4 \pm 1 | 1840 \pm 95 |

Patterns of sapling establishment were further explored by examining the interaction between sapling distributions and the establishment opportunities resulting from different modes of tree death. Dying standing, bole snapping, and uprooting create a mosaic of microsite opportunities for species to establish. After a tree dies standing or by bole snapping, forest floor sites and mounds around the base of the tree become available, although the stumps and bole itself may not be available for successful establishment until the decay process advances. In contrast, however, uprooting instantly creates a mound up to 3 metres high, a pit, exposed mineral soil on the mound sides and around the pit edges from roots being ripped up, and forest floor sites.

Saplings of different species showed distinct preferences for particular microsites after different forms of tree death (Table 12). *Dacrydium* saplings were observed to be mainly distributed in the wetter soils particularly around uproot pit depressions particularly in an area of intense uprooting in the centre of the plot (Fig. 24a). Statistically, *Dacrydium* saplings showed a significant positive association with these sites (Table 12). Although

not statistically significant, *Dacrycarpus* saplings had a tendency to be positively associated with uprooted trees at short distances, but had a wider distribution in the plot (Fig. 24a). Furthermore, both *D. cupressinum* and *Dacrycarpus* saplings showed negative associations after tree death with less associated soil disturbance (dead standing trees and bole snaps - Table 12).

Species on elevated sites (*W. racemosa*, *N. fusca*, *N. menziesii*) showed either significant positive associations with bole snapping and uproot mounds, or were randomly distributed reflecting the ability to take advantage of the establishment opportunities offered by different forms of tree death (Table 12). *Nothofagus fusca* and *N. menziesii* saplings were abundant wherever there are better drained elevated sites (Plate 2), especially logs for *N. menziesii*. *Nothofagus menziesii* seedlings were able to prolifically colonise logs at an earlier stage of decay compared to other species (appendix: - Table B2), and were more abundant on these types of microsites than seedlings of other species (Table 14.)

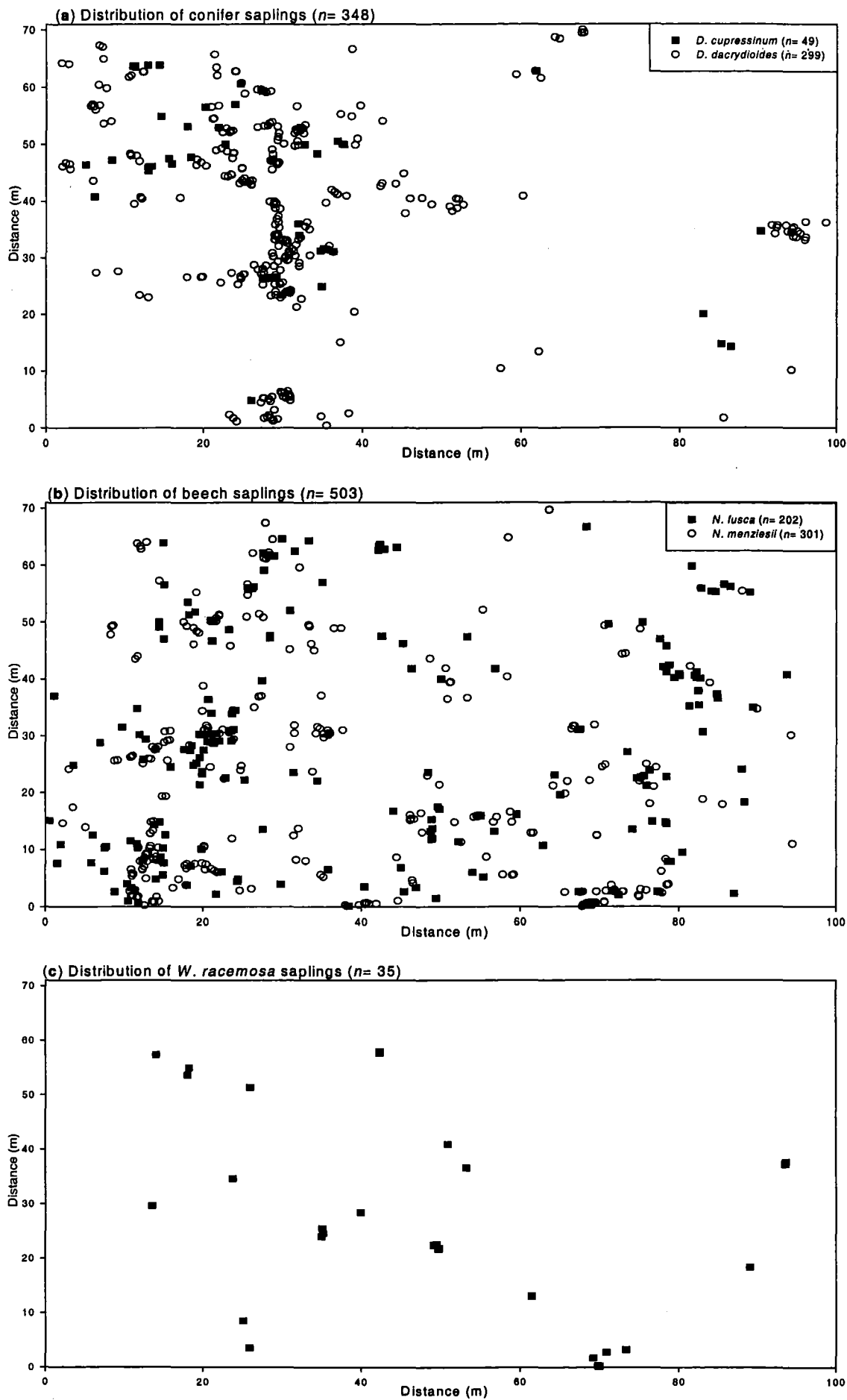


Figure 24: Maps of actual number of saplings recorded of different species distributed around plot C (a) *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*, (b) *N. fusca* and *N. menziesii*, (c) *W. racemosa* (only species > 30 individuals mapped).



Plate 3: *Dacrycarpus* saplings (middle) & *Dacrydium* (foreground) on wet forest floor sites in plot B.



Plate 4: *N. fusca* saplings and small diameter trees on an uproot mound in plot B.

3.3 WELL DRAINED STAND - PLOT C

3.3.1 Stand composition, structure and soils

The beeches *Nothofagus fusca* and *N. menziesii*, and non-beech hardwoods *Weinmannia racemosa* and *Quintinia acutifolia* were the dominant species in terms of stem density and basal area on the well-drained soils in plot C (Table 15). *Weinmannia racemosa* and *N. menziesii* were the most abundant species, and although there were substantially fewer *N. fusca* they were the basal dominant. Structurally, *N. fusca* and *N. menziesii* dominated the canopy tier with associated *Q. acutifolia*, and *W. racemosa* was the main understorey and sub-canopy species (Table 15).

Conifers were scarce, with few *Dacrydium cupressinum* and *Prumnopitys ferruginea* and no *Dacrycarpus dacrydioides* present. There was only one dead *Dacrydium* and four dead *P. ferruginea* stems identified, suggesting conifer density was also low in the recent past. There was only one tree of the other non-beech hardwood species *Elaeocarpus hookerianus* located in this plot.

Table 15: No. trees (≥5 cm dbh) in different height tiers, basal area and no. identifiable dead stems in 0.3ha plot C. All values converted to a per hectare basis.

| Species | Understorey (2-5 m) | Subcanopy (5-15 m) | Canopy (15-25 m) | Emergent (> 25 m) | TTL live stems/ ha | Dead stems/ ha | Basal area m ² / ha |
|----------------------|------------------------|-----------------------|---------------------|----------------------|-----------------------|----------------------|--------------------------------------|
| <i>N. fusca</i> | 3 | 23 | 143 | 23 | 192 | 173 | 26.6 |
| <i>N. menziesii</i> | 40 | 170 | 213 | 3 | 426 | 90 | 16.0 |
| <i>W. racemosa</i> | 163 | 463 | 3 | | 629 | 50 | 13.6 |
| <i>Q. acutifolia</i> | 17 | 53 | 57 | | 127 | 10 | 4.7 |
| <i>Dacrydium</i> | | 3 | | 7 | 10 | 13 | 2.6 |
| <i>P. ferruginea</i> | | 6 | 20 | | 26 | 13 | 2.9 |
| Total | | | | | 1410 | 349 | 66.4 |

Plot C was dominated by extensive well-drained yellow-brown Ahaura silt loams (YBE) placing it in the well-drained portion of the drainage sequence (see appendix for soil profile descriptions). The typical horizon sequence comprised an *L*, *F*, *H* layer over an *Ah*, *Bw* and *C* layer. Soil profiles were shallow throughout this plot compared to the poorer drained plots, extending down to underlying gravels at depths of 30-60 cm. There were

some small associated patches (200 m² and 250 m²) of poorly-drained gleyed yellow-brown earth soils (G-YBE) in low-lying depressions in the centre and left of the plot.

Extensive pit and mound topography covered the right side of the plot, and there were abundant closely spaced stems of between 15-35 cm diameter in this area. In contrast, in the other side of the plot, stems were larger and more widely spaced, and micro-topography was more variable with stumps and dead standing spars common.

3.3.2 Stand size and age structure

Beeches

Nothofagus fusca had a bimodal age-class frequency distribution with peaks evident between 200-275 yrs and 75-125 yrs ago suggesting distinct periods of recruitment and/or mortality (Fig. 25a). The cored trees ranged in age from 64-260 yrs with few trees > 125 yrs. More than 60% of trees were in one age class (75-100 yrs), with an abrupt drop off in trees in younger age classes suggesting a pulse of establishment occurred over a relatively short period. There were only 15 saplings located within the plot, which age/diameter regressions suggested were aged between 55-70 yrs (appendix: Table C1). The *N. fusca* size class distribution also suggested a relatively recent pulse of recruitment, most live stems were in the 15-44.9 cm diameter range with a peak in the 25-34.9 cm class, and few small stems or saplings (Fig. 25b). Dead stems were spread throughout the mid to larger size classes with > 50 % of dead stems in the 15-44.9 cm range, possibly indicating recent mortality due to thinning of an even-aged population. Age/diameter regressions suggested that most dead stems were aged between 85-135 yrs.

The multi-modal age-class distribution for *N. menziesii* had a discontinuous structure with minor peaks evident in the 300-350 yrs, 250-275 yrs, 200-225 yrs and 50-125 yrs classes (Fig. 25c). The cored trees mostly ranged in age between 49-255 yrs with a gap of c. 50 yrs to three older trees aged 308-331 yrs. There were fewer trees in older age classes, most trees were in younger age classes with the largest peak for cored trees in the 75-100 yrs class coinciding with *N. fusca* (Fig. 25c). There were only 34 saplings found, which age/diameter regressions indicated were < 50 yrs old, suggesting a tapering off of recent establishment (appendix: Table C1). The *N. menziesii* size class distribution showed a unimodal shape peaking in the 5-14.9 cm class (Fig. 25d), also suggesting a recent pulse of establishment. Dead stems were spread across different size classes with most (c. 80 %) between 10-45 cm dbh also suggesting thinning of an even-aged population.

Non-beech hardwoods

The age-class distribution for *Q. acutifolia* had most stems (c. 80 %) aged between 50-125 yrs also suggesting a distinct pulse of establishment (Fig. 25e). The cored trees ranged in age from 60-254 yrs with few stems in older age classes. The age of the oldest stems corresponded to the oldest *N. fusca* and the beginning of the main upsurge in *N. menziesii* establishment, suggesting a synchronous pulse of establishment c. 250 yrs ago. The size-class distribution had a unimodal distribution with few stems in larger size classes and most trees between 5-24.9 cm, further supporting a recent pulse of stem establishment (Fig. 25f). There were only two saplings indicating that conditions have been unfavourable for recent establishment.

The age structure for *W. racemosa* showed most stems (c. 80 %) were aged between 50-150 yrs with decreasing numbers of stems in older age classes (Fig. 25g). The cored stems ranged in age from 50-254 yrs with two older stems > 300 yrs. The cored stems show a unimodal shape with a peak in the 100-150 yrs class suggesting a distinct pulse of establishment, with fewer stems in younger age classes and only 15 saplings indicating a tapering off of recent establishment (Fig. 25h). However, there were more *W. racemosa* aged between 150-200 yrs than other species indicating that recruitment and/ or mortality patterns differed and were more continuous than the other species. The unimodal shape of the size-class distribution showed > 75% stems in the smaller size classes (5-24.9 cm) providing support for a relatively recent upsurge of stem establishment.

All abundant canopy species had a coincidental upsurge in stem numbers beginning in the 100-125 yr age class that dominated the age-class frequency distributions in this plot, and there are few saplings present throughout the plot. This pattern most likely reflects the synchronous establishment of many stems in this plot commencing c. 100-125 yrs ago. The combined age-class frequency distribution for the beeches and hardwoods showed two pulses of establishment commencing 250-275 yrs ago, and a distinctive, more recent pulse 100-125 yrs ago with a clear peak 75-100 yrs ago (Fig. 26). Extensive areas of similarly-sized beech and hardwood stems were also densely packed outside the plot area suggesting that there was a larger establishment pulse on the terrace.

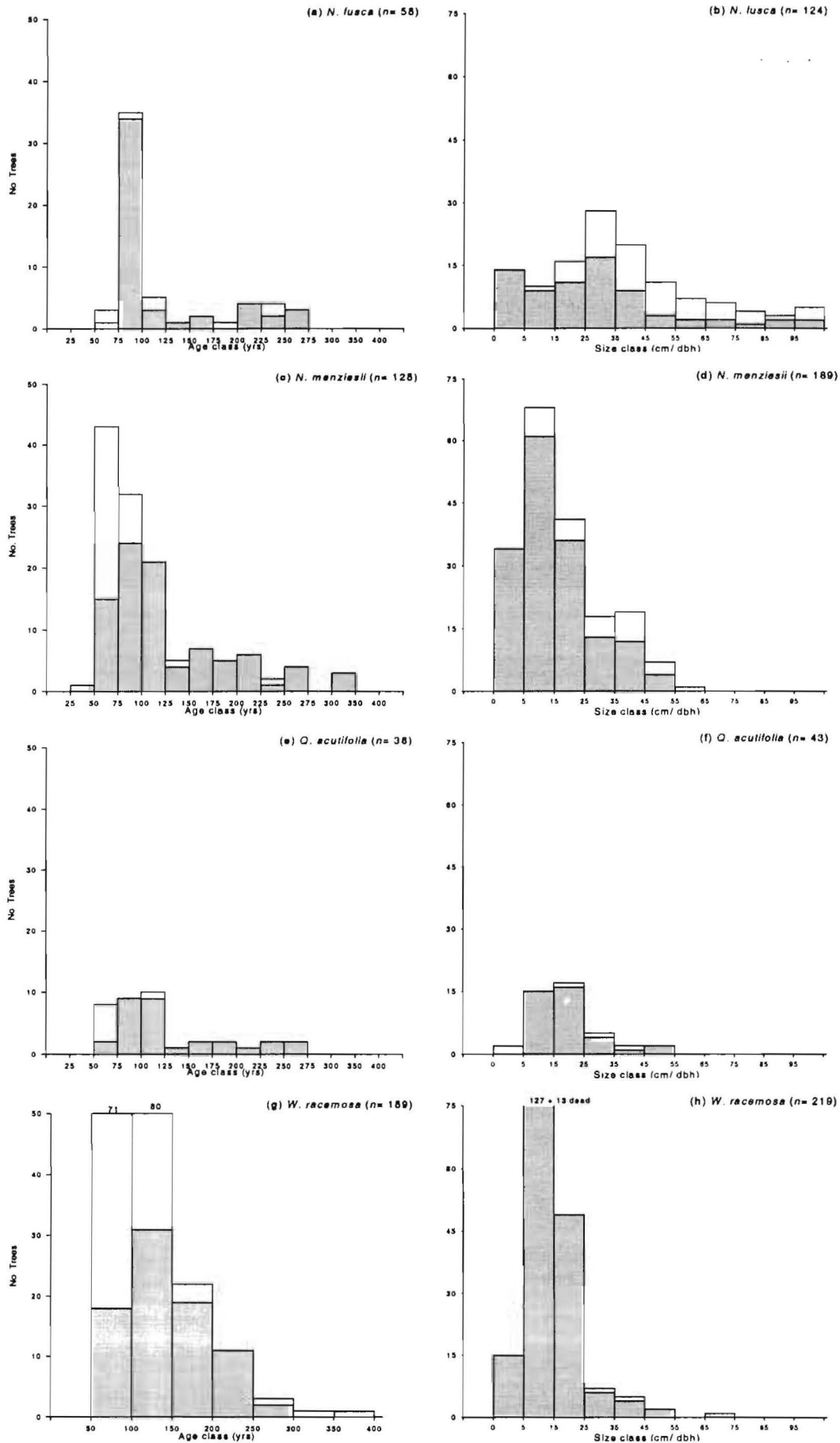


Figure 25: Age- and diameter class frequency distribution diagrams for the main overstorey species. Unfilled bars in the age-class diagrams (a, c, e, g) represent ages estimated from age/diameter regressions for unaged trees. Unfilled bars in the size class diagrams (b, d, f, h) represent diameter class of dead stems. 0-5 cm = saplings in the size-class diagrams.

Conifers

Conifer ages recorded indicated sporadic recruitment of these species over the last 550 yrs, two *P. ferruginea* trees were aged 170-173 yrs, one aged 274 yrs, and the other four were aged between 483-548 yrs. One *Dacrydium* tree was aged 226 yrs and two others 443 yrs and 448 yrs. These conifers were all confined to the left side of the plot. Six *Dacrycarpus* saplings and only one *Dacrydium* sapling were located in the plot, and there were no *P. ferruginea* saplings.

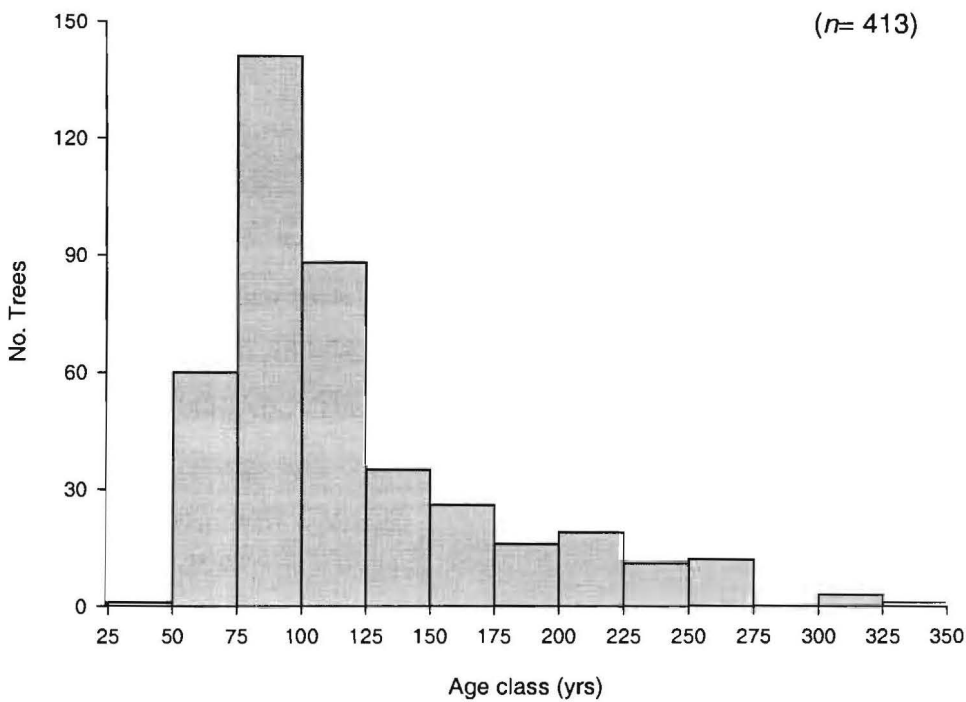


Figure 26: Combined age-class frequency distribution diagrams for the main overstorey species in well-drained plot C (*N. fusca*, *N. menziesii*, *W. racemosa* and *Q. acutifolia*).

3.3.3 Spatial distribution of tree ages

The right side of the plot had abundant closely packed stems < 35 cm diameter of different species and a general paucity of larger stems and few saplings, which suggested a stand-building phase. In the left side, stems of varying size were more widely spaced and there were many more saplings. To investigate whether these size patterns reflected patchiness in the spatial distribution of tree ages, I constructed a spatial correlogram of the combined ages of the four main canopy species (Fig. 27a).

This combined correlogram of all *N. fusca*, *N. menziesii*, *W. racemosa* and *Q. acutifolia* ages had a significant spatial structure suggesting there were even-aged patches of trees within the plot (Fig. 27a). A significant positive value in distance classes 1-9 (1-27 m) indicated that trees of similar ages were clustered together within approximately each half of the plot. Significant negative values in distance classes 12-20 (33-60 m) probably reflected the differences in age between the two halves of the plot.

Beeches

Individual tree age distributions were also examined for evidence of patchiness. Both beech correlograms had similar general shapes to the combined correlogram indicating patchiness in tree ages (Figs. 27b-c). Positive values at short distances up to 24-27 m indicated that trees of similar age were grouped together in about half the plot, and negative values in distance classes > 30 m was attributed to the distance between patches of different age.

For *N. fusca*, subsequent cluster analysis identified two groups that were distinct in age, the first aged 145-260 yrs and the second 64-111 yrs (Table 16). These groups were found in different parts of the plot reflecting distinct periods of establishment, the 145-260 yrs group was found scattered mainly in the left side (Fig. 28a) and the 64-111 yrs group predominantly clustered in the right side of the plot (Fig. 28b).

For *N. menziesii*, three groups that were distinct in age were identified after cluster analysis: 308-331 yrs, 133-255 yrs, 49-131 yrs (Table 16), and they were mostly found in different parts of the plot, especially the two younger groups, suggesting distinct periods of recruitment (Fig. 29). The oldest group of three trees (308-331 yrs), were scattered around the plot and may have been a remnant of a more extensive patch in the past (Fig. 29a). The 133-255 yrs group was mainly in the left side with a distinct cluster of trees in the bottom left corner, and around the centre of the plot. The 49-131 yrs group was predominantly clustered in the right side of the plot, with smaller clumps and individual trees around the plot centre (Fig. 29b).

Non-beech hardwoods

In contrast, the correlogram for *W. racemosa* did not show a significant spatial structure that would suggest stems of similar age were grouped together in separate parts of the plot (Fig. 27d). Stems of all ages were distributed around the plot suggesting a continuous pattern of stem establishment over the last 250 yrs (Fig. 30). Stems were divided into two age groups (> 125 yrs and < 125 yrs) which roughly coincided with

similarly-aged groupings of the beeches (Figs. 30a-b, Table 16). In contrast to the other species, stems of both age groups were spread throughout the plot.

A correlogram could not be constructed for *Q. acutifolia* due to insufficient sample size in each distance class. This was explained by its restricted distribution in only the left and centre of the plot (Fig. 31). Stems were also divided into two age groups (> 125 yrs and < 125 yrs) and stems of all ages were mixed together with no evidence of patchiness in tree age distributions (Fig. 31).

For different species, patches with broadly corresponding age ranges were placed into three broad age groups (Table 16). Within these three broad groups, the spatial distribution of each patch of trees was compared to see whether trees of different species were recruited at similar times in the same general area of the plot.

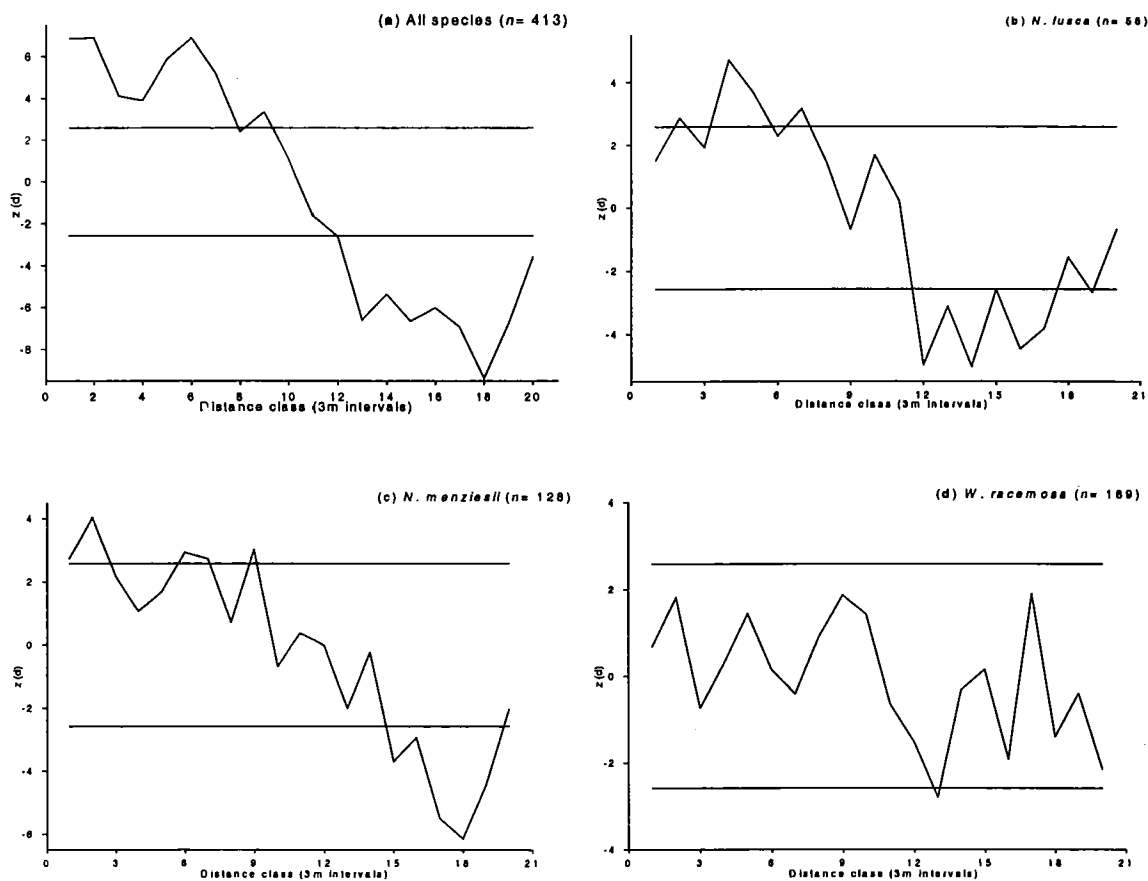


Figure 27: Spatial correlograms of tree ages for (a) all species (b) *N. fusca*, (c) *N. menziesii* and (d) *W. racemosa*. Horizontal lines of significance at $I=0.01$ level for individual distance classes. Bonferroni correction test showed that the spatial correlograms for all species, for *N. fusca* and *N. menziesii* to be globally significant at $\alpha=0.01$ level.

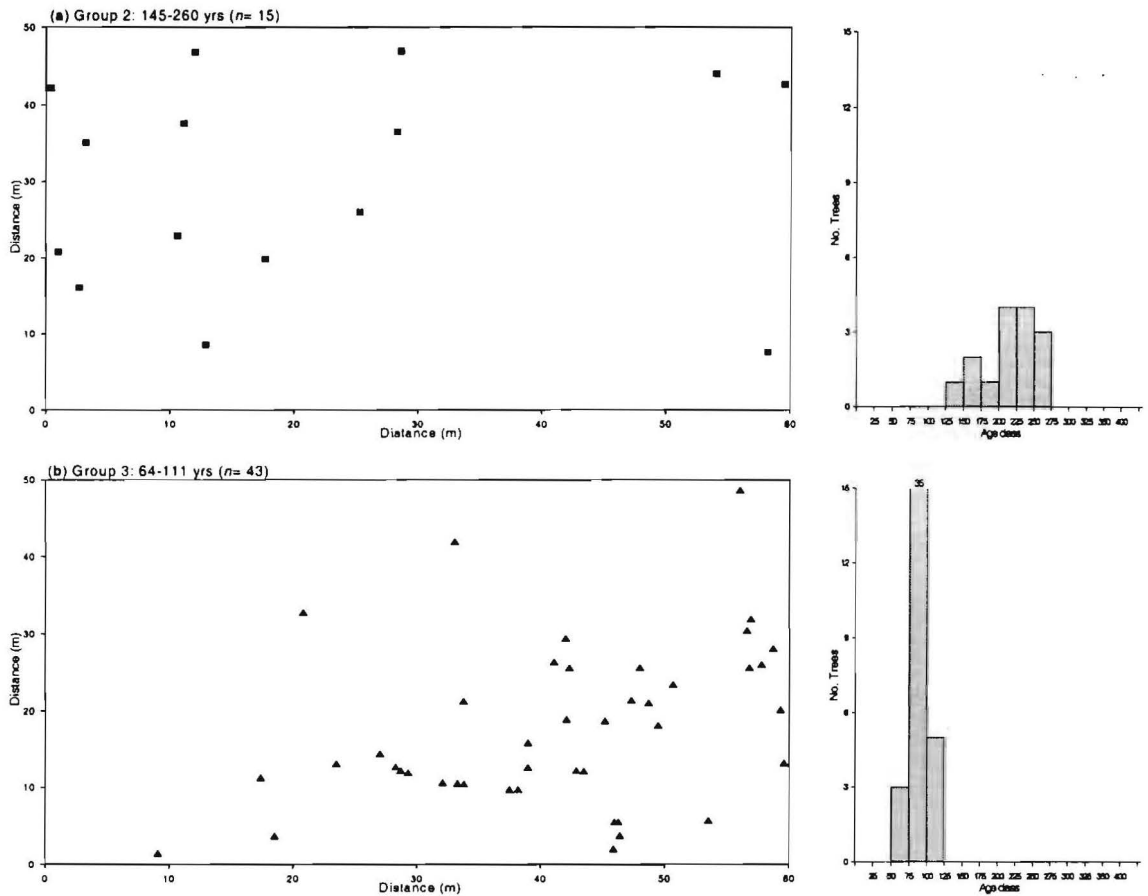


Figure 28: Stem maps & age-class frequency distributions of *N. fusca* groups (a) 145-260 yrs (b) 64-111 yrs.

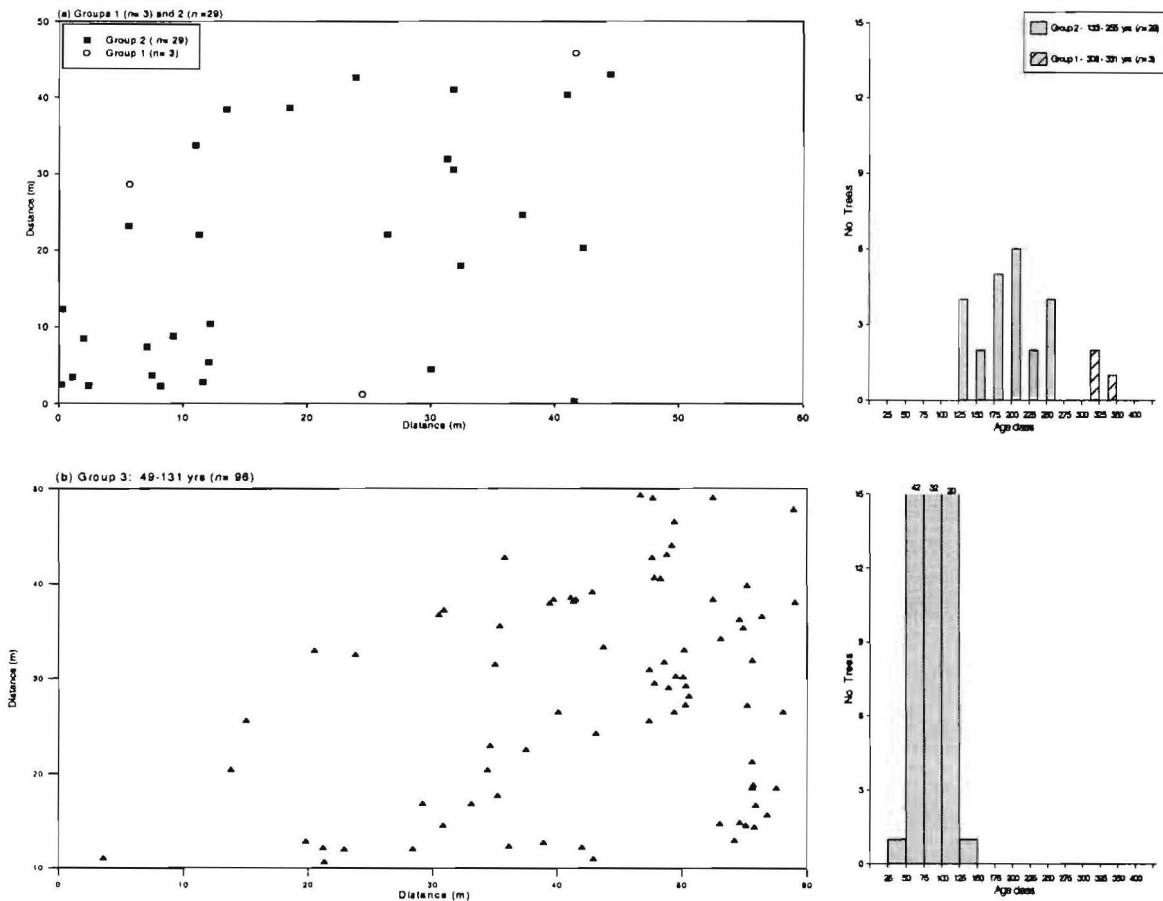


Figure 29: Stem maps and age-class frequency distributions for *N. menziesii* age groups (a) 308-331 yrs - group 1 and 133-255 yrs - group 2 and (b) 49-131 yrs - group 3.

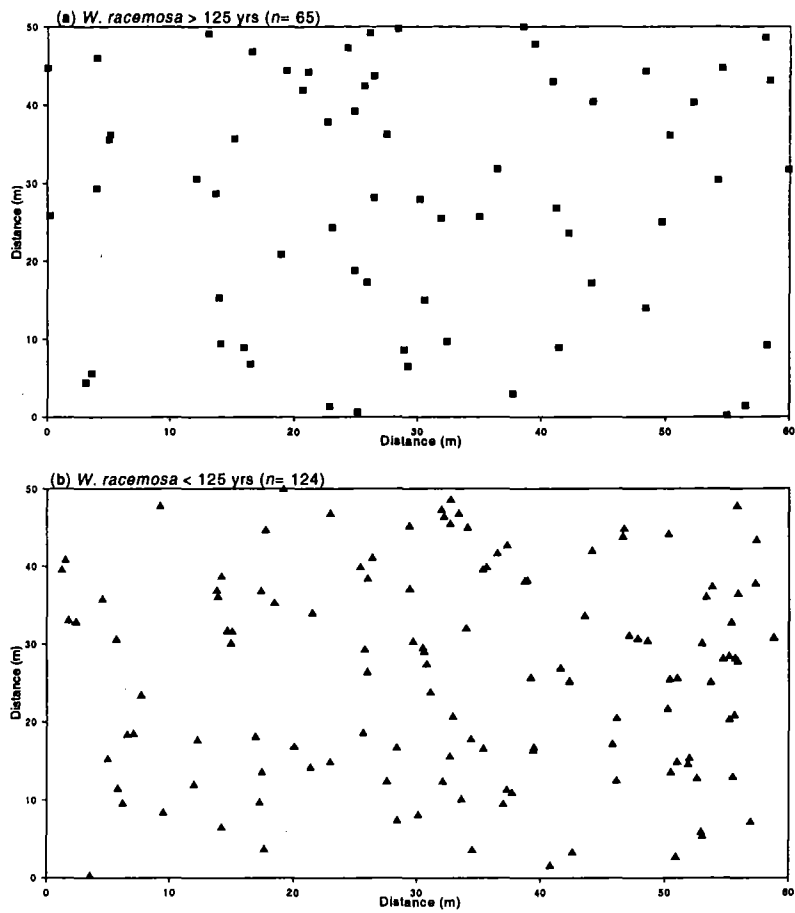


Figure 30: Stem maps for *W. racemosa* (a) > 125 yrs (b) < 125 yrs.

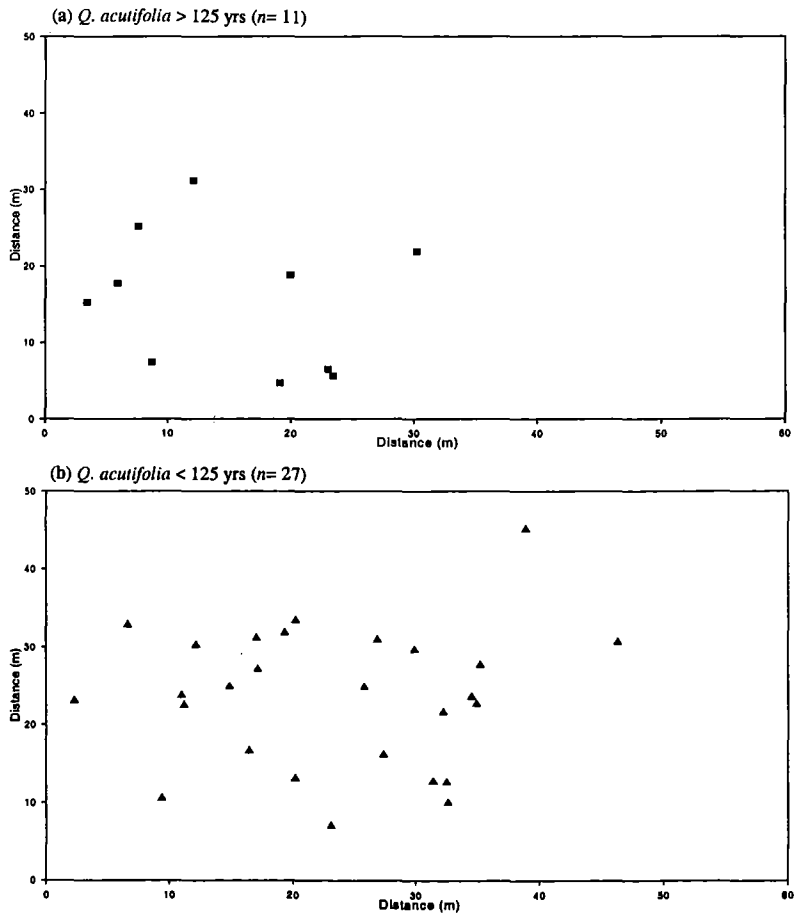


Figure 31: Stem maps for *Q. acutifolia* (a) > 125 yrs (b) < 125 yrs.

Table 16: Age groups identified from cluster analyses for *N. fusca*, *N. menziesii* and *Q. acutifolia*.

| Group | Species | No. trees | Age range (yrs) | mean age \pm 1 s.d (yrs) | Max. distance between trees (m) |
|-------|---------------------|-----------|-----------------|----------------------------|---------------------------------|
| 1 | <i>N. menziesii</i> | 3 | 308-331 | 318 \pm 12 | 40 |
| 2 | <i>N. fusca</i> | 15 | 145-260 | 213 \pm 36 | 50 |
| 2 | <i>N. menziesii</i> | 29 | 133-255 | 189 \pm 40 | 45 |
| 3 | <i>N. fusca</i> | 43 | 64-111 | 87 \pm 10 | 50 |
| 3 | <i>N. menziesii</i> | 96 | 49-131 | 79 \pm 20 | 55 |

3.3.4 Overhead cover and microsite preferences

Aside from the three *N. menziesii* trees in group 1 scattered around the plot, most trees of *N. menziesii*, and *N. fusca* were in two distinct age groups (groups 2 and 3) with similar overlapping age ranges and maximum ages, reflecting at least two distinct synchronous pulses of establishment (Table 16). The beeches were distributed in the same parts of the plot (Figs. 28-29).

Age-class diagrams of each age group suggested there were differences in species' regeneration strategies. Most *N. fusca* trees in group 2 (> 70%) were clustered between 200-260 yrs old, suggesting an even-age pulse of establishment with sporadic subsequent recruitment (Fig. 28a). In contrast, only c. 40 % of *N. menziesii* stems were aged > 200 yrs, most were aged between 133-192 yrs, suggesting either more protracted establishment than *N. fusca*, slower growth to coring height, or subsequent recruitment in response to further openings in the canopy (Fig. 29a). There were no microsite differences between species that could explain these spatial patterns, with most stems establishing on elevated sites such as mounds and logs (Table 17).

Table 17: Numbers of trees of each species established on different microsities for each approximately even-aged group identified after spatial analysis of tree age distributions.

| Group | Species | Elevated Logs | Elevated Mounds | Elevated Stumps | Non-Elevated Forest floor | Total N |
|-------|--------------------------------|---------------|-----------------|-----------------|---------------------------|---------|
| 1 | <i>N. menziesii</i> | | 3 | | | 3 |
| 2 | <i>N. fusca</i> | 1 | 13 | | 1 | 15 |
| 2 | <i>N. menziesii</i> | 6 | 18 | 2 | 3 | 29 |
| | <i>Q. acutifolia</i> > 125 yrs | | 10 | 1 | 1 | 12 |
| | <i>W. racemosa</i> > 125 yrs | 4 | 53 | 2 | 6 | 65 |
| 3 | <i>N. fusca</i> | 3 | 30 | 2 | 8 | 43 |
| 3 | <i>N. menziesii</i> | 15 | 55 | 7 | 19 | 96 |
| | <i>Q. acutifolia</i> < 125 yrs | 3 | 10 | 10 | 3 | 26 |
| | <i>W. racemosa</i> < 125 yrs | 9 | 94 | 10 | 11 | 124 |

There were also distinct differences in species age structures in group 3. *Nothofagus fusca* ages were more tightly clustered with most stems (> 80%) in the 75-100 yrs age class, in contrast *N. menziesii* had more stems spread between the 50-125 yrs classes suggesting advance regeneration and more protracted establishment (Figs. 28b and 29b). Most *N. fusca* had established in open conditions and although the majority of *N. menziesii* were also under open canopy cover but there were more trees in shadier situations than *N. fusca* (Table 18). The younger hardwoods < 125 yrs were also mainly in shadier situations than *N. fusca* (Table 18.) There were subtle microsite differences between the beeches and the hardwood *Q. acutifolia* stems < 125 yrs, more *Q. acutifolia* had established on decaying stumps (10) than the beeches, and the proportion of stems on stumps (37%) was the greatest of any species (Table 17).

Table 18: No. of trees for each of the most abundant species in overhead cover classes in plot C.

| Species | Open | Intermediate | Closed | Total |
|-------------------------------|------|--------------|--------|-------|
| <i>N. fusca</i> | 53 | 3 | 2 | 58 |
| <i>N. menziesii</i> | 78 | 25 | 25 | 128 |
| <i>Q. acutifolia</i> <125 yrs | 14 | 5 | 8 | 27 |
| <i>Q. acutifolia</i> >125 yrs | 10 | 1 | | 11 |
| <i>W. racemosa</i> <125 yrs | 5 | 39 | 80 | 124 |
| <i>W. racemosa</i> >125 yrs | 20 | 27 | 18 | 65 |

3.3.5 Patterns of tree ring release and disturbance history

To investigate whether establishment of these relatively even-aged groups of trees was linked to the influence of historical disturbances, I examined the patterns of annual growth ring release in *N. menziesii* trees. Major periods of tree ring growth releases that coincided with increases in tree recruitment in the three groups indicated evidence of past disturbances causing openings in the canopy (Fig. 32). Releases were considered significant if they were present in ≥ 20 % cores in one decade. The corresponding maximum ages for each species in group 2 (clustered between 250-260 yrs) probably represent a synchronous response to a disturbance around this time. However, there was only one tree with a ring series long enough to examine this and it had a release 270-280 yrs ago (appendix: - Fig. C1).

The largest periods in release were between 190-220 yrs with a peak 200-210 yrs ago, and 70-100 yrs with a peak 80-90 yrs ago. Between 120-200 yrs ago there were periods where there with few or no releases detected, with the exception of releases in three trees 150-140 yrs ago. The upsurge in releases 100 yrs ago that continued until 60-70 yrs

ago coincided with the pulse of recruitment in this plot which commenced in the 100-125 yrs age class. These ages do not take into account the time taken for trees to grow to coring height. However, the majority of *N. fusca* were in a tight age cluster between 75-100 yrs ago suggesting a distinct pulse of establishment that responded relatively quickly to extensive opening (s) of the canopy. The peak in releases 200-210 yrs ago corresponded with an increase in *N. menziesii* recruitment evident in the 200-225 yrs class. Several *N. menziesii* trees showed a > 300 % increase in annual tree ring width c. 200 yrs ago, suggesting they were preexisting saplings (advance regeneration) that experienced a significant growth release around this time (appendix -Fig. C2).

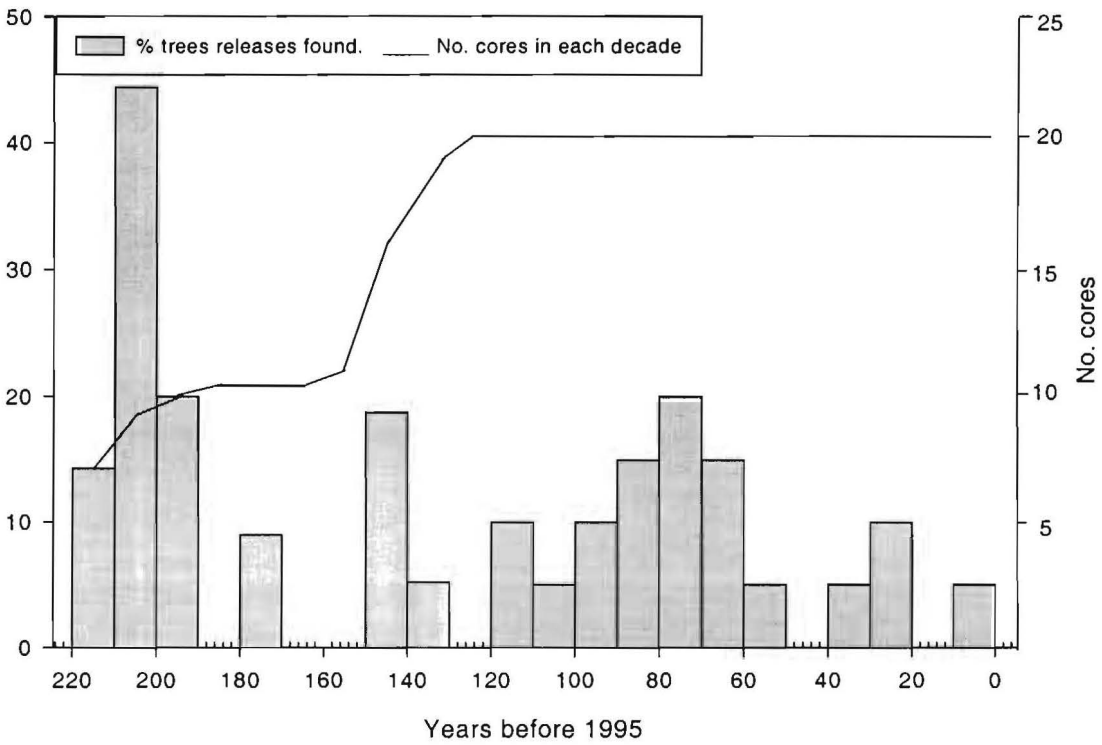


Figure 32: Temporal distribution of growth releases in each decade over last 220 yrs using uncross-matched cores ($n=23$ trees). Filled bars are relative proportion of trees with releases in each decade, and line represents total number of cores measured in each decade.

The distribution of *N. fusca* and *N. menziesii* stems in group 3 closely coincided with an area of abundant uprooting and associated tip-up pit and mound topography in the plot (Fig. 33a). However, there were some differences between their distributions; *N. fusca* was concentrated almost exclusively amongst the uprooted stems, whereas *N. menziesii* was more spread out with a number of stems also amongst the area of dead standing trees (Figs. 28b, 29b, 33b).

The cause of this uprooting appears to have been windthrow as the uprooted trees had all fallen in a general N-NW direction. The synchronous regeneration evidenced by the establishment of similarly-aged trees on mounds and adjacent forest floor sites also suggested uprooting caused disturbance to the canopy. *Nothofagus fusca* accounted for 77% of uprooted trees identified in this area (Fig. 33a). The distribution of uproots with few surviving trees suggests that the windthrow resulted in a large, relatively continuous opening in the canopy in the right side of the plot.

In contrast, dead standing trees scattered amongst many surviving trees in the left of the plot resulted in more patchy, smaller light gaps. Trees that died standing or were bole snapped dominated the other side of the plot (Fig. 33b: note only trees > 35 cm diameter were included as mortality of trees < 35 cm dbh was unable to be determined from causes such as exogenous disturbance or self-thinning). This is the area dominated by *Q. acutifolia* stems < 125 yrs along with many *W. racemosa* < 125 yrs stems (Figs. 31b and 30b).

Mortality of trees identified and recorded as dead standing likely occurred at different times in the past. Spatial patterns of older stems of *N. menziesii* (group 2) and *W. racemosa* aged > 125 yrs were compared with dead standing trees. These species were found to be positively associated with dead standing trees and stumps, suggesting that these species may have responded to openings in the canopy created by the death of individual trees scattered throughout the plot at different times ($P < 0.01$, $n = 60$, and $P < 0.05$, $n = 45$ respectively).

Soil differences between the sides of the plot could not account for why trees in one side of the plot were blown down and the other side experienced less extensive disturbance and different types of tree death c. 100 yrs ago. Soils were similar in drainage, depth to underlying gravels (range 30-65 cm) and texture (Ahaura silt loams) throughout the plot (31 of 42 pits and drainage holes were well-drained YBE soils and 11 were GYBE soils).

There were differences in the size and age of *N. fusca* trees in the two sides of the plot c. 100 yrs ago that could have influenced susceptibility of trees to blow down in the right side of the plot. The size class structure of the uprooted trees in this side of the plot was examined and > 50 % were found to be between 50 cm – 1 m in diameter (Fig. 34). Age/diameter regressions for *N. fusca* suggested these trees may have been aged between 147 ± 16 yrs to 240 ± 46 yrs when they were uprooted (appendix: Table C1). In contrast, the *N. fusca* that survived the blow down c. 100 yrs ago were younger, aged between 68-150 yrs, and smaller, ranging in diameter from 10 - 60 cm (two-tailed Kolmogorov-Smirnov test between age distributions = 0.818, $P < 0.001$, $n = 38$). This suggests the basal

dominant *N. fusca* in the two sides of the plot were of different size and age prior to the synchronous upsurge in establishment that occurred c. 100 yrs ago.

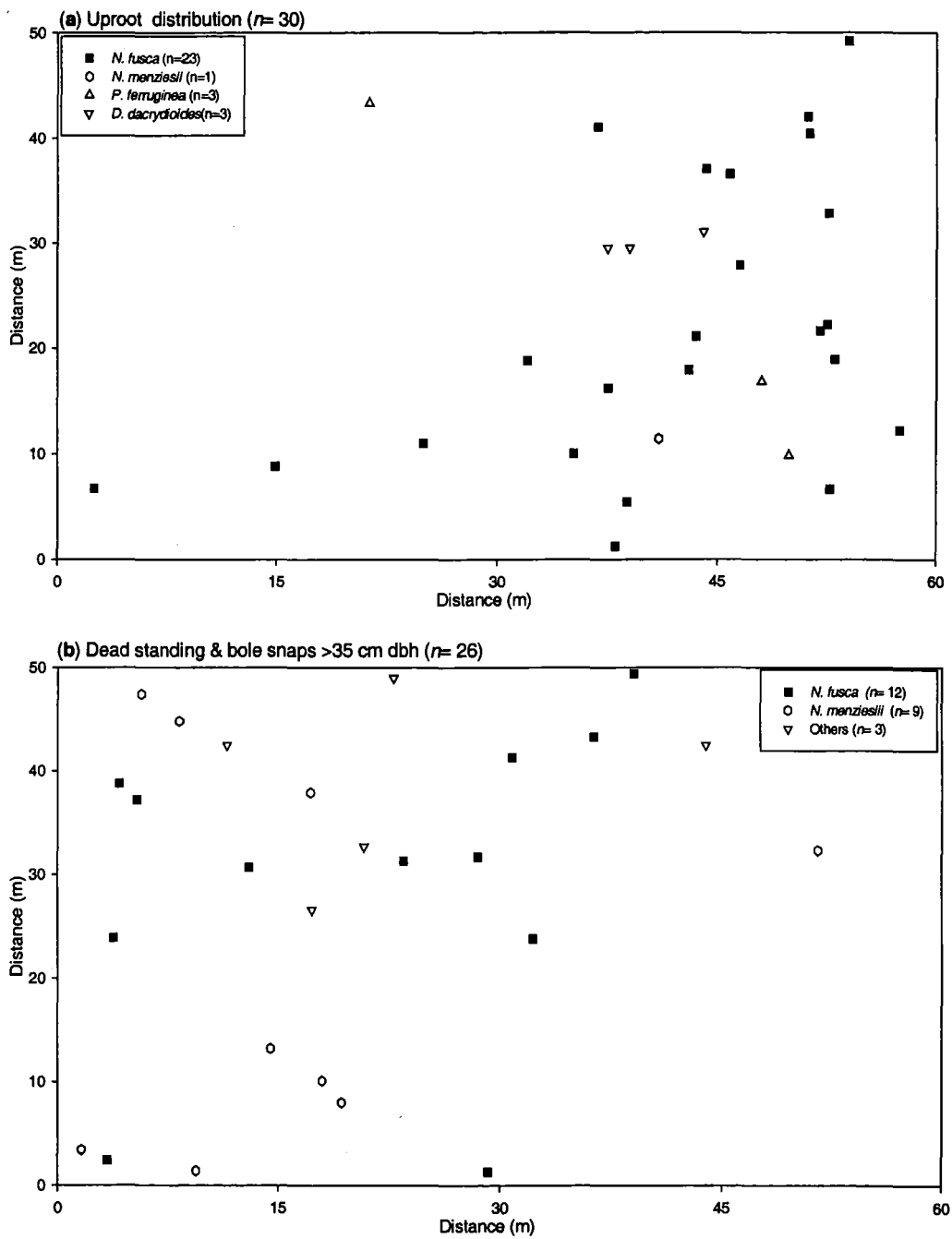


Figure 33: (a) Spatial distribution of uproots: note corresponding distribution of *N. menziesii* and *N. fusca* in Figs. 28b-29b (b) Spatial distribution of dead standing trees: note the distribution of *Q. acutifolia* in Fig. 31b.

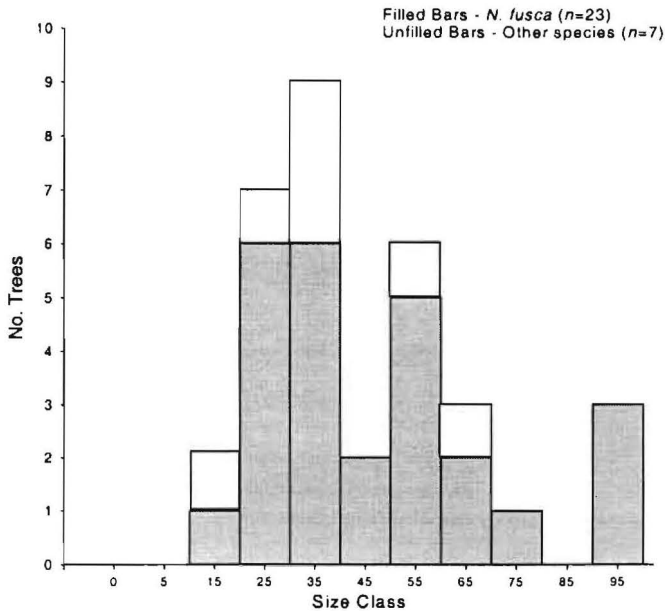


Figure 34: Size-class frequency diagram of *N. fusca* and other species uprooted in the right side of the plot c. 100 yrs ago (n= 30).

3.3.6 Current regeneration patterns

Most trees of the main canopy species established on elevated microsites such as mounds, logs or stumps (Table 17). This suggests that differences in microsite preferences could not account for differences in the relative abundances of these species. Not many beeches or hardwoods established on non-elevated sites despite their availability.

The few conifers present had established on the forest floor (*D. cupressinum*), or on mounds and forest floor sites (*P. ferruginea*). Seedlings of all the conifers were reasonably abundant on all both elevated and non-elevated microsites, but consistently appear unable to reach sapling height on any microsite type, despite the availability of microsites created by large disturbances that struck the plot over the last 200 yrs (Table 19). Similarly, the hardwood *E. hookerianus* was almost completely absent from this plot, being found only in the wetter gleyed yellow-brown earth patches along with the *D. dacrydioides* saplings.

The yellow-brown loams of the forest floor sites in this plot are much better drained and are not permanently saturated compared with the peats of plots A and B, and are more similar to mounds in terms of their drainage and soil characteristics. It may be that the lack of saturated or wetter sites may preclude the widespread establishment success of the conifers or, alternatively, there may be intense competition with the beeches and hardwoods on the well-drained elevated and non-elevated microsites within this well-drained plot.

Table 19: Comparison of number of saplings (<5 cm dbh, >1.4 m tall) and seedlings (<1.4 m tall) + 1 s.d. of different species across different microsites in an 0.3 ha well poorly drained plot (all values converted to a per hectare basis).

| Species | | Forest Floor | Pits | Logs | Stumps | Mounds | TOTAL (ha ⁻¹) |
|----------------------|-------|--------------|--------|------------|----------|-------------|---------------------------|
| <i>N. fusca</i> | sapls | 7 | | 20 | 7 | 13 | 47 |
| | seedl | 4195 ± 210 | 24 ± 1 | 3835 ± 318 | 500 ± 25 | 17632 ± 881 | 26186 ± 1309 |
| <i>N. menziesii</i> | sapls | 20 | | 23 | 13 | 57 | 113 |
| | seedl | 4667 ± 233 | 24 ± 1 | 1752 ± 88 | 283 ± 14 | 16983 ± 849 | 23709 ± 1185 |
| <i>W. racemosa</i> | sapls | 3 | | 10 | 7 | 30 | 50 |
| | seedl | | | 129 ± 6 | 19 ± 1 | 767 ± 38 | 915 ± 46 |
| <i>Q. acutifolia</i> | sapls | | | | 3 | 3 | 6 |
| | seedl | | | 55 ± 3 | 151 ± 8 | 944 ± 47 | 1150 ± 58 |
| <i>Dacrydium</i> | sapls | | | | | 3 | 3 |
| | seedl | 629 ± 31 | | 129 ± 6 | 94 ± 5 | 1533 ± 77 | 2385 ± 119 |
| <i>Dacrycarpus</i> | sapls | 17 | 3 | | | | 20 |
| | seedl | 734 ± 37 | 48 ± 2 | | | 413 ± 21 | 1195 ± 60 |
| <i>P. ferruginea</i> | sapls | | | | | | |
| | seedl | 629 ± 31 | | | 28 ± 2 | 944 ± 47 | 1601 ± 80 |

The few beech saplings present in the plot were found mostly in the left side of the plot, with the lack of saplings in the right side reflecting the lack of establishment opportunities under the dense canopy of young trees in the blowdown area (Fig. 35). Most *N. fusca* saplings were clumped in the top left side of the plot in a recently created canopy gap, whereas *N. menziesii* saplings were also located around centre of the plot (Fig. 35a). *Weinmannia racemosa* saplings were situated in the centre and right of the plot around existing trees, and there were none in the canopy gap dominated by *N. fusca* and *N. menziesii* in the top left of the plot (Fig. 35b). The one *Q. acutifolia* sapling in this canopy gap was elevated 2 m off the ground on a stump above the competing beech saplings, which had established on logs and mound microsites.

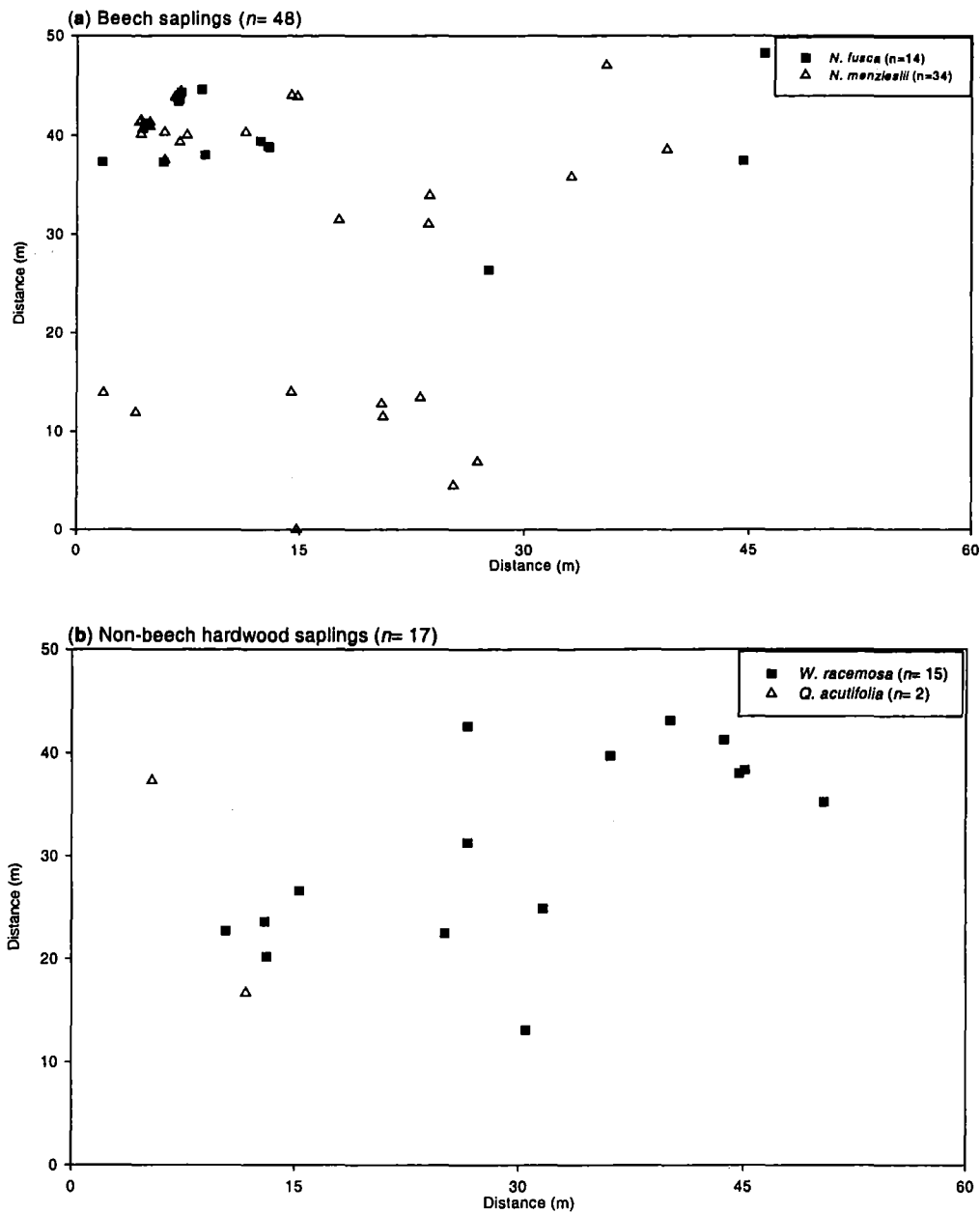


Figure 35: (a) Map of *N. fusca* and *N. menziesii* saplings (n= 48) and (b) Map of *W. racemosa* and *Q. acutifolia* saplings (n= 17) in well drained plot C at Mt Harata.

3.4 SYNTHESIS OF FOREST HISTORY IN THE THREE PLOTS

All overstorey species showed population structures indicating had been successfully recruited within the study area during the last 450 years and appeared to be able to coexist indefinitely, assuming conditions that allow their recruitment continue. However, there were differences in the structure and composition of stands on surfaces that differed in drainage. As drainage got progressively better across the terrace there was an associated increase in beech and non-beech hardwood stem density and basal area, and a corresponding decrease in conifer density and basal area with few conifers present on the well drained site.

At different points along the drainage gradient, there have been distinct and synchronous upsurges of establishment for more than one species, in particular for the conifers and *Nothofagus fusca* at intervals of *c.* 50-100 yrs. These are attributed to the influence of disturbances that caused openings in the canopy, consistent evidence for these was found across all plots from tree age structures, the spatial distribution of tree ages, and patterns of tree ring growth releases.

Several periods of establishment coincided between plots suggesting that at certain times these disturbances were not localised in their impacts. Four major pulses of establishment that occurred in more than one plot in the last 450 yrs were identified: 375-425 yrs, 275-300 yrs, around 200 yrs ago and between 100-125 yrs ago (Table 20).

Two main patterns were evident in how species responded to disturbances over the last 450 yrs: first, there appears to have differential species responses to the same disturbance across the plots (Table 20). This reflects the strong gradient in drainage and soil development across the terrace. In general, at this larger scale, the same event favours the beeches and non-beech hardwoods on drier sites and mainly conifers and beeches on wetter sites. At the smaller within-plot scale, species were able to coexist by partitioning microsites based on drainage characteristics with beech and hardwoods on better drained elevated sites (logs, stumps, mounds, litter cones), whereas conifers and the hardwood *E. hookerianus* established on poorly drained sites (forest floor and pit edges). Second, at the same site, different suites of species have been recruited at different times. For example, in plot B, following a disturbance 375-425 yrs ago, a pulse of conifer (*Dacrydium*, *Dacrycarpus*) and beech (*N. menziesii*, *N. fusca*) establishment occurred, while 200 yrs ago predominantly *N. menziesii*, *W. racemosa* and *Q. acutifolia* recruitment occurred. This suggests there was something different about the nature of disturbances and their extent at different times in each plot that favoured different sets of species.

Table 20: Approximate timing of disturbances that occurred in more than one plot that initiated widespread establishment of the main tree species on differently drained surfaces.

| Approx. disturbance date (yrs B.P) | Well- drained Plot C | Poorly- drained Plot B | Very Poorly- drained Plot A |
|------------------------------------|--|---|---|
| 100-125 yrs | <i>N. fusca</i> <i>N. menziesii</i> <i>W. racemosa</i> <i>Q. acutifolia</i> | <i>N. fusca</i> <i>N. menziesii</i> <i>Dacrycarpus</i> <i>E. hookerianus</i> | |
| 200 | <i>W. racemosa</i> | <i>N. menziesii</i> <i>W. racemosa</i> <i>Q. acutifolia</i> | <i>Dacrydium</i> <i>Dacrycarpus</i> <i>N. menziesii</i> |
| 275-300 | <i>N. fusca</i> <i>N. menziesii</i> <i>W. racemosa</i> <i>Q. acutifolia</i> | <i>N. menziesii</i> <i>W. racemosa</i> | <i>Dacrydium</i> <i>Dacrycarpus</i> <i>L. bidwillii</i> <i>P. hallii</i> |
| 375-425 | <i>N. menziesii</i> | <i>Dacrydium</i> <i>Dacrycarpus</i> <i>N. menziesii</i> <i>N. fusca</i> | <i>Dacrycarpus</i> <i>N. menziesii</i> |
| 650 | | <i>Dacrydium</i> | |
| 850 | | <i>Dacrydium</i> | |

Differences in patch sizes between species can aid in understanding the extent of different disturbances. For example, if tree distributions within patches were densely packed in an area with few or no older surviving trees, this reflects a large discrete opening in the canopy. Alternatively, if species in a patch were interspersed amongst trees from older patches, this suggests that disturbances caused more patchy impacts to the canopy at these times.

Conifers

Few *Dacrydium cupressinum* were recruited into the canopy across the terrace in response to more recent disturbance periods, with the last substantial pulse of establishment beginning around 275-300 yrs ago (Table 20). Patch size varied in the poorly drained plots but generally covered large areas (> 1000 m²), stems were densely packed in discrete areas with few surviving older trees in plots A and B. These patterns reflected regeneration in response to extensive perturbation to the canopy at different times.

Dacrycarpus dacrydioides established along with *Dacrydium* after large disturbances 275-300 yrs and 375-425 yrs ago in the poorly drained plots but, in contrast to *Dacrydium*, had more recent recruitment into the canopy (Table 20). The clumping of

stems in small groups on the forest floor, particularly around uprooted trees in plot B, suggested gap-phase recruitment after more recent disturbances.

Libocedrus bidwillii and *Podocarpus hallii* were found only in the very poorest drained peats in small even-aged populations of similar age, coinciding with the pulse of plot-wide *Dacrydium* and *Dacrycarpus* establishment c. 275-300 yrs ago in plot A.

Scattered *Prumnopitys ferruginea* were found across the terrace, with ages spread from 35-635 yrs, suggesting sporadic and intermittent establishment. No saplings were found in any plot despite the canopy gaps and closed forest surveyed.

Beeches

In all plots, groups of relatively even-aged *N. fusca* trees were periodically recruited into the canopy although there were differences between plots (Table 20). In poorly drained plot A, groups of similarly-aged *N. fusca* were distributed in canopy gaps amongst older surviving trees in the general absence of older, pre-existing subcanopy hardwoods. In contrast, the population in the well drained plot was dominated by one extensive patch that established in a large continuous canopy opening after extensive wind throw c. 100 yrs ago. There were few trees recruited into the canopy at other times.

Nothofagus menziesii was the most consistently abundant species across the plots, and had a more all-aged structure than *N. fusca* or the conifers, suggesting recruitment occurred more frequently in response to a range of disturbances of different extent (Table 20). Even-aged patches of trees in discrete areas were evident after extensive disturbance, in a series of large clumps in the left of plot A c. 200 yrs ago, and after blowdown in the well drained plot c. 100 yrs ago. Similarly-aged small groups and single trees that progressively established in a mosaic of canopy gaps between surviving trees, occurred in response to patchy mortality in all plots.

Non-beech hardwoods

Weinmannia racemosa exhibited all-aged population structures consistent with establishment in response to a range of disturbances. There were more *W. racemosa* trees aged between 100-200 yrs than any other species, during a period when patterns of tree ring releases over the last 200 yrs suggested a history of less extensive, smaller scale disturbances within plots. Relatively few stems established over the last 100 yrs when extensive establishment of beech and *Dacrycarpus* occurred in poorly drained plot B.

Quintinia acutifolia increased in abundance as drainage improved. In poorly drained plot B, the spatial distribution of *Q. acutifolia* ages suggested establishment co-

occurred along with *N. menziesii* and *W. racemosa* after patchy disturbance created by trees mainly dying standing. In well drained plot C, *Q. acutifolia* captured patchy light gaps following the standing death of individual trees, and around the edges of the large uproots.

Elaeocarpus hookerianus showed the reverse distributional pattern from the other hardwoods, becoming more abundant as drainage became progressively poorer. Periodic establishment in canopy gaps occurred for this species, with trees in small groups associated with *Dacrycarpus* and *N. fusca* after uprooting in plot B c. 100 yrs ago, and after disturbance c. 160 yrs ago in plot A along with *N. fusca*, *Dacrycarpus* and *N. menziesii*.

4. DISCUSSION

4.1 Species recruitment patterns

The spatial distribution of tree ages suggested that species differed in their regeneration strategies across the drainage gradient stemming from the interaction of three key factors: underlying drainage, disturbance extent, and availability of certain microsites. Population structures suggest the conifers and *N. fusca* were recruited into the canopy periodically, with the peaks in the age-class distributions most likely reflecting pulses of tree establishment in response to infrequent disturbances that caused extensive damage to the canopy. In general, large disturbances favoured one set of species (especially the conifers and *N. fusca*), smaller patches resulting from more frequent disturbances such as gaps created by the death of one tree or small groups favoured another set (*N. menziesii*, *W. racemosa*, *Q. acutifolia*). This suggests that species also partitioned establishment sites depending on the amount of overhead cover, in addition to the availability of different types of suitable establishment sites.

Conifers

The emergent *Dacrydium* had substantially greater longevity than other species, and probably was recruited into the canopy after extensive disturbances. Other studies in north Westland have also noted *Dacrydium* populations in mixed stands were dominated by large, old stems, with fewer young trees and saplings compared with other species (Burrows *et al.* 1975; June, 1982). These authors did not explicitly link the regeneration of *Dacrydium* to large disturbances at these sites, rather other possible explanations were invoked. For example, June (1982) interpreted *Dacrydium* age-class peaks between 300-

600 yrs ago as representing a continuous regeneration pattern that was interrupted by a major disturbance c. 300 yrs ago, rather than these peaks representing past pulses of establishment in response to large disturbances. June argued that a disturbance that occurred about 300 yrs ago led to the suppression of further *Dacrydium* establishment by vigorous angiosperm regeneration. The apparent failure of recent *Dacrydium* recruitment in conifer/angiosperm forests throughout Westland (the so-called 'regeneration gap') has been keenly debated over the last 50 yrs (e.g., Cockayne, 1928; Holloway, 1954; Robbins 1962; Wardle 1963, 1980; Clayton-Greene, 1977; Veblen and Stewart, 1982; June 1982), and elsewhere in the mixed conifer/angiosperm forests of New Caledonia and Papua New Guinea (Wormsley, 1958; Aubréville, 1964, 1965; Whitmore, 1966; Havel, 1971; Gray, 1975), and South America (Kalela, 1941; Schmithüsen, 1960). One traditional school of thought accepted conifer regeneration failure in New Zealand as a given, and various explanations were advanced to explain this pattern. In 1928, Cockayne advanced the idea that conifers represented a penultimate stage in a successional trajectory towards an angiosperm climax. A change toward cooler and drier climates around 1200 A.D. underpinned Holloway's (1954) hypothesis to explain the apparent lack of conifer regeneration in the last few centuries. Wardle (1963) placed this climate change as occurring at 1300 A.D. In part, these theories were premised around the idea that conifers were evolutionally inferior to the more competitive angiosperms, and their presence in forests was therefore relictual (Wormsley, 1958; Robbins, 1962). More recent work to aid in explaining this relictual status suggested that, aside from climate, other factors were involved in triggering suppression of conifers, such as vigorous angiosperm regeneration in response to large disturbances (June, 1982) or the extinction of the large herbivorous moa (Wardle, 1985). However, other work in Southern Hemisphere forests has shown that the regeneration gap postulated for some conifers can be explained a lack of infrequent, large scale or catastrophic disturbances that allow conifer regeneration (Whitmore, 1966; Gray 1975; Clayton-Greene, 1977; Veblen and Stewart, 1981, 1982; Ogden, 1985; Read and Hill, 1988; Duncan, 1993; Ogden and Stewart, 1995; Veblen *et al.* 1995; Wells, 1998). For example, at other sites in Westland, disturbance history was an important factor in determining the relative abundances of conifers and angiosperms (Veblen and Stewart, 1981). At Rahu Saddle in north Westland, these authors found the conifer *Libocedrus bidwillii* and the beeches *Nothofagus solandri* var. *cliffortioides* and *N. menziesii* were all recruited into the canopy after catastrophic disturbance, but the beeches captured subsequent treefall gaps except in wetter areas where their vigour was reduced. The relative basal area and abundance of mixed *L. bidwillii*, *N. solandri* var. *cliffortioides* and

non-beech hardwood forest in the North Island was also found to be determined by the severity and nature of past disturbances (Ogden *et al.* 1993).

Conifers responding to processes occurring at larger scales has lead to conifer/angiosperm forests being described as 'two-component' systems (Veblen and Stewart, 1981, 1982; Ogden and Stewart, 1995). There has been a conceptual model of conifer cohort structure proposed to account for the way in which this two-component model operates, the 'lozenge-model' of forest development (Ogden, 1985; Ogden and Stewart, 1995). Groups of even-aged conifer trees establish in response to large disturbances and, as they mature and senesce, secondary smaller cohorts of trees establish leading to a spreading out of ages. These smaller cohorts are relatively patchy, because most subsequent canopy gaps are captured by angiosperms (Ogden and Stewart, 1995). Several other studies have also shown that conifer densities decline in the absence of large disturbances (Ogden *et al.* 1987; Veblen and Lorenz, 1987). The age structure of *Dacrydium* in plot B provides support for this model, with the imposition of a more recent, smaller cohort aged 300-400 yrs in the top right of the plot on the extensive patches of trees > 600 yrs old that covered the rest of the plot (Fig. 17). In this light, the age structure and spatial extent of *Dacrydium* that established in plot A may represent the first stage of the model after extensive plot-wide disturbance (Fig. 6a). *Dacrydium cupressinum* regeneration abruptly commenced about 275 yrs ago, and covered most of the plot with very few surviving, interspersed older trees of any species, suggesting catastrophic mortality of the canopy at that time, which allowed extensive recruitment to occur. A subsequent pulse of younger stems in the top left of the plot represents the second stage of the lozenge model (Fig. 6b). This pattern of different aged *Dacrydium* patches in the two plots at different points along the terrace is consistent with what other workers have found in south Westland, where groups of relatively even-aged *Dacrydium* dominate forests in a mosaic of different aged patches (Hutchinson, 1932; Six Dijkstra *et al.* 1985; Cornere, 1992; Rogers, 1995; Stewart *et al.* 1998; Van Uden, 1998). Although, this research occurred where beeches were absent, on strongly leached soils under higher rainfall in south Westland.

Dacrycarpus dacrydioides established along with *Dacrydium* after large disturbances in the poorly drained plots but, in contrast, intermittent gap-phase recruitment occurred after more recent and less intense disturbances. *Dacrycarpus dacrydioides* has been viewed as a species that responds to large scale disturbances, commonly regenerating in dense stands on flood plains and fertile alluvial terraces after flooding (Wardle, 1974; Smale, 1984; Duncan, 1993). A widespread paucity of young stems and reliance on poorly

drained silts on floodplain surfaces meant this species was considered to be mostly dependent on catastrophic disturbances such as flooding for recruitment, with existing seedlings and saplings viewed as ephemeral (Smale, 1984; Duncan, 1993). However, on this old stable terrace 120 m above the Grey River, no evidence of large scale flooding was found. There are several small streams that flow across the terrace, and it is likely that they periodically deposit pulses of silty material on the forest floor when water levels are high. Sapling regeneration was vigorous, particularly in canopy gaps, and these may not necessarily be ephemeral.

The conifers, *Libocedrus bidwillii* and *Podocarpus halli*, displayed small even-aged populations that were restricted in their distribution in very poorly drained plot A only, and no evidence was found that these species were present in the other plots. Other studies have shown *L. bidwillii* populations to be commonly composed of relatively even-aged groups that establish after large disturbances such as landslides or earthquakes, with few stems recruited at times of less extensive disturbance (Veblen and Stewart, 1982; Stewart and Rose, 1989; Wells, 1998). Live and dead stems in plot A were in the right side of the plot close to where species composition and structure changed to lower statured *Nothofagus solandri* var. *cliffortioides*, *Phyllocladus aspleniifolius* (toatoa), *Lagarostrobos colensoi* (silver pine), *Leptospermum scoparium* (manuka) vegetation in extremely poorly drained basin peats of the terrace centre. This distribution pattern, with respect to drainage, occurs elsewhere in north Westland; in the nearby Hochstetter forest (c. 20 km S) Veblen and Stewart (1981) found *L. bidwillii* restricted to very poorly drained areas, whereas *N. solandri* var. *cliffortioides* and *W. racemosa* were more abundant in better-drained areas.

The few *Prumnopitys ferruginea* identified were recruited into the canopy infrequently in the three plots, which is consistent with patterns found in a range of studies throughout Westland, where other workers found intermittent and gap-phase patterns of recruitment of this relatively shade-tolerant conifer species (Duncan, 1993; Rogers, 1995; Lusk and Smith, 1998; Stewart *et al.* 1998; Van Uden, 1998). *Prumnopitys ferruginea* produce large amounts of seeds in mast years, and dispersal is prolific across the landscape, being widely dispersed by native wood pigeons (kereru - *Hemiphaga novaseelandiae*) (Clout and Tilley, 1992). Seedlings are able to persist under the canopy for long periods in shady situations in different forest types (Ogden and Stewart, 1995), and at this site, *P. ferruginea* seedlings were numerous on a range of different soils. It appears to be a classic slow growing 'tortoise' (0.10 ± 0.04 cm/yr, $n=28$; cf appendix - Table D1) with a strategy to plod away once it gets successfully underway on differently drained soils. Lusk and Ogden (1992) reported trees of > 700 yrs in the North Island, and considered *P. ferruginea*

was the most shade-tolerant of the conifers regenerating in slight canopy openings. It was the second longest-lived species in this study (maximum age 634 yrs), and appears to have the opposite regeneration strategy to the other long-lived conifer *D. cupressinum* at the site. *Prumnopitys ferruginea* did not appear dependent on infrequent, large openings in the canopy, but could regenerate sporadically under the canopy, and hold sites for long periods once established.

Beeches

In plot A, the *N. fusca* population was composed of relatively even-aged groups of trees that had established in canopy gaps in different parts of the plot at different times. The most recent pulse of establishment occurred in the last 50 yrs following the death of the older *L. bidwillii*. Abundant saplings around the bases of dead standing trees, and the litter cones of live conifers, suggest this establishment pulse is ongoing. When the first pulse of *N. fusca* recruitment occurred c. 160 yrs ago, > 100 yrs after the initial pulse of conifer establishment, there were few subcanopy hardwoods in the plot. The overstorey comprised conifers probably over an understorey of tree ferns (*Dicksonia squarrosa* and *Cyathea smithii*). Currently, there is a dense understorey of tree ferns, and a number of *Dacrydium* had branched low above the fern cover reflecting a lack of competition in the lower height tiers. Gaps created in the understorey and/or the development and availability of suitable elevated microsites enabled successful *N. fusca* establishment commencing about 160 yrs ago. The ability of tree ferns to cast deep litter and shade inhibiting seedling establishment on the forest floor (Beveridge, 1973; Wardle, 1991) meant that elevated microsites were important sites for *N. fusca* establishment in this plot.

The type of tree death and extent of canopy openings influenced the successful recruitment of *N. fusca* trees into the canopy in plot B, where subcanopy hardwoods were abundant. Most *N. fusca* trees < 100 yrs old established on mounds (60%) following uprooting, particularly around the centre of the plot. The ongoing canopy collapse of senescent *Dacrydium* created large openings as mortality struck trees up to 100 cm dbh (> 600 yrs old). There were comparatively few *N. fusca* stems aged between 100-300 yrs ago in this plot, despite extensive *N. menziesii* and subcanopy hardwood recruitment in gaps created by dead standing trees during this time. In contrast, *N. menziesii* patch size varied with similarly-aged groups of several trees spread amongst surviving trees in a mosaic of small gaps in this plot. Other workers have found *N. menziesii* to have all-aged structures reflecting establishment in response to frequent disturbances (Stewart, 1986; Allen, 1988).

In mixed-species forest in Fiordland, for example, Stewart (1986) found *N. menziesii* was highly dependent on canopy openings for successful establishment.

In well drained plot C, both beech species responded in abundance to the blow down c. 100 yrs ago, but their recruitment patterns differed. *Nothofagus fusca* was mainly located within the windthrown area and had a tight age clustering. In contrast, *N. menziesii* was more numerous and tree ages were spread out suggesting advance regeneration and more protracted establishment than *N. fusca*. In addition to the main uproot area, *N. menziesii* established in smaller gaps created by trees that had died standing. Other workers have found *N. fusca* and *N. menziesii* to co-occur as even-aged stands, with *N. menziesii* having a wider age range, and greater numbers of stems in smaller sized classes, suggesting that *N. fusca* dominates in larger gaps and *N. menziesii* in smaller gaps (Wardle, 1984; Ogden, 1985, 1988; Smale *et al.*, 1987). Recruitment of even-aged *Nothofagus* stands in response to catastrophic disturbances has been recorded in a number of southern temperate forests (see reviews in Read and Brown, 1996; Ogden *et al.*, 1996; Veblen *et al.* 1996a).

Non-beech hardwoods

In very poorly drained plot A, there were only two saplings and two small *W. racemosa* trees, and no *Q. acutifolia*, suggesting underlying drainage conditions influenced their distributions. *Weinmannia racemosa* seedlings were negatively associated with poorly drained forest floor sites in plot B ($X^2 = 4.8$, $P < 0.05$, 1 d.f) possibly suggesting that seedlings do not like excessive moisture inundation in these saturated peats. On waterlogged sites in the Toaroha catchment in central Westland, these species were also scarce and restricted to logs, or epiphytic establishment occurred on large trees (Veblen and Stewart, 1981).

In poorly drained plot B, *W. racemosa* showed a pattern of recruitment after less extensive disturbances suggesting stem establishment occurred in small or ephemeral openings. *Weinmannia racemosa* stems had a more all-aged structure than other species in the well-drained plot. Stewart (1986) also found *W. racemosa* to have differential recruitment strategies to a range of gap sizes on well-drained sites in Fiordland, being recruited along with *N. menziesii* after windthrow and capturing a range of subsequent smaller gaps. Other workers have found all-aged structures reflecting continuous recruitment patterns for *W. racemosa*, along with the other hardwood *Quintinia acutifolia*, suggesting that they are more shade tolerant than other species (Veblen and Stewart, 1981; Stewart and Veblen, 1982; Lusk and Ogden, 1992; Duncan, 1993; Lusk and Smith, 1998;

Stewart *et al.*, 1998). *Weinmannia racemosa* and *Q. acutifolia* both have the ability to reproduce vegetatively and from root suckering, *W. racemosa* can resprout from the base following the death of the main leader (Moorhouse, 1939; Wardle, 1991). These are useful strategies following disturbances that enable these species to respond vigorously to increased light, and gives them a decided advantage in small gaps over the faster-growing beech which establish from seed (Moorhouse, 1939; Wardle, 1984; Stewart, 1986).

Elaeocarpus hookerianus also differed from the other hardwoods in its recruitment patterns, being periodically recruited into the subcanopy in response to gaps created by disturbances. In plots A and B, recruitment occurred along with distinct pulses of *Dacrycarpus*, *N. fusca* and *N. menziesii* recruitment. *Elaeocarpus hookerianus* is a heteroblastic, divaricating species, with differences in growth strategies between the seedling and sapling stages (Day and Gould, 1997). Seedlings are strongly divaricating which represents a plastic and energy efficient growth form. In other words, it can hang around for a long time amassing resources for eventual vertical extension (Day *et al.* 1997). Once increased light becomes available, it switches its growth form of the adolescent or sapling phase and redistributes its resources to maximise height growth in canopy gaps (Day *et al.* 1997). Hence, periodic disturbances can release a pool of seedlings, creating the pattern of relatively similarly-aged trees grouped together in different parts of the plots A and B.

4.2 Disturbances and microsite heterogeneity

Microsite availability

Disturbances are critical in providing the environmental variability that enables different species to coexist, by releasing resources such as light and making available, or creating, a range of microsite types for different species to establish. There were two broad groups of species that partitioned microsites according to drainage characteristics: beech and hardwoods on well drained microsites, and conifers and *E. hookerianus* on poorly drained microsites. On poorly drained microsites, *Dacrydium*, *Dacrycarpus* and *E. hookerianus* trees and saplings were associated with forest floor sites or around pit edges. In other mixed stands in north Westland, species also partitioned establishment sites according to drainage, with the conifer *L. bidwillii* on wetter sites, and *N. menziesii* on well drained sites (Veblen and Stewart, 1982). June (1982) observed *Dacrydium* seedlings were positively associated with pit edges and up on logs in mixed north Westland stands. Duncan (1993) found that in gleyed recent flood material in south Westland *Dacrycarpus*

established on wet sites, whereas *Dacrydium cupressinum* seedlings established on raised substrates. Other workers describe *E. hookerianus* as inhabiting damp or poorly drained areas (Veblen and Stewart, 1981; Wardle, 1991).

Elevated microsites such as logs, stumps, and mounds have been recognised in Aotearoa forests as important safe sites for the successful establishment of species, such as beeches, due to a range of factors inhibiting recruitment on the forest floor including fern competition and deep litter layers (P. Wardle, 1980, 1991; J. Wardle, 1984; Norton *et al.* 1988; Stewart and Rose, 1990; Duncan, 1993; Duncan *et al.* 1998). Variation in the dense tree fern understorey in the poorer drained areas, and crown fern cover in the well drained sites, influenced successful species regeneration at this site. Therefore, perturbation of the fern understorey and/or the creation of elevated sites by disturbances were important in providing opportunities for species to successfully regenerate. Elsewhere in north Westland, June (1982) noted *N. fusca* seedlings favoured logs. Other workers have observed *N. menziesii* to prefer raised bryophyte-covered logs, since beech seedling survival was generally poor under dense fern or shrub cover (Wardle, 1984; Stewart, 1986; Allen, 1987). Beveridge (1973) noted the pattern of prolific *W. racemosa* seedling establishment on the stems of tree ferns.

The availability and distribution of better drained mounds also enables species to establish in areas where they would not normally be found, such as *N. fusca* in very poorly drained areas (Adams and Norton, 1991). On the poorly drained peats, elevated microsites also provide species with safe sites to establish away from mortality agents such as moisture inundation (Harper, 1977). In coastal Chilean rainforest, *Nothofagus betuloides* was able to avoid competition and survive in *Drimys winteri* dominated areas by establishing on root mounds (Rebertus and Veblen, 1993). In swamp forest in the US, Putz and Sharitz (1991) found that species such as *Acer rubrum* generally found on better drained surfaces in swamp margins, were able to exist at the edge of their environmental tolerance range in very poorly drained areas after establishment on logs or uproot mounds.

In plot A, the spatial and temporal pattern of microsite creation and availability provided species with differential opportunities for establishment over the last 300 yrs. Following the disturbance c. 275-300 yrs ago, conifers mostly established on forest floor sites with apparently little corresponding successful beech or hardwood regeneration. It is possible that the absence of evidence of beeches or hardwoods establishing around this time was a function of their shorter life-expectancy compared to the conifers on the very poorly-drained soils. There were two *N. menziesii* trees > 300 yrs in the plot, and two *N. fusca* > 250 yrs indicating that beech predated and immediately postdated the disturbance,

and there have probably also been stems that established around that same time but have since died (Table 1). However, in the very poorly drained peats of the plot centre where *Dacrydium* uncharacteristically branched low over the fern overstorey from the lack of interspecific competition, it appears that other factors limited widespread beech establishment c. 275-300 yrs ago. Delays in beech establishment could be due to the availability of suitable elevated microsites, for example > 50 % of *N. menziesii* recruited after disturbance c. 200 yrs ago were up on logs. Similarly, many *N. fusca* and *N. menziesii* that responded to the disturbance 150-160 yrs ago established on logs (Table 4). Over time, more recent establishment of beech occurred on the mounds of dead standing trees especially around the bases of dead *L. bidwillii* trees. These tree bases or litter cones are elevated and better drained than forest floor sites, and are composed of accumulated sloughed litter, bark and moss over centuries. This is reflected in a drier organic layer with a distinguishable litter, fermentation and humic layer, compared to a saturated organic layer on the forest floor. This suggests two conclusions. First, the distribution and availability of microsites reflects the importance of past disturbances in creating sites suitable for different species (Grubb, 1977; Whittaker and Levin, 1977; Christy and Mack, 1984; Eriksson and Ehrlén, 1992; Duncan, 1993). Second, some species require amelioration of site conditions (decay of logs, build up of drier material in the saturated peats and changing nature of microsite conditions) before they can successfully colonise openings in the canopy. Site amelioration was previously identified in gleyed floodplain soils in south Westland, where, following a stand-initiating flood delayed, recruitment of *W. racemosa* occurred c. 100 yrs after conifers, once suitable elevated microsites for successful establishment became available such as logs, mounds or tree fern bases (Duncan, 1993).

Different types of tree death also provided a heterogenous mosaic of microsites to which species responded differentially (Schaetzel *et al.* 1989). For example, conifer saplings were negatively associated at short distances with dead standing trees or bole snaps in plot B. However, saplings were more positively associated with areas around uproots (Table 14). In contrast, beech and hardwoods were associated with sites created by all types of tree death. This suggests that some form of soil disturbance may be a factor influencing conifer establishment patterns by enabling them to establish away from ground cover such as moss or competing understorey vegetation. Evidence of this has been found in south Westland conifer forests, where high recruitment rates of *Dacrydium* seedlings on disturbed ground, resulting from ground-based logging, have been recorded (James and Franklin, 1978).

Microsite partitioning after disturbance

In plot A, spatial patterns of similarly-aged *Dacrydium* and *Dacrycarpus* trees that established after disturbance c. 275-300 yrs ago could be influenced by differences in peat composition at the plot scale with species possibly partitioning parts of the plot along a gradient of organic matter concentration. Different types of peats were broadly found in different areas of the plot, with the more organic Kini peats found towards the middle and Rotokuhu peats on the outsides of the plot (Table 5). Kini peats are typically formed from *Dacrydium* litter and sphagnum moss and usually complexed with other soils such as Rotokuhu peats (Mew and Ross, 1980). Rotokuhu peats are derived mainly from *Dacrycarpus* litter with some alluvium (Mew, 1980) (Plate 2). Whether *Dacrycarpus* and *Dacrydium* established on these different peats, or the trees themselves are a causative factor in forming these peats, is unknown. The elevated, spreading root plates observed for about half the *Dacrydium* in the centre of the plot, may be a mechanism to give stability in the most saturated peats, or the roots are splayed due to the shallow depth of anaerobic soil. At a landscape level, *Dacrycarpus* is found on flood plains and recent terrace soils rejuvenated by flooding (Foweraker 1929, Wardle, 1974; Norton and Leathwick, 1990; Duncan, 1993) and in flat low lying hollows and back-swamps on low terraces (Mew and Ross, 1980); whereas *Dacrydium* is prevalent on more nutrient poor, leached and acidic organic soils on older surfaces (Chavasse, 1962; Sowden, 1986; Almond, 1997). One possibility is that these peats were different in terms of nutrient availability although no data were collected in this study. In a set of glasshouse trials, Hawkins and Sweet (1989) found that *Dacrycarpus* had a greater relative response to elevated nutrient levels than *Dacrydium*, but that *Dacrydium* had a greater efficiency of N and P uptake and slower growth considered good adaptations for its tolerance of more nutrient-poor sites.

4.3 Drainage and conifer distributions

Drought versus competition

Conifer trees and saplings were scarce in the well-drained plot despite the history of large and small disturbances in the area. At a landscape level in mixed species forests in Westland, *Dacrydium* are not abundant on well drained sites and are scattered on hillslopes and terrace edges (J. Wardle, 1984; DeVelice, 1988; P. Wardle, 1991; Lusk and Smith, 1998). Different ideas have emerged to explain these conifer distribution patterns. One set of explanations involves the influence and role of natural disturbances on conifer regeneration on these sites. For example, June (1983) argued that *Dacrydium* was shade-

tolerant spending 100-400 yrs in the subcanopy awaiting small gaps to reach the canopy. In contrast, a more recent study linked periodic establishment of *Dacrydium* on well-drained moraines to large, infrequent disturbances (Stewart *et al.* 1998). Another idea to explain infrequent *Dacrydium* recruitment on well-drained hillslopes surrounds life-history differences between conifers and angiosperms (Lusk and Smith, 1998). In the absence of large disturbances, a long life-span and canopy residence time (up to 700 yrs), compared with the more abundant shorter-lived beeches and hardwoods, means that sooner or later opportunities for sporadic *Dacrydium* recruitment would arise by chance. However, these ideas do not appear to offer a full explanation for the relative scarcity of *Dacrydium* and *Dacrycarpus* on well drained sites.

In the well-drained plot, the lack of moist microsites could be a key factor limiting successful *D. cupressinum* and *Dacrycarpus* establishment. The few conifer saplings present were found in the wetter forest floor depressions. Another possible explanation is that competition between conifers and angiosperms for elevated sites could limit conifer recruitment success. *Nothofagus fusca* were the fastest growing species in both the well drained and poorly drained sites and were between 2-3 times faster growing than *Dacrydium* and *Dacrycarpus* (Appendix - Table D1 from Ulrich *et al.* 1999). Although conifer seedlings were found on a range of elevated and non-elevated microsites in the well-drained plot, the lack of conifer saplings on well drained sites and their relative abundance on poorer drained sites could be interpreted in light of Bond's (1989) 'tortoise and hare' model. Slower growing, longer lived 'tortoises' (conifers) are restricted to poorer sites (in this study - poorly drained sites), and the faster growing 'hares' (angiosperms) capture the favourable (better drained) sites on more fertile soils. This pattern has also been observed by Wardle (1991) on the infertile gley podsols of south Westland, where herbaceous angiosperms were sparse under open canopies and regeneration of conifers tolerant of low fertility was relatively unrestrained. On fertile soils, Wardle argued opportunities for conifer regeneration are limited in time and space due to angiosperm competition. Support for the competition hypothesis is linked to the idea of the conifers having the functional constraint of a less efficient vascular system, as a mechanism that inhibits conifer competitiveness versus angiosperms on some sites (Bond, 1989; Midgley and Bond, 1991). This is especially critical in the juvenile stage because conifers have low maximum rates of conductance or photosynthesis, meaning that they have slow early growth rates (Midgley *et al.* 1995). Bond (1989) and Midgley *et al.* (1995) hypothesise that this means they will be prone to be out-competed by angiosperms where conditions are conducive for rapid growth, or where disturbance return time is less than the

conifer age to maturity, meaning that conifers should be restricted to areas where angiosperm vigour is reduced. Some evidence of this comes from seedling growth trials in south Westland, where few naturally establishing *Dacrydium* seedlings after logging disturbance survived shading from fern competition (James, 1998). Planted seedlings grew taller and denser in unshaded situations, and once seedlings were able to outgrow the competing understorey vegetation in open situations, survival rates were over 85% after 17 years (James, 1998).

However, there is another alternative physiological explanation in attempting to explain lack of conifer recruitment on well drained sites which may be related to the poorly developed, root networks of conifer seedlings making them prone to desiccation. For example, Cameron (1963) found *Dacrydium* seedlings to be lacking a tap root or extensive lateral root system, and were therefore susceptible to drought. *Dacrydium cupressinum* saplings observed outside the plot in well drained areas were mainly confined to wet depressions such as uproot pits, their sporadic recruitment implying that they needed a 'window of opportunity' of wet microsites combined with a suitable large canopy opening on these otherwise drier sites (*cf* Lusk and Smith, 1998). In *Austrocedrus* forests in Patagonia, spring and summer drought limited initial seedling establishment and caused conifer seedling mortality on dry microsites (Villalba and Veblen, 1997). In the US, the conifers *Tsuga heterophylla* and *Abies amabilis* were prone to desiccation on well drained sites, these species used available soil moisture for growth but became highly stressed when water supply was exhausted (Livingston and Black, 1988). These authors found that the poor stomatal control of these conifers meant they were unable to prevent desiccation and mortality in the face of high evaporative demand, and they suggested putting available reserves into growth would be a successful strategy when moisture was not limited.

Clearly, further studies on drought versus competition hypotheses needs to be done on seedling and sapling dynamics in these mixed north Westland forests to further understand species' distributions. There are additional physiological considerations that would also need testing between the species that may also have an influence on stand structure, in terms of relative competitive abilities to acquire nutrients in the seedling/sapling establishment phase. Conifers and hardwoods have different nutrient acquiring characteristics via their different mycorrhizal associations to beech (Baylis, 1980; Francis and Read, 1994). Conifers and hardwoods have vesicular-arbuscular (V-A) mycorrhizae, which live in or on plant roots (endomycorrhizae). The advantage of this system is that the root networks of the plant do not have to be so extensive, as the hyphae can extend out great distances and mobilise nutrients beyond the immediate root zone (Fitter, 1997). In

contrast, beech have ectomycorrhizal associations with a quite different set of fungi, which do not penetrate the cell walls but form a sheath around the roots (Fitter, 1997). Ectomycorrhizal associations may be better at accessing nutrients contained in organic resources (Francis and Read, 1994), and in drier forest floor microsites in well-drained areas with abundant organic matter, one hypothesis is beech seedlings could possibly be favoured in gathering resources, over the conifers with their more poorly developed root networks.

4.4 Patterns of stand development

Poorly drained

The dynamics of stand composition change in plots A and B were influenced by a range of different disturbances that varied in type and extent, inferred from stand structure, spatial patterns and tree ring releases. These patterns suggest large, infrequent disturbances that opened large discrete areas of the canopy allowed for the even-aged recruitment of *Dacrydium*, which appeared highly dependent on these sorts of infrequent occurrences for successful establishment along with the other conifers *L. bidwillii* and *P. hallii* in the very poorly drained soils. *Dacrydium cupressinum* populations comprising even-aged, spatially discrete patches with a distinct upsurge of establishment followed by declining numbers of stems in younger age classes, reflect the general pattern of stand development following large disturbances described by Oliver (1981). This model of stand development describes stands going through several distinct phases following large, infrequent disturbances: *stem initiation* with synchronous regeneration of large numbers of stems, followed by *stem exclusion* as thinning of stems occurs from competition, *stem reinitiation* from establishment in canopy gaps as stems age and die, then *old growth* where there is a mosaic of age and size classes and tiers in the stand. Most trees that establish after these major events typically do not face competition when they regenerate into the large canopy openings from surrounding canopy trees as they would in smaller gaps (Oliver, 1981), although they can face intraspecific competition from their peers in the initiation and stem-exclusion phases. In this respect, the establishment of conifers in plot A c. 275-300 yrs ago, probably reflects regeneration after a major disturbance. Subsequent smaller openings were primarily captured by *Dacrycarpus*, *N. menziesii*, *N. fusca* and *E. hookerianus* as the stand moved into the old-growth phase, with the beech becoming more prolific as site conditions were ameliorated by the development of suitable elevated microsites.

The larger poorly drained plot B is currently in the old-growth phase. Over the last 900 yrs, there have been several infrequent, large disturbances that produced sufficiently large openings to which *Dacrydium* responded in discrete patches. The last major one was between 375-425 yrs ago, to which *Dacrycarpus* and *N. menziesii* also responded. Subsequent canopy openings have been captured by two different sets of species but not *Dacrydium*. From 100-300 yrs ago, *N. menziesii*, *W. racemosa* and *Q. acutifolia* dominated in small gaps resulting from the death of one or a few dead standing trees. In a series of gaps created by uprooting in the last 100 yrs, particularly of large senescent conifers around the centre of the plot, *Dacrycarpus* and *E. hookerianus* were recruited into the canopy on forest floor sites, and *N. fusca* and *N. menziesii* on elevated sites. In the absence of major disturbances, where individual tree death was the main form of gap formation, population structures and species' regeneration patterns suggest the beech and hardwoods would become more abundant, and *Dacrydium* less so as mortality thins out the large *Dacrydium* patches.

Well drained

On well drained microsites and in the well drained plot, there were no differences in microsite preferences between the beeches and hardwoods that could explain coexistence. Instead, differences in relative shade tolerances suggested gap partitioning after disturbances as an explanation for coexistence of beeches and hardwoods. For example, in the well drained plot, *N. fusca* trees were almost exclusively found in the uprooted area following blowdown. *Nothofagus menziesii* trees were located together with *N. fusca* in the uproot area, and also around the edges of the uprooted area amongst surviving trees in gaps created by dead standing trees. *Quintinia acutifolia* stems were situated amongst the area of dead standing trees and mostly around the edges of the uprooted area, whereas *W. racemosa* stems were throughout the plot in a range of small and large canopy openings suggesting an order of shade tolerance: *N. fusca* < *N. menziesii* < *Q. acutifolia* < *W. racemosa*. In the absence of large disturbances such as blowdown, population structures and species regeneration patterns suggest that the hardwoods and *N. menziesii* would become more dominant and *N. fusca* less so. The tight age clustering of *N. fusca* following large-scale blowdown reflects their relative shade-intolerance, similar patterns of shade-intolerant species that establish in large gaps in mixed US forests include black cherry (*Prunus serotina*) and yellow poplar (*Liriodendron tulipifera*) (Poulson and Platt, 1989). These are species that typically do not regenerate under close canopy and need adequate

light caused by multiple treefalls to allow recruitment of new individuals (Oliver and Stephens, 1977; Poulson and Platt, 1989).

In poorly drained plot B, differences in relative shade-tolerance between the beeches could explain why *N. menziesii* frequently captured small gaps on elevated microsites. In nearby beech-dominated Maruia Valley (c. 30 km N), there were no microsite differences between *N. fusca* and *N. menziesii* that could explain coexistence in forests dominated by frequent small-scale disturbances (Stewart and Rose, 1990). Instead, differences in life histories influenced the relative recruitment success of these species, with *N. menziesii* more shade tolerant and with a greater ability to survive periods of suppression than *N. fusca* which exhibited a faster growth rate in the centre of canopy openings, greater juvenile mortality, greater adult survivorship and longevity (Runkle and Stewart, 1989; Stewart and Rose, 1990; Stewart *et al.* 1991; Runkle *et al.* 1995; Runkle *et al.* 1997; Stewart, 1997).

Following blow down c. 100 yrs ago in the well drained plot, the differential damage to one side of the plot compared with the other may be a function of variability of stand size and age at the time. Several *N. fusca* trees uprooted in the right of the plot exceeded 100 cm dbh and it appears that *N. fusca* stems in this side of the plot were generally larger and older than the other side of the plot. Other studies have shown that factors such as stand age, size, architecture and/or composition can influence the susceptibility of *Nothofagus* stands to wind damage (Jane, 1986; Rebertus *et al.* 1997).

Disturbances in Westland

One of the intriguing patterns that emerged from these plots is why, despite widespread establishment of beech and *Dacrycarpus* stems in the last 50-100 yrs, there are few *Dacrydium* of similar age. Disturbance history is considered influential in understanding variations in tree population age structures, particularly in understanding the different conditions that result after different disturbances (Lorimer, 1985; Foster, 1988a). Natural disturbances are frequent in Westland with a number of different types of regional disturbance events recorded or reconstructed in the region over the last 400 yrs (Hutchinson, 1928; Foster, 1931; Moorhouse, 1939; Benn, 1990, 1992; Wells *et al.* 1998; Wells *et al.* 1999).

There have been many storms with gale force winds and flooding recorded in most decades in north Westland over the last 150 yrs (Benn, 1990). Storms not only cause extensive blowdown, but also defoliation and bole snapping of individual trees. A storm recorded as causing massive mortality in *N. fusca*/*N. menziesii* forests in the Reefton

district c. 40 km from Mt Harata in 1898 (Roche, 1929; Foster, 1931; Moorhouse, 1939) was suggested as a cause of growth release responses in the nearby Maruia Valley around 80-95 yrs ago (Stewart *et al.* 1991) and in other north Westland sites (Vittoz *et al.* 2000; Cullen, pers comm). Other large storms with gale force winds were frequently recorded between 1905-1913 (Benn, 1990), including one major storm in 1912 that caused widespread blowdown in the nearby Waipuna Valley only 5 km from the study site (Ken Ferguson, pers comm). One observer, Roche (1929), found a 80 hectare terrace stand of *N. fusca* near Ikamatua in 1922 (c. 20 km west from study site) had been windthrown in a NW direction sometime in the recent past from winds emanating from the SE, the same direction as those trees windthrown in the well drained plot. June (1982) also noted that areas of historic windthrow faced the same NW direction. In south Westland terrace forests, the largest areas of windthrow have also been recorded as being on flat terrace sites (Foweraker and Hutchinson, 1934; Six Dijkstra *et al.* 1985).

Drought is also another factor causing mortality in trees in north Westland, Stewart *et al.* (1991) reported 1930 was the driest year on record this century at Reefton followed by below average rainfall for 6 of the next 8 years. Insect attacks causing mortality in drought stressed trees have been noted in the nearby Maruia Valley in the 1970s, particularly affecting *N. fusca* trees (Milligan, 1974, 1979; Hosking and Kershaw, 1985). However, drought is more likely to result in gaps created by individual trees dying standing in the well-drained silt loams, a pattern of tree death that appears to favour the more shade-tolerant species.

Earthquakes have recently been shown to result in episodic, synchronous multiple stand establishment throughout north and south Westland, with a consistent pattern of conifer stand initiation from a number of studies, commencing 280 and 380 yrs ago (Wells 1998; Wells *et al.* 1998). Three catastrophic Alpine Fault earthquakes of $M_w 8 \pm 0.25$ have been reconstructed in the last 600 yrs; these events ruptured along > 400 km of the fault and resulted in multiple stand regeneration in Westland (Wells *et al.* 1999). These events occurred about 280 yrs, 370 yrs and around 540 yrs ago (Wells *et al.* 1999). No movement of the central Alpine Fault has been recorded in European settlement times over past 150 yrs (Adams, 1980; Benn, 1992; Yetton *et al.* 1998). Mt Harata is within 15 km of the Alpine Fault and is in the most intense isoseismal shaking zone (Yetton *et al.* 1998) and it is likely it received severe impacts during past earthquakes. Other studies have shown that stands located near the epicentre of earthquakes are subject to the greatest impacts (Kitzberger *et al.* 1995; Allen *et al.* 1999).

4.5 Summary

In summary, species recruitment across the drainage gradient appears to be able to be explained by the interactions of three key factors:

1. Underlying drainage.
2. Extent of disturbances.
3. Types and availability of microsites created by disturbances.

It appears that underlying drainage gradient influenced species composition along the drainage gradient, and disturbance history regulated species relative abundances.

On well drained soils in plot C, the lack of suitable wet microsites and/ or competition from angiosperms may explain the scarcity of conifers despite large openings created by blowdown and frequent smaller disturbances.

In contrast, species abundance and diversity increases on poorly drained sites due to the mosaic of elevated and non-elevated micro-topography. This heterogeneity allowed conifers and *E. hookerianus* to successfully establish on non-elevated sites, and beeches and other hardwoods on elevated sites. The nature of canopy damage and size of the canopy opening was important in influencing which species can reach the canopy on these different microsites depending on the relative shade-tolerances of individual species. The type and availability of microsites left after different forms of tree death, was also important in creating this microsite heterogeneity.

Therefore, two questions emerge from the patterns observed in these three plots and are addressed in the next section at a larger landform (*between-stand*) scale:

1. How general are those patterns across the terrace and how extensive on soils of different drainage are the events identified in all three plots?
2. What is driving these patterns of species recruitment in terms of the relative importance of disturbance type and extent in influencing coexistence on soils of different drainage and development?

CHAPTER TWO

Effects of different large, infrequent disturbances on coexistence in mixed conifer/ beech/ hardwood forest, north Westland, Aotearoa/ New Zealand.

Abstract

Across the forest landscape, species distributions are influenced by environmental gradients and the effects of complex disturbance regimes at different points along these gradients. I studied how different types of large, infrequent disturbances (wind, earthquakes) interacted with variation in underlying soil drainage conditions to create differential opportunities for species regeneration and coexistence in a mixed conifer/ beech/ hardwood forest, north Westland, Aotearoa/ New Zealand. I selected a large (0.8 km²) lowland postglacial terrace which had a strong gradient in drainage and soil development, with marked shifts in forest structure and species composition along it. To understand the complex effects of the different disturbances, I reconstructed stand history from age structures and microsite establishment preferences in 20 circular plots (>1250 m²). Ordination of species age structure was used to group together plots that showed a similar age structure and species composition, and to infer the extent of establishment following major disturbance across the terrace.

Different large, infrequent disturbances resulted in extensive regeneration of the five main overstorey species 75-100 yrs ago which was attributed to (a) storm (s), and 200-275 yrs and 350-450 yrs ago, which were probably Alpine Fault earthquakes. These disturbances had different effects on species' establishment across the terrace, due to underlying drainage, variation in impacts of disturbances at different points along the gradient, and the availability of different microsites.

On well drained sites, species' distributions were influenced by drainage despite the heterogeneity of establishment opportunities created by earthquakes, storms and more frequent small-scale tree death. Differential response to variation in the size of canopy openings at different times regulated the abundance of the canopy beeches (*Nothofagus fusca* and *N. menziesii*) and the subcanopy hardwood (*Weinmannia racemosa*). The regeneration of *N. fusca* primarily occurred in large even-aged cohorts in response to the major disturbances, whereas the other species were also recruited into the overstorey after more frequent less extensive disturbances.

The same disturbances resulted in different species establishing in different parts of the terrace. Following the earthquake c. 280 yrs ago, the beeches and hardwoods regenerated on well drained sites, whereas the conifers *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* and the beech *N. menziesii* regenerated in poorly drained areas. In the poorly drained plots, species partitioned microsites based on drainage with the beeches and hardwoods on better-drained elevated sites (logs and mounds) and the conifers on forest floor sites.

Different suites of species regenerated at different times on the same sites in response to the large, infrequent disturbances. Following the earthquake c. 280 yrs ago, the conifers and *N. menziesii* regenerated on poorly drained sites; in contrast following the storm c. 100 yrs ago mainly *N. fusca*, *Dacrycarpus*, *N. menziesii* responded. This was linked to the relative extents of the different events. The extent of the earthquake impacts was found to be an important factor in enabling the widespread establishment of the conifer *Dacrydium* in poorly drained areas. The earthquake c. 280 yrs ago affected much of the terrace. Trees in the *Dacrydium* cohorts were found in large patches (often > 1000 m²) with few or no interspersed surviving trees, suggesting establishment occurred in extensive, continuous canopy openings, on unstable, saturated peats prone to liquefaction. In contrast, the effects of the storm c. 100 yrs ago varied on different surfaces of different drainage, with extensive windthrow on well drained soils around the terrace edges and more patchy smaller-scale damage in the poorly drained areas. Few *Dacrydium* successfully regenerated after the storm, compared with establishment of the other conifer *Dacrycarpus* together with the beeches in smaller patches amongst trees that survived this event.

Therefore, the underlying edaphic conditions influence species composition along the drainage gradient and disturbance history regulates the relative abundances of species. These results also suggest the 'two-component' coexistence model of conifers regenerating after large disturbances, and beeches and hardwoods after smaller disturbances, can be further developed by examining the type and extent of different large, infrequent disturbances in creating establishment conditions suitable for different species, and taking into account the variable influence of disturbances along underlying environmental gradients.

Keywords:

Disturbance, coexistence, beech, conifer, hardwoods, earthquakes, wind, lowland forest, drainage gradient, regeneration niche, Alpine Fault, Westland, Aotearoa/ New Zealand.

Nomenclature:

Allan (1961) with changes suggested in Connor and Edgar (1987) and Hill and Jordan (1993).

1. INTRODUCTION

1.1 Landscape disturbance dynamics - coexistence and succession

The forest landscape has been called a 'shifting mosaic' composed of different age and size patches and successional status formed by disturbances (Heinselman, 1973; Bormann and Likens, 1979; Shugart, 1984; Runkle, 1982). The development of the non-equilibrium patch dynamics perspective in forest ecology has emphasised the importance of these natural disturbance regimes on landscape diversity patterns (Pickett and Thompson, 1978; Sousa, 1984; Pickett and White, 1985; Veblen *et al.* 1996b).

Much research into patch dynamics has focussed on mechanisms of coexistence between tree species in small scale treefall gaps (see review in *Ecology* 1989 vol 70: pp 535-576; Hubbell *et al.* 1999). However, emphasis has also been recently placed on the importance of large, infrequent disturbances (LIDs - after Turner and Dale, 1998) such as fire, floods, earthquakes and vulcanism in causing extensive mortality of pre-existing vegetation, and acting as dominant forces in structuring subsequent and long term composition, and ecosystem processes on the forest landscape (Veblen and Ashton, 1978; White, 1979; Veblen and Lorenz, 1987; Turner and Dale, 1998; Foster *et al.* 1998; Turner *et al.* 1998; Romme *et al.* 1998; Wells, 1998).

These large disturbances may be qualitatively different from smaller, more frequent disturbances as they can trip thresholds that redirect succession and create opportunities for changes in species composition to occur (Romme *et al.* 1998). These are particularly important for providing periodic establishment of relatively shade-intolerant species (Clayton-Greene 1977; Veblen and Stewart, 1982; Ogden and Stewart, 1995). Succession following large disturbances can be influenced by various factors such as survival of existing propagules and individuals after these episodes (the so-called 'residuals'), colonisation (e.g., time of arrival and distance to a site), dispersal limitation, and edaphic conditions (Turner *et al.* 1998). Moreover, species life-history attributes are interconnected with the disturbance regime and may have evolved or adapted in response to these disturbances (see Pickett and White, 1985, for synthesis; Lusk and Smith, 1998).

The variation in the intensity of disturbance impacts within and across landforms creates a spatially heterogeneous mosaic of opportunities for succession (Foster, 1988b; Duncan, 1993; Turner *et al.* 1998). The biological legacies left in terms of physical structures, such as new surface formation, windthrow mounds, soil churning, and coarse woody debris, all influence opportunities for different species establishment (Harmon *et al.*

1986; Duncan, 1993; Foster *et al.* 1998; Wells, 1998). Species can coexist by differential response to the environmental variation created by these disturbances in terms of differences in the regeneration niche (*sensu* Grubb, 1977), by partitioning different microsites created by the death of trees (Beatty, 1984; Duncan, 1993; Duncan *et al.* 1998), or differences in light availability (gap partitioning) (Veblen, 1985; Whitmore, 1989; Stewart *et al.* 1991; Runkle *et al.* 1995).

The landscape patterns of damage that result from large disturbances are controlled by the interactions between these disturbances, variations in impacts across gradients in abiotic conditions such as topography and soils (Romme and Knight, 1981, Foster, 1988a, 1988b; Bellingham, 1991), and composition and structure of the pre-existing vegetation (Foster, 1988b; Veblen *et al.* 1992; Foster *et al.* 1998). Species' distributions along broad environmental gradients have been described along landform and edaphic gradients (e.g., Whittaker, 1956; Wardle, 1984; Stewart *et al.* 1993; Clark *et al.* 1998), but to more fully understand the distribution of species along environmental gradients, disturbance effects from different types of disturbance must be considered (Harmon *et al.* 1983; Foster, 1988a, 1988b; Ishizuka and Sugawara, 1989; Veblen *et al.* 1992; Crawley, 1997).

There is growing recognition that different types of large disturbances vary in their importance spatially across the landscape and that species respond differently to these disturbances along environmental gradients (Oliver *et al.* 1981; Romme and Knight, 1981; Harmon *et al.* 1983; Veblen *et al.* 1992; Rebertus *et al.* 1997). Species can also respond differently to these large, infrequent disturbances depending on the presence or absence of other species at different points along an environmental gradient (Veblen, 1989).

1.2 Large, infrequent disturbances and vegetation dynamics in mixed-species forests of Aotearoa

In Aotearoa/New Zealand, catastrophic influences of vulcanism (McKelvey, 1963; Ogden *et al.* 1993), fire (Ogden *et al.* 1998), flooding (Wardle, 1974; Duncan, 1993), storms (Hutchinson, 1928; Roche 1929; Foster, 1931; Wardle, 1984; Jane, 1986), and earthquakes (Cornere, 1992; Wells, 1998; Wells *et al.* 1999) have had extensive long term impacts across the landscape on vegetation patterns (Lusk and Ogden, 1992; Ogden and Stewart, 1995).

These large disturbances have impacted areas dominated by all of the three main compositional forest types of Aotearoa, these being conifer, beech and non-beech (broadleaved) hardwoods (Wardle, 1991). There has been much research on the dynamics

of pure beech and beech/hardwood forests (see Wardle, 1984 and Ogden *et al* 1996 for summaries), and on conifer or conifer/hardwood forests excluding beech (Norton *et al.* 1988; Ogden and Stewart, 1995). Many studies have demonstrated the importance of catastrophic disturbance events in structuring these forest stands and maintaining the dominance of certain canopy species (e.g., Norton, 1983*b*; Duncan, 1993; Wells, 1998). However, research on the dynamics of forests where these three groups occur together as mixed conifer/beech/hardwood forest has been limited (Veblen and Stewart, 1981; June, 1982; Stewart 1986; Allen, 1988; Rogers, 1989; Lusk and Smith, 1998), especially in relation to the role of large disturbances in determining the composition and structure of stands. This is despite the fact that such forests presently cover over 1 million ha of Aotearoa (Wardle, 1984; Newsome, 1987).

Historically, the dynamics of these mixed stands were assumed to be unstable with the more evolutionarily advanced beech and hardwoods suppressing and replacing the conifers (Robbins, 1962; Holloway, 1954; Wardle, 1963; June, 1982). More recently, a 'two-component' system enabling coexistence has been proposed, in which long-lived conifers are periodically recruited in response to infrequent, stand-destroying disturbances, and angiosperms are recruited at more frequent intervals (Veblen and Stewart, 1982; Ogden and Stewart, 1995; Enright and Ogden, 1995; Ogden *et al.* 1996).

In north Westland, Aotearoa, large areas of mixed conifer/beech/hardwood forest are present, in combination with clear evidence of catastrophic impacts on the forests of the region. Storms and earthquakes are key disturbances in the Westland forest landscape, in providing much of the environmental variation to which species respond differentially (Norton *et al.* 1988; Stewart *et al.* 1991; Duncan, 1993; Wells, 1998). Recorded historical storms over the past 150 yrs have been frequent in Westland (Roche, 1922; Hutchinson, 1928; Foster, 1931; June, 1982; Benn, 1990; Stewart *et al.* 1991). These tend to be localised in their effects, for example, a storm in 1898 blew down large areas of beech forest around Reefton in north Westland (Foster, 1931). In comparison, Alpine Fault earthquakes, which occurred around 1630 and 1717, resulted in more regional patterns of damage and widespread, synchronous species establishment across a range of landforms (Yetton *et al.* 1998; Wells *et al.* 1998; Wells *et al.* 1999).

The recruitment dynamics, where the widespread abundant emergent conifers *Dacrydium cupressinum* (rimu), *Dacrycarpus dacrydioides* (kahikatea) (both Podocarpaceae) and the similarly common canopy beech *Nothofagus fusca* (red beech) and *N. menziesii* (silver beech - Nothofagaceae) co-occur in lowland and mid altitudes of the region, are poorly understood, despite their ecological, conservation and management

significance. The influence of different types of large, infrequent disturbances in mixed north Westland forests offers an opportunity to test the two-component idea, to examine whether species respond differently to different types of these disturbances; and, if so, to determine how species recruitment patterns reflect qualitative differences in disturbance impacts and regeneration conditions at different times that enable different conifers, beeches and hardwoods to coexist.

1.3 Background to mixed forest regeneration in north Westland

Drainage is a key environmental variable influencing forest patterns in north Westland (Mew, 1975; Ross *et al.* 1977; Stewart *et al.* 1993). In chapter 1 of this study, I examined regeneration patterns along a drainage and soil gradient on a postglacial terrace at Mt Harata forested with mixed stands of conifer, beech and hardwood trees. I found the underlying edaphic conditions influenced species' composition along the drainage gradient and disturbance history regulated the relative abundances of species. Regeneration of the groups of species varied with drainage conditions, but also with different disturbance types and intensities at individual sites where drainage was constant over time.

In a well drained stand, conifers were scarce and their recruitment was sporadic, while gap partitioning for light between beeches and hardwoods enabled coexistence in response to a range of different sized openings resulting from disturbances of different extent. In poorly drained areas, *Dacrydium*, *Dacrycarpus* and *N. fusca* showed discontinuities in age structures suggesting periodic recruitment in response to infrequent disturbances, whereas *N. menziesii* and the hardwood *Weinmannia racemosa* (kamahi - Cunoniaceae) had more all-aged structures. Species coexisted by partitioning the light environment with respect to the amount of overhead cover, and species also partitioned microsites based on drainage characteristics, with conifers on forest floor sites and beeches and hardwoods mainly on better drained elevated mounds and logs.

Synchronous pulses of recruitment of different conifer and beech species that occurred in well drained and poorly drained plots also suggested large disturbances had catastrophically impacted across a large portion of the landscape at intervals of around 100-200 years. Furthermore, regeneration of *Dacrydium* following some of these disturbances but not others suggests that different types of large disturbances have resulted in different sets of conditions suitable for regeneration.

1.4 Study Aims

In light of these findings, the aim of this study was to examine and test whether the patterns of disturbance and regeneration identified at a within-stand scale (chapter 1) reflected processes that were operating at a whole landform (between-stand) scale across an entire 0.8 km² post-glacial terrace. Specifically, the objectives of this study were to:

1. Reconstruct and examine the nature and spatial extent of large, infrequent disturbances across the entire terrace, and examine their impacts to the forest on soils of different drainage.
2. Understand how the conditions created by disturbances of different type and extent influenced the compositional variation and coexistence of species across the terrace gradient in drainage and soil development.

2. METHODS

2.1 Site selection

Mount Harata, in north Westland, South Island, Aotearoa/New Zealand (42° 22' S, 171° 51' E) is a granitic dome located in the Upper Grey River Valley c. 15 km from the Alpine Fault and c. 30 km south of Reefton (Stewart *et al.* 1993, see chapter 1). Rainfall at the site is likely to be around 2500 mm/annum (Stewart *et al.* 1993).

The lowland forests of Mt Harata contain a high diversity of tree species where the beech dominated forests of the Maruia Valley in the north come together with the conifer/hardwood forests that dominate the post-glacial outwash surfaces and floodplains of south Westland. The large Otiran post-glacial terrace where plots were placed in chapter 1 was extensive enough to be suitable for examining landform processes in this chapter. There are at least eight conifer, three beech, and three main non-beech hardwood tree species on the terrace (Stewart *et al.* 1993).

Structurally, the conifers *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* were commonly emergent over a canopy of beeches and a hardwood sub-canopy across the terrace. Beeches were very abundant in the canopy with *Nothofagus fusca* and *N. menziesii* found across the terrace on a range of soils, except in the most extremely poorly drained organic peats. I concentrated on the well and poorly drained sites dominated by red and silver beech. The subcanopy non-beech hardwood *Weinmannia racemosa* (kamahi) was selected for study as it was the most abundant hardwood species across the terrace.

The c. 1 km long by c. 800 m wide terrace has broad variation in soils at different stages of development and drainage status with a soil drainage gradient running from the terrace edge to the terrace centre (Stewart *et al.* 1993; see chapter 1). Soils of the terrace edges are predominantly well-drained yellow-brown earth soils (Ahaura series - Mew and Ross, 1980) and there are some associated patches of imperfectly- and poorly-drained gleyed yellow-brown earths. Toward the terrace centre, well-drained soils grade into poorly drained gley soils (Maimai series) and fluid mineral peats, and eventually into very poorly drained organic peats (Kini series) close to the terrace centre.

2.2 Plot selection

Six transect lines that run across the entire length of the terrace along a North-South axis placed by Stewart *et al.* (1993) in 1988-89, were relocated in 1998-1999. Spaced at 150 m intervals, these transect lines encompass the range of drainage variability across the

terrace, from well drained yellow-brown loams of the terrace edges to progressively more poorly drained peats towards the terrace centre (Table 2 in Stewart *et al.* 1993).

At 100 metre intervals along each transect, forest reconnaissance (RECCE) plots were placed by Stewart *et al.* (1993) to investigate changes in vegetation composition with respect to soil development and drainage. These RECCE plots had a subjective drainage assessment noted, in which soils had been grouped into classes from well-drained to very poorly drained. However, for this study I subdivided the plots into just two groups: well-drained and poorly drained soils. This was done for two main reasons. First, the boundaries between well-drained and poorly drained soils are generally abrupt and easily detected. However, the boundaries between poorly drained and very-poorly drained soils are difficult to detect, and soil drainage can switch between poorly drained and very poorly drained within metres depending on sub-surface topography. This makes it problematic to adequately delineate them in the field where they are complex. Second, differences in stand composition were marked between the well drained site (plot C in chapter 1) where conifers were almost absent, and the poorer drained plots (plots A and B) which had the same conifer and beech species in abundance. Therefore, I placed poorly drained and very poorly drained soils together into one category and well-drained in another.

Ten well-drained and 10 poorly drained RECCE plots were randomly selected. In each of these plots, I relocated the original central point that was marked with flagging tape. If the tape was not present, I estimated 100 m distance from the next closest marked RECCE point located along the same compass bearing, and matched the composition and height tiers of vegetation with that recorded on the original RECCE plot sheet. At this central point, I identified the nearest 15 trees (≥ 5 cm dbh) of each of the main conifer (*Dacrydium*, *Dacrycarpus*), beech (*N. fusca*, *N. menziesii*) and hardwood (*W. racemosa*) species up to a maximum radius of 20 m (1256 m²) in any direction in well-drained areas and 25 m (1963 m²) in poorly drained areas. This gave a maximum of 75 trees per plot (ie, up to a desired maximum of 15 for each species)

This sampling scheme represented a trade-off between the number of trees that could be physically aged of each species in each plot, and the extensive coverage gained from sampling 20 plots across the terrace to enable terrace-wide recruitment patterns to be detected. The maximum radius in the differently drained plot types was pre-selected after examining the density of species in the well drained and poorly drained plots in chapter 1.

2.3 Stand dynamics

In each plot, I measured the distance and compass bearing from the central point to the centre of the closest 15 trees of each species to calculate relative densities and basal area per hectare for each species, using the following equations.

$$F = \frac{\pi r^2}{10000}$$

Where F = is the conversion factor to convert the area represented by the distance to the farthest tree to a per hectare basis

r = distance to farthest tree in plot (m)

Density per hectare was calculated as $D = Fn$

where n = no. trees of the species measured in that plot.

Basal area per hectare was calculated as $B = Fa$

Where a = basal area of the species measured in that plot.

Each tree (≥ 5 cm dbh) was tagged and the diameter at breast height (1.4 m above ground level) was recorded. The largest stem of multi-stemmed trees was measured. Increment cores were extracted from the longest axis of each tree at 1 m above ground level. For the larger conifers and beeches, a second core was often taken to improve aging accuracy. Over 84 % of cores used for aging in this thesis either hit the pith or had arcs within 10 mm of the pith enabling robust interpretation of age data (see Fig. 2 in chapter 1). For cores that missed the pith but had visible arcs, Duncan's (1989) geometric model for calculating the missing portion was used. Trees that had arcs > 50 mm were rejected and ages were estimated from age/diameter relationships within each plot. For rotten cores that were short of the chronological centre, age was estimated by assuming the distance to the geometric centre also represented the distance to the chronological centre (Norton *et al.* 1987). Cores that were $< 70\%$ in length to the estimated geometric centre were rejected, and ages were estimated from age/ diameter relationships within each plot.

Cores were mounted, air-dried then sanded using progressively finer grained sandpaper so the growth rings were clearly visible (chapter 1). Rings were counted to ascertain ages, and as no correction was made for age to coring height, ages will be underestimates of the true age. Ages were grouped into 25 yr classes for the beeches and conifers. The clarity and distinction of rings varied in many *W. racemosa* cores, making it difficult to confidently place this species in 25 yr classes. Hence, to minimise possible

counting errors 50 yr age classes were considered more appropriate for analysing population structures.

2.4 Microsite patterns and soil drainage

To assess species establishment patterns, I recorded the microsite type (forest floor, mounds, stumps, logs) for each tree. Drainage in each plot was assessed by digging a hole within 3 m of the central point. Drainage and soil characteristics assessed in each of these plots matched the visual drainage assessment recorded in each of the original RECCE plots (Stewart *et al.* 1993).

2.5 Plot classification

The age-class data were analysed by ordination analysis to determine if there were differences in species composition and stand age structures between differently drained surfaces. This was done by comparing the frequency of stems in different age-classes for each species in every plot. The data were arranged in 18 age classes (25-74 yrs, 75-124 yrs...875-924 yrs) reflecting the range of cored tree ages across the terrace. A matrix of association (Bray-Curtis similarity measure) was constructed using the PATN programme (Belbin, 1989), and non-metric multi-dimensional scaling was performed to arrange these association measures in a two-dimensional graph format. Plots were then visually grouped on the graph on the basis of their spatial locations on the terrace and their similarity in species age-class distributions.

3. RESULTS

3.1 Combined age structures across the terrace

Tree ages were combined for each species in the poorly drained and well drained plots to see if there were corresponding periods of establishment that would suggest terrace wide disturbance events, that could explain the synchronous periods of regeneration between the plots identified in chapter 1. There were several clear peaks that coincided for different species both on poorly drained and well drained plots. These suggest at least three major periods of terrace wide regeneration of species in response to large disturbances: 75-100 yrs (**Event 1**) and 200-275 yrs (**Event 2**) and, in the poorly drained plots, 350-450 yrs ago (**Event 3**) (Fig. 1). These also coincide with three of the four major periods of establishment identified in chapter 1. There were also several peaks found only in the long-lived *Dacrydium*, between 500-650 yrs and 800-850 yrs; these broadly coincide with the two oldest *Dacrydium* cohorts identified in plot B in chapter 1, which probably also signified past extensive disturbance events.

The age-class peaks in the last 450 yrs coincide for different species but not all species show peaks at the same time. This suggests differential responses of species to different disturbances (Fig. 1). For example, the peak 75-100 yrs ago is evident in the *Dacrycarpus*, *N. fusca* and *N. menziesii* age structures but not in the *Dacrydium* age-class distribution, whereas the peak 250-275 yrs ago is more pronounced for *Dacrydium* than the other species (Fig. 1a).

Age-class distributions for each species differed across the drainage gradient, further suggesting that establishment patterns varied across the terrace after the same disturbance event. *Nothofagus fusca*, *N. menziesii*, and *W. racemosa* had a more pronounced peak in the 75-100 yrs class in well drained plots (Fig. 1), whereas *Dacrycarpus* had a coinciding pulse of establishment in only the poorly drained plots.

To investigate the extent of these disturbance events and to see whether there were groups of plots in close proximity with similar age structures, plots were grouped by ordination analysis of their species age structures and the results displayed in an ordination diagram (Fig. 2).

Poorly drained

Well drained

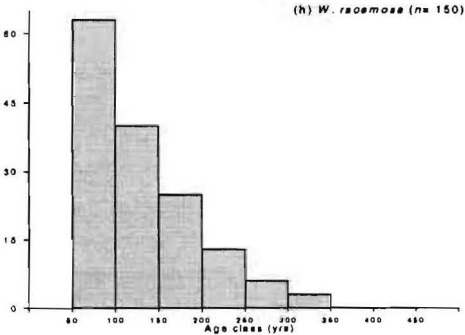
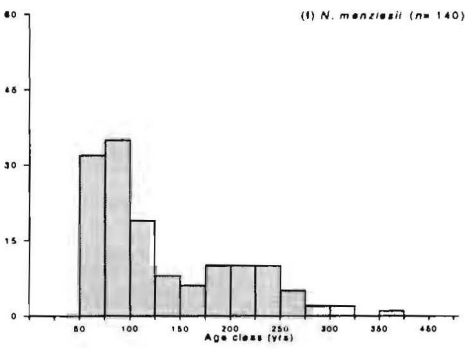
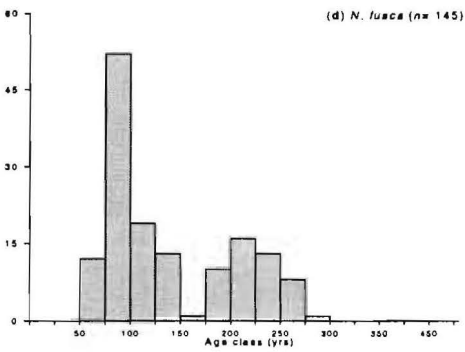
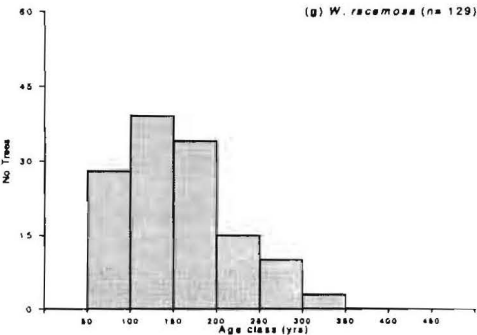
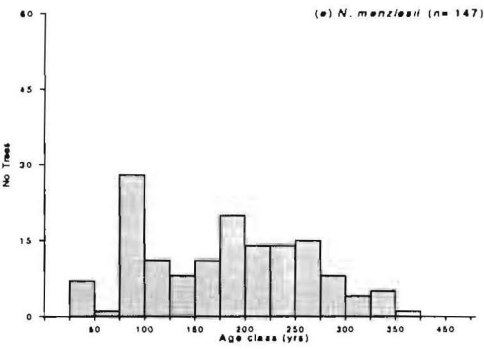
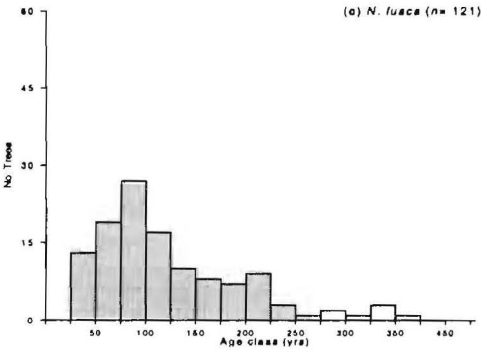
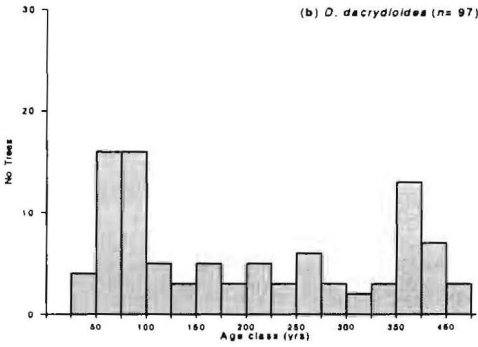
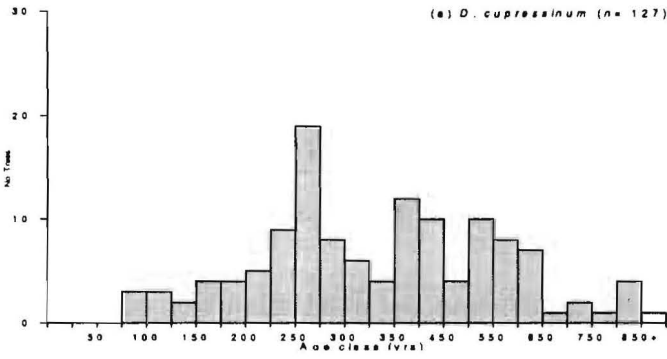


Figure 1: Age-class frequency distributions of all main canopy species (≥ 5 cm dbh) (n= 1056) from all combined circular terrace plots at Mt Harata on both **poorly drained** sites for (a) *Dacrydium* (b) *Dacrycarpus* (c) *N. fusca* (e) *N. menziesii* (g) *W. racemosa*; and **well drained** sites for (d) *N. fusca*, (f) *N. menziesii* and (h) *W. racemosa*.

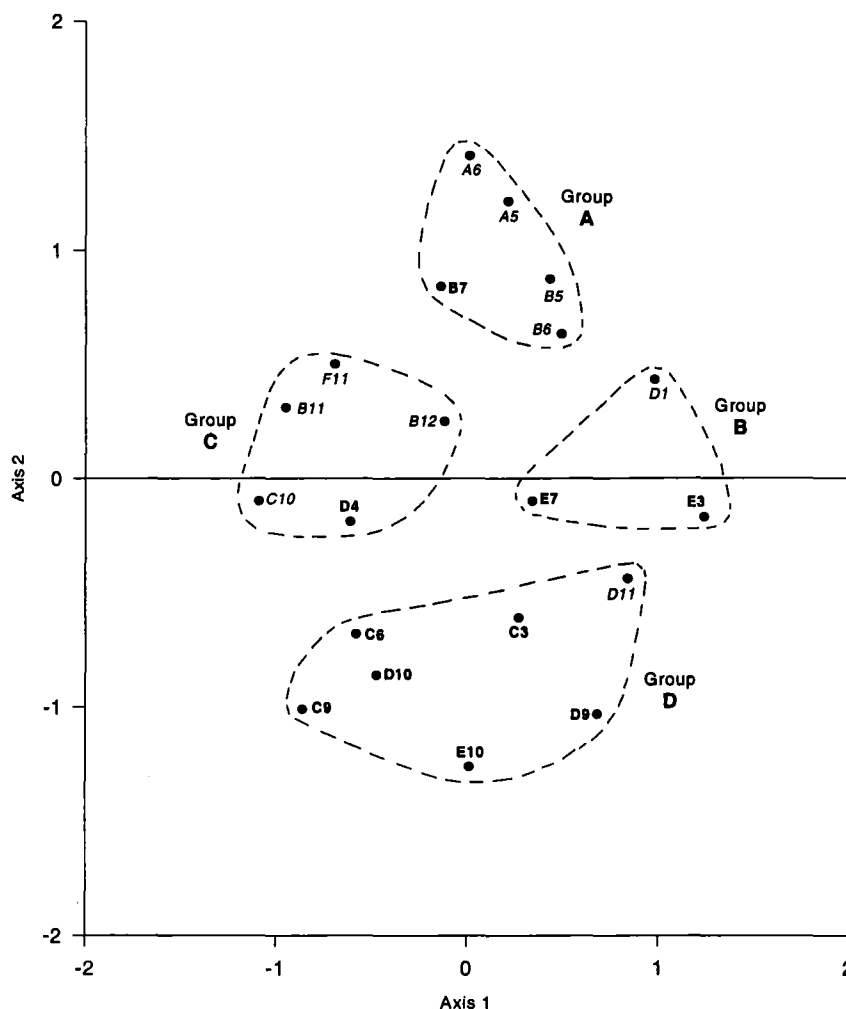


Figure 2: Ordination diagram showing plots grouped together that were similar in their age structures and spatial location. Well drained plots are in normal text and *italicised*, poorly drained plots are in **bold** ($n = 20$).

Four groups of plots were identified from the ordination diagram (Fig. 2). Group A contained plots that were characterised by a large synchronous pulse of *N. fusca*, *N. menziesii*, and *W. racemosa* establishment following **Event 1** (Fig. 3), and that were predominantly well-drained and located together in the north-west corner of the terrace (Fig. 4). Although the beeches and hardwoods in group A plots were similar in age and density, *N. fusca* was generally dominant in terms of basal area suggesting *N. fusca* was faster growing (Table 1).

Group B plots also had a synchronous pulse of *N. fusca* and particularly *N. menziesii* establishment after **Event 1**, but, in contrast to Group A, also had a small pulse of coinciding *Dacrycarpus* establishment (Fig. 3). These plots were located in the south-eastern and upper centre of the terrace and were mainly poorly drained (Fig. 4). The

conifers were a larger basal component of these mainly poorly drained plots, along with *N. menziesii* (Table 1).

In addition to **Event 1**, older disturbance events were evident in the age structures of the mainly well-drained Group **C** plots around the terrace edges, and in the mostly poorly drained Group **D** plots in the centre of the terrace (Figs. 3 and 4). Species basal area and density patterns reflected underlying drainage in these groups with decreasing *N. fusca* and *W. racemosa* and increasing conifers and *N. menziesii* as drainage deteriorated (Table 1), and was consistent with the broader compositional patterns related to drainage identified in chapter 1.

The large disturbance events had two main effects on species' establishment: a *drainage effect* and an *event effect*. In addition there were within-plot differences in regeneration patterns between species. From the grouped age-class distributions, underlying drainage (the *drainage effect*) resulted in different species establishing on soils of differing drainage after terrace-wide events (Fig. 3). For example, in the north-eastern corner of the terrace following **Event 2**, *D. cupressinum* and *Dacrycarpus* regeneration in Group **D** was effectively confined to the poorly drained plots (D9, D10, E10) with associated *N. menziesii*. In comparison, in the nearby well drained plots (D11 in Group **D** and F11 and C10 in Group **C**), a simultaneous pulse of *N. fusca*, *N. menziesii* and *W. racemosa* occurred (appendix- Figs. E1 and E3).

There were also clear differences in the extent and distribution of establishment following different terrace-wide disturbance events suggesting an *event effect*. This is most clearly seen in the differential regeneration patterns across the drainage gradient following the two most recent events. **Event 2** covered most of the terrace, with all species establishing at some point along the drainage gradient in groups **C** and **D**. In contrast, fewer species responded to **Event 1** and there were different scales of establishment within plots. Greater establishment occurred near the terrace edges, and on other soils that were predominantly well-drained. There were more trees that survived **Event 1** on well-drained sites towards the back of the terrace, and farther in towards the terrace centre where establishment was more patchy on the poorer drained soils after this event.

Evidence of establishment in response to **Event 2** in Group **A** plots could have been largely destroyed by the catastrophic effects of **Event 1** (Fig. 3). There were few older *N. fusca*, *N. menziesii* or *W. racemosa* found in the well drained plots of Group **A**, although the *Dacrydium* that survived **Event 1** in the one poorly drained Group **A** plot (B7) had established in response to **Event 2**. Establishment in response to **Event 2** also occurred close to Group **A** plots in nearby plot **C** (Fig. 4) where large synchronous pulses of beech

and hardwood establishment were identified in response to **Events 1** and **2** in the different halves of the plot (chapter 1).

The extent of the canopy openings created by **Event 2** compared with **Event 1** in the poorly drained plots could also provide an explanation for the regeneration of *Dacrydium* at some times but not others (Group **D**). The extensive establishment of all species (including *Dacrydium*) from **Event 2** across much of the terrace suggests this disturbance had catastrophic effects. In poorly drained plots where there was a single, even-aged cohort of *Dacrydium* after **Event 2** (e.g., plots D9, B7 and C3 and plot A in chapter 1), there were few older surviving trees (appendix - Fig. E3), suggesting that in these areas there were large continuous canopy openings that enabled successful *Dacrydium* regeneration. In contrast, the more patchy regeneration of species after **Event 1** in poorly drained areas amongst or close to emergent large diameter conifers, implies that there were more, smaller-scale openings in the canopy after this disturbance that *Dacrydium* was not able to take advantage of.

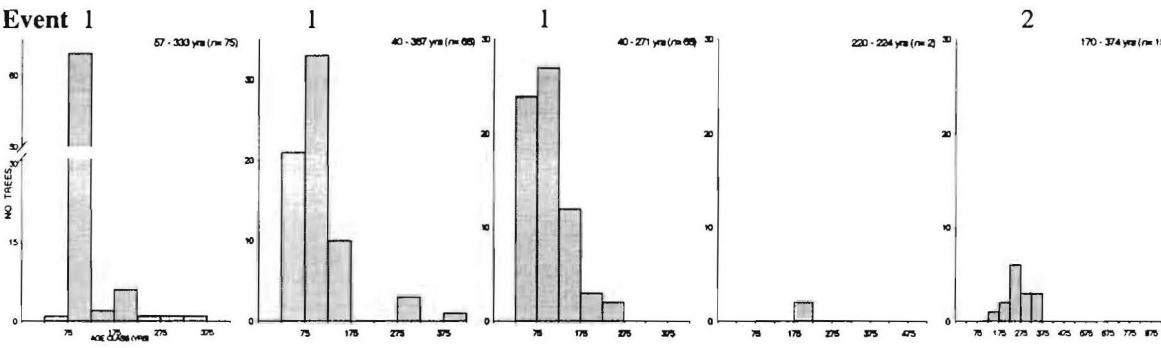
The extent of the canopy openings in individual poorly-drained plots after **Event 1** also appeared to be a critical factor in *N. fusca* regeneration in these plots. *N. fusca* stem density was high and it was the basal dominant in the poorly drained plots where there was a large even-age pulse of establishment after this event (B7 and E7 in groups **A** and **B** Table E1; appendix - Fig. E3). In contrast, *N. fusca* was low in basal area and density in group **D** plots where there was less establishment after **Event 1**, and in plots dominated by the other beech *N. menziesii* after **Event 2** such as in plots C6, C9 and D4.

There were also differences in the establishment patterns of different species within plots after the same event that reflected differences in their regeneration strategies. For example, in Group **A** following **Event 1**, *N. fusca* typically established in extensive even-aged groups on well drained plots (appendix - Figs. E1 and E2). This is evident in its basal dominance in well drained groups **A** and **C** (Table 1). In contrast, associated *N. menziesii* and *W. racemosa* had overall cohort ages that were more spread out reflecting more advanced regeneration and protracted establishment, as well as (in the case of *W. racemosa* in plots A5 and A6) the persistence of surviving stems after the disturbance.

N. fusca *N. menziesii* *W. racemosa* *Dacrycarpus* *Dacrydium*

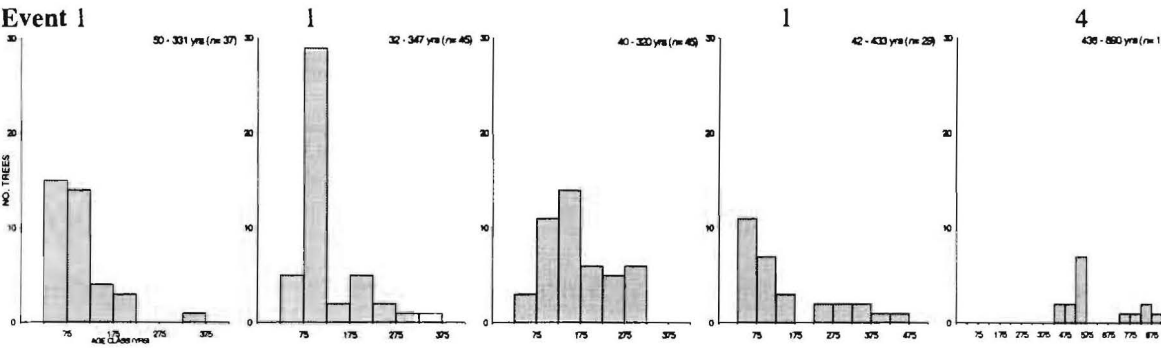
GROUP A

(4 Well drained plots, 1 Poorly drained)



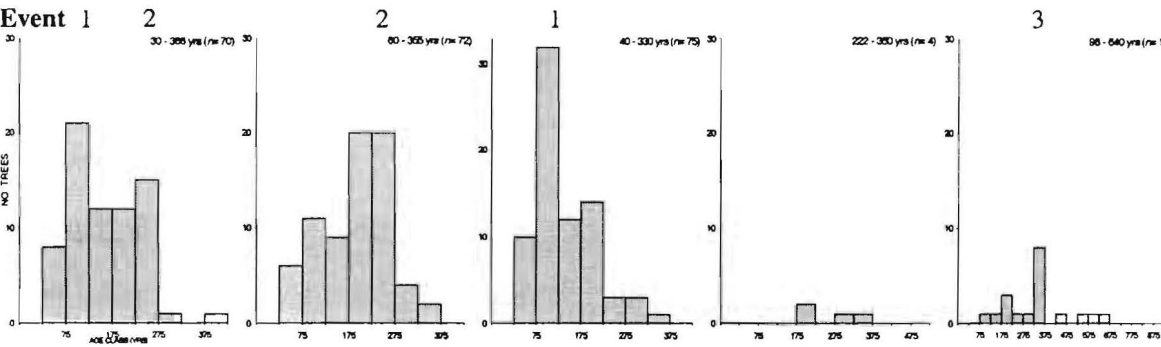
GROUP B

(1 Well drained plot, 2 Poorly drained)



GROUP C

(4 Well drained plots, 1 Poorly drained)



GROUP D

(1 Well drained plot, 6 Poorly drained)

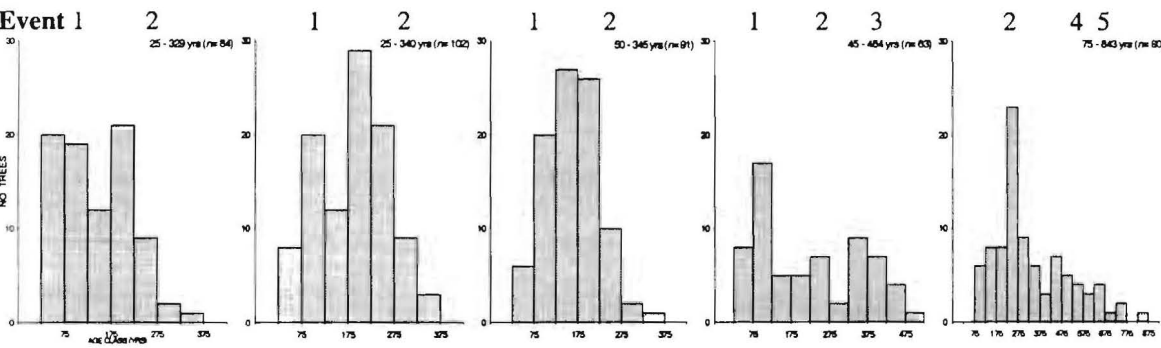


Figure 3: Age-class frequency distributions of combined tree ages for each of the 4 Plot Groups identified from Fig. 2 on a lowland post-glacial terrace, Mt Harata.

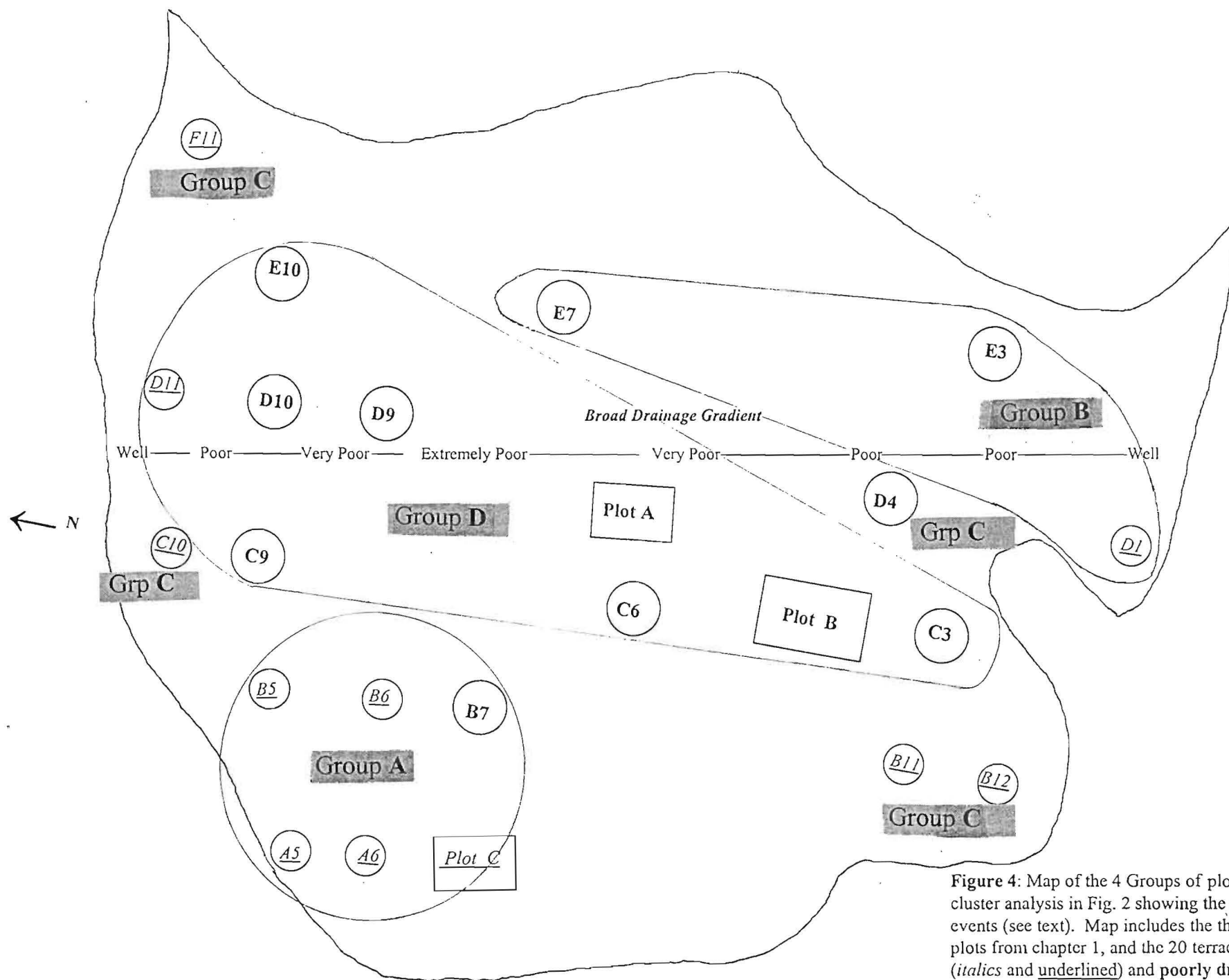


Figure 4: Map of the 4 Groups of plots identified from cluster analysis in Fig. 2 showing the extent of the disturbance events (see text). Map includes the three large permanent plots from chapter 1, and the 20 terrace well drained plots (*italics and underlined*) and **poorly drained plots** (**bold**) from chapter 2.

Table 1: Basal area (m²/ ha) of species and stem density per ha (≥ 5 cm dbh) in the 4 groups of plots across the terrace, Mt. Harata.

| Basal area | | | | | |
|-------------------|---------------------|-------------|------------|--------------|--------------------|
| Group | Species | mean | s.d | range | Freq/ plots |
| A | <i>N. fusca</i> | 40.3 | 10.6 | 24.3 - 53.2 | 5 |
| | <i>N. menziesii</i> | 6.5 | 3.1 | 3.1 - 10.6 | 5 |
| | <i>W. racemosa</i> | 7.9 | 4.3 | 1.2 - 12.0 | 5 |
| | <i>Dacrycarpus</i> | | | 1.3 | 1 |
| | <i>Dacrydium</i> | | | 14.4 | 1 |
| B | <i>N. fusca</i> | 24.0 | 16.6 | 4.9 - 34.1 | 3 |
| | <i>N. menziesii</i> | 16.3 | 9.6 | 7.1 - 26.2 | 3 |
| | <i>W. racemosa</i> | 5.3 | 3.4 | 3.3 - 9.2 | 3 |
| | <i>Dacrycarpus</i> | 8.8 | 3.3 | 6.5 - 11.1 | 2 |
| | <i>Dacrydium</i> | 18.6 | 9.6 | 11.8 - 25.4 | 2 |
| C | <i>N. fusca</i> | 27.6 | 13.3 | 7.4 - 38.9 | 5 |
| | <i>N. menziesii</i> | 12.7 | 6.4 | 5.7 - 22.5 | 5 |
| | <i>W. racemosa</i> | 8.7 | 3.2 | 5.8 - 13.5 | 5 |
| | <i>Dacrycarpus</i> | 3.4 | 1.1 | 2.6 - 4.2 | 2 |
| | <i>Dacrydium</i> | 4.6 | 5.4 | 0.4 - 12.6 | 5 |
| D | <i>N. fusca</i> | 14.2 | 12.7 | 4.5 - 38.8 | 7 |
| | <i>N. menziesii</i> | 14.8 | 14.2 | 1.8 - 42.3 | 7 |
| | <i>W. racemosa</i> | 5.3 | 4.1 | 0.1 - 13.4 | 7 |
| | <i>Dacrycarpus</i> | 8.8 | 6.3 | 0.8 - 18.7 | 6 |
| | <i>Dacrydium</i> | 16.4 | 8.4 | 1.6 - 28.6 | 7 |
| Density | | | | | |
| A | <i>N. fusca</i> | 264 | 68 | 204 - 381 | 5 |
| | <i>N. menziesii</i> | 210 | 94 | 68 - 306 | 5 |
| | <i>W. racemosa</i> | 390 | 231 | 57 - 677 | 5 |
| | <i>Dacrycarpus</i> | | | 14 | 1 |
| | <i>Dacrydium</i> | | | 126 | 1 |
| B | <i>N. fusca</i> | 234 | 190 | 37 - 417 | 3 |
| | <i>N. menziesii</i> | 368 | 193 | 237 - 590 | 3 |
| | <i>W. racemosa</i> | 199 | 164 | 100 - 388 | 3 |
| | <i>Dacrycarpus</i> | 97 | 1 | 96 - 97 | 2 |
| | <i>Dacrydium</i> | 45 | 13 | 36 - 54 | 2 |
| C | <i>N. fusca</i> | 160 | 59 | 81 - 247 | 5 |
| | <i>N. menziesii</i> | 167 | 80 | 96 - 301 | 5 |
| | <i>W. racemosa</i> | 422 | 210 | 210 - 765 | 5 |
| | <i>Dacrycarpus</i> | 16 | 1 | 15 - 16 | 2 |
| | <i>Dacrydium</i> | 31 | 13 | 20 - 54 | 5 |
| D | <i>N. fusca</i> | 85 | 44 | 39 - 163 | 7 |
| | <i>N. menziesii</i> | 171 | 97 | 61 - 337 | 7 |
| | <i>W. racemosa</i> | 187 | 144 | 16 - 413 | 7 |
| | <i>Dacrycarpus</i> | 60 | 19 | 31 - 85 | 6 |
| | <i>Dacrydium</i> | 97 | 48 | 38 - 189 | 7 |

Clearly, not all establishment on the terrace was a consequence of the large, infrequent disturbance events, and more frequent smaller-scale recruitment into the overstorey occurred at other times. Different species were recruited into the canopy in differing abundances during the periods of less extensive disturbances between the two most recent large events. Overall, the hardwood *W. racemosa* had more establishment during times of less extensive disturbances 100-200 yrs ago in the individual poorly drained plots than any other species (Fig. 1g; appendix - Fig. E3), and in the well drained plots *W. racemosa* had more patchy establishment after **Event 1** in fine-scale gaps or underneath the older surviving beech cohorts from **Event 2** (Fig. 1h; appendix - Fig. E1).

3.2 Microsite establishment patterns

There were clear differences between the conifers, beeches and hardwoods in their microsite preferences (Table 2). Almost all the conifers had established on forest floor sites in the poorly drained areas (groups **B** and **D**), whereas the beeches and hardwoods were mostly on elevated sites (mounds, logs and stumps). In the well drained areas, the beeches and hardwoods had established on a range of elevated and forest floor sites (groups **A** and **C**). Poorly drained forest floor sites typically had surface ponding and/ or saturated organic forest floor layers, and were different in drainage and soil characteristics to the drier litter layers of the forest floor sites in well drained loams (appendix for soil profile photos; Table E2).

Species that established at the same time in the poorly drained plots also showed differences in their microsite preferences, suggesting partitioning of establishment sites after disturbances. For example, following **Event 1** in groups **B** and **D**, *Dacrycarpus* established on forest floor sites whilst beeches commonly established on nearby elevated sites. Following **Event 2** in group **D**, the conifers established on forest floor sites whereas *N. menziesii* established on mounds and logs in the same plots.

On well-drained plots (groups **A** and **C**) there were no obvious differences in microsite preferences between the beeches and hardwoods that could explain coexistence (Table 2). However, in poorly drained plots, more *N. menziesii* had established on logs (both overall and in individual plots) compared with *N. fusca* and *W. racemosa*, suggesting this type of microsite favours its establishment (appendix - Table E3). In the poorly drained plot **B** in chapter 1, *N. menziesii* was able to colonise logs in greater abundance at an earlier stage of decay than *N. fusca* and *W. racemosa* (appendix - Table B2).

In the poorly drained plots, both *Dacrydium* and *Dacrycarpus* occupied forest floor sites and were able to coexist by differential establishment at different times, with *Dacrycarpus* having more frequent establishment (43 vs 7 trees) during the last 200 yrs.

Table 2: Comparison of no. trees (≥ 5 cm dbh) of species on different microsites in the 4 groups from Fig. 2, across the terrace, Mt Harata, north Westland.

| Group | Species | Mounds | Logs | Stumps | TOTAL Elevated | Forest Floor TOTAL Non Elevated |
|-------|---------------------|--------|------|--------|-------------------|---------------------------------------|
| A | <i>N. fusca</i> | 30 | 9 | 1 | 40 | 35 |
| | <i>N. menziesii</i> | 23 | 15 | 2 | 40 | 28 |
| | <i>W. racemosa</i> | 32 | 6 | 4 | 42 | 26 |
| | <i>Dacrycarpus</i> | | | | | 2 |
| | <i>Dacrydium</i> | | | | | 15 |
| B | <i>N. fusca</i> | 14 | 5 | 2 | 21 | 16 |
| | <i>N. menziesii</i> | 17 | 15 | 1 | 33 | 12 |
| | <i>W. racemosa</i> | 22 | 7 | 1 | 30 | 15 |
| | <i>Dacrycarpus</i> | | | | | 29 |
| | <i>Dacrydium</i> | | | | | 16 |
| C | <i>N. fusca</i> | 18 | 7 | 3 | 28 | 42 |
| | <i>N. menziesii</i> | 22 | 4 | | 26 | 46 |
| | <i>W. racemosa</i> | 29 | 5 | 2 | 36 | 39 |
| | <i>Dacrycarpus</i> | | | | | 4 |
| | <i>Dacrydium</i> | 1 | | | 1 | 18 |
| D | <i>N. fusca</i> | 66 | 6 | 2 | 74 | 10 |
| | <i>N. menziesii</i> | 51 | 38 | 1 | 90 | 12 |
| | <i>W. racemosa</i> | 62 | 7 | 2 | 71 | 20 |
| | <i>Dacrycarpus</i> | 2 | | | 2 | 96 |
| | <i>Dacrydium</i> | 1 | 2 | | 3 | 83 |

3.3 Probable causes of the large infrequent disturbance events

Event 1 was probably related to a powerful storm that caused extensive windthrow in plot C (refer to chapter 1). This agrees with the finding that **Event 1** was most extensive on the well-drained plots of Group A in the north-west corner of the terrace (Fig. 4). Large numbers of windthrown boles were observed in these plots, and the extensive even-sized beeches that dominated this area had established on the uprooted mounds and the adjacent forest floor. A storm is also an explanation consistent with the more patchy establishment of species in the poorly drained plots, particularly in poorly drained plot B in chapter 1 where large numbers of *N. fusca* (<100 yrs old) had established on uproot mounds, along with *Dacrycarpus* of similar age that had successfully colonised the disturbed edges of uproot pits.

Flooding can be rejected as a cause of **Event 2** due to a consistent lack of a distinct silt lamina in soils across the terrace, and the elevation of the terrace (< 120 m above the Grey River) means direct river flooding is improbable. There was also no evidence of extensive landsliding or fan deposits in the plots, suggesting that frequent and extensive landsliding is an unlikely cause of the forest history across the terrace (Fig. 4). Prehistorical earthquakes are an alternative plausible cause of widespread synchronous mortality across the terrace, resulting from intense shaking and soil liquefaction in the poorly drained waterlogged peats. Recent dating of large Alpine Fault earthquakes suggests these occurred at times that closely coincide with **Events 2** and **3** and possibly **Event 4** (Wells *et al.* 1999).

4. DISCUSSION

4.1 Identifying the nature of past disturbance events

Patterns of species establishment across the terrace reflect the strong influence of large, infrequent disturbances that struck the terrace at intervals of 100-200 yrs over the last few centuries. The disturbances that occurred 75-100 yrs, 200-275 yrs and 350-450 yrs ago, resulted in synchronous establishment of species across the terrace on differently drained soils. Results show species coexisted by differential establishment patterns following these different disturbances depending on the extent and intensity of the effects across the terrace, underlying drainage, and the consequent availability of suitable microsites for establishment. In this respect, patterns of species regeneration across the whole terrace landform reflected those identified in chapter 1.

Species age structures suggest that these disturbances had different impacts across the drainage gradient. The scale of species establishment across the terrace after the event 200-275 yrs ago suggests it had catastrophic effects in the poorly drained plots and also a number of well drained plots in group C, whereas fewer species established after the most recent event 75-100 yrs ago and establishment varied in different parts of the terrace and on soils that differed in drainage. This latter event resulted in extensive tree toppling in the well-drained terrace edges directly above the Grey River, with extensive even-aged cohorts establishing as a consequence; however, farther in towards the terrace edge many more trees survived and establishment was more patchy.

This suggests the two events were fundamentally different either in their intensity and/or their type. Good evidence exists for (a) storm (s) at the site 75-100 yrs ago from the

directional patterns of uprooting around the terrace edges, and the subsequent establishment on the uprooted mounds and adjacent forest floor sites of many similar aged trees. It appears the storm or a series of storms occurred some time between 1898-1912. Storms that caused extensive mortality in forests occurred periodically in the north Westland region between 1898-1912 (Foster, 1931; Moorhouse, 1939; June 1982; Benn, 1990). The 1898 storm that caused widespread *N. fusca* and *N. menziesii* mortality around Reefton c. 40 km from Mt. Harata (Foster, 1931) was suggested as a cause of growth release responses in the nearby Maruia Valley around 80-95 yrs ago (Stewart *et al.* 1991), and in other north Westland sites (Vittoz *et al.* 2000; Cullen, pers comm).

Variability in the impacts of the storm was evident in the more patchy establishment of species amongst many trees that survived in the terrace interior. Following the storm, gaps created by windfalls were mainly colonised by the conifer *Dacrycarpus dacrydioides* and the beeches on these poorly drained sites. However, patterns of stand establishment in the poorly drained interior 200-275 yrs ago were different, with large, discrete areas of *Dacrydium cupressinum* regeneration (often > 1000 m²) and few surviving trees, suggesting impacts were greater in these areas at that time. Widespread even-aged beech establishment also simultaneously occurred in the group C plots along the terrace edges in the south-west and north-east of the terrace suggesting disturbance impacts were also extensive on better-drained soils.

This suggests that either there was a storm of even greater magnitude that occurred 200-275 yrs ago that had similar effects across the whole terrace, or there is another cause. The timing of Alpine Fault earthquakes suggests an alternative mechanism and represents a more likely explanation of the terrace-wide establishment patterns around this time. Recent work in reconstructing the timing and magnitude of historical Alpine Fault earthquakes has resulted in probable dates of M_w 8 events that ruptured along the fault length about 280 yrs ago (1717 A.D.), 370 yrs (1630 ± 25 yrs), and around 540 yrs ago (1460 ± 25 yrs) (Wells *et al.* 1999). These catastrophic earthquakes resulted in widespread, synchronous establishment of conifers (particularly *Dacrydium*, *Dacrycarpus* and *Libocedrus bidwillii*) throughout Westland on new and existing surfaces (Wells *et al.* 1999). The two most recent Alpine Fault earthquakes coincided closely with the timing of distinct pulses of *Dacrydium* and *Dacrycarpus* regeneration, along with the beeches 200-275 yrs and 350-450 yrs ago at this site. Previous pulses of *Dacrydium* regeneration between 500-650 yrs and 800-900 yrs ago could also well reflect past earthquakes. Whatever the cause of Event 2 around 275 yrs ago, it was clearly much more severe and

impacted with more intensity in the poorly drained areas than the storm (s) 75-100 yrs ago. For this discussion, I assume it was earthquake caused.

Mount Harata is within 15 km of the Alpine Fault and is within the most intense isoseismal shaking zone (Yetton *et al.* 1998), and it is likely it received severe impacts during past earthquakes. Other studies have shown that stands located near the epicentre of earthquakes are subject to the greatest impacts (Kitzberger *et al.* 1995; Allen *et al.* 1999). There has not been an Alpine Fault movement in the last 150 yrs, since European settlement, and it appears unlikely that there was an Alpine Fault earthquake in the last 200 yrs (Adams, 1980; Yetton, 1997). Tree ring releases suggest that more recent less intense, localised earthquakes in Westland in 1929 and 1968 had minor effects relative to the Alpine Fault events (Vittoz *et al.* 2000 - appendix: Fig. C2). The epicentres of these recent earthquakes were all located > 60 km away in Arthur's Pass, Murchison (both 1929) and Inangahua (1968), and Mt. Harata experienced relatively minor shaking on the Mercalli index (Adams *et al.* 1968; Downes, 1995). A recent study of the M_w 6.7 Arthur's Pass earthquake that occurred in 1994 found localised impacts on the forests near the epicentre, with rapid decay in effects as distance increased out from the epicentre (Allen *et al.* 1999).

There were also periods of more localised disturbances that occurred in different parts of the terrace, and also more frequent smaller-scale within-plot disturbances that influenced species' regeneration. The disturbance 190-200 yrs ago identified in the poorer drained plots in chapter 1 was not as widespread or evident within the terrace plots, although there were one or two plots where an upsurge of establishment also commenced in the 200-225 yrs class (plots C3 for *N. fusca* and E7 for *N. menziesii*). These plots were close to the poorer drained plots in chapter 1, hinting at the possibility of an intermediate scale event around the poorer drained terrace centre.

4.2 Differentiating earthquake and storm effects

Earthquake effects

The scale of the impacts is an important factor in understanding why *Dacrydium* regenerated after the two historical earthquakes but not the storm. Establishment patterns across the terrace suggest the last earthquake opened up large areas of the forest canopy by causing widespread mortality of trees. Earthquakes can cause extensive forest damage and mortality, with severe shaking effects including root shearing, limb breakage or toppling (Sheppard and Jacoby, 1989; Wiles *et al.* 1996). Trees on soils with high water tables such

as organic soils are particularly susceptible to toppling due to liquefaction (Almond, 1997; Yetton *et al.* 1998). Organic soils provide weak rooting mediums as they lack structure and can be very fluid, and consequently in an earthquake are likely to move causing extensive treefall (Almond, 1997). On poorly drained outwash terraces in south Westland large patches 1-20 ha have been disturbed following earthquakes, with smaller patches (< 2 ha) on better drained moraines (James, 1987; Norton *et al.* 1988). Forest damage and tree mortality from intense shaking varies according to differences in substrate stability within landforms, and across the landscape on unstable landform surfaces (Kitzberger *et al.* 1995). Areas with abundant senescent trees are also more likely to be severely affected than young stands of the same species (Kitzberger *et al.* 1995). Clearly, earthquakes could account for the widespread synchronous pulses of establishment evident in the age structures on both well and poorly drained sites 200-275 yrs and 350-450 yrs ago.

Storm effects

The most extensive establishment following the storm was concentrated in at least two discrete sections of the terrace (groups A and B). This suggests either there was some factor (s) that predisposed stands to being blown down (in group A in particular), or alternatively the storm's effects were ameliorated in the other well drained and poorly drained areas where trees also commonly died standing or were bole snapped (chapter 1). The former idea implies that the storm's intensity was not uniform across the terrace, whereas the latter idea suggests that even if disturbance intensity was uniform, trees simply survived better on some sites due to a range of ameliorating factors. Wind strength and direction is a primary factor in uprooting, but there are many important interacting secondary factors that also influence the susceptibility of sites to blowdown (Foster, 1988b, Schaetzl *et al.* 1989). These secondary factors include differences in species' autecology, stand age, composition and structure, and variability in edaphic conditions (Jane, 1986; Foster 1988a, 1988b; Foster and Boose, 1992; Bellingham *et al.* 1995; Rebertus *et al.* 1997).

The location of the group A plots could have exposed them to more intense winds than the terrace interior. The direction of the uproots in these plots were lying N-NW indicating the winds were from the S-SE (chapter 1; see also Roche, 1929, June 1982). The location of these plots around the terrace edges in the north-western corner was most likely exposed to the path of the storm front. This corner lies directly in the path of southerly winds that funnel down the steep Clarke River catchment. Sites where winds are funnelled and concentrated generally experience more wind damage than sheltered areas

(Jane 1986; Schaetzel *et al.* 1989). Storm impacts have been found to be greater on exposed sites that bear the full force of storms, although wind direction and velocity may vary across short distances due to meteorological factors and the topographic environment (Foster, 1988b). Variation in wind velocity is a dominant factor in controlling the intensity of storm disturbances (Foster and Boose, 1992). Impact intensities from large winds can create intricate landscape patterns in terms of size and shape of damaged areas, as differential intensity of disturbance means damage is not uniform across the landscape, and can vary across landforms depending on exposure to prevailing wind velocity and direction (Bellingham, 1991; Foster and Boose, 1992; Bellingham *et al.* 1995). The degree of site exposure can therefore be one factor in explaining why certain areas are impacted more than others following the storm.

Another factor influencing site susceptibility is differences in soil depth, and this provides a partial explanation of why extensive areas in different groups were blown down in group A plots. Soil profiles were shallower in group A plots (25-50 cm) than nearby terrace interior group D poorly drained plots (50-100 cm) (appendix - Table E1). However, soil depth was also shallow in the well drained group C plots (30-50 cm) where extensive uprooting did not occur. A number of studies have shown extensive uprooting to occur on shallow soils during storms, as trees are not as windfirm as in deeper rooted sites (Wood, 1970; see Schaetzel *et al.* 1989, for summary). In a swamp forest in the US after Hurricane Hugo in 1989, uprooting was greater in well-drained areas than poorly drained soils (Putz and Sharitz, 1991). These authors noted that uprooted trees in better drained soils had originally established on logs or previous uproot mounds, sites which were mechanically unstable in high winds.

Species' autecology also provides a partial explanation why extensive uprooting of *Nothofagus fusca* occurred on the shallow soils in group A plots. Several studies have shown that species can be differentially affected by hurricanes with some species more susceptible to being damaged than others (Foster 1988b; Bellingham *et al.* 1995). For example, some species may be more prone to uprooting than others due to their rooting patterns (Foster 1988b, Schaetzel *et al.* 1989). Foster found that canopy-dominant pioneer species with shallow root plates and large crowns preferentially uprooted during a large hurricane, than co-dominants that had deep taproots. *N. fusca* shares those attributes typically having a large spreading root plate, and is generally shallow rooted making it prone to uprooting on shallow soils (Wardle, 1984; Stewart *et al.* 1991). However, it was also a major component of the other well-drained group C plots that were not blown down suggesting there are other factors that need to be considered.

Other factors that predispose stands to blowdown include stand age and size structures (Jane, 1986; Foster 1988a, 1988b; Rebertus *et al.* 1997). Differences in stand age and size were identified in the well drained plot in chapter 1, that suggested *N. fusca* blown down in one half of the plot were of different size and age to the other part. The trees that survived were of the same age as those in group C, and it is possible that the blowdown plots contained older *N. fusca* that were preferentially blown down on shallow soils.

Differences in stand architecture between well and poorly drained plots could also have ameliorated the effects of the storm (s). The areas that experienced less blowdown in the poorly drained plots were architecturally more complex than the well drained plots. Stands typically comprised an emergent conifer layer, canopy beeches and subcanopy hardwoods over a dense tree fern and shrub understorey which possibly inhibited wind velocity. In contrast, well drained sites were more architecturally simple with a much more open understorey, characterised by a beech canopy and hardwood subcanopy over sparse understorey with many forest floor crown ferns. Other studies have shown that areas that differ in species composition and tree architecture can be differentially affected by storm impacts (Foster 1988b, Foster and Boose, 1992).

In summary, there are probably many contributing and interacting factors that influenced the effects of the storm (s) across the terrace. Two key points emerge from considering the storms' effects. First, the complex mosaic of effects that occur across a range of scales influenced the differential establishment of species in differently drained areas. Second, the smaller scale of establishment in the poorly drained terrace interior suggested the storms' effects led to conditions that favoured the regeneration of a different set of species (*N. fusca*, *N. menziesii* and *Dacrycarpus*), compared to the effects of the last Alpine Fault earthquake (*Dacrydium*, *Dacrycarpus*, *N. menziesii*)

4.3 Drainage and microsite influences

Species also partitioned the regeneration conditions resulting from these events with respect to drainage at the broad scale and at the within-plot microsite scale, with conifers on wetter sites and beeches and hardwoods on drier sites. On well drained terrace sites, despite the large disturbances and more frequent smaller-scale disturbances during the interval between them, few conifers are able to successfully regenerate into the overstorey. This is likely due to the lack of suitably moist edaphic conditions and/ or competition from faster-growing angiosperms. This could be a key factor in understanding

the patterns of scattered emergent conifers over dense beech and beech/hardwood canopies on well-drained hillslopes in the region, with *Dacrydium*, in particular, confined to wet depressions, stream channels, gully sides or slope benches (where slopes flatten off).

On poorly drained sites, the type of disturbance was critical in the creation and availability of suitable better drained microsites. Uproot mounds and fallen logs provided opportunities for beech and hardwood establishment in permanently wet areas where, ordinarily, species such as *N. fusca* would struggle (Rogers, 1989; Adams and Norton, 1991). These findings agree with other studies in mixed forests, for example, in a study of mixed *L. bidwillii*/*N. fusca* in the North Island, Rogers (1989) concluded that disturbance history and the availability of suitable seedling establishment sites (logs) limited beech spread into conifer areas. In mixed *L. bidwillii*/*N. menziesii*/*N. solandri* var. *cliffortioides* stands in north Westland, Veblen and Stewart (1981, 1982) found that large disturbances resulted in even-aged stands of all species, but subsequent smaller canopy gaps were captured by the beeches except in wetter areas where their vigour was reduced. Wardle (1991) also noted that angiosperm vigour was reduced on poorly drained areas in south Westland, allowing for more conifer regeneration in these areas.

Following earthquake shaking, better drained microsites may not have been immediately available for colonisation in some poorly drained areas which could explain the lack of *N. fusca* regeneration. The sudden pulse of organic debris (boles, leaf canopies) into the poorly drained peats results either in this debris becoming eventually available for future colonisation by beeches and hardwoods as decay processes advance, or the weight of many stacked trees sinking into the fluid soils creates anaerobic conditions in places due to increased organic loadings, suitable for establishment of species such as *Dacrydium* tolerant of very organic soils (see chapter 1). Tip-up mounds in the very poorly drained deep peats also have different characteristics from soils with mineral material. The fluid, fibrous material around the root mass can quickly slough off leaving exposed roots, and limiting establishment until decay advances (pers obs; Almond pers comm). The ability of *N. menziesii* to capture these types of log microsites in poorly drained sites may also explain its relative abundance compared with *N. fusca* after the last earthquake.

4.4 Regeneration patterns in well-drained plots

Regeneration patterns in the poorly drained plots reflected those identified in chapter 1, where disturbance history was found to be important in mediating coexistence between *N. fusca*, *N. menziesii* and *W. racemosa*. There were no significant microsite

differences between species. Patterns of stand development following the different large disturbances emphasise the importance these events had in structuring stands on the well-drained surfaces and particularly for the maintenance of *N. fusca* in these areas. Group A *N. fusca* stands that regenerated after complete stand destruction following the storm, were in the stem-exclusion or thinning phase of stand development (*sensu* Oliver, 1981) as reflected in their high stem densities and large basal area (Table 1). In well-drained group C stands, where there was partial damage from the storm, small patches of *N. fusca/N. menziesii* in canopy gaps reflected stem reinitiation in older stands. The relative paucity of *N. fusca* regeneration between the large disturbances suggests that in the absence of these events, *N. menziesii* and *W. racemosa* would probably become more abundant and *N. fusca* less so (cf *N. pumilio* - *N. betuloides* - *Drimys winteri* forests in southern Chile - Rebertus and Veblen, 1993). Other studies have shown that in co-dominant *N. fusca/N. menziesii* stands with a history of large disturbances, *N. fusca* occurs as even-aged populations with regeneration prevalent in larger gaps whereas *N. menziesii* regeneration is greater in more frequently created smaller gaps (Wardle, 1984; Ogden, 1985, 1988).

4.5 Regeneration patterns on poorly drained plots

Different types of large disturbances, along with more frequent types of smaller-scale disturbances from the death of one or several trees, provided the variability in light conditions and created different microsites to which species responded differentially, and enabled the coexistence of all five overstorey species in poorly drained areas across the terrace. Patterns of stand development in these poorly drained plots and differential species responses to disturbances reflected those in chapter 1, and suggested an order of shade tolerance of *W. racemosa* > *N. menziesii* > *N. fusca* > *Dacrycarpus* > *Dacrydium*.

Conifers

Dacrydium cupressinum established infrequently mostly after earthquakes. Less successful regeneration at other times suggests it is relatively shade-intolerant compared to the beeches, hardwoods and *Dacrycarpus*. The dependence on large disturbances for widespread *Dacrydium* regeneration is well understood on glacial outwash terraces and moraines in south Westland (Hutchinson, 1928; Cornere, 1992; Rogers, 1995; Stewart *et al.* 1998; Van Uden, 1998), but not as well in mixed conifer/beech/hardwood stands in north Westland. Two previous studies noted an apparent recruitment gap in *Dacrydium* from 300 yrs ago to the present, in mixed-species forests also in the Grey Valley (Burrows

et al. 1975; June 1982). However, these studies did not link *Dacrydium* regeneration in response to the conditions created by large disturbances. Rather, June (1982; 1983) proposed that a large disturbance 300 yrs ago favoured vigorous angiosperm regeneration, which suppressed *Dacrydium*. More recently, Lusk and Smith (1998) proposed that infrequent establishment of *Dacrydium* in well-drained hillslope *Dacrydium*/*N. menziesii*/*W. racemosa* forest in south Westland, was due to chance, sporadic capture of canopy openings. Differences in life-history characteristics and a substantially longer canopy residence time (>700 yrs) meant that there was a high probability that one or two trees could reach the canopy per century to maintain *Dacrydium* in the forest. However, the age data presented by June (1982) and Lusk and Smith (1998) could support an alternative interpretation of establishment in response to large disturbances. At June's Callaghans Ridge site 30 km away from Mt Harata, the *Dacrydium* age structure was characterised by an abrupt upsurge in establishment that commenced in the 600-700 yrs class and peaked in the 500-600 yrs class (1982: 117) which corresponds in timing to establishment pulses identified at Mt Harata. There was also a tailing off of establishment in the last 300 yrs that could reflect the interval since large disturbance affected that site. At the Jackson River site in south Westland studied by Lusk and Smith (1998: 799), the age data appear to broadly show two different age groups that most trees fall into: 500-700 yrs and 200-400 yrs. The age groupings also relate to differences in size classes with the older trees > 60 cm dbh, and the smaller 30-60 cm trees were younger. These data could also plausibly be reflecting pulses of establishment after large disturbances identified previously in south Westland (Wells *et al.* 1998; Wells *et al.* 1999).

The shorter-lived conifer *Dacrycarpus* had more frequent and recent gap-phase regeneration. *Dacrycarpus dacrydioides* regenerated after the more recent storm, and also responded to the earthquakes along with *Dacrydium* but, in several plots, trees of the same age were spatially separated after disturbances. In chapter 1, differences in peat composition in different areas were found, with *Dacrycarpus* establishing on peats with incorporated silty material but less so on the most organic peats where *Dacrydium* was abundant. These patterns reflect landscape level distributions, with *Dacrycarpus* is found on flood plains and recent terrace soils rejuvenated by flooding (Foweraker 1929, Wardle, 1974; Duncan, 1991, 1993; Norton and Leathwick, 1990) and in flat low lying hollows and back-swamps on low terraces (Mew and Ross, 1980); whereas *Dacrydium* is prevalent on more nutrient poor, leached and acidic organic soils on older surfaces (Chavasse, 1962; Sowden, 1986; Almond, 1997).

Beeches and hardwoods

The size of the canopy opening after disturbance was an important factor in *N. fusca* regeneration in small, even-aged groups in areas with suitable microsites. In contrast, *N. menziesii* regenerated more frequently from single tree to groups of similarly-aged trees amongst older *Dacrydium* trees. *Weinmannia racemosa* had an all-aged structure reflecting recruitment after a range of disturbances of different extent in most of the poorly drained plots (appendix - Fig. E3). There were more stems recruited into the subcanopy at times when other species establishment was low, especially the conifers and *N. fusca*. Less *W. racemosa* establishment in response to the storm could reflect the intense competition for available microsites in canopy gaps. In areas where *W. racemosa* responded to the storm, such as plot E7, stems were scattered underneath the established canopy of *Dacrydium* in shadier, less open situations reflecting its shade-tolerance.

4.6 Coexistence between conifers, beeches and hardwoods

Gradients and species distributions

In this study, the underlying edaphic conditions influenced species composition along the drainage gradient and disturbance history regulated the relative abundances of species. Different sets of species responded to the variation in scale of the different large disturbances reflecting the heterogeneity created by these events. One strength of this study is that it examined the influence of the drainage gradient in controlling differential establishment patterns across the terrace following disturbance. In this respect it adds to the small but growing number of studies that have shown the importance of understanding how the disturbance regime interacts with environmental gradients in influencing species distributions across the forest landscape. For example, Romme and Knight (1981) found that subalpine forest composition in Wyoming (USA), was determined by the frequency of fires and the rate of secondary succession along a topographic moisture gradient. Where fire frequency was high in the drier uplands, *Pinus contorta* dominated, but in the sheltered ravines and wetter valley bottoms, less frequent fires and rapid succession resulted in *Picea engelmannii* and *Abies lasiocarpa* dominated stands. In the Great Smoky Mountains (USA), Harmon *et al.* (1983) examined species' responses to modifications of the disturbance regime by human activities, and found that fire suppression, logging and pathogens altered the intensity and frequency of the disturbance regime on xeric and mesic sites causing shifts in species distributions and community composition. Variation in hurricane intensity on differently drained soils affected conifer and hardwood species

differentially following a hurricane in Harvard Forest, USA (Foster 1988a, 1988b; Foster and Boose, 1992). These authors found that there were changes in species abundances occurring as a result of the hurricane, conifers were particularly susceptible to damage, and there was vigorous hardwood regeneration following the release of resources. These studies and others have shown that differences in species' ability to survive disturbances and their regeneration strategies also influence post-disturbance composition on different sites (Veblen, 1989; Ishizuka and Sugawara, 1989; Veblen *et al.* (1992); Bellingham *et al.* 1995).

Two-component model of coexistence

The 'two-component' model proposed by Ogden and Stewart (1995) in describing interactions and coexistence between conifers and angiosperms, suggests that these groups of species respond to different influences and occupy different strata of the forests. Conifers are typically emergent and regenerate in large, even-aged stands after large disturbances, whereas more frequent smaller disturbances favour the faster-growing generally shorter-lived canopy and subcanopy angiosperms. Results show that this model is a useful tool in understanding conifer, beech and hardwood coexistence; however, results also suggest that the 'two-component' idea can be further advanced in three ways. First, the two-component system is *drainage related* in these forests, applying in the poorly drained plots only where all three groups of species coexist. Second, the *scale of effects* is the important factor in influencing conifer regeneration on poorly drained sites with some large disturbances not providing the conditions necessary for abundant regeneration. Third, the conifer (large disturbance regenerator), angiosperm (smaller disturbance regenerator) dichotomy does not encompass notable differences in the *variability* of species regeneration patterns identified.

In understanding the *drainage related* species distributional patterns across the terrace with few conifers on well-drained sites, Bond (1989) argued that due to the functional constraints of relatively inefficient vascular conductance, conifer seedlings would be out-competed by angiosperms on productive sites. Conifers would be restricted to the colder and more infertile sites in shady situations where angiosperm vigour would be reduced. The lack of conifer trees on well drained sites may be related to competition with beeches and hardwoods, or alternatively a poorly developed root network and susceptibility to drought conditions on well drained sites could also explain these patterns (Cameron, 1963; Livingston and Black, 1988). The restriction of conifers to the few moist edaphic microsites available in well drained areas suggest wetter sites may be a realised niche in

these mixed forests, but whether *Dacrydium* and *Dacrycarpus* have a wider ecological amplitude or fundamental niche but are restricted to these sites by angiosperms needs further investigation (chapter 1).

The storm and earthquakes were different in terms of the *scale* of their effects, which was the key to whether large pulses of *Dacrydium* regeneration occurred. The resulting size of the canopy openings and the regeneration conditions left behind determined the mix of species that regenerate at some times but not others in poorly drained areas. It also appears that Alpine Fault earthquakes could be a major force in structuring forest composition and structure in north Westland forests as they are in south and central Westland forests (Wells *et al.* 1998; Wells *et al.* 1999). However, the extent and effects of these earthquakes need further investigation across a range of different landforms in other parts of the north Westland region.

Third, the *variability* in species regeneration patterns suggest that the beech *N. fusca* behaved like the conifer component of the model on well-drained sites with populations composed of extensive even-aged patches that regenerated after the large disturbances. Similarly, the conifer *Dacrycarpus* behaved like the angiosperm component regenerating in a gap-phase manner after less extensive disturbances.

These forests on poorer drained areas could also conceivably be described heuristically as 'three component' systems. In this study conifers, beeches and hardwoods had different responses to disturbances in respect of their relative shade and environmental (microsite) tolerances, they occupied different strata in the forest (conifers – *emergent*, beeches – *canopy*, hardwoods – *subcanopy*) and there were differences in their longevity.

Longevity and coexistence

The greater longevity of *Dacrydium* (600-900 yrs) compared with other species means that only one or two catastrophic events need to occur during its lifespan for successful recruitment of the next generation. The relative longevity of *Dacrydium* is analogous to the other dominant Aotearoa conifer *Agathis australis* (kauri - Araucariaceae) as a long-lived pioneer. The persistence of long-lived *A. australis* has seen it described as a 'long-lived pioneer' which holds sites for many centuries after establishment following large disturbances (Ogden, 1985). During this time, several generations of angiosperms may occur, and as the long-lived *A. australis* seedlings can not readily penetrate angiosperm canopies, this implies their recruitment and mortality operate over a different time scale (Ogden, 1985). However, a high basal-area of *A. australis* does not imply a reduction of the associated angiosperms, termed the 'additive basal area' hypothesis

(Enright, 1982; Ogden, 1985), rather the basal area of these long-lived emergent conifers may be largely independent of the angiosperms. This was not directly tested in this study, although there were no significant differences in basal area between the four groups of plots identified in Figure 2 (Table 1- Kruskal Wallis test = 1.179, $P = 0.76$, $n = 20$).

Longevity is a tradeoff between growth rates and plant defence effort, with longer lived species tending to have slow relative growth rates and high plant defences (Loehle, 1988). Enright and Ogden (1995) argued that for southern conifers, longevity is a natural consequence where the frequency of major disturbance is low, since time to maturity is prolonged and extinction is the likely alternative under high disturbance regimes. Other studies have also noted that conifer densities decline in the absence of large disturbances (Ogden *et al.* 1987; Veblen and Lorenz, 1987), but that due to extreme longevities conifers may persist in the landscape over many centuries in the absence of large disturbances. Therefore, large infrequent disturbances preclude rapid competitive displacement of conifers and allow coexistence between angiosperms and conifers (Enright *et al.* 1995).

CONCLUDING SUMMARY

This thesis has investigated the structure, regeneration dynamics, and forest disturbance history in a mixed conifer, beech and non-beech terrace forest across an environmental drainage gradient, and applied this information to gain an improved understanding of the interactions and coexistence between different species. This study set out to better understand the processes that influence the regeneration ecology of mixed species forests in what is a relatively common forest type but a poorly studied one. This involved the reconstruction of regeneration dynamics and disturbance history at both a within-stand and a whole landform scale in response to small scale frequent tree death, and infrequent, violent storms and catastrophic Alpine Fault earthquakes.

In Chapter 1, I conducted a detailed study of three large rectangular plots (0.3 ha - 0.7 ha) placed at different points along a gradient in soil development and drainage, on a 1 km long by 0.8 km wide post-glacial terrace of Otiran age at Mt. Harata in north Westland. The analysis of stand age structures, spatial distribution of tree ages, microsite preferences, tree ring releases, and mortality patterns in the plots provided a clear picture of different species regeneration strategies after a range of disturbances of different extent. Species composition was found to be influenced by soil drainage with few conifers on well drained plots and, in poorly drained plots, species partitioned available microsites according to drainage characteristics. Species also partitioned the light environment with respect to the amount of overhead cover on these poorly drained sites. There were distinct periods of regeneration that closely corresponded between plots suggesting large, infrequent disturbances had been a major factor in influencing long term forest patterns and processes.

In Chapter 2, I investigated whether these corresponding periods of regeneration reflected larger patterns across the terrace in a series of stratified random circular plots placed in poorly- drained and well- drained areas. This study confirmed and refined the extent of three coinciding regeneration periods in the last 450 yrs, and showed there were clear differences between species in their regeneration patterns after different types of large, infrequent disturbances that enabled them to coexist. This chapter examined the impacts of storms and infrequent Alpine Fault earthquakes and the differential intensity of stand damage, and found them to be important influences in structuring long-term forest pattern in differently drained areas.

Given the ecological importance of these lowland forests, being at the juncture where the beech dominated forests of the north come together with the conifer/hardwood forests of the south, understanding the influence of disturbances at different points along an environmental drainage gradient provides insights into the mechanisms at work that enables the maintenance of a high level of tree species diversity. Some insights into long-standing biogeographical debates on disjunct species distributions may also emerge from this study. These forests are also important in a management sense, and the size of the managed extraction openings may need to be reevaluated if management seeks to maintain long term compositional diversity and mimic natural processes of stand replacement (Urlich *et al.* 1999).

Overall, the substantial age and spatial information collected has provided a framework to understand the processes that influence mixed tree species coexistence in north Westland, specifically, the partitioning of environmental conditions (edaphic, light) following different types of tree death. This study reinforces past studies that have also identified these factors as critical in the maintenance of tree species diversity in Westland. It has also added to our increasing understanding of the landscape effects of Alpine Fault earthquakes as a dominant force in shaping the forest landscape over the last millennium in Westland.

In respect of the questions this study sought to answer regarding species interactions and mechanisms of coexistence in mixed conifer, beech and hardwood forests of north Westland, the following conclusions can be made.

1. The underlying edaphic conditions influence species composition along the drainage gradient and disturbance history regulates the relative abundances of species. Few conifers were found on well-drained areas despite the range of disturbances of different type and size that occurred over the last 400 yrs.
2. As drainage became progressively poorer *Nothofagus fusca*, *Weinmannia racemosa* and *Quintinia acutifolia* became less abundant, whereas *N. menziesii*, *Elaeocarpus hookerianus*, *Dacrydium cupressinum* and *Dacrycarpus dacrydioides* increased in abundance.
3. Species were able to coexist by a combination of microsite partitioning, with conifers on poorly drained sites, and beeches and hardwoods on well drained microsites,

and differential regeneration responses to variation in the size of canopy openings following different disturbances.

4. The type of tree death was found to be an important factor in influencing successful regeneration of species, with small gaps from dead standing tree death favouring the more shade-tolerant species *N. menziesii*, *W. racemosa*, and *Q. acutifolia*. In contrast, uprooting in poorly drained areas provided suitable microsites and openings large enough to allow successful regeneration of *N. fusca*, *Dacrycarpus* and *E. hookerianus* to occur together. Soil disturbance caused by uprooting was also found to be an important factor in the successful establishment of *Dacrycarpus* and *Dacrydium* saplings.
5. The disturbance regime at Mt Harata has been characterised and punctuated by large, infrequent disturbances that cause massive mortality and synchronous regeneration of species, interspersed with periods of continuous smaller scale individual or several tree mortality. Terrace-wide disturbances were identified that occurred in the last 450 yrs around 75-100 yrs, 200-275 yrs, 350-450 yrs; and possibly 575 yrs, 650 yrs and 850 yrs ago.
6. Different sets of species regenerated on differently drained sites in response to these large, infrequent disturbances, generally with conifers and beeches on poorly- drained sites, and beeches and hardwoods on well-drained sites reflecting the underlying drainage gradient.
7. The large, infrequent disturbances caused different effects in stands at different times that favoured regeneration of different species. *Dacrydium cupressinum* regeneration appeared to be largely linked to the conditions caused by severe, infrequent Alpine Fault earthquakes that struck the terrace at periodic intervals over the last millennium, but few stems were recruited after the storm 75-100 yrs.
8. The results of this study further develop the two-component theory of mixed-species conifer/angiosperm coexistence. This model can be advanced by first understanding the important influence of underlying drainage on species distributions. Second, by recognising that not all types of large, infrequent disturbances create the conditions that enable conifer regeneration - the scale of effects is an important factor. Third, that not all conifers or angiosperms fit the regeneration dichotomy reflected in the model.

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APPENDIX

Representative Soil Profile Descriptions

PLOT C

Pit 1: Location co-ordinates $x=55, y=25$.
Soil Series - Ahaura (Mew and Ross, 1980)
Soil Class - Yellow-brown earth (YBE) - (Stewart *et al*, 1993)
NZ Soil Classification - Acidic Orthic Brown soil (Hewitt, 1998)
USDA Taxonomy - Spodic Drystrudepts

Depth to gravels - 45 cm.
Drainage - Well drained.



| Layer Depth Description | | | Plate 5 |
|-------------------------|----------|---|---------|
| L | 0-3 cm | Litter layer, boundary with Ah abrupt and distinct. | |
| Ah | 3-10 cm | 10YR 3/3 (Dark brown). Silt loam. Fine nut and crumb structure. Very intensely rooted, very abundant fine to medium sized roots (60%). Occasional stone (4 cm across). Very low penetration/ resistance. Diffuse and irregular boundary with Bw. | |
| Bw | 10-45 cm | 10YR 5/6 (Yellowish-brown). Stony silt loam. Large stones up to 15 cm long in layer (5 to 50%). High penetration/ resistance. Slightly firm resistance to crushing. Very occasional roots. Variable depth, in some places Bw comes within 5 cm of surface. Boundary indistinct and wavy with C. | |
| C | 45 cm - | 2.5YR 5/4 (olive brown). Weathered fine to medium gravels and occasional large stones (up to 15 cm across). 65% fine P gravels. 35% 1-3 cm stones. Granitic gravels are rounded (alluvial). High penetration/ resistance. Churned over by periodic uprooting. Large area of uprooting surrounding this pit. | |

Pit 2: Location co-ordinates $x=16, y=28$.
Soil Series - Ahaura (Mew and Ross, 1980)
Soil Class - Yellow-brown earth (YBE) (Stewart *et al*, 1993)
NZ Soil Classification - Acidic Orthic Brown soil (Hewitt, 1998)
USDA Taxonomy - Spodic Dystrudepts

Depth to gravels - 45 cm.
Drainage - Well drained.



| Layer Depth | | Description | Plate 6 |
|-------------|----------|--|---------|
| L | 0-2 cm | Litter layer, boundary with Ah abrupt and distinct. | |
| Ah | 2-15 cm | 10YR 3/3 (Dark brown). Silt loam. No mottles. Fine nut and crumb structure. Very intensely rooted, very abundant fine to medium sized roots (60%). Occasional stone (3 cm across). Very low penetration/ resistance. Slightly firm resistance to crushing. Wavy and distinct boundary with AB. | |
| AB | 15-20 cm | 10YR 5/1 (Brownish grey). Silt loam. Many fine live roots. Diffuse and wavy boundary with Bw. | |
| Bw | 20-45 cm | 10YR 6/6 (Brownish-yellow colour). Stony loamy silt. Very occasional roots. Variable depth, in some places Bw comes within 5 cm of surface. Large stones up to 20 cm long in layer. Some gleying around several large stones along one side of pit. However, this is localised and not prevalent, although this pit is slightly wetter than pit 1 in this plot and is in an area of less recent large scale disturbance. High penetration/ resistance. Slightly firm resistance to crushing. Boundary with C layer is indistinct and wavy. | |
| C | | Underlying gravels (Same as for pit 1). | |

General soil limitations: "Many (Ahaura) profiles are shallow or stony; excess stones may limit tree rooting and/ or lead to instability. The soils are generally of low nutrient status. Some are subject to summer drought" Mew and Ross 1980: p 17.

PLOT B

Pit 1: Location co-ordinates $x=10, y=60$.
Soil Series - Rotokuhu (Mew and Ross, 1980)
Soil Class - Peat (Stewart *et al*, 1993)
NZ Soil Classification - Mellow humic organic soil (Hewitt, 1998)
USDA Taxonomy - Sapric Haplohemists

Depth to gravels - 1 m.
Drainage - Very poorly drained.



| Layer Depth Description | | | Plate 7 |
|-------------------------|-----------|---|---------|
| O | 0-5 cm | 10YR 4/2 (Dark greyish brown). Organic layer, matted fine roots. Boundary sharp and distinct. | |
| O | 5-25 cm | 10YR 4/4 (Brownish black). Loamy peat . Variable depth 20 cm-50 cm, generally about 20 cm. Black casts (5%). Indistinct and diffuse boundary with Bhr. Breaks into aggregates 0.5 to 1 cm, quite friable. A lot of rooting along boundary with Bhr. Also packed with dead wood and rotting roots particularly concentrated at Bhr boundary. No gravels. Low penetration/ resistance. Weak resistance to crushing. | |
| Bhr | 25-90 cm | 10YR 3/3 (Dark brown). Silty peat. Variable in depth. Intense fine to medium rooting. No gravels. Very low penetration/ resistance. Very fluid. Boundary with Br wavy and distinct. | |
| Bg | 90-100 cm | 5 Y 6/3 (Greyish olive). Sandy loam Very slightly gravelly (5%). Very low penetration/ resistance. Slightly firm resistance to crushing. Boundary with C distinct and irregular. | |
| C | 100 cm | Weathered fine to medium gravels and occasional large stones (up to 15 cm across). 65% fine P gravels. 35% 1-3 cm stones. Gravels are rounded (alluvial). Yellow-brown stain. High penetration/ resistance. | |

Pit 2: Location co-ordinates $x=70, y=40$.
Soil Class - Peaty-Gley (Stewart *et al*, 1993)
NZ Soil Classification - Mellow humic organic soil (Hewitt, 1998)
USDA Taxonomy - Terric Haplohemists

Depth to gravels - 80 cm.
Drainage - Poorly drained.



| Layer | Depth | Description | Plate 8 |
|-------|----------|--|---------|
| O | 0-5 cm | 10YR 4/2 (Dark greyish brown). Organic layer, matted fine roots. Boundary sharp and distinct. | |
| O | 5-40 cm | 10YR 3/2 (Brownish black). Loamy peat. Black wormcasts. Fine roots throughout. No gravels. Moderately sticky. Boundary with Ah diffuse and wavy. | |
| Ah | 40-55 cm | 10YR 5/3 (Dull yellowish brown). Peaty loam. Occasional roots up to 5 cm in diameter. Very low penetration/ resistance. Weak resistance to crushing. Slightly sticky. Diffuse and wavy boundary with Bg. | |
| Bg | 55-80 cm | 5Y 7/4 (Light yellow). Silt loam. Fine roots (10%). Slightly gravelly (up to 1 cm in diameter). Moderate penetration/ resistance. Wavy and indistinct boundary with C. | |
| C | 80 cm | Weathered fine to medium gravels and occasional large stones (up to 15 cm across). 65% fine P gravels. 35% 1-3 cm stones. Gravels are rounded (alluvial). Yellow- brown stain. High penetration/ resistance. | |

PLOT A

Pit 3: Location co-ordinates $x=35, y=20$. *Depth to gravels* - 85 cm. *Drainage* - Very poorly drained.
Soil Series - Kini (Mew and Ross, 1980) *Soil Class* - Peat (Stewart *et al*, 1993)
NZ Soil Classification - Mellow humic organic soil (Hewitt, 1998) *USDA Taxonomy* - Sapric Haplohemists



| Layer | Depth | Description | Plate 9 |
|-------|----------|--|---------|
| O | 0-5 cm | 5YR 2/2 (Brownish black). Organic layer, matted fine roots. Prevalent rimu litter from surrounding trees. Boundary with next organic layer distinct but wavy. | |
| O | 5-15 cm | 5YR 3/1 (Brownish black). Peat with no mineral material (Table 3). Very strongly decomposed dark brown/ black material. Abundant moderate to fine roots. Abundant large earthworms throughout layer. Boundary with next O layer distinct but irregular. | |
| O | 15-40 cm | 5YR 3/2 (Dark reddish brown). Weakly decomposed dark brown material, pure peat (Table 5). Organic material still has structure with recognisable fine forest floor litter with small fine twigs (up to 0.5 mm), ferns fronds, fibrous material, leaves, and intact pieces of wood (up to 0.5 m length). Buried red beech tree in this layer. Identified by wood colouring, smell, and wide, distinct growth rings (sample taken). No red beech in immediate vicinity approx. 10 metres in each direction. Flat micro-topography in this area and even-aged cohort of rimu (<i>Dacrydium</i>) with associated <i>Cyathea</i> and <i>Dicksonia</i> tree ferns. | |
| O | 40-70 cm | 7.5YR 3/3 (Dark brown). Peat. Semi-decomposed chocolate brown material, mushed up pieces of wood up to 10 cm across. No roots present. There is a bad smell possibly indicating presence of hydrogen sulphide caused by material decaying under anaerobic conditions. Boundary with Bg smooth and abrupt. | |
| Bg | 70-85 cm | 5Y 6/4 (Olive-yellow). Sandy loam . Coarse material (30%) with stones up to 2 cm across. No roots. Low penetration/ resistance. Weak resistance to crushing. Boundary with C indistinct and irregular. | |
| C | 85 cm - | Weathered fine to medium gravels and occasional large stones up to 15 cm across). 65% fine P gravels. 35% 1-3 cm stones. Yellow- brown stain. Gravels are rounded (alluvial). High penetration/ resistance. | |

General soil limitations:. Composed of organic matter, mainly from sphagnum moss and rimu, with some alluvium (granite). No chemical analysis available. Main limitation is high water table (Mew & Ross 1980:37).

Pit 4: Location co-ordinates $x=55, y=20$.
Soil Series - Rotokuhu (Mew and Ross, 1980)
Soil Class - Peat (Stewart *et al*, 1993)
NZ Soil Classification - Mellow humic organic soil (Hewitt, 1998)
USDA Taxonomy - Sapric Haplohemists

Depth to gravels - 60 cm.
Drainage - Very poorly drained.



| Layer Depth Description | | | Plate 10 |
|-------------------------|----------|---|----------|
| O | 0-5 cm | 10YR 4/2 (Dark greyish brown). Organic layer, matted fine roots. Prevalent litter from surrounding trees. Boundary with next organic layer distinct but wavy. | |
| O | 5-8 cm | 10YR 2/2 (Brownish black). Loamy peat (Table 5). Very strongly decomposed dark brown with black concretions, slightly sticky. | |
| O | 8-30 cm | 10YR 2/3 (Brownish black). Loamy peat (Table 5). Weakly decomposed fine leaves, twigs, intact pieces of wood. | |
| Bhr | 30-60 cm | 7.5YR 3/3 (Greyish brown). Silty peat muck (description after Almond 1997), silt material identified after ignition (Table 5). Very wet fluid soil, abundant live roots down to gravels (Photo unclear as face not cleaned up properly) | |
| C | (60 cm) | Weathered fine to medium gravels and occasional large stones up to 15 cm across). 65% fine P gravels. 35% 1-3 cm stones. Yellow- brown stain. Gravels are rounded (alluvial). High penetration/ resistance. | |

In this plot, four pits dug across a transect were briefly described in Table 3.
Pit 2 ($x=20, y=24$) is similar to pit 1 in peat composition (*Kini*). Depth to gravels - 80 cm
Pit 1 ($x=5, y=20$) is similar to pit 4 in peat composition (*Rotokuhu*). Depth to gravels - 60 cm
General soil limitations:. Composed of organic matter, derived mainly from flax and kahikatea (*Dacrycarpus*), with some alluvium (granite)...found in flat low lying hollows or back-sloping parts of low glacial outwash terraces. Usually complexed with Maimai soils. Extremely acid, but high cation exchange of Mg, K and Na...(although) limited data because waterlogging makes observation difficult...correlated with *Kini* peats. Main limitation is high water table (Mew & Ross 1980: 24-25).

DRAINAGE CLASSES

(Adapted from Taylor and Pohlen, 1970; and Canadian Soil Science Drainage Assessment 1987).

Very Poorly Drained: Water is removed so slowly that the water table remains at or on the surface the greater part of the time. Groundwater flow and subsurface flow are the major sources of water, precipitation is less important except where there is a perched water table. Soils of this drainage class occupy level or depressed sites and are frequently ponded. They commonly have peaty surface layers.

Poorly Drained: Water is removed so slowly in relation to supply that the soil remains wet (moisture status is above field capacity) for a comparatively large part of the time. Poorly drained conditions are due to a high water table from subsurface flow, groundwater flow, precipitation, a slowly permeable layer within the profile, to seepage, or to some combination of these conditions. A perched water table may also be present. They have peaty surface layers and grey subsoil colours or other evidence of gleying.

Well drained: Water is removed from the soil readily; excess water flows downward into underlying pervious material or laterally as subsurface flow. These soils commonly retain optimum amounts of moisture for plant growth after rains for lengthy periods. In the case of Westland soils, these are likely to be yellow-brown earth soils commonly of a silt loam or stony silt loam texture (Brown soils - Hewitt, 1998).

TABLES and FIGURES

Table A1: Best fit regression equations for estimating age (y) from diameter at breast height (x) for dominant species in very poorly drained plot (A), Mt. Harata. P<0.001 for all species. MAI is the mean annual ring width (mm/ year) increment for species >20 stems

| Species | N | Dbh range (cm) | Equation | R ² | MAI (mm/ year) | Fishers LSD between means |
|-----------------------|----|----------------|------------------|----------------|----------------|---------------------------|
| <i>N. fusca</i> | 35 | 5 - 51.2 | y = 24.8 + 3.4x | 0.75 | 0.24 ± 0.09 | A |
| <i>Dacrydium</i> | 40 | 11.3 - 62.5 | y = 100.6 + 2.8x | 0.65 | 0.18 ± 0.05 | B |
| <i>N. menziesii</i> | 48 | 5.8 - 70.2 | y = 38.44 + 9.5x | 0.72 | 0.17 ± 0.07 | B C |
| <i>E. hookerianus</i> | 22 | 10.5 - 49.6 | y = 62.1 + 3.9x | 0.58 | 0.15 ± 0.04 | B C |
| <i>Dacrycarpus</i> | 42 | 8.9 - 75.6 | y = 80.9 + 4.2x | 0.74 | 0.15 ± 0.04 | C |

Table A2: Patterns of spatial dispersion for trees (≥5 cm dbh) and saplings (>1.4m ht, <5 cm dbh) by species. Letters indicate significant (P< 0.05) deviation from a random distribution at distance t based on values of the function K(t): U = uniformly distributed: C = clumped distribution: . = random distribution. Sapl = saplings >1.4m ht, ≤5 cm dbh; n = no individuals.

| Type | Species | t (metres) | | | | | n |
|-------|---|--------------|--------------|--------------|----|----|-----|
| | | 1 | 5 | 10 | 15 | 20 | |
| trees | <i>Dacrydium cupressinum</i> | | CCCCC | CCCCCCCCCCCC | | | 41 |
| trees | <i>Dacrydium</i> (live & dead) | | CCCCC | CCCCCCCCCCCC | | | 53 |
| trees | <i>Dacrycarpus dacrydioides</i> | | | | | | 42 |
| trees | <i>Dacrycarpus</i> (live & dead) | | CCC | CCC | C | | 66 |
| sapl | <i>Dacrycarpus</i> | CCCCCCCCCCCC | CCCCCCCCCCCC | | | | 34 |
| trees | <i>Nothofagus fusca</i> | | | | | | 39 |
| trees | <i>N. fusca</i> (live & dead) | | | | | | 52 |
| sapl | <i>N. fusca</i> | CCCCCCCCCCCC | CCCCCCCCCCCC | | | | 275 |
| trees | <i>Nothofagus menziesii</i> | | | | | | 51 |
| trees | <i>N. menziesii</i> (live & dead) | | CC | CCCCCCCCCCCC | | | 80 |
| sapl | <i>N. menziesii</i> | CCCCCCCCCCCC | CCCCCCCCCCCC | | | | 71 |
| trees | <i>Elaeocarpus hookerianus</i> | | | | | | 25 |
| sapl | <i>E. hookerianus</i> | CCCCCCCCCCCC | CC | | | | 20 |
| trees | <i>Libocedrus bidwillii</i> (live & dead) | | CC | CCCCCCCCCCCC | | | 19 |

Table B1: Best fit regression equations for estimating age (y) from diameter at breast height (x) for dominant species in very poorly drained plot B. P<0.001 for all species except *Q. acutifolia* which was not statistically significant and is not presented. MAI is the mean annual ring width (mm/ yr) increment for species >20 stems.

| Species | N | Dbh range (cm) | Equation | R ² | MAI (mm/ year) | Fishers LSD between means |
|-----------------------|-----|----------------|--|----------------|----------------|---------------------------|
| <i>N. fusca</i> | 81 | 5.2 - 96.0 | y = 37.24 + 0.18 x + 0.04x ² | 0.84 | 0.29 ± 0.12 | A |
| <i>N. menziesii</i> | 109 | 5.4 - 75.8 | y = 45.77 + 4.19x | 0.63 | 0.17 ± 0.09 | B |
| <i>Dacrycarpus</i> | 23 | 5.1 - 75.8 | y = -20.87 + 11.66x - 0.08x ² | 0.96 | 0.15 ± 0.05 | B C |
| <i>W. racemosa</i> | 81 | 5.9 - 43.4 | y = 68.56 + 3.81x | 0.44 | 0.14 ± 0.05 | C |
| <i>Dacrydium</i> | 36 | 14.3 - 111.8 | y = 7.89 + 8.83x | 0.80 | 0.12 ± 0.03 | C |
| <i>P. ferruginea</i> | 14 | 9.1 - 52.7 | y = -34.01 + 12.98x | 0.89 | | |
| <i>E. hookerianus</i> | 13 | 7.4 - 37.3 | y = 4.63 + 5.49x | 0.78 | | |

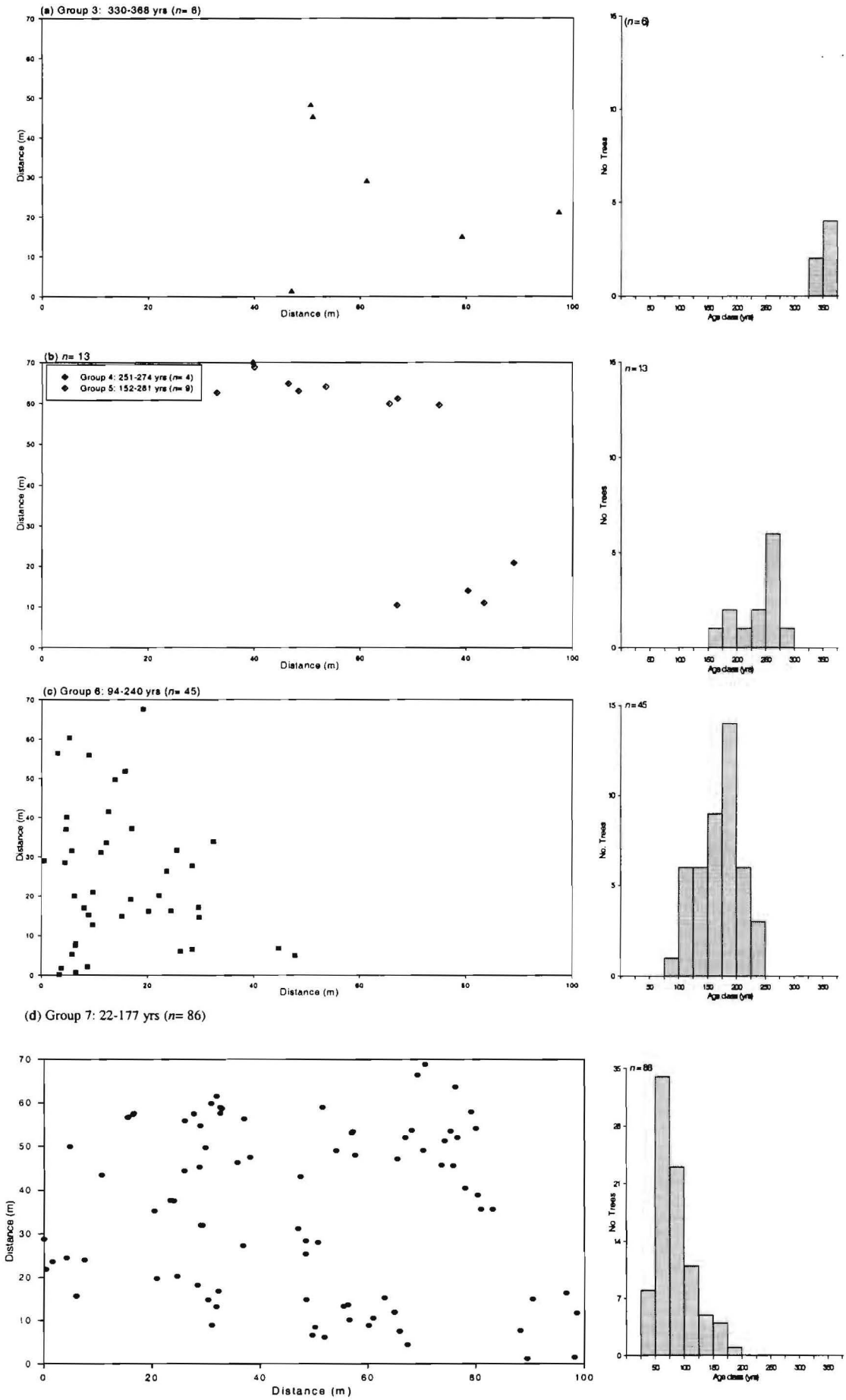


Figure B1: Stem maps and age-class frequency distributions for *N. menziesii* age groups identified from cluster analysis.

Table B2: Seedlings on logs at different stages of breakdown by log decay class (adapted from Stewart and Burrows, 1994).

| Species | L1 | L2 | L3 | L4 | TOTAL |
|---------------------|----|-----|-----|----|-------|
| <i>N. menziesii</i> | 24 | 223 | 102 | 48 | 397 |
| <i>N. fusca</i> | | 12 | 18 | 20 | 50 |
| <i>W. racemosa</i> | 1 | 10 | 11 | 16 | 38 |
| <i>Dacrydium</i> | 2 | 12 | 12 | 14 | 40 |
| <i>Dacrycarpus</i> | | 13 | 23 | 13 | 49 |

Table C1: Best fit regression equations for estimating age (y) from diameter at breast height (x) for dominant species in well drained plot (C), Mt. Harata. P<0.001 for all species. MAI is the mean annual ring width (mm/year) increment for species >20 stems

| Species | N | Dbh range (cm) | Equation | R ² | MAI (mm/year) | Fishers LSD between means |
|----------------------|----|----------------|---------------------|----------------|-----------------|---------------------------|
| <i>N. fusca</i> | 50 | 9.5 - 92.3 | $y = 54.83 + 1.86x$ | 0.80 | 0.30 ± 0.12 | A |
| <i>N. menziesii</i> | 86 | 5.0 - 56.3 | $y = 27.6 + 4.41x$ | 0.84 | 0.18 ± 0.06 | B |
| <i>Q. acutifolia</i> | 31 | 7.0 - 53.0 | $y = 29.74 + 4.83x$ | 0.80 | 0.16 ± 0.03 | B |
| <i>W. racemosa</i> | 82 | 8.2 - 65.8 | $y = 52.24 + 4.91x$ | 0.89 | 0.13 ± 0.04 | C |

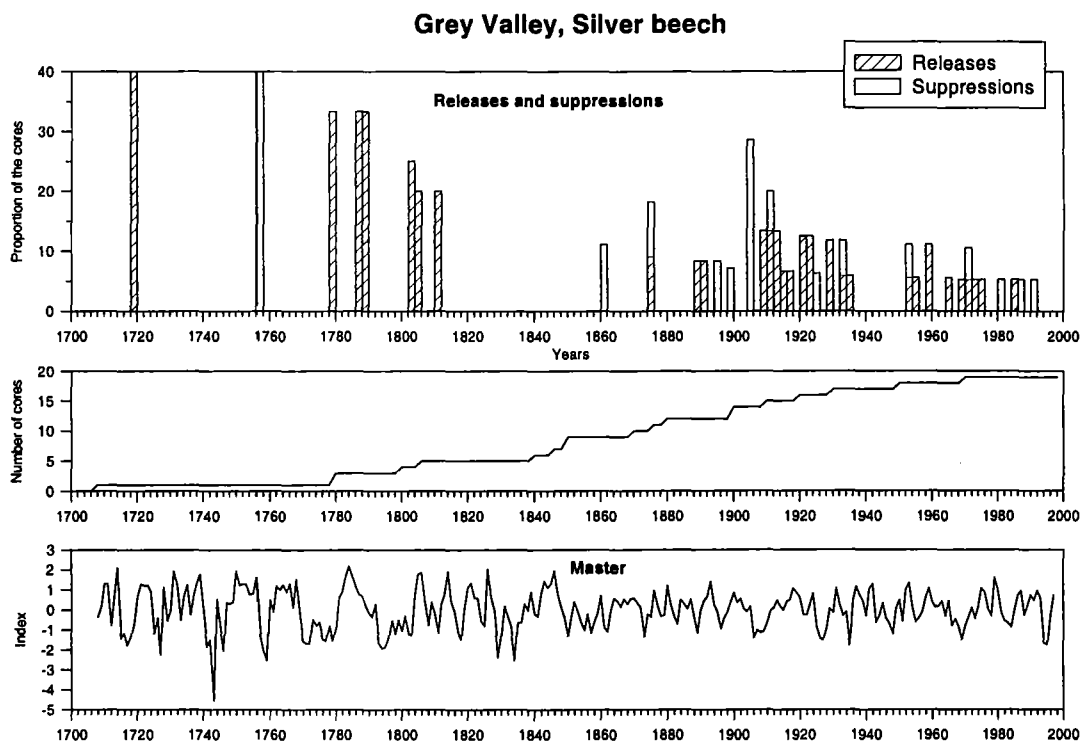


Figure C1: Selection of *N. menziesii* cores able to be successfully cross-dated from plot C, Mt Harata as part of a wider study of earthquake impacts in north Westland in the last century (kindly used with authors permission - Pascal Vittoz). Note there are some differences to releases detected from those in this study (Fig. 32), as I also used uncross-matched cores from the same plot but broad patterns of significant upsurges in releases are similar.

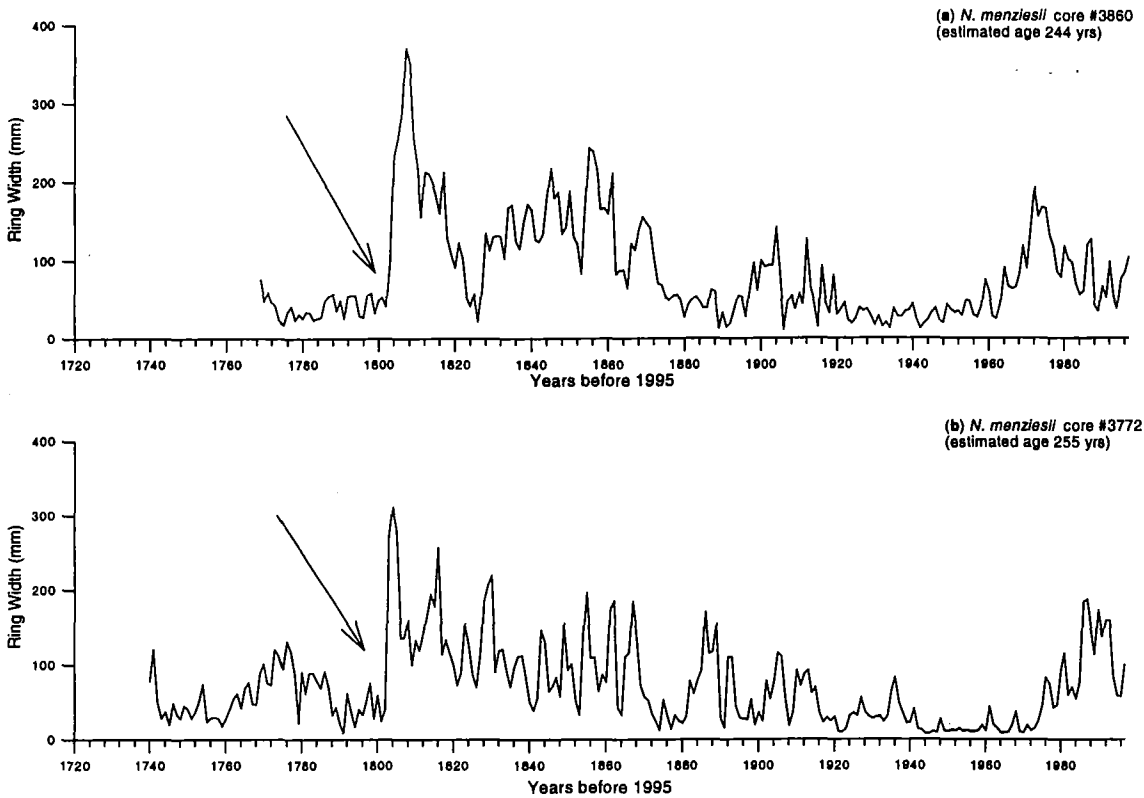


Figure C2: Examples of *N. menziesii* cores in plot C showing substantial synchronous growth increases c. 200 yrs ago (marked by arrows) after release from slower initial growth.

Table D1: Mean annual ring width increment rates (cm/ yr) for individual species (>20 cm dbh) on differently drained surfaces at Mt. Harata. Min MAI refers to the slowest growing individual, Max MAI refers to the fastest growing individual of each species. Figures in brackets are diameter of slowest and fastest growing individuals. The letters in the Fishers LSD column represent significant differences ($P<0.001$) in growth rates between species except kahikatea-rimu ($P<0.01$). (Table 5 from Ulrich *et al*, 1999).

| Species | <i>n</i> | MAI (cm/yr) | s.d | Min MAI (cm/yr) | Max MAI (cm/yr) | Fishers LSD between spp |
|-----------------------|----------|-------------|------|-----------------|-----------------|-------------------------|
| Poorly drained | | | | | | |
| Red beech | 105 | 0.31 | 0.13 | 0.13 (22) | 0.67 (42) | A |
| Silver beech | 136 | 0.18 | 0.07 | 0.07 (21) | 0.51 (25) | B |
| Kahikatea | 84 | 0.17 | 0.04 | 0.08 (21) | 0.32 (64) | B |
| Rimu | 174 | 0.14 | 0.04 | 0.07 (25) | 0.26 (63) | C |
| Well drained | | | | | | |
| Red beech | 159 | 0.36 | 0.13 | 0.12 (30) | 0.80 (65) | X |
| Silver beech | 110 | 0.21 | 0.8 | 0.08 (21) | 0.50 (30) | Y |

Table E1: Horizonation description and classification (after Stewart *et al*, 1993), overall depth of soils in 20 circular plots across the terrace.

| <i>Well</i> | | <i>Drained</i> | <i>Plots</i> | | | | | | | |
|-----------------------|-------|----------------|--------------|-----------------|-------|-----------------------------|-----------------------------|----------------------------|---------------------|--|
| A5 | A6 | B5 | B6 | B11 | B12 | C10 | D1 | D11 | F11 | |
| <i>Horizonation</i> | | | | | | | | | | |
| L,F,H | L,F,H | L,F,H | L,F,H | L,F,H | L,F,H | L,F,H | L,F,H | L,F,H | L,F,H | |
| AB | Ah | Ah | Ah | Ah | Ah | Ah | Ah | Ah | Ah | |
| Bw | Bw | Bw | Bw | Bw ₁ | Bw | Bwg | Bwg | Bw | Bw ₁ | |
| | | | | Bw ₂ | | | | | Bw ₂ | |
| <i>Depth</i> | | | | | | | | | | |
| 25cm | 25cm | 40cm | 50cm | 35cm | 30cm | 40cm | 60cm | 40cm | 50cm | |
| <i>Classification</i> | | | | | | | | | | |
| YBE | YBE | YBE | YBE | YBE | YBE | YBE-GYBE | YBE-GYBE | YBE | YBE | |
| <i>Notes</i> | | | | | | Some areas signs of gleying | Soils have signs of gleying | Large areas of wet hollows | Silt lamina 20-35cm | |

| <i>Poorly</i> | | <i>drained</i> | <i>Plots</i> | | | | | | | |
|-----------------------|----------------|----------------|--------------|------------|-------|------------|-------|------|-------|--|
| B7 | C3 | C6 | C9 | D4 | D9 | D10 | E3 | E7 | E10 | |
| <i>Horizonation</i> | | | | | | | | | | |
| O | O ¹ | O | O | O | O | O | O | O | O | |
| Bg | Peat | Peat | Peat | Peat | Peat | Peat | Peat | Peat | Peat | |
| | | Bg | Bg | Bwg | | Bg | | | Bg | |
| <i>Depth</i> | | | | | | | | | | |
| 50cm | 100cm | 60cm | 65cm | 50cm | 100cm | 50cm | 100cm | 70cm | 100cm | |
| <i>Classification</i> | | | | | | | | | | |
| Gley | Peat | Peaty-Gley | Peaty-Gley | Peaty-Gley | Peat | Peaty-Gley | Peat | Peat | Peat | |

Notes
¹ O layer is top 5 cm layer that is fibrous and saturated, Peat is O layer differentiated from top 5 cm.

Table E2: Basal area (m²/ ha) and stem density per ha (≥ 5 cm dbh) in the 10 well-drained and 10 poorly drained circular plots across the terrace.

| BASAL AREA | | | | | Plot no | | | | | |
|-----------------------------|-------------|-------------|-------------|-------------|----------------|-------------|-------------|-------------|-------------|-------------|
| Well drained plots | A5 | A6 | B5 | B6 | B11 | B12 | C10 | D1 | D11 | F11 |
| <i>N. fusca</i> | 45.2 | 40.8 | 38.2 | 53.2 | 33.7 | 38.9 | 20.9 | 33.0 | 38.8 | 36.9 |
| <i>N. menziesii</i> | 3.8 | 3.1 | 7.1 | 10.6 | 5.7 | 10.9 | 14.7 | 7.1 | 5.9 | 9.9 |
| <i>W. racemosa</i> | 6.9 | 11.2 | 8.2 | 12.0 | 9.8 | 13.5 | 8.3 | 9.2 | 13.4 | 5.8 |
| <i>Dacrydium</i> | | | | | 0.9 | 1.4 | 0.4 | | 1.6 | 7.7 |
| <i>Dacrycarpus</i> | | | | | 2.6 | | | | | |
| Total | 55.9 | 55.1 | 53.5 | 75.8 | 52.7 | 64.7 | 44.3 | 49.3 | 59.7 | 60.3 |
| Poorly drained plots | B7 | C3 | C6 | C9 | D4 | D9 | D10 | E3 | E7 | E10 |
| <i>N. fusca</i> | 24.3 | 20.8 | 5.9 | 6.1 | 7.4 | 4.5 | 18.0 | 4.9 | 34.1 | 5.6 |
| <i>N. menziesii</i> | 7.9 | 1.8 | 24.3 | 42.3 | 22.5 | 7.1 | 7.6 | 26.2 | 15.7 | 14.3 |
| <i>W. racemosa</i> | 1.2 | 5.7 | 3.7 | 3.7 | 6.0 | 0.1 | 4.6 | 3.4 | 3.3 | 6.1 |
| <i>Dacrydium</i> | 14.4 | 11.7 | 22.2 | 17.5 | 12.6 | 17.2 | 28.6 | 25.4 | 11.8 | 16.0 |
| <i>Dacrycarpus</i> | 1.3 | 7.6 | 8.6 | 4.6 | 4.2 | 12.6 | 18.7 | 6.5 | 11.1 | 0.8 |
| Total | 49.1 | 47.6 | 64.7 | 74.2 | 52.7 | 41.5 | 77.5 | 66.4 | 76.0 | 42.8 |
| STEM DENSITY | | | | | | | | | | |
| Well drained plots | A5 | A6 | B5 | B6 | B11 | B12 | C10 | D1 | D11 | F11 |
| <i>N. fusca</i> | 244 | 381 | 204 | 234 | 247 | 169 | 81 | 417 | 163 | 160 |
| <i>N. menziesii</i> | 68 | 196 | 199 | 306 | 156 | 161 | 96 | 278 | 119 | 119 |
| <i>W. racemosa</i> | 374 | 677 | 326 | 518 | 332 | 765 | 402 | 388 | 413 | 402 |
| <i>Dacrydium</i> | | | | | 28 | 27 | 20 | | 38 | 25 |
| <i>Dacrycarpus</i> | | | | | 15 | | | | | |
| Total | 686 | 1254 | 729 | 1058 | 778 | 1122 | 599 | 1083 | 733 | 706 |
| Poorly drained plots | B7 | C3 | C6 | C9 | D4 | D9 | D10 | E3 | E7 | E10 |
| <i>N. fusca</i> | 258 | 118 | 51 | 39 | 144 | 66 | 58 | 37 | 247 | 99 |
| <i>N. menziesii</i> | 283 | 140 | 266 | 337 | 301 | 111 | 61 | 590 | 237 | 161 |
| <i>W. racemosa</i> | 57 | 343 | 100 | 79 | 210 | 16 | 173 | 100 | 109 | 182 |
| <i>Dacrydium</i> | 126 | 109 | 107 | 64 | 54 | 189 | 94 | 54 | 36 | 76 |
| <i>Dacrycarpus</i> | 14 | 85 | 57 | 31 | 16 | 73 | 64 | 96 | 97 | 47 |
| Total | 738 | 795 | 581 | 550 | 725 | 455 | 450 | 877 | 726 | 565 |

Table E3: No. trees that established on logs and (% of microsites established on) in all poorly drained plots from chapter 1 and chapter 2.

| Plot | <i>N. menziesii</i> | <i>N. fusca</i> | <i>W. racemosa</i> |
|------------------|----------------------------|------------------------|---------------------------|
| Plot A | 23 (45%) | 14 (36%) | 0 |
| Plot B | 64 (43%) | 36 (33%) | 12 (12%) |
| 10 Terrace Plots | 52 (35%) | 13 (11%) | 13 (10%) |
| TOTAL | 139 (40%) | 63 (24%) | 25 (10%) |

N. fusca

N. menziesii

W. racemosa

Group A

Plot (all well-drained)

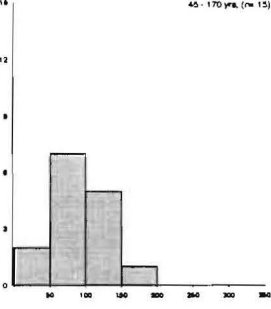
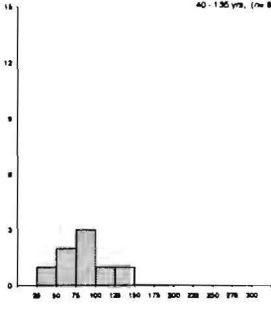
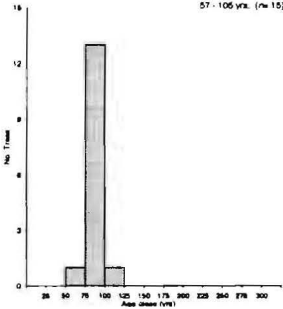
A5

1

Event

1

1

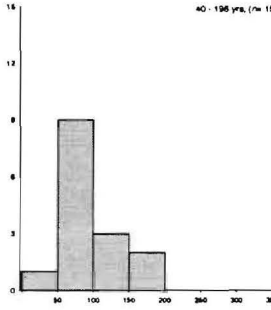
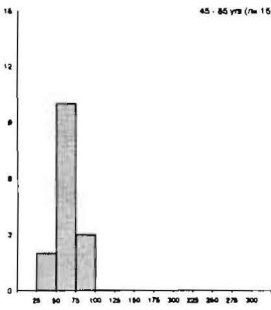
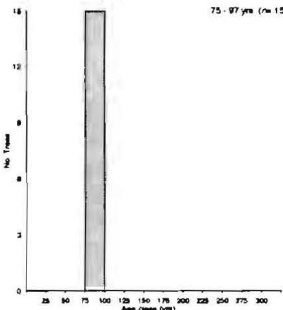


A6

1

1

1

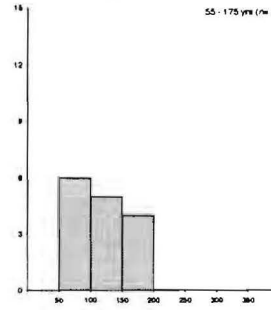
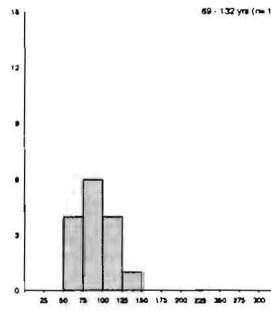
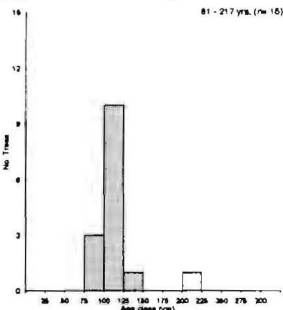


B5

1

1

1

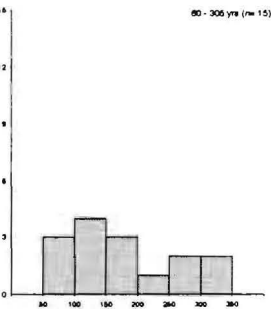
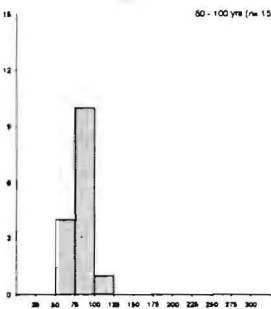
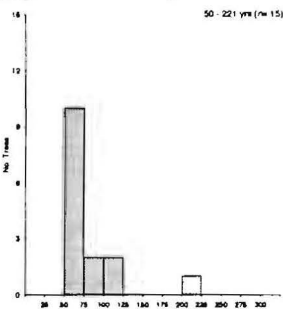


D1

1

1

1

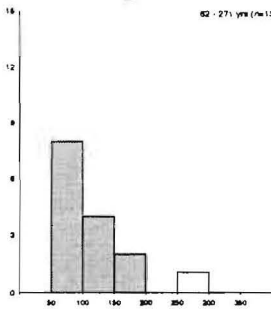
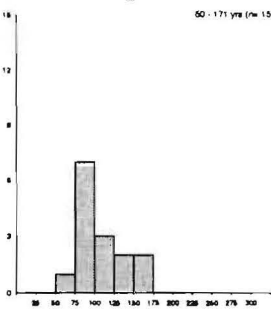
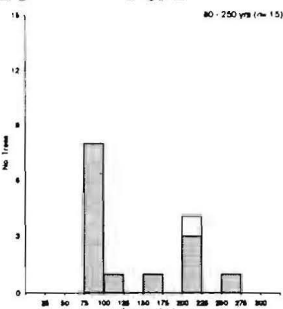


B6

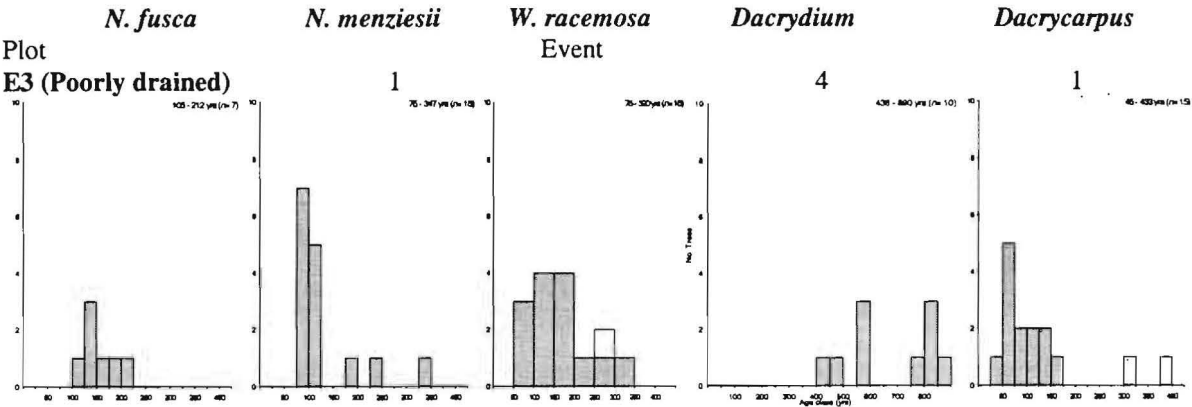
1 & 2

1

1



Group A (continued)



Group B

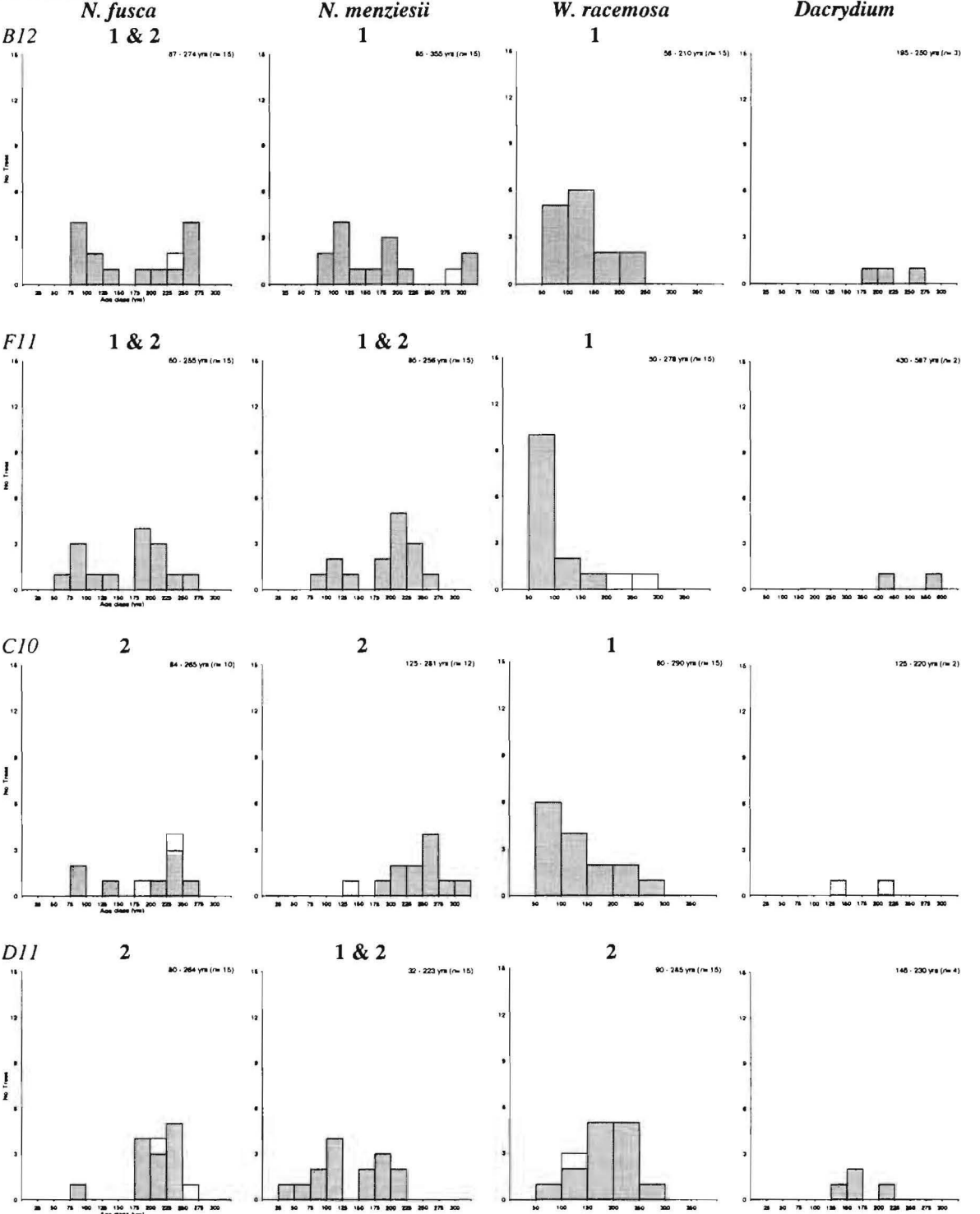


Figure E1: Age-class frequency distributions for Groups A and B across the terrace in Groups from Fig. 2.

N. fusca

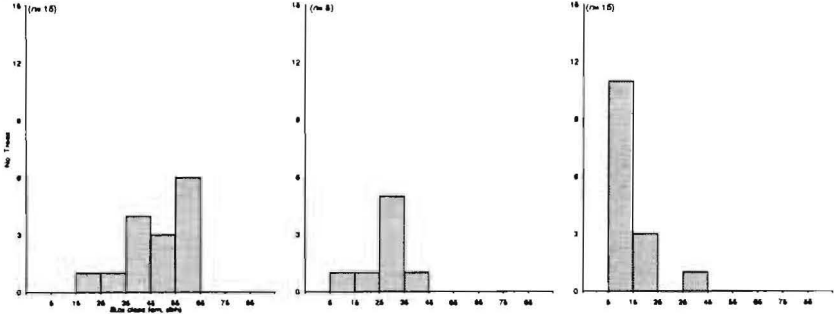
N. menziesii

W. racemosa

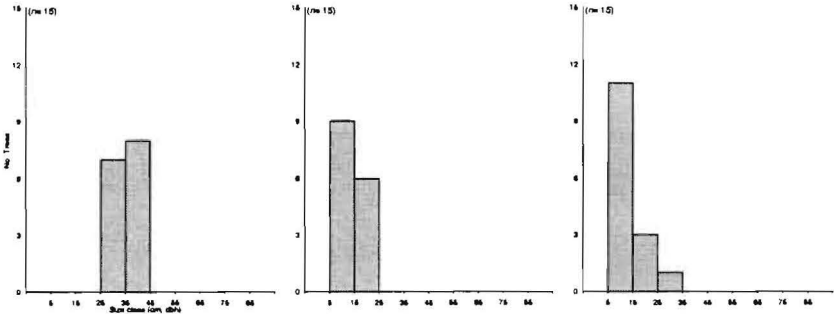
Dacrydium

GROUP A

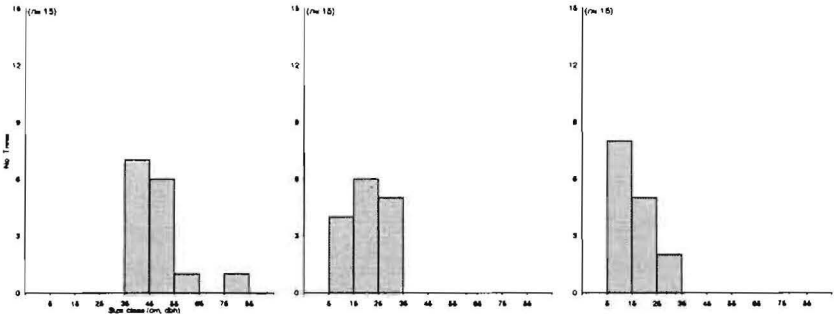
A5



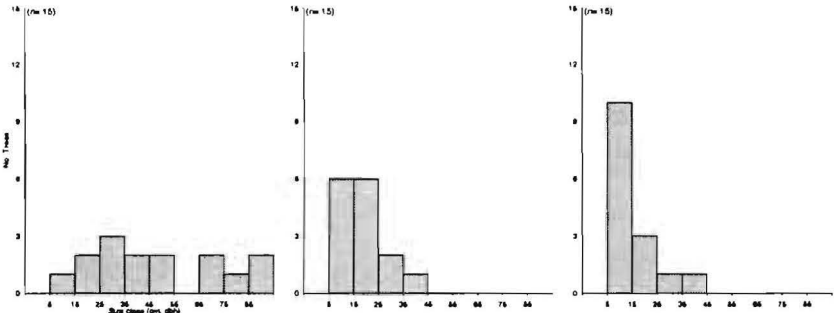
A6



B5

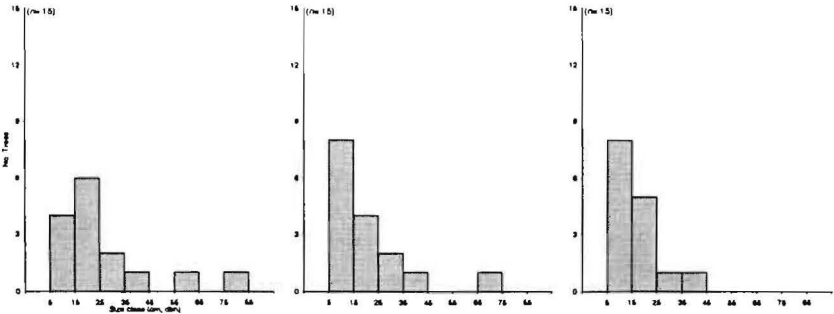


B6



GROUP B

D1



N. fusca

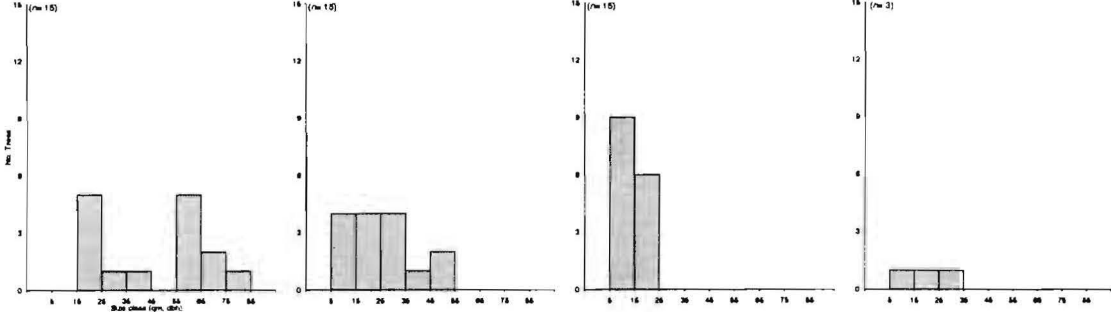
N. menziesii

W. racemosa

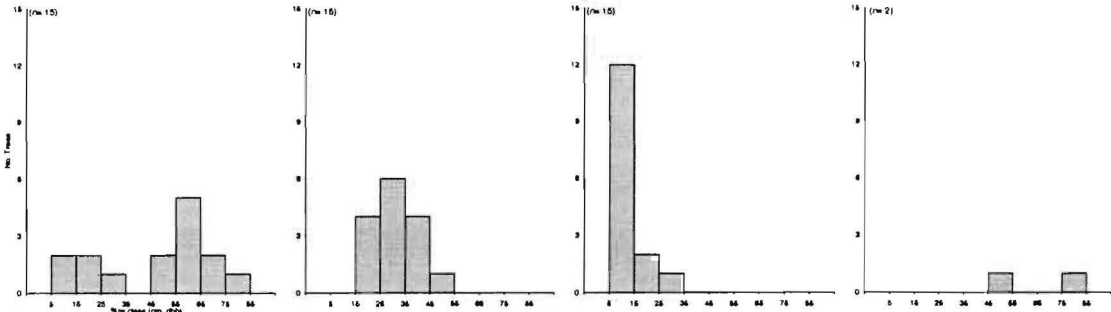
D. cupressinum

GROUP C

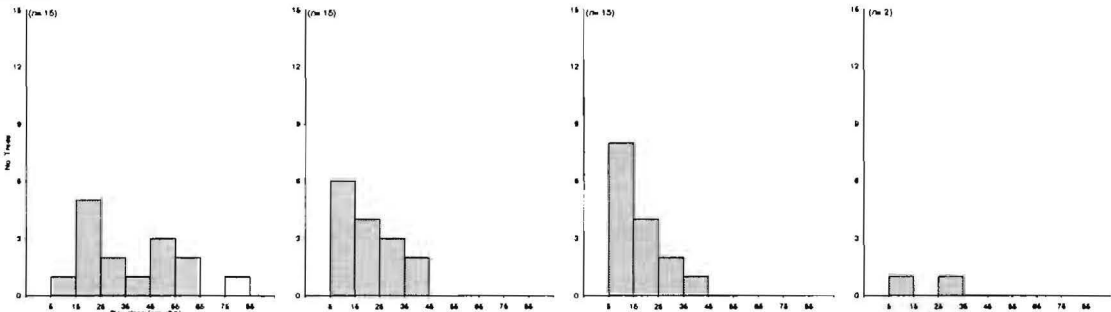
B12



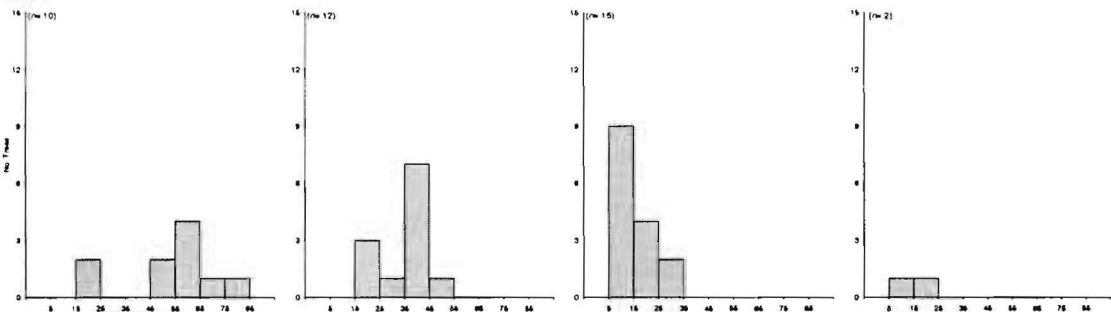
F11



B11



C10



GROUP D

D11

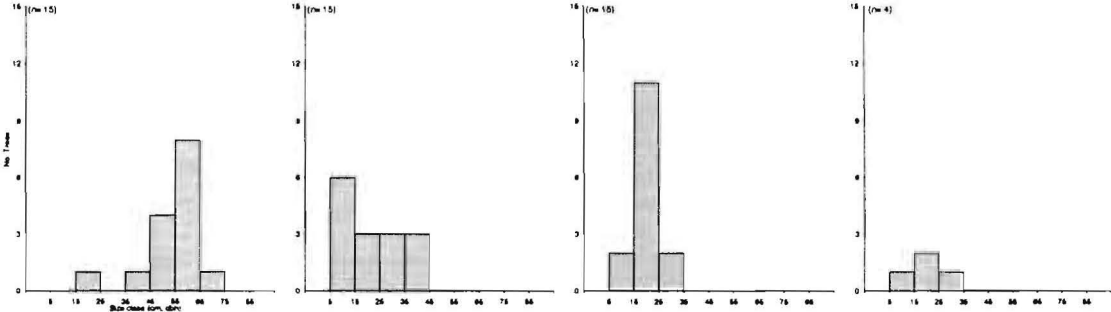
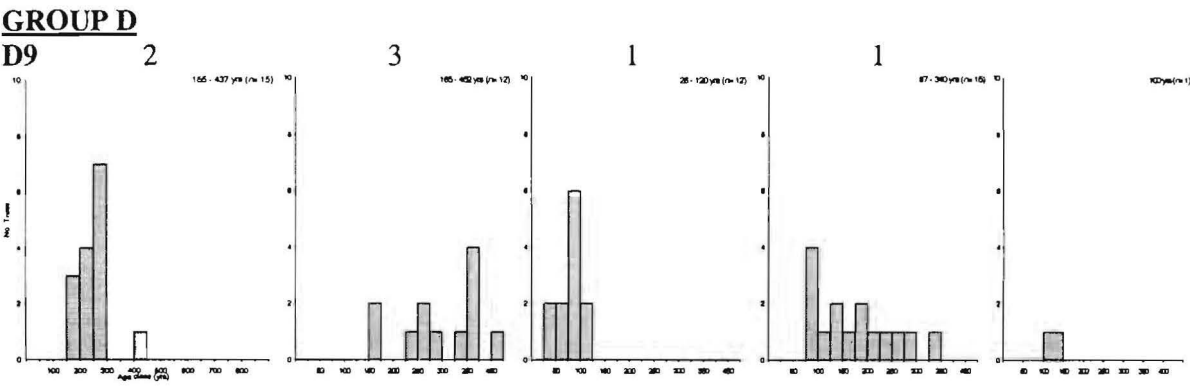
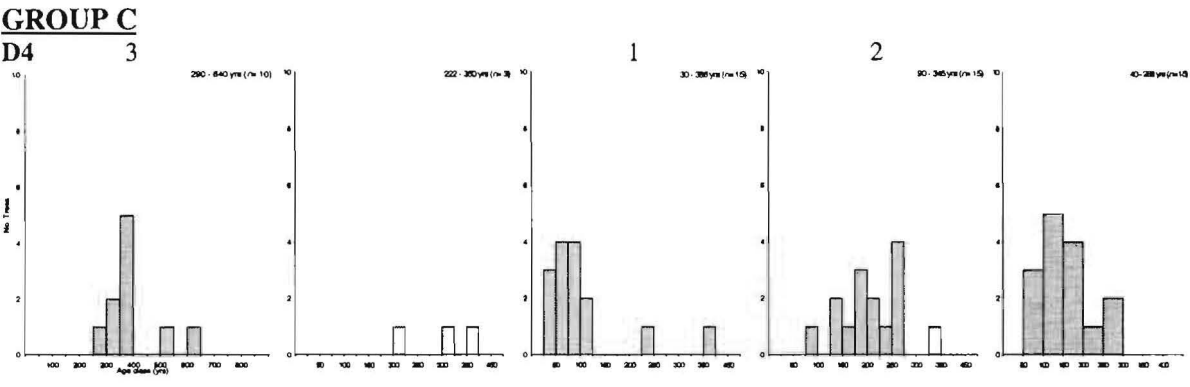
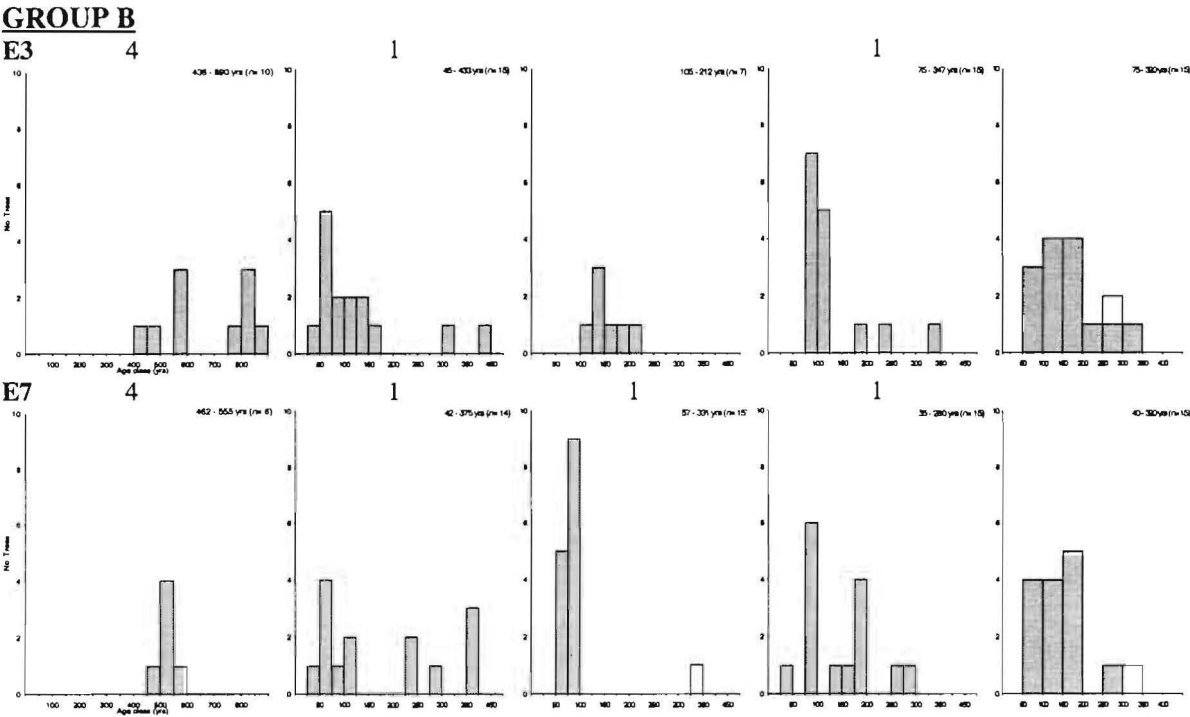
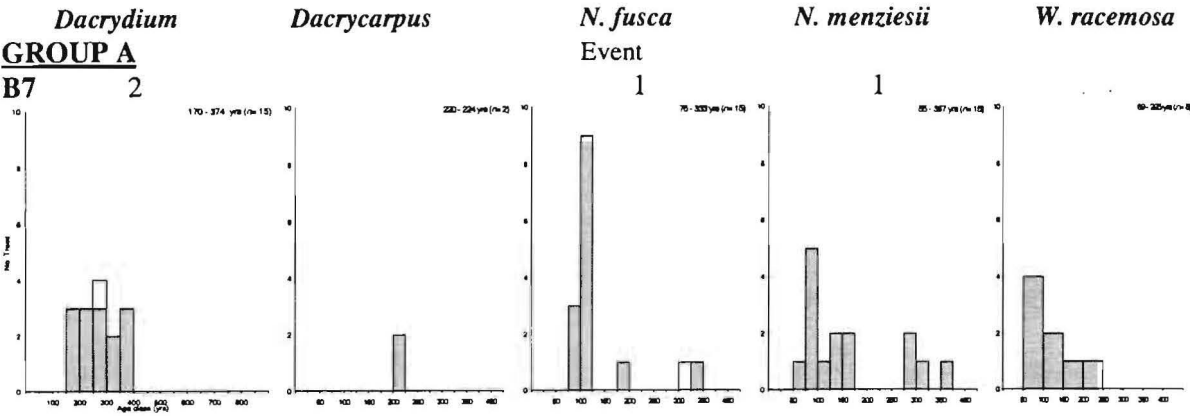


Figure E2: Size-class frequency distributions for all species on well drained plots in Groups from Fig. 2.



Dacrydium
GROUP D (Continued)

Dacrycarpus

N. fusca
Event

N. menziesii

W. racemosa

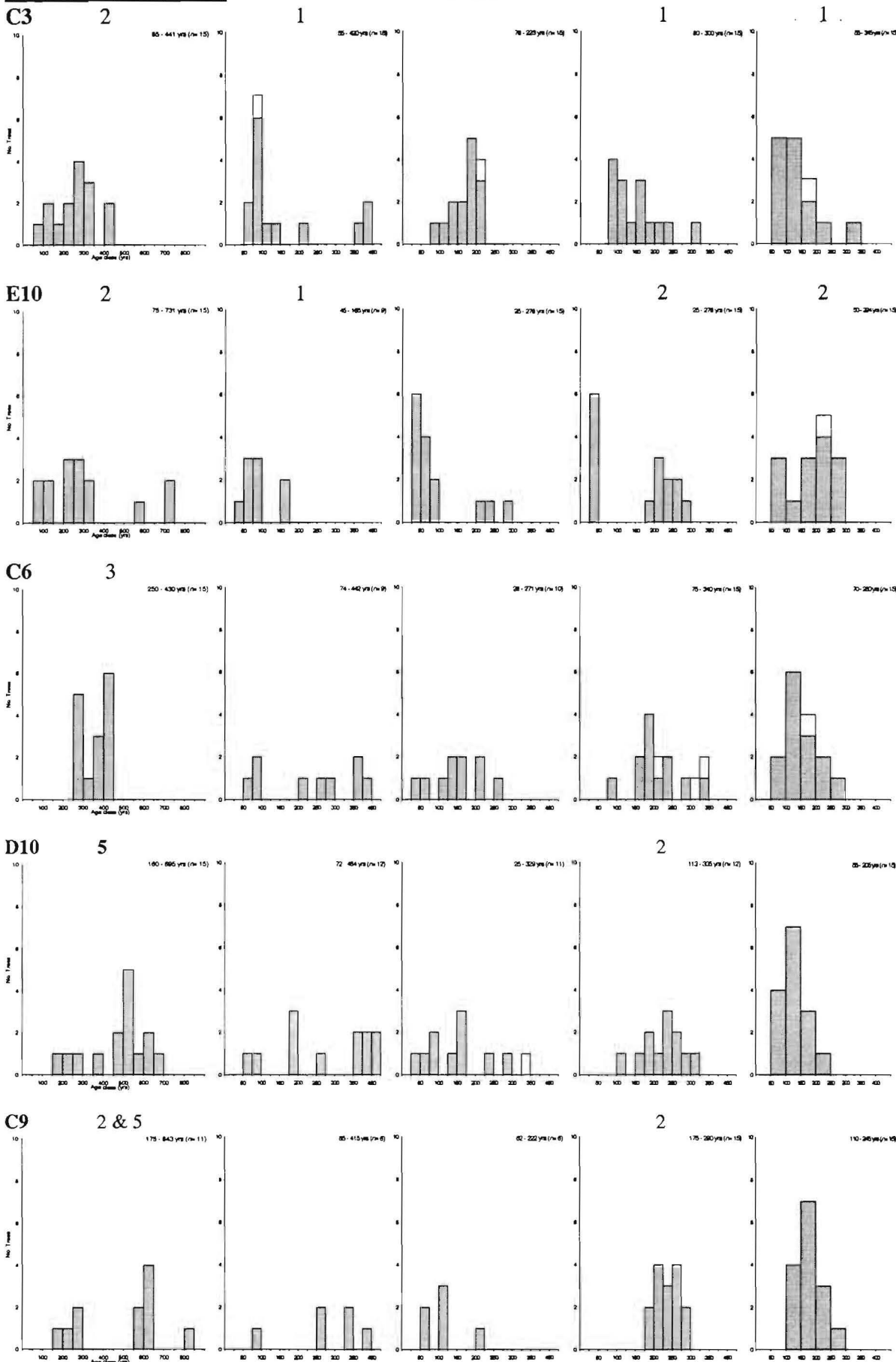


Figure E3: Age-class frequency distributions for all species on poorly drained plots in Groups from Fig. 2. Unfilled bars represent ages determined from age/ diameter regressions for unaged trees. All regressions significant at $\alpha=0.01$ level except *N. menziesii* in plot C6 where regressions significant at $P=0.09$.

Dacrydium
GROUP A

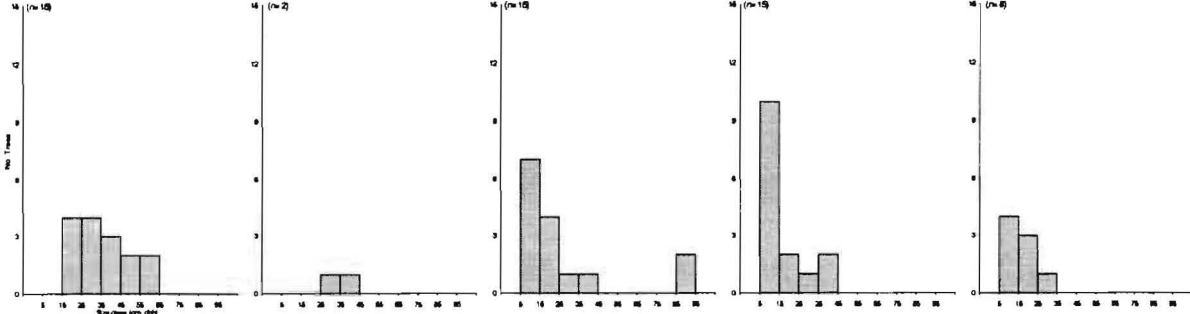
Dacrycarpus

N. fusca

N. menziesii

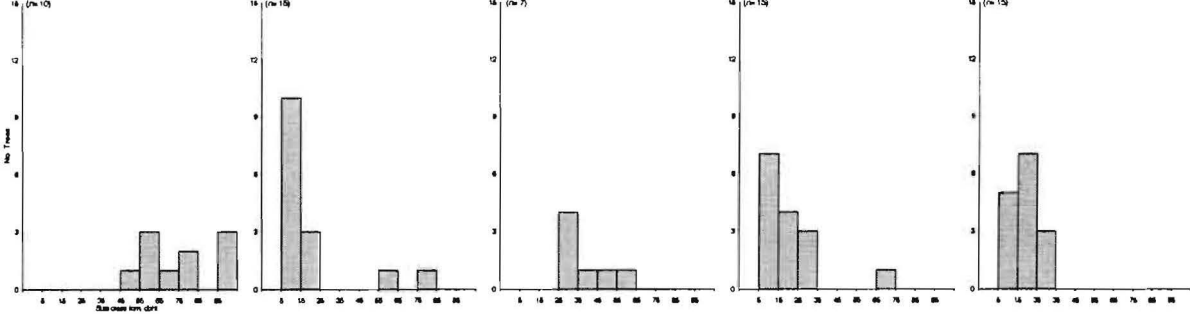
W. racemosa

B7

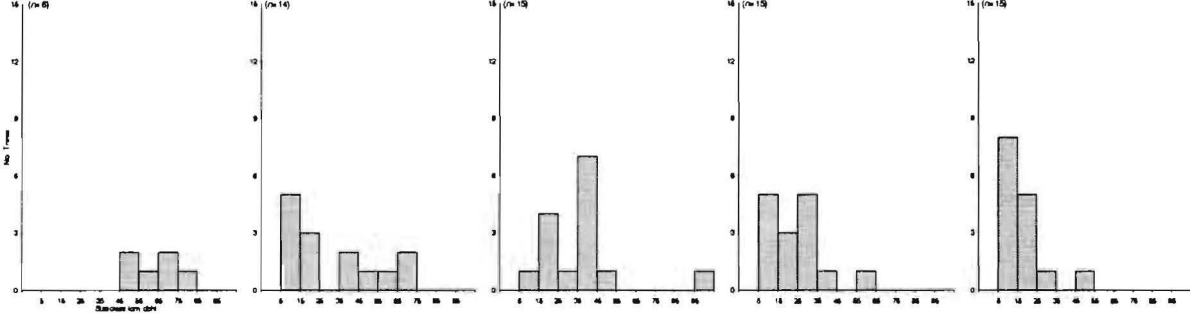


GROUP B

E3

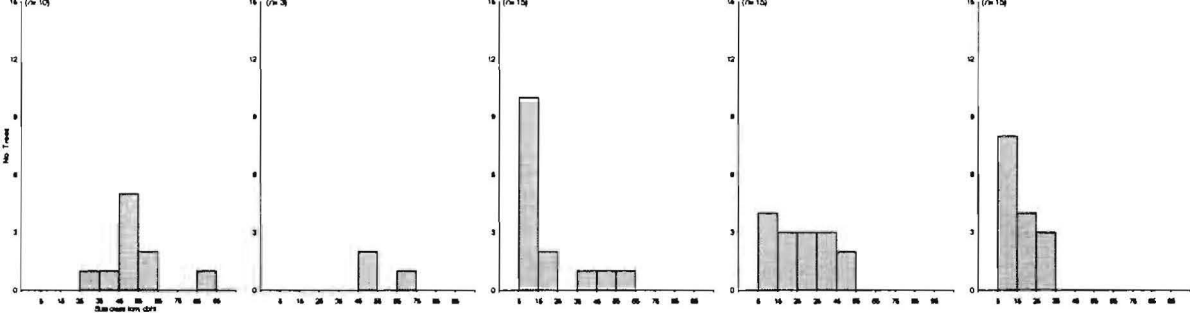


E7



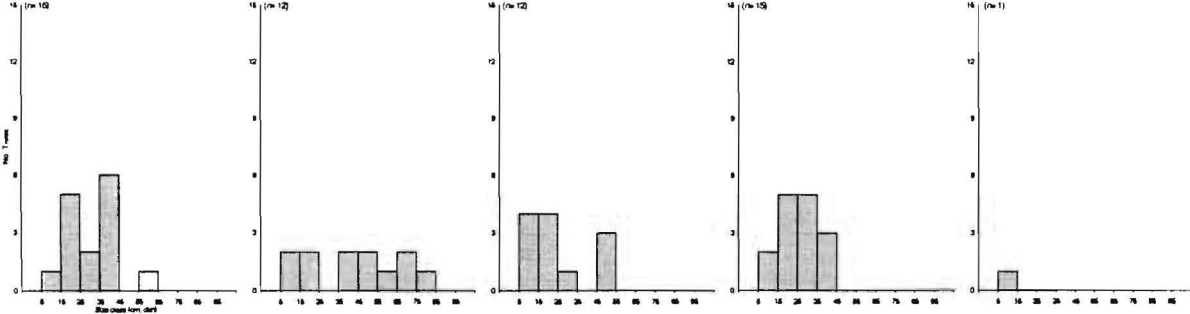
GROUP C

D4



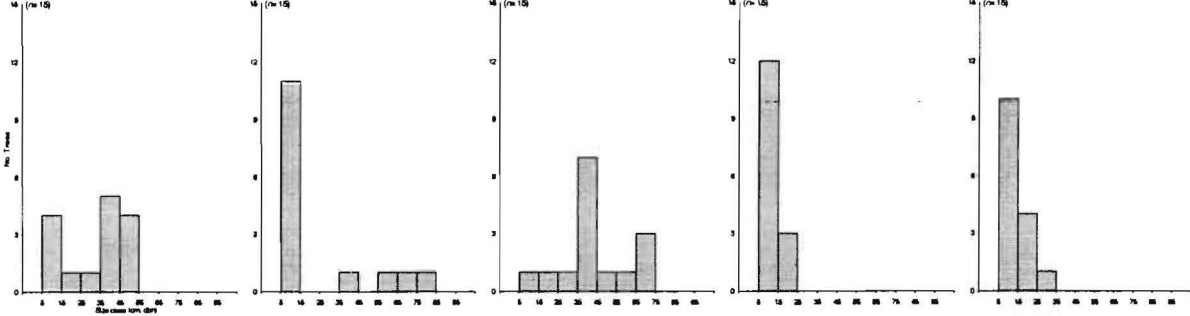
GROUP D

D9

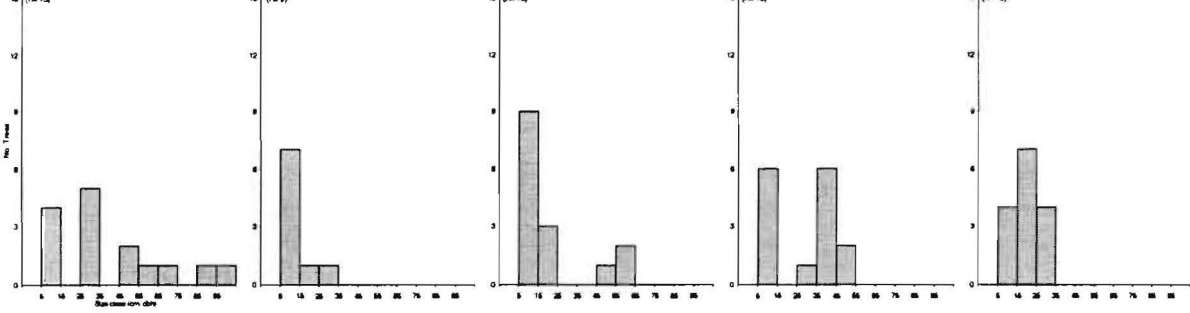


GROUP D (Continued)

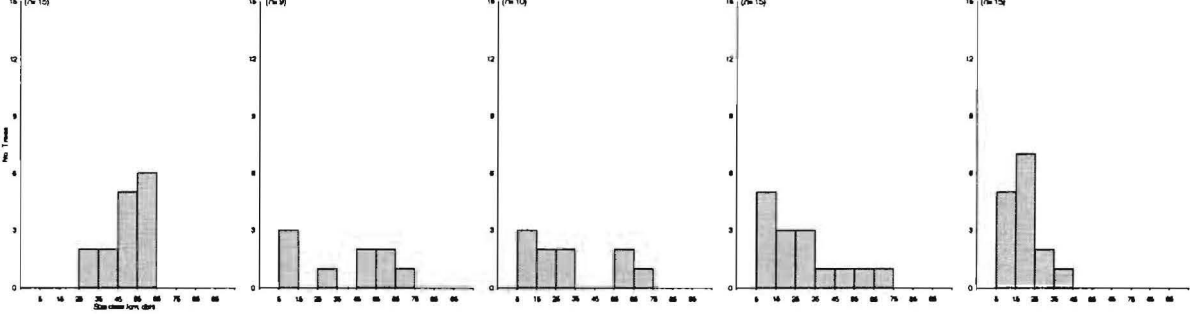
C3



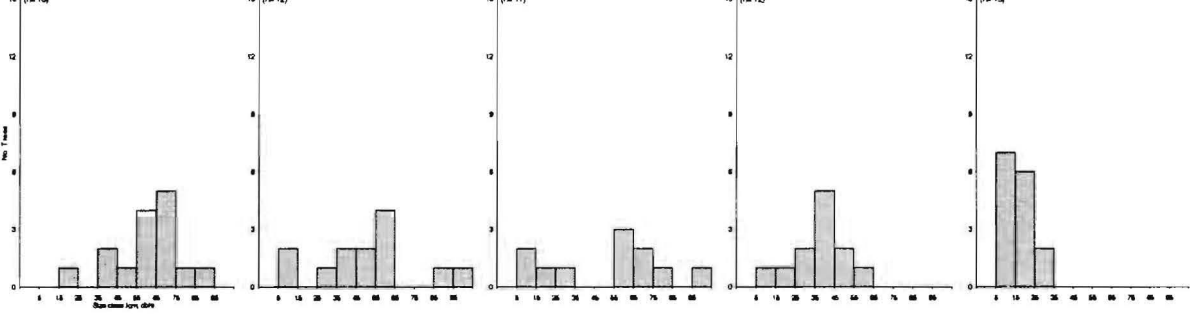
E10



C6



D10



C9

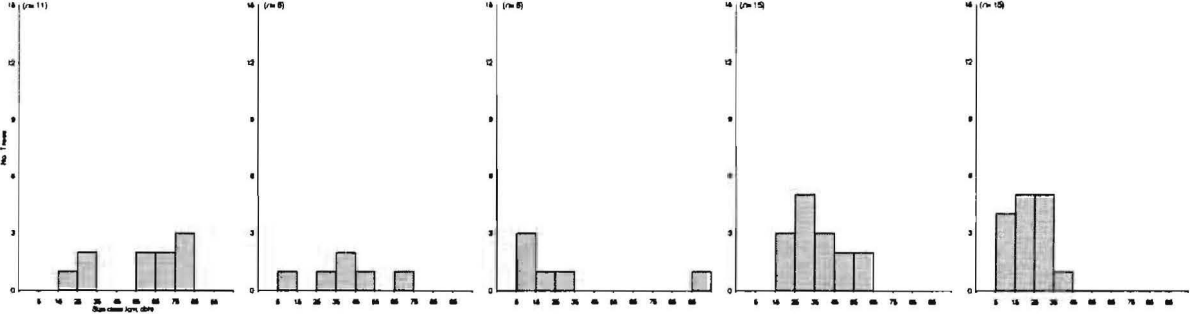


Figure E4: Size-class frequency distributions for all species on poorly drained plots in Groups from Fig. 2.