PETER HAASE

Dyckerhoffstrasse 3, 4540 Lengerich, Federal Republic of Germany.
Present address: School of Forestry, University of Canterbury, Private Bag, Christchurch, New Zealand.

POPULATION STUDIES OF ISOLATED *NOTHOFAGUS FUSCA* STANDS IN THE LOWER OTIRA VALLEY, SOUTH ISLAND, NEW ZEALAND

Summary: Population size and structure of 52 isolated *Nothofagus fusca* stands were investigated in the lower Otira Valley, 3-6 km from a major population centre in the upper Taramakau catchment. The approximate age of *N. fusca* pioneer trees, estimated from partial increment cores and calculations based on diameter growth rates, indicated that nearly all isolated stands originated after 1600 AD, predominantly during the periods 1600-1760 AD and 1865-1910 AD. Age and location of pioneer trees from the latter time span suggest that their establishment was a result of human disturbance associated with European settlement of the region. Most of the sites occupied by the older *N. fusca* outliers are prone to intermittent natural disturbance, creating temporary gaps in the generally forested habitat. Reduced competition from both other tree species and ground cover in these habitats may have allowed establishment of *N. fusca* pioneer trees, but subsequent recruitment was limited except in floodplain stands. The comparatively abrupt regional geographical limit of *N. fusca* is discussed in relation to the local rainfall regime.

Keywords: *Nothofagus fusca;* population structure; pioneer stands; tree-age estimates; disturbance; vegetation history; climatic gradients; plant biogeography; Fagaceae.

Introduction

Isolated stands of *Nothofagus fusca*[1] and *N. menziesii* occur in podocarp-broadleaved forest and subalpine scrub up to 20 km beyond the accepted regional geographical limits of *Nothofagus*-dominated forests in the South Island of New Zealand (Wardle, 1980a,b; June, 1982; Allen, 1987). Such outlier stands are presumed to indicate present invasion of other vegetation types by *Nothofagus* during the process of re-immigration into areas of Pleistocene forest extinction as a result of the Otira Glaciation (Wardle, 1963, 1964, 1988; Burrows, 1965). The comparatively late spread of *Nothofagus* has been attributed to its assumed restricted seed dispersal ability (e.g., Preest, 1963). Other authors, however, suggest that the discontinuous distribution of *Nothofagus* in New Zealand is a result of present climate and biological competition and assume that *Nothofagus* may be excluded in regions with mild and superhumid climates (McGlone, 1985; Sweetapple, 1985; Haase, 1990).

A recent study of isolated *N. fusca* stands in Deception Valley, Arthur's Pass National Park, indicated a narrowed ecological range of this species towards its regional geographical limits (Haase, 1989). Large stands had persisted for at least 1000 years without significant population growth, but all younger outlier stands had established since 1650 AD, implying a relatively recent environmental change in favour of *N. fusca* establishment. Since only a limited number of outlier stands occurs in the Deception Valley, a follow-up study was undertaken in the neighbouring lower Otira Valley, where *N. fusca* is locally abundant near the Otira-Taramakau confluence and southern outlier stands are more numerous. Population structures and estimated dates of establishment of these outlier stands were investigated in order to describe the population dynamics of *N. fusca* at the regional *Nothofagus*/ podocarp-broadleaved forest boundary.

Study area

The study area covers the catchment of the lower Otira River from its confluence with the Taramakau (240 m a.s.l.) to 1 km upstream of the Deception River mouth (320 m a.s.1.; Fig. 1). The valley slopes rise steeply to the Kelly Range (1394 m) to the. north-west and to One Shot Hill (1210 m) and the north face of Goat Hill (1649 m) to the south-east.

[1]Nomenclature follows Allan (1961) except where other authors are cited.

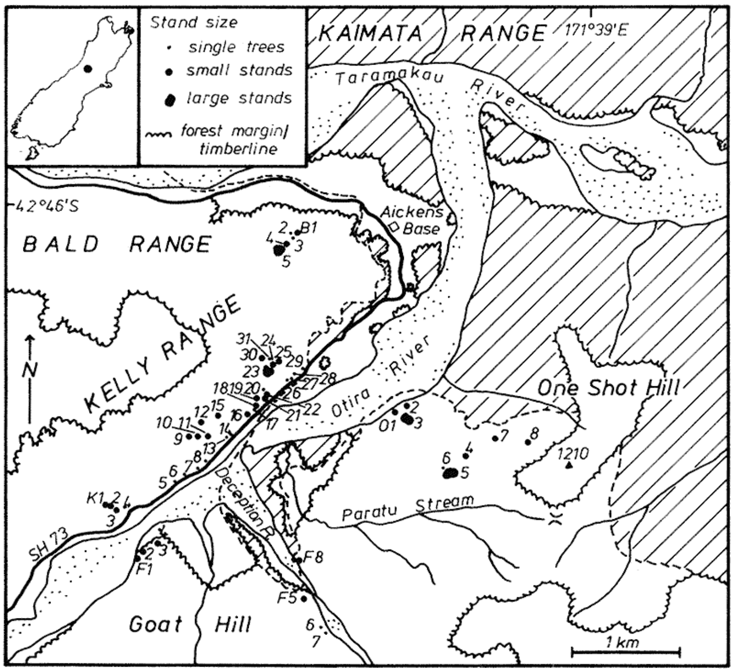

Figure 1: *Map of the study area in the lower Otira Valley with the location of* Nothofagus fusca *sample stands (B: Bald Range stands; F: Otira-Deception floodplain stands; K: Kelly Range stands; 0: One Shot Hill stands). The distribution of* Nothofagus fusca *dominated forest is indicated by hatching.*

The local climate is mild and superhumid and strongly influenced by the Westland weather pattern. Annual rainfall is 5042 mm at Otira, 6 km to the south-west of the study area (New Zealand Meteorological Service, 1983). Estimates of mean air temperature for Aickens Base (255 m; Fig. 1) give an annual mean of to.8∞C (February 15.9∞C; July 5.l∞C; Norton, 1985).

Two major forest types can be distinguished in the study area. *Nothofagus fusca* is the dominant forest tree in most floodplain forests and on the northern part of One Shot Hill, where it forms the upper forest limit. Goat Hill, the Kelly Range, and the south-western part of One Shot Hill support montane podocarp-broadleaved forest with only small and scattered *N. fusca* stands up to I km south of the Deception River mouth. Above the upper forest limit there is a belt of subalpine scrub dominated by woody composites and epacrids.

Massive human disturbance began in 1865 during the construction of the first Christchurch-Hokitika road and the area was settled in 1869 by farmers at Jacksons and Aickens (Arthur's Pass National Park, 1986). Large areas of the Otira-Taramakau and Otira-Deception floodplains were later deforested and converted to pasture; most of the remaining groves of *N. fusca* floodplain forest have been severely modified by logging.

Methods

Fifty-two isolated *Nothofagus fusca* stands in the transition zone between *Nothofagus-dominated* forest of the upper Taramakau catchment and podocarp-broadleaved forest in the lower Otira Valley were located by their conspicuously coloured spring foliage. All located stands were surveyed in the summer of 1988-89. Young trees in man-made habitats at the eastern road-bank of State Highway 73 were not considered. In every stand (see Fig. 1 for nomenclature of stands), stem diameter at breast height (d.b.h.) of all *N. fusca* trees including dead standing and fallen logs was determined and stems were grouped into 5 cm diameter classes. Environmental variables (aspect, slope, altitude) of the sample stands were determined.

In 16 isolated stands, and at a stand near timberline on One Shot Hill, the presumed pioneer tree (tree with the largest diameter) and/or 3-5 apparently healthy trees were cored (1 core per tree) in order to estimate average annual radial increment and approximate age. Growth rings were counted and measured in decades to the nearest 0.2 mm.

Annual height increment of *N. fusca* seedlings (<135 cm tall) was determined using external indications for annual shoot growth (bud scale scars, leaf cohorts) in order to estimate the time for growth to coring height or breast height.

Because of the hard wood and the widespread presence of heart-rot, most of the cored trees yielded only partial cores, and tree-age estimates were based on extrapolations using individual growth rate/diameter relationships. Such estimates normally contain errors due to eccentricity of the pith and different growth rates during the juvenile stage (Norton, Palmer and Ogden, 1987).

Assuming that *N. fusca* pioneer seedlings only grow to mature trees under favourable conditions and therefore possess at least average growth rates, stem diameter of pioneer trees not cored was used to calculate tentative age estimates of isolated stands. These estimates are meant to give a general impression of the time scales involved in the local history of *N. fusca* outlier formation, rather than suggesting discrete ages for individual trees. Some small isolated stands which lack remains of a pioneer tree are characterised by distinct cohorts of large diameter stems which were interpreted as first on-site regeneration of now decayed pioneers, disregarding the possibility of multiple invasion. An estimate of the average time from establishment of a pioneer tree to first successful on-site regeneration was calculated from the differences in stem diameter between pioneer trees and the next smaller stem in the stand or in nearby satellite stands. This figure was added to the estimated age of the largest living stem in stands lacking a presumed pioneer tree.

Isolated stands (>20 m from the nearest potential seed source) are split into two classes. "Outlier stands" are stands or single trees >200 m from the nearest potential seed source; this distance is usually regarded as the maximum range of most seed dispersal (e.g., Preest, 1963; Wardle, 1980a; Allen, 1987). Stands or single trees at 20-200 m distance are termed "satellite stands" (Haase, 1989).

Results

Local distribution of *Nothofagus fusca*

The large floodplain at the Otira-Taramakau confluence still supports remnants of former, presumably more or less continuous *Nothofagus fusca*-dominated forest.

On the floodplain of the Otira River, scattered *N. fusca* forest remnants and isolated trees are restricted to the western bank of the river up to 700 m north of the Deception River mouth (Fig. 1). *N. fusca* is still locally dominant on the north bank of the Deception River mouth, but there is an abrupt transition to pure podocarp-broadleaved forest at the foot of One Shot Hill, and towards podocarp floodplain forest at the south-eastern end of the floodplain. On the south bank of the Deception River mouth, small floodplain stands of *N. fusca* occur at the riverside margins of other forest types. This area has been modified by logging and farming and, except for very few large-diameter trees, the local *N. fusca* population post-dates European settlement of the region and forest disturbance by humans has probably assisted the observed local population growth.

On the south-east slopes of the Kelly Range, *N. fusca* has a more or less continuous presence in small stands and as scattered trees in montane podocarp-broadleaved forest from Aickens Base for another 1.5 km south (Fig. 1). Four small *N. fusca* outlier stands (K14), containing large senescent pioneer trees with very few smaller stems, mark the south-western limit of isolated stands on the western side of the Otira River. On the Kelly Range, most isolated stands occur below 500 m altitude and none ascends above 620 m.

One large stand, two small outliers, and two single trees of *N. fusca* are located on the northern slope of the Bald Range.

N. fusca is the physiognomic forest dominant on the north-west slope of One Shot Hill and forms a locally well defined treeline at 800-900 m. Within a north-south distance of only 500 m, the upper limit of *N. fusca* forest drops from the subalpine treeline to the floodplain of the Otira River (300 m a.s.l.) and only few outlier stands occur further south on the western slopes of One Shot Hill.

Ecological habitat of isolated stands

The habitats of the sample stands are listed in Appendix I. In the study area, *Nothofagus fusca* forest remnants are comparatively common on stabilised floodplains and river terraces, but only few natural isolated stands could be identified (F1-8, O2). The most common sites of hillslope stands on the Kelly Range are drainage lines which often have the form of steep gullies. *N. fusca* trees are frequently located near the top of the south-western gully slope which provides drier soils and more sunny NNE to NE aspects. The *N. fusca* outlier stands K1-4 are located in tall podocarp-broadleaved forest on a broad old talus fan of a creek draining a comparatively large catchment of the Kelly Range. Their pioneer trees probably became established after local disturbance, probably fluvial deposition of rock debris.

All *N. fusca* stands on the Bald Range occupy northern aspect sites.

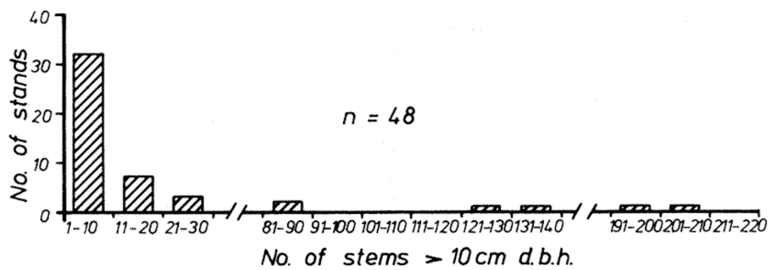

Figure 2: *Size-frequency distribution of the* 48 *isolated* Nothofagus fusca *stands which have stems >10 cm db.h.*

Four *N. fusca* outlier stands on the southern part of One Shot Hill (03,4,7,8) are situated on steep NW-facing slopes; at one site recent disturbance by slips is evident. The large *N. fusca* stand 05 on One Shot Hill occurs on a more level site (10-30∞) with indications of impeded drainage.

Population size and structure of isolated *Nothofagus fusca* stands

The isolated *Nothofagus fusca* stands are classified according to their population size (counting only stems > 10 cm d.b.h.; Fig.2). Of the 48 stands considered, 87.5% have 1-30 stems, and only 8.3% (B5, K23, O3, O5) have an established population of more than 100 stems (large outlier stands). Except for stand B5, the large stands contain 29-43% of their stems in the 0-5 cm class. After a marked reduction in the 5-10 cm class, stem numbers decrease only slowly in the larger size classes (Fig. 3).

Of the small isolated stands shown in Fig. 4, stand O1 contains few mature trees, but has a dense population of large seedlings. This size-class distribution characterises an intermittently regenerating stand. Partial erosion of the river bank and the apparently synchronous death of several, possibly even-aged canopy trees in this stand has probably recently created a sunny forest fringe habitat which provided suitable conditions for *N. fusca* regeneration. Stand F5 reveals an intermediate stage of stand development after an earlier flush of regeneration. Maximum stem numbers occur in the 10-50 cm d.b.h. class and there is a present lack of smaller stems. The size-class diagram for podocarps, mostly *Podocarpus hallii,* in an 800 m^2 sample plot within stand F5 shows very young tree populations. The young podocarps (other than *P. halli*) should eventually overtop the present *N. fusca* canopy and form tall podocarp floodplain forest in the absence of further disturbance. A small population of *N. fusca* in podocarp floodplain forest on the north bank of the Deception River (stand F8) exhibits an advanced stage of stand development.

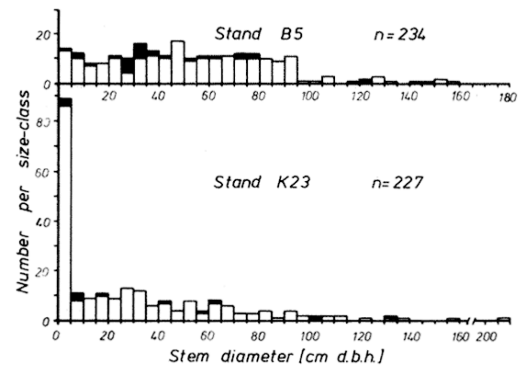

Figure 3: *Size-class distribution of two large* Nothofagus fusca *outlier stands. Dead trees are shown in black.*

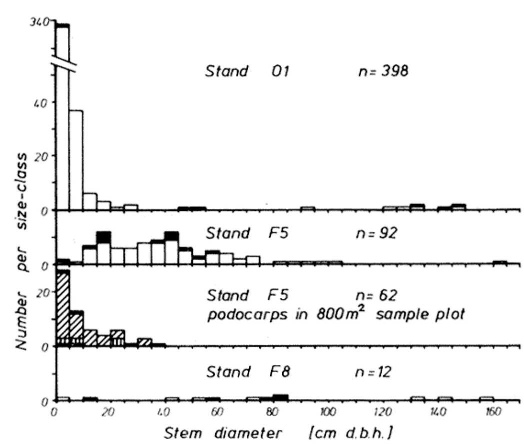

Figure 4: *Size-class distribution of three small isolated* Nothofagus fusca *stands selected to depict different stages of stand development. The podocarp population of a sample plot in stand F5 is shown for comparison. Hatching indicates* Podocarpus hallii *with dead* P. hallii *shown in black; vertical hatching stands for* Dacrydium cupressinum. *the remainder are* Dacrycarpus dacrydioides *and* Prumnopitys taxifolia.

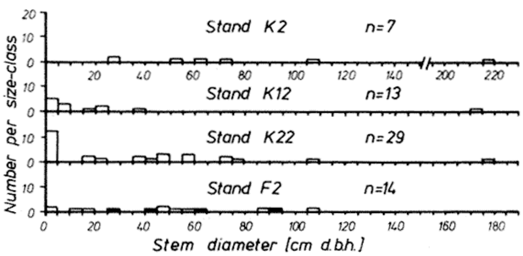

Figure 5: *Size-class distribution of four small isolated* Nothofagus fusca *stands.*

Although recruitment has generally been rare (Fig. 5), all small stands have been able to maintain themselves (some for up to 400 years). No local extinction of isolated stands, i.e., single, dead *N. fusca* trees or stumps, was observed during the field work.

Average annual radial increment and tree-age estimates

Mean annual radial increment of 25 sample trees (including seven pioneers) at selected altitudes is given in Table l. Annual radial increment of the pioneer trees (70-120 cm d.b.h.) was 5.00 mm (49.95±l.95 mm decadal increment; mean ± s.e.; n=34) which is 30.8% above the average growth rate.

Average annual height increment of 21 *N. fusca* seedlings was 104.3±5.4 mm (n=57).

The mean time to first reproduction of pioneer trees was calculated to be 116.9±10.9 years (n=32). Estimated dates of establishment of isolated *N. fusca* stands are given in Appendix I.

Discussion

Habitat disturbance and tree recruitment

The upper Taramakau catchment supports extensive *Nothofagus* forests which are disjunct from the main areas of distribution in north Westland-Nelson and east of the main divide. *N. fusca* is the dominant forest tree in the upper Taramakau Valley from the Otira to the Otehake River, but small stands and scattered trees of *N. solandri* var. *cliffortioides, N. truncata,* and *N. menziesii* are also present.

In the study area, the isolated *N. fusca* stands on river terraces and floodplains are always located near the riverside margin of podocarp forest where active erosion and deposition of debris at the riverbank provides intermittently disturbed habitats suitable for regeneration of the species. The preferred habitats of isolated *N. fusca* hillslope stands are steep slopes (>40∞), usually associated with sites of former or present disturbance, e.g., drainage lines, healed slips, talus fans, and bedrock outcrops. The distribution of isolated *N. fusca* stands on the south-eastern slopes of the Kelly Range coincides with a local "podocarp gap" which extends over a distance of 2 km from north-east of the cluster K1-4 to stands K27, 28 (Fig. 1). The local forest is dominated by broadleaved trees and, except for three records of *Prumnopitys ferruginea* and *Podocarpus hallii,* mature podocarps are absent. The lack of tall podocarps is probably a result of the unstable nature of the terrain; the hillslopes are usually >40∞steep and the local parent rocks weather easily into small fragments and are prone to erosion.

The habitats of isolated *N. fusca* stands in the study area are similar to those at the southern limit of the species in north Westland, which were described as "steep-sided gullies, well-lit terrace edges, and low open-canopied forest" (June, 1982).

Only seven isolated stands (K11,13,19,27, F1 O1,2) contain comparatively large numbers of small stems (0-10 cm d.b.h.) and may, at the moment, be regarded as growing populations (compare columns 6 and 7 in Appendix 1.). In the larger stands, tree populations are probably maintained by occasional recruitment of seedlings in a "gap-phase" regeneration mode, which appears to be typical for *Nothofagus* stands not recently subjected to major disturbance (Wardle, 1980a; Mark and Lee, 1985).

Ogden (1978) investigated diameter growth rates of *N. fusca* in different parts of New Zealand and calculated a mean decrease of 0.38 mm annual radial increment per 100 m altitude (from 5.00 mm at sea level). The average ring widths determined for *N. fusca* in the study area relate well to the calculated rates for diameter growth based on Ogden's regression equations.

Table 1: *Average decadal radial increment of* Nothofagus fusca *at different altitudes (determined from partial cores).*

Altitude (m)	Stand No.	No. of cores scored	No. of decades scored	Decadal growth (mm) Mean ±: s.e.	Av. ann. radial increment (mm) (after Ogden, 1978)
285-330	K8, 13, 17, 18,21,27,28,29 FI-3,01	15	97	38.19 ± 1.38	3.86
490-510	K15,23	7	36	29.49 ±: 2.08	3.10
900	Timberline One Shot H.	3	31	14.03 ±: 0.92	1.58

Local vegetation history

Age estimates for the oldest living *Nothofagus fusca* pioneer trees in the study area are 300-350 years, but a large hollow stump (stand K10) probably dates from about 1600 AD (Appendix I). Prior to 1600 AD, *N. fusca* probably had a more restricted distribution in the lower Otira Valley. Only five hillslope stands (B5, K23, O3, O5, O8) pre-date 1600 AD, and remains of very large *N. fusca* trees on the north bank of the Deception River mouth also indicate presence in the local floodplain forest before that date. A pronounced peak of outlier formation occurred from 1600-1760 AD when most hillslope stands established and *N. fusca* attained its present southern limit in the Otira Valley. It is possible that only three more stands established between 1760-1865 AD (B1, B3, K18), but subsequent disturbance through construction, deforestation, and farming created suitable forest fringe habitats and resulted in another peak of outlier formation from 1865-1910 AD. All recently established pioneers are associated with roadside habitats on the western (forested) side of State Highway 73 and were dated from 1958-1967 AD.

If age estimates for pioneer trees are more or less correct, the peak of *N. fusea* outlier formation from 1600-1760 AD is interpreted as a period of increased environmental disturbance, e.g., mass movement triggered by tectonic activity, storminess, and/or high rainfall intensity. In this process, erosion scars on mountain sides provided pioneer sites for hillslope stands and the related aggradation of floodplains formed suitable conditions for alluvial *N. fusca* stands on the valley bottoms. Stewart and Rose (1989) found a distinct peak of Libocedrus bidwillii establishment in the Alexander Range, to km to the north-west of the study area, between 1600 and 1800 AD and postulated stand origin after mass movement or windthrow. The authors suggested that the observed lack of *Libocedrus* regeneration during the last 200 years reflects a lack of disturbance over that time. The time scale for the proposed regional disturbance history is confirmed by the results of the present study.

Distribution of *Nothofagus fusca* and climatic gradients

The north-western part of One Shot Hill and the broad Otira-Taramakau floodplain mark the regional south-western limit of continuous *N. fusca* forest in the study area. The comparatively abrupt transition to montane podocarp-broadleaved forest towards the west and south is possibly a result of particular local geomorphological features which create steep climatic gradients. As opposed to *N. fusca*-clad One Shot Hill, the slopes of the Kelly Range possess east to south-east aspects with a presumed less favourable climate for *N. fusca* (Haase, 1989). Results of the present study show that *N. fusca* stands on the slopes of the Kelly Range are preferentially located on the south-western margins of steep drainage lines, which present more suitable north to north-east aspect sites on a local scale.

The extreme south-western limit of *N. fusca* floodplain and lower hillslope stands in the Otira Valley coincides with a sudden constriction of the valley from a basal width of 1.0-1.2 km north of the Otira-Deception confluence to only 400-600 m further upstream which may affect the local rainfall regime (Griffiths and McSaveney, 1983). South of the Deception mouth, even the potentially more suitable north and west slopes of Goat Hill lack *N. fusca* stands which extend 6 km upstream on similar sites in the neighbouring Deception Valley (Haase, 1989).

Although the study area receives large amounts of precipitation (5042 mm at Otira), its annual distribution is distinctly more seasonal than at stations in the "*Nothofagus-gap*" of central Westland, e.g., Franz Josef Glacier, and summer rainfall is characterised by a higher annual variability (New Zealand Meteorological Service, 1983). Whereas the climate at Otira is regarded as "marginally unsuitable" for *N. fusca,* climatic conditions at Aickens with presumably slightly lower precipitation and higher summer temperatures are apparently suitable for the species.

Burrows (in Burrows and Greenland, 1979) assumed from botanical evidence that precipitation in the Taramakau catchment was much higher "perhaps 500 years or more ago". This putative change in rainfall regime pre-dates 1600 AD and supports subsequent spread of *N. fusca* outlier stands in the study area.

Conclusions

The lower Otira Valley constitutes a regional ecotone between *Nothofagus*-dominated forest in the upper Taramakau catchment and podocarp-broadleaved forest to the south and west. Habitat and population structure of isolated *N. fusca* stands within this ecotone reveal a restriction of pioneer tree establishment to recently disturbed sites followed by little recruitment of trees on stabilised sites.

It is suggested that the observed range extension of *N. fusca* in the Otira Valley was the result of high-frequency forest disturbance through mass movement or storm damage during the period 1600-1760 AD. The competitiveness of *N. fusca* may have additionally been supported by a possible decrease in precipitation or a change to a more seasonal rainfall regime prior to that time.

Acknowledgements
The field work for this study was carried out in Arthur's Pass National Park and 1 thank the staff of the Department of Conservation, Arthur's Pass, for friendly support. The Department of Conservation, Hokitika, made its Aickens Base available for accommodation in the field. The Department of Plant and Microbial Sciences, University of Canterbury, supplied field equipment and also provided accommodation at the Cass Field Station. Rainer Haase and Hans-Joachim Klepsch provided computing facilities and technical advice for the preparation of the manuscript. Rainer also reviewed the draft manuscript.

References
Allan, H.H. 1961. *Flora of New Zealand Vol. I.* Government Printer, Wellington, New Zealand. 1085 pp.

Allen, R.B. 1987. Ecology of *Nothofagus menziesii* in the Catlins Ecological Region, South-east Otago, New Zealand. (I) Seed production, viability, and dispersal. *New Zealand Journal of Botany 25*: 5-10.

Arthur's Pass National Park 1986. *The story of Arthur's Pass National Park*. CobblHorwood Publications and Department of Lands and Survey, Auckland, New Zealand. 128 pp.

Burrows, C.J. 1965. Some discontinuous distributions of plants within New Zealand and their ecological significance. Part II: Disjunctions between Otago-Southland and Nelson-Marlborough and related distribution patterns. *Tuatara 13:* 9-29.

Burrows, C.J.; Greenland, D.E. 1979. An analysis of the evidence for climatic change in New Zealand in the last thousand years: Evidence from diverse natural phenomena and from instrumental records. *Journal of the Royal Society of New Zealand 9*: 321-373.

Griffiths, G.A.; McSaveney, M.J. 1983. Distribution of mean annual precipitation across some steep land regions of New Zealand. *New Zealand Journal of Science 26*: 197-209.

Haase, P. 1989. Ecology and distribution of *Nothofagus* in Deception Valley, Arthur's Pass National Park, New Zealand. *New Zealand Journal of Botany 27:* 59-70.

Haase, P. 1990. Environmental and floristic gradients in Westland, New Zealand, and the discontinuous distribution of *Nothofagus*. *New Zealand Journal of Botany 28:* 25-40.

June, S.R. 1982 (unpublished). *Ecological studies in the indigenous forests of North Westland, New Zealand*. Ph.D. Thesis, University of Canterbury, Christchurch, New Zealand. 300 pp.

Mark, A.F.; Lee, W.G. 1985. Ecology of hard beech *(Nothofagus truncata)* in southern outlier stands in the Haast ecological district, South Westland, New Zealand. *New Zealand Journal of Ecology 8*: 97-121.

McGlone, M.S. 1985. Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand Journal of Botany 23*: 723-749.

New Zealand Meteorological Service 1983. *Summaries of climatological observations to 1980*. New Zealand Meteorological Service Miscellaneous Publications 177. Ministry of Transport, Wellington, New Zealand. 172 pp.

Norton, D.A. 1985. A multivariate technique for estimating New Zealand temperature normals. *Weather and climate 5*: 64-74.

Norton, D.A.; Palmer, J.G.; Ogden, J. 1987. Dendrochronological studies in New Zealand I. An evaluation of tree age estimates based on increment cores. *New Zealand Journal of Botany 25*: 373-383.

Ogden, J. 1978. On the diameter growth rates of red beech *(Nothofagus fusca)* in different parts of New Zealand. *New Zealand Journal of Ecology 1:* 16-18.

Preest, D.S. 1963. A note on the dispersal characteristics of the seeds of the New Zealand podocarps and beeches and their biogeographical significance. *In:* Gressit, J.L. (Editor), *Pacific Basin biogeography,* pp. 415-424. 10th Pacific Science Congress. Bishop Museum Press, Honolulu. 561 pp.

Stewart, G.H.; Rose, A.B. 1989. Conifer regeneration failure in New Zealand: dynamics of montane *Libocedrus bidwillii* stands. *Vegetatio 79*: 41-49.

Sweetapple, P.J. 1985 (unpublished). *The lowland distribution of beech* Nothofagus *north of the Haast River, South Westland*. B.For.Sci. Thesis, University of Canterbury, Christchurch, New Zealand. 67 pp.

Wardle, P. 1963. Evolution and distribution of the New Zealand flora, as affected by Quaternary Climates. *New Zealand Journal of Botany 1:* 3-17.

Wardle, P. 1964. Facets of the distribution of forest vegetation in New Zealand. *New Zealand Journal of Botany 2*: 352-366.

Wardle, P. I 980a. Ecology and distribution of silver beech *(Nothofagus menziesii)* in the Paringa district, South Westland, New Zealand. *Nell' Zealand Journal of Ecology 3*: 23-36.

Wardle, P. 1980b. Primary succession in Westland National Park and its vicinity, New Zealand. *Nell' Zealand Journal of Botany 18:* 221-232.

Wardle, P. 1988. Effects of glacial climates on floristic distribution in New Zealand I. A review of the evidence. *Nell' Zealand Journal of Botany 26:* 541-555.

Appendix 1: *Site parameters, stem number, and age estimates of isolated* Nothofagus fusca *stands. Habitat codes: 1 roadside; 2 disturbed forest margin on river terrace/floodplain; 3 disturbed forest margin on steep slope; 4 drainage line on steep slope; 5 slip scar; 6 bedrock outcrop; 7 low subalpine forest; 8 tall (podocarp-) broadleaved forest; + indicates evidence of recent (post-1864) disturbance, e.g., slips, fluvial erosion/deposition, treefalls, construction and farming. In the last column, years in bold print are based on partial increment cores; years in normal print are calculated from stem diameter using mean growth rates; years in brackets are based on putative second generation trees and include an addition of 117 years (mean time span for first on-site regeneration).*
** Man-made habitat indicates post-1864 establishment.*
*** Ridge crest aspect.*
D Dead pioneer trees; age includes estimate since time of death.

Stand No.	Alt. (m)	Aspect	Slope (°)	Habitat	Stem No.	Stems >10cm dbh	Max. Stem dbh	Est. Age 1988	Year of estimated establishment
K1	400	SE	10-20	8	9	3	168	254	(1616)
K2	380	SE	5-15	8	7	7	216	316	1671
K3	360	SE	5-15	8	8	4	145	215	(1658)
K4	350	E	20-30	8	1	1	79	121	1866
K5	305	-	-	1+	1	0	7	26	1961
K6	305	-	-	1+	1	0	1	20	1967
K7	305	-	-	1+	1	0	8	27	1960
K8	315	ESE	40-45	3+	1	1	81	85	1902
K9	580	E	25-30	4+	11	5	138	259	1728
K10	515	ESE	40-45	4+	13	4	178D	385	1602
K11	470	SE	35-40	4+	46	11	115	191	(1679)
K12	620	E	cliff	6	13	5	172	343	1644
K13	315	ESE	40-45	3+	27	1	114	125	1862-
K14	305	-	-	1+	2	0	8	27	1960
K15	490	ESE	40-45	8	29	23	130D	270	1717
K16	300-320	SE	20-30	4	29	11	160	224	1763
K17	310	SE	20-30	3+	4	1	99	99	1888
K18	305-320	SE	20-30	4	19	10	130	185	1802
K19	365	ESE	25-30	8	76	2	143	297	1690
K20	370	ESE	35-40	4+	7	1	111	295	1695
K21	300	SE	40-45	3/6+	4	3	56	86	1901
K22	320-350	SE	30-40	5/4+	29	17	179	330	1657
K23	455-520	ESE**	20-40	8	227	127			pre-1600
K24	460	E	40	5+	46	21	140	231	1756
K25	450	NE	<40	4	2	2	64	111	1876
K26	300	SSE	20-30	4/3+	1	1	12	29	1958
K27	300	ESE	20-30	3/6+	30	1	90	113	1874
K28	320	SSE	30	8	1	1	67	123	1864-
K29	295	SE	20-25	3+	1	1	84	108	1879
K30	565	ENE	40-50	4+	13	8	119		fused double stem
K31	520	SE	>45	4+	1	1	41	84	1906
B1	440	N	cliff	6	19	5	113	183	1804
B2	500	N	5	8	1	1	161	264	1723
B3	500	N	cliff	6	2	1	100	174	1813
B4	540	NNE	5-30	8	18	15	221	217	(1653)
B5	600-670	NNW	40-45	6+	234	206			pre-1600
F1	315	-	-	2+	42	16	73	76	1911
F2	315	-	-	2+	14	12	105	227	1760
F3	315	-	-	2	4	4	86	91	1897
F4	315	-	-	2+	1	1	49	79	1908
F5	330	-	-	2+	92	89	162	228	1759
F6	335	-	-	2+	1	1I	88	131	1856-
F7	335	-	-	2+	1	1	47	76	1911
F8	330	-	-	2+	12	11	160	226	(1644)
01	300	NW	5-10	2+	398	28	146	260	(1610)
02	295	-	-	2+	88	3	89	127	1860
03	360-510	NW	30-45	6/4+	236	135			pre-l600
04	600	NNW	>40	7/6	14	9	106	207	(1663)
05	750-780	WNW	10-30	7	322	196			pre-1600
06	745	WNW	20	7	2	2	37	100	1890
07	700	NW	30-35	8	6	4	92D	241	1749
08	760-780	WNW**	30-45	6	115	90			pre-1600