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BEECH AND CONIFER COMMUNITY INTERACTIONS IN MOAWHANGO ECOLOGICAL REGION, NORTH ISLAND, NEW ZEALAND

Summary: Relict forests within tussock grassland and abundant subsoil charcoal indicate that prior to Polynesian conflagrations, conifer forests dominated by kaikawaka covered the upper montane plateaux in Moawhango Ecological Region. Much forest remains in peripheral districts where the plateaux border the encircling Kaimanawa, Kaweka and Ruahine greywacke uplands; in these districts, beech forest of the ranges extends on to plateau surfaces as a narrow, variable-width strip intermixed with conifer forest.

Factors considered in an investigation of the dynamics of the boundary zone between beech and conifer forest include the distribution pattern of beech outlier stands within conifer forest, stand structure, tree architecture and age hierarchies at the boundary, spreading rates of beech, seedling microsite requirements and radial increment growth rates. The study shows a centripetal spread of beech from the ranges at the expense of the conifer community. Range expansion occurs by both the slow marginal spread of beech trees and the establishment of outlier stands of beech within the conifer community. Spreading rates are comparable to those deduced from South Island forests. The chief limitation to beech spreading is lack of opportunities for seedling establishment beneath the dense, lower canopy of small trees and shrubs of the conifer community. Population growth of beech in the late Holocene, which is evident in the palynological records from the adjacent Ruahine Range, has probably been regulated by slope and how closely regional environments approximate the optimum conditions for beech.

Keywords: Plant migration; species interactions; tree growth rates; seedling microsites; *Nothofagus*; *Libocedrus bidwillii*; last glaciation.

Introduction

Evidence for an expansion of *Nothofagus* (beech) forest into adjoining communities has been reported in South Island studies (Wardle, 1980b; June, 1982; Allen, 1988). These studies of range expansion usually examine population structures and spatial relationships of communities at major discontinuities in the provincial distribution of beech. This expansion process is viewed primarily as a result of a long post-glacial readjustment to range dislocation and contraction in the last glaciation induced by harsher climates and glaciation (Cockayne, 1926; Molloy, 1969). For instance, both Wardle (1980b) in the Paringa District and June (1982) in North Westland, in studies centred at the northern and southern ends of a 240 km gap in beech distribution in central Westland (Wardle, 1980a), claim that beech is slowly migrating back into areas from which it was eliminated in the last glaciation. Wardle (1980b) suggested an early post-glacial phase of rapid range expansion of *Nothofagus menziesii* (silver beech) with subsequent gradual population growth. At the northern beech boundary, June (1982) attributed the present distribution and structure of the forests to a gradual, post-glacial spread from cold-climate isolated refugia plus the establishment of further isolated outlier

stands by seed dispersal over distances up to 6 km. In Catlins forests, Allen (1988) concluded that silver beech is expanding at the expense of a range of other forest types. Furthermore, Holloway (1954) found evidence of beech expansion in Westland and Southland, Wardle (1962) and Franklin (1967) in the northern Tararua Range, Elder (1962, 1965) in the Kaimanawa Mountains and Ruahine Range and McKelvey (1973) in the Urewera region.

On plateaux of the Moawhango Ecological Region, situated south of the Kaimanawa Mountains, montane conifer and beech forests do not exist in an apparently predictable spatial relationship explicable in terms of environmental gradients. Kaikawaka dominated conifer forest covers plateaux while beech is largely confined to plateau margins at similar altitudes. The extent and configuration of these two forest communities not only contrasts with patterns in the surrounding greywacke ranges, where beech is extensive and montane conifer forest restricted, but also suggests a range expansion of beech.

This paper examines the evidence for a spread of beech trees on plateau margins at the expense of conifers, by surveying community composition, stand structure and growth rates of trees in the boundary zones.

Moawhango environment

Landforms are predominantly of late Cenozoic marine sediments forming montane plateaux (e.g. Mounganui, Ngamatea (Owhaoko) and Mangaohane; Fig. 1). However, in the southwest Kaimanawa foothills landforms are a series of gently undulating greywacke ranges and intermontane basins infilled with Taupo Pumice. The entire region and the bordering ranges are mantled in Holocene andesitic ash derived from the Tongariro volcanoes. At altitudes above 1000 m, particularly on plateau surfaces, the ash sequence is entirely post-glacial (following the stratigraphy of Topping, 1973), and overlies unweathered bedrock. This unconformity indicates that the plateaux were largely unvegetated in the last glaciation.

Rainshadows from the Tongariro, Kaimanawa, Kaweka and Ruahine uplands dominate weather

patterns, restricting annual rainfall (891 mm, Moawhango; 1092 mm, Ngamatea; N.Z. Meteorological Service) and inducing summer droughts particularly in western districts. However, frequent easterly rain in the Ruahine Range provides for higher rainfall (1731 mm, Ruahine Corner; Rogers, 1987) and more equable humidity in the eastern districts.

Results

Patterns of conifer and beech forest

Only remnant pockets of *Libocedrus bidwillii* (kaikawaka) conifer forest within widespread tussockland remain on plateaux after Polynesian deforestation dated at 450-600 yr B.P. (Rogers, 1987). The remnants are more continuous where plateaux abut the greywacke ranges (Fig. 2). It is here that a

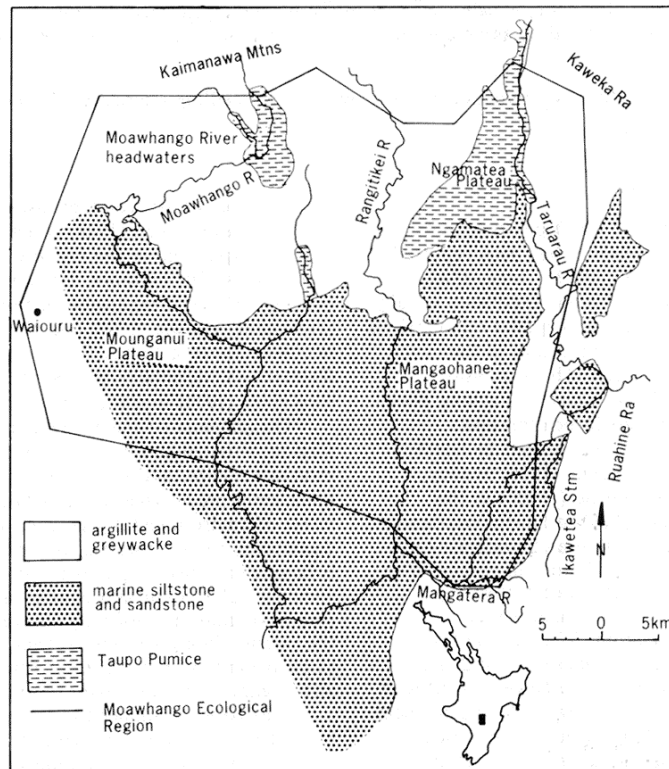


Figure 1: The geology of Moawhango Ecological Region (based on Grindley, 1960 and Kingma, 1962).

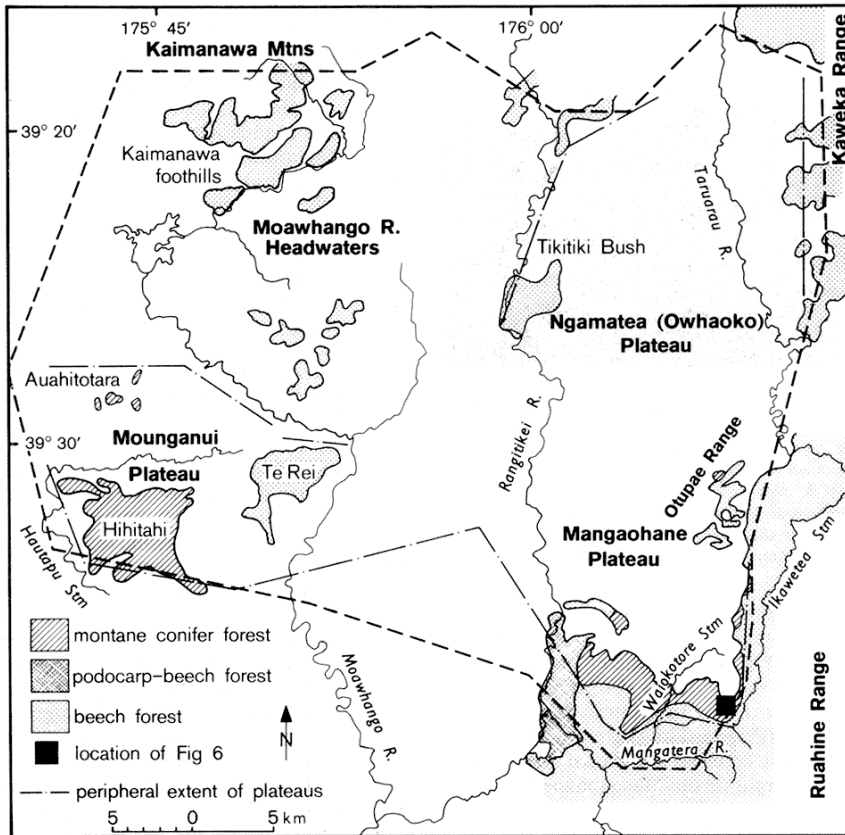


Figure 2: The distribution of the major forest classes in Moawhango Ecological Region.

discontinuous, variable-width strip of beech forest occurs. The transition zone between the conifer and beech communities has discrete outlier stands of beech within a matrix of conifer forest. Whereas conifer forest was extensive on plateaux of the Moawhango Ecological Region from 850 to 1250 m, in the adjacent western Ruahine Range, of more dissected relief, conifer forest is restricted to narrow treeline belts from 1100 m to 1250 m above extensive red beech forest (Elder, 1965). Although this latter pattern appears explicable in terms of an altitudinal gradient, plateau forest patterns are not.

On plateaux, beech and conifer trees are generally separated into discrete communities. Kaikawaka, with

two associates, *Podocarpus hallii* (mountain totara) in the drier west and *Halocarpus biformis* (pink pine) in the humid south-east, dominate conifer stands. In the south of the district bordering the western Ruahine Range, extensive stands remain in the Waiokotore Stream catchment and about Ohutu Ridge (Fig. 2). Another extensive stand remains at Hihitahi in the west and several isolated stands occur at Auahitotara at the northern extent of the plateaux (Fig. 2). Others remain along the eastern margin of Mangaohane Plateau.

Beech forest abuts most of these conifer forests on plateau margins. In the east Waiokotore basin, *Nothofagus fusca* (red beech) extends from the



Figure 3: The southern margin of Mangaohane Plateau, in the east Waiokotore basin, where it meets the Mangatera River catchment of the Ruahine Range. The boundary zone between red beech on the left and kaikawaka dominant conifer forest on the right occurs some way in from the plateau margin. Several outlier stands of red beech, including individual trees, occur within a matrix of conifer forest to the right of the boundary zone. Photo A.P. Druce.

Mangatera River catchment of the Ruahine Range on to the southern Mangaohane Plateau with a transition zone about 1180 m (Fig. 3). Immediately to the north, *Nothofagus solandri* var. *cliffortioides* (mountain beech) similarly extends onto the plateau from the Ikaweteta catchment (Fig. 2). This pattern in the Ikaweteta catchment is repeated northward at intervals along the eastern margin of the Mangaohane Plateau (Fig. 2).

To the west of Ohutu Ridge, on the southwest corner of Mangaohane Plateau, where it dips gently down to the Rangitikei River, montane red beech has an irregular upper limit of 1000-1100 m in the south descending to 925-1000 m in the north. Kaikawaka forest, affected by dieback, extends above this to near the summit of Ohutu Ridge.

At Auahitotara, 5 km east of Waiouru, the several forest pockets in tussockland are of red and mountain beech stands within a matrix of conifer forest. At Hihitahi to the south of Auahitotara, only two small enclaves of red beech occur in the 2200 ha conifer forest. The main body of beech, in relation to these outlier stands, exists to the north in the southern Kaimanawa foothills. The extensive red beech forest, Te Rei Bush (Fig. 2), to the east of Auahitotara, constitutes part of the variable width strip of beech forest on the northern plateau margins.

Nature of the boundary zone

The boundary zone is not correlated with habitat changes or altitude (Fig. 3), being some way in from plateau margins. As the region is mantled in 2-3 m of homogeneous andesitic ash, soil profiles are remarkably uniform. There is generally a clearly defined structural and compositional demarcation between the two communities. Kaikawaka, mountain totara and pink pine seldom appear in stands of beech and never form discrete outlier stands in beech forest. Beech forms a closed canopy 18-25 m high whereas the emergent conifers form a sparse upper canopy (Fig. 3) of approximately 10% cover. Not only are there striking canopy differences but pronounced lower stratum differences accompany this change. Beech understoreys are sparse with *Pseudowintera colorata*, *Rubus cissoides* and *Griselinia littoralis* most important. In contrast the conifer stands have a dense sub-canopy and understorey at 2-7 m of shorter conifers, broadleaved trees and small leaved shrubs. Whereas *Coprosma* sp. (t), *Rubus cissoides* and *Chionochloa conspicua* dominate in the more humid eastern forests at Waiokotore, *Pseudowintera colorata* is overwhelmingly dominant in the drier forest of Hihitahi.

Beech trees bordering the conifer community typically show asymmetric branch development, weighted toward and overtopping the 2-7 m high conifer subcanopy. Beneath the open-grown limbs, beech juveniles mostly establish near the outer extent of beech foliage when plants of the overtopped conifer understorey succumb. It is suspected that light exclusion and moroid profile development associated with the beech contribute to the death of the conifer understorey.

An abrupt boundary is commonly characterised by standing dead conifer stems overtopped by taller stature beech indicating a recent, but narrow, expansion of beech. In addition to the abrupt boundary condition, wide transition zones of limited extent are evident where emergent stems of the two communities intermingle, often but not exclusively, near the upper altitudinal limit of beech. The spatial arrangement of stems were mapped in two quadrats in the east Waiokotore (Fig. 4) spanning these two boundary conditions. Fig. 4a shows an example of an abrupt boundary zone where canopy stems of the two communities interact in a 10 m wide zone. However, seedlings and saplings of the conifer community occupy the beech understorey up to 40 m back from the boundary. It is apparent from the arrangement of

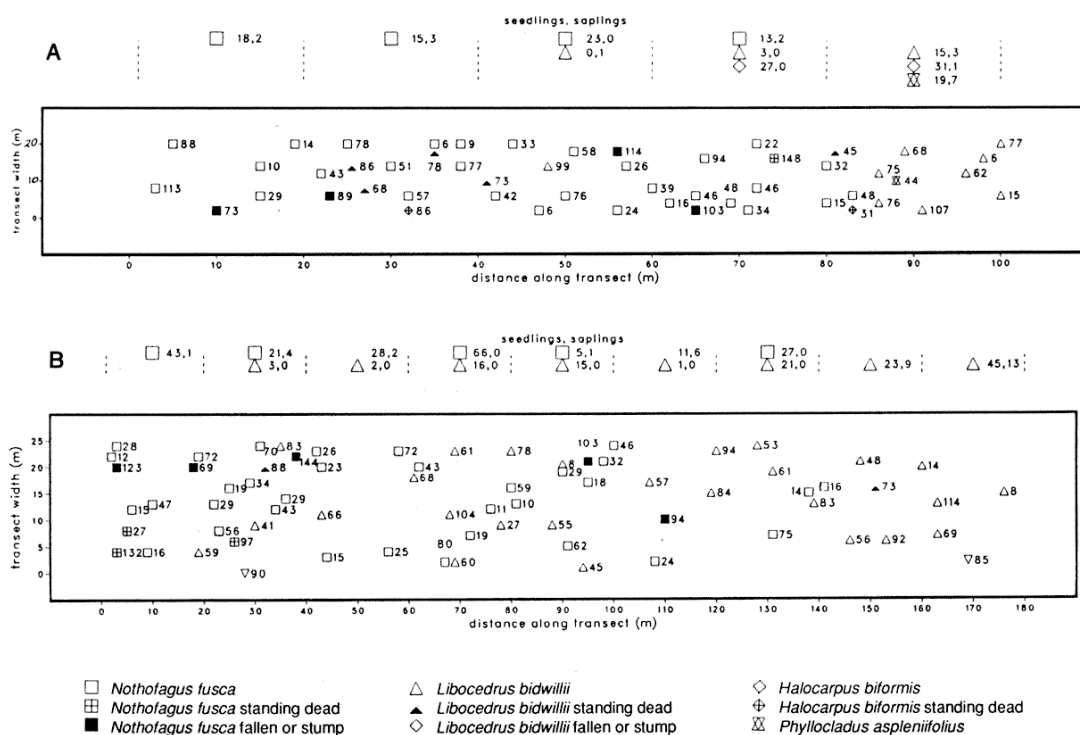


Figure 4: The configuration and diameter at 1 m (d1m) of beech and conifer stems (> 4cm) in quadrats straddling the boundary and transition between red beech on the left and kaikawaka dominant forest on the right. 25 x 20 m subquadrat counts of seedlings and saplings appear above. a) A 20 x 100 m quadrat spanning an abrupt boundary zone. b) A 25 x 180 m quadrat spanning a wide transition zone.

beech stems at the boundary that there has been a recent expansion of the margin by juveniles originally derived from the 148 cm (diameter at one metre, d1m) standing dead tree.

In contrast, Fig. 4b depicts a 120 m wide transition zone of mostly healthy stems of beech and conifers, separating exclusive stands of each community. The size-classes of conifer and beech suggest an original and low density influx of beech into the adjoining conifer stand over some 100 m with subsequent population growth.

The size-classes of intermixed conifer and red beech in one of the two beech outlier stands at Hihitahi (T21/458825) suggested a recent rapid expansion of beech into the surrounding conifer community. To investigate the origin and dynamics of

this 0.2 ha outlier stand, the size-class and representative age-class distributions were prepared from a 20x50 m plot; results appear in Fig. 5. Stem sizes and ages are evenly distributed for all three species although mortality is high in the *Libocedrus* and *Podocarpus* populations. The sample of red beech ages is consistent with establishment in mast years. The advanced *Libocedrus* mortality has resulted from intrastand competition from beech through overtopping and from root competition.

The entire red beech outlier stand is composed of stems of size-class 8 or less with no evidence of older generation trees except a decomposing, 135 cm diameter red beech log, at one end of the stand. It is concluded that this tree was the original outlier nucleus and that the present generation represents a

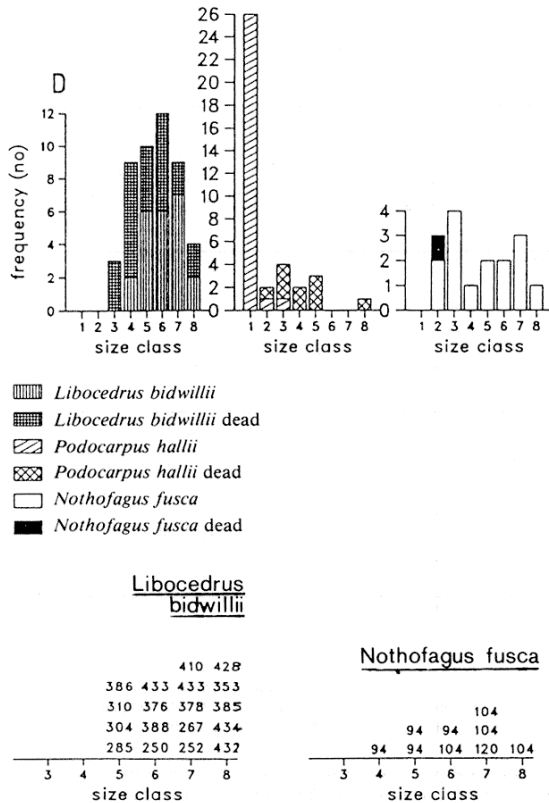


Figure 5: Size and age-class frequency distributions from an outlier red beech stand at Hihitahi. Size-classes are (d1m = diameter at 1m): 1, 0-4 cm d1m; 2, 5-14 cm d1m; 3, 15-24 cm d1m; 4, 25-34 cm d1m; 5, 35-44 cm d1m; 6, 45-54 cm d1m; 7, 55-64 cm d1m; 8, 65-74 cm d1m. A sample of aged trees in different size classes for two species appears below the histograms.

rapid expansion from that parent tree. The outlier stand apparently represents a rapid range expansion of beech in the last 120 years.

Evidence of range expansion of beech

The apparently poor dispersal capacity of beech compared to other tree species has been commented on frequently (e.g. Darlington, 1965; Wardle, 1984). But dispersal distances of 6 to 12 km as inferred by the distribution of outlier stands in relation to each other and to the main body of continuous beech are

reported by Wardle (1980b), June (1982) and Allen (1987a). Long-distance dispersal of *Nothofagus* is also reported from south-east Australia by Howard and Ashton (1973).

Outlier stands of beech in conifer forest at Waiokotore also suggest seed dispersal over moderate distances (Fig. 3). An outlier stand is defined as a discrete stand of beech at > 30 m from more continuous beech forest. Favoured sites for outlier establishment include knolls, and escarpment rims and slopes, sites probably experiencing disturbance such as slumping and windthrow.

The distribution of outlier stands in relation to the main body of beech was mapped in the east Waiokotore catchment (Fig. 6; cf June, 1982). The frequency distribution of the size of outlier stands and the distance of each outlier stand from the nearest likely seed source appear in Fig. 7. The frequency of successful seedling establishment should decline with increasing distance from seed source (Harper, 1977); this is reflected in an exponential decline in the frequency of distance to outlier stand from the nearest likely seed source. Seventy-eight percent of the 51 red beech stands are within 250 m of the nearest likely seed source. The most distant is 525 m away. Similarly, most outliers are small; 37% are single trees and 65% are < 0.1 ha. There is a moderate degree of association between stand size and distance to likely seed source ($r^2 = 0.418$); that is, large outlier stands tend to occur more frequently at greater distances from the nearest potential seed source. This correlation is consistent with long-distance outlier stands being isolated for long periods. Smaller, and generally younger outlier stands have a shorter independent lifespan near the boundary, disappearing as the boundary position adjusts forward.

Thirteen outlier stands of mountain beech are also included in Fig. 6 on the south-eastern margin of Mangaohane Plateau. Three are single trees. Stand size shows a high level of correlation with distance ($r^2 = 0.873$), but the sample of 13 is small. The mean sizes of outlier stands of red and mountain beech were not significantly different (unpaired comparison, Student's t-test, $p > 0.05$), neither were their mean distances from likely seed sources.

The presence of single trees and the spatial arrangement of stems in outlier stands indicate that the stands originate from the establishment of a single tree with subsequent expansion by the recruitment of incomplete concentric rings of juveniles. However, there can be no theoretical relationship between the time since establishment and the size of outlier stands

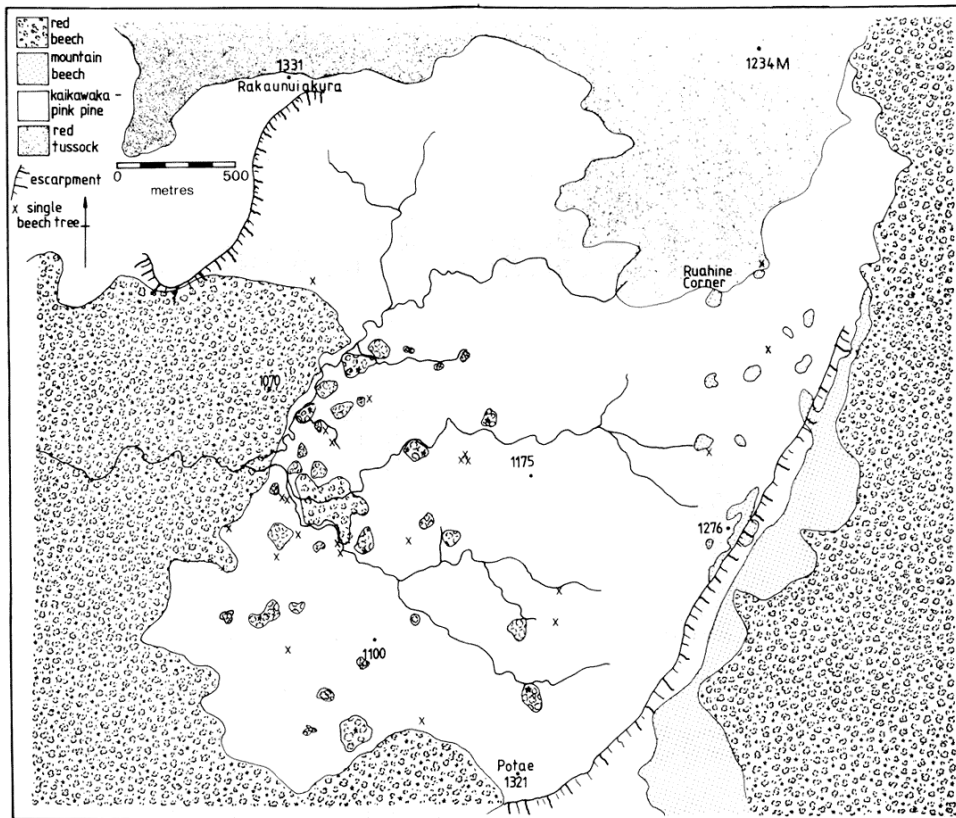


Figure 6: The distribution pattern and size of beech outlier stands in conifer forest in the east Waiokotore basin.

because recruitment of juveniles at the margins does not occur at regular intervals.

The beech boundary is often marked by senescent trees or standing dead stems demonstrating several centuries of boundary stasis. Equally commonly, tree size hierarchies indicate recent boundary expansion where juveniles have been recruited at the margin of spreading limbs of adult trees. Leak and Graber (1974) detail a method of detecting margin expansion based on adult/juvenile age profiles. The age and distance differentials between parent and offspring can provide an estimate for the rate of local boundary expansion. To this end, 45 individual pairs of different generation trees at the beech boundary were sampled. The derived spreading rates and means for five regional sectors are presented in Table 1.

Individual rates of spread range between 3.6 and 15.4 m/century and the means of all five sectors range between 5.5 and 8.0 m/century. The differences in spreading rates between red and mountain beech were found to be not significant (unpaired comparison, Students t-test, $p > 0.05$). The mean distance separating parent and offspring for both species is 11.38 ± 3.4 m and the mean age difference is 180 ± 63 years. These latter two figures represent the average radial spread of foliage and the likely time for canopy gaps to develop in adjoining vegetation beneath the limbs of parent trees which are then exploited by beech juveniles.

Estimates of spreading rates for beech in north Westland (June, 1982) from 41 samples ranged between 9 and 12 m/century (95% confidence limits

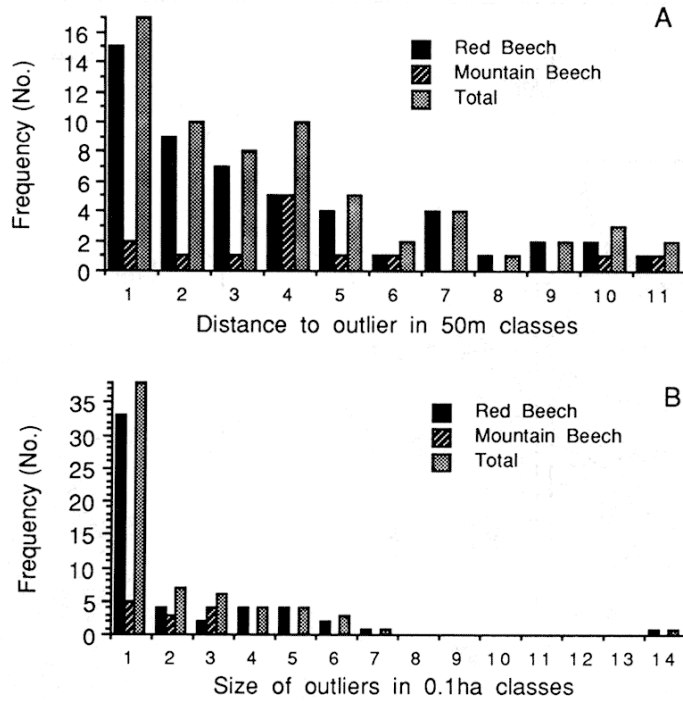


Figure 7: The size and distance to nearest likely seed source of outlier stands of beech in the east Waiokotore basin. a) Frequency distribution of the distance of outlier stands from the nearest potential seed source. b) Frequency distribution of the size of outlier stands.

of the mean rate of 11 m/century, were 7 to 13 m/century). Wardle (1980b) derived a mean rate of 6 m/century for 16 samples of silver beech in south Westland, a rate within the range from this study. According to Wardle (1980b), spread into a discontinuous cover of plants in heathland is relatively more rapid than into closed vegetation.

Radial growth rates

A comparison was made of radial growth rates of mature trees of beech and conifer species from Hihitahi and the Waiokotore boundary zones as a measure of the growth supremacy of beech over conifers. Growth rates are based on single increment cores that intersect the chronological centre of trees judged to be healthy and free from severe hierarchical suppression of growth. Growth increments per decade were compared using the Pearson product moment correlation coefficient to obtain correlations between

cores for trees of broadly similar ages (cf. Clayton-Greene, 1977). Both positive and negative correlation coefficients were obtained for each group of similarly aged trees with only a limited number of trees in each significantly correlated at the 5% level. Within the resulting correlation groups, each tree was significantly correlated ($p < 0.05$) with every other tree. Mean growth rates/decade for each correlation group were computed. Results for 4 species from Waiokotore appear in Fig. 8 and those for three species from Hihitahi appear in Fig. 9.

The correlation groups mostly display a common growth pattern, that is, increasing initially then, with small oscillations, progressively declining. For both districts the three conifer species grow more slowly than the beech species and at more uniform rates though sampled beech stems were substantially younger than the conifers. At Hihitahi (1040 m), the mean growth rates for two kaikawaka, 680 years old,

Table 1: Marginal expansion rates of *Nothofagus into adjoining communities*. *Age of older tree estimated from incomplete radial core.

Location and Species	Altitude (m)	Marginal expansion rate (m/century)	Number, mean and standard error
Hihitahi Red beech	940	6.0 6.3. 9.6 5.1	n=4 x=6.8 se = 0.64
Waiokotore Red beech	1100	8.1* 8.25.8 7.1 7.2* 5.8*. 5.8 5.6 3.5 4.9 8.5 5.1 3.4 10.2 6.7*. 3.3 6.1	n= 17 x=5.9 se = 0.47
Waiokotore Mountain beech	1180	7.1* 3.6 5.3 5.0 6.4	n=5 x=5.5 se = 0.43
Auahitotara Red beech	1000	6.9 13.2* 10.1 3.9* 4.9 15.4 8.8 3.8 11.3 10.4* 7.0 4.3 6.6 4.9	n= 14 x=8 se=0.87
Ohutu Ridge Red beech	1120	11.9* 7.0 10.2 5.7* 4.8*	n=5 x=7.9 se=0.79

are 4.79 ± 1.51 and 5.65 ± 1.82 mm/decade. Two trees of mountain totara grew at almost twice the rate of kaikawaka at 8.80 ± 2.18 and 9.20 ± 4.30 mm/decade. The lower stature pink pine grew at similar rates to kaikawaka.

The magnitude of short-term oscillations in growth rate is less in conifer species than in beech, where, even within a 50 year period, wide fluctuations are apparent. Interestingly, there is no chronological coincidence in the cycles of growth between the respective groups of trees suggesting endogenous influences are responsible rather than a widespread environmental factor.

The average growth rate for four trees of red beech in group 1 at Waiokotore is 11.95 ± 0.21 mm/decade, substantially below the approximately 30 mm/decade rate derived by Ogden (1978) from age:diameter regressions for red beech on Mt. Colenso, 16 km to the south. However, for younger trees at Hihitahi, growth rates are similar to those derived by Ogden. Radial increments would be expected to decline with increasing diameter. Nevertheless, red beech at 1160 m, near the regional upper altitudinal limit of the species, is capable of substantial growth in the first 200 years. As the red beech rapidly attain optimal growth rates, crown development probably occurs early in each tree's life,

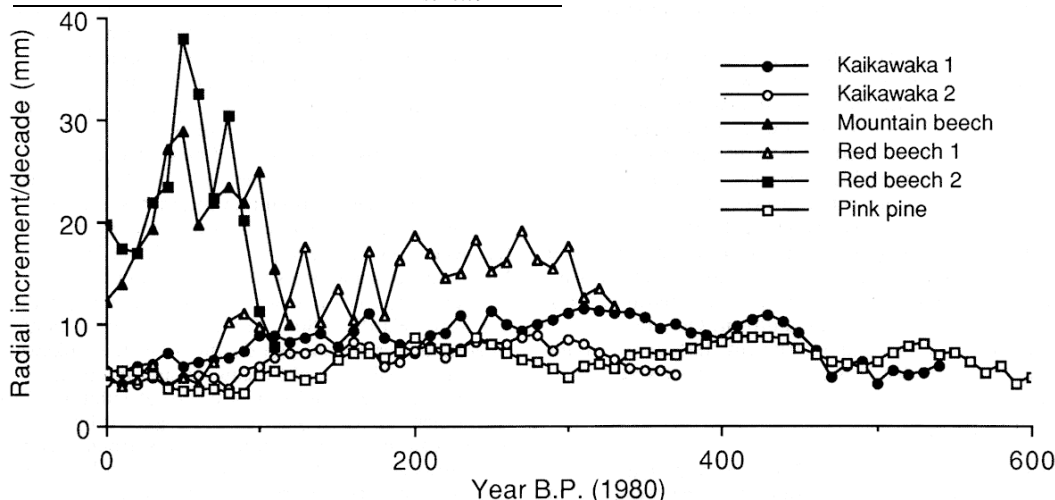


Figure 8: Mean growth rate/decade plots for groups of trees with positively correlated growth rates in the east Waiokotore basin. The number of positively correlated trees in each age group are: Kaikawaka - group 1: 5 from 11; group 2: 5 from 13. Mountain beech - 6 from 17. Red beech - group 1: 4 from 10; group 2: 4 from 7. Pink pine - 3 from 3.

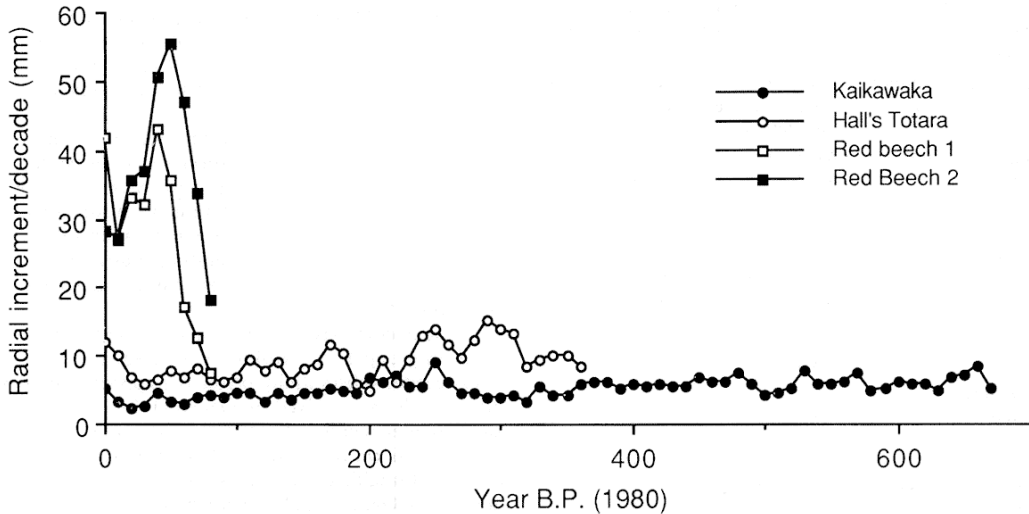


Figure 9: Mean growth rate/decade plots for groups of trees with positively correlated growth rates at Hihitahi. The number of positively correlated trees in each age group are: Mountain totara - 2 from 5. Kaikawaka - 2 from 4. Red beech-group 1: 3 from 7; group 2: 3 from 8.

particularly if the tree experiences less community competition for light at the boundary with the conifer forest (Fig. 3).

The wide growth rate variations during the life of beech trees dictate caution in drawing growth rate comparisons among individual populations and with other species. For instance growth of red beech, which may eclipse that of conifers in early life, may decline later to rates comparable with conifer species (Fig. 8). Soil fertility levels influence growth rates as shown by Wardle (1980b) for silver beech in the Paringa District. However, given the undulating landforms and geomorphic stability of the homogenous andesitic ash regolith mantling the plateaux, substrate fertility levels are expected to be relatively uniform. Only on calcareous outcrops and escarpment flush-zones would elevated fertility levels prevail, but such sites are limited.

Stand structure

Cockayne (1926), Zotov (1938), June and Ogden (1965) and Wardle (1980b) found that the regeneration and spread of *Nothofagus* is influenced by forest stand structure, particularly the shading effects of canopy and understorey layers. Size-class distributions

of all canopy and sub canopy species were obtained from NZ Forest Service National Forest Survey plots as a means of assessing regional differences in stand structure and its likely influence on community interactions at the boundary zone. For instance, possible recruitment gaps or dieback events in conifer forest may enhance the spread of beech.

The kaikawaka forest at Hihitahi has a preponderance of larger trees with very low numbers of juveniles whereas mountain totara has a more continuous range of size-classes diminishing in frequency toward the larger classes (Table 2). Mountain totara appears to be continuously regenerating, consistent with a steady-state population structure (Wardle 1980b; Veblen and Stewart, 1980) whereas a recruitment gap distinguishes the kaikawaka population. Dieback of kaikawaka and mountain totara on steeper relief is widespread at Hihitahi. Past recruitment cycles may have been triggered by widespread mortality or large scale disturbance events. In contrast, the red beech stands at Te Rei have an uneven diameter-class frequency distribution suggesting more continuous recruitment. Range expansion of beech may be enhanced by widespread, periodic mortality in adjacent kaikawaka stands.

Table 2: Mean number and standard deviation of stems in diameter classes from 0.4 ha plots at different locations in Moawhango Ecological Region. Data are from NZ Forest Service National Forest Survey plots.

Species	Diameter classes (cm)					no of plots
	10<30	30<50	50<75	75<100	>100	
Waiokotore red beech forest (1100 m) - 5 plots: U21/780688; U21/789687; U21/794698; U21/799698; U21/795688						
<i>Nothofagus fusca</i>	0.8 ±0.8	9.8 ±4.3	8.0 ±4.4	5.2 ±3.4	5.8 ±2.8	5
<i>Griselinia lucida</i>	4.0 ±4.2	10 ±0				3
<i>Fuchsia excorticata</i>	0.8					1
<i>Pseudopanax simplex</i>	0.4 ±0.5					2
<i>Carpodetus serratus</i>	0.4 ±0					2
Waiokotore kaikawaka forest (1180 m) - 3 plots: U21/804687; U21/809688; U21/821698						
<i>Libocedrus bidwillii</i>	14.6 ±12.5	15.7 ±2.6	14 ±7.1	3 ±1.6	3 ±1.6	3
<i>Halocarpus biformis</i>	11.7 ±14.4	18 ±9.4	4 ±0.8	1 ±0.8		3
<i>Phyllocladus aspleniifolius</i>	6.3 ±1.2	6.7 ±2.9	0.7 ±0			3
<i>Pseudopanax simplex</i>		0.3 ±0				1
Hihitahi kaikawaka forest (1020 m) - 6 plots: T21/443816; T21/444833; T21/451816; T21/461816; T21/477815; T21/486815						
<i>Libocedrus bidwillii</i>	1.5 ±0.7	0.7 ±0.8	4.5 ±4.0	9.2 ±7.2	2.7 ±2.5	6
<i>Podocarpus hallii</i>	1.5 ±1.0	3.8 ±4.7	2.8 ±2.8	0.8 ±0.8	0.2 ±0.5	5
<i>Dacrydium cupressinum</i>			4.0 ±0	1.0 ±0	1.0 ±0	1
<i>Plagianthus regius</i>	1.8 ±1.0	3.3 ±1.0	0.3 ±0.5			4
<i>Griselinia littoralis</i>	2 ±0.8	2.3 ±2.1	2.3 ±1.9	1.3 ±1.3		4
<i>Carpodetus serratus</i>	1 ±0	4.5 ±0.7	0.5 ±0.7			2
Te Rei Bush red beech forest (980 m) - 9 plots: T21/542844; T21/548844; T21/551845; T21/555850; T21/555839; T21/564842; T21/573842; T21/580844; T21/556843						
<i>Nothofagus fusca</i>	14.1 ±13.5	28.2 ±18.3	11.8 ±7.1	4.8 ±4.0	0.7 ±0.9	9
<i>Podocarpus hallii</i>	1.0 ±0	2.3 ±2.3	0.3 ±0.6			3

In Waiokotore and Ruahine Corner quadrats in the more humid east (Table 2), continuous recruitment is evident. Such a pattern may result from composite size-frequencies of a mosaic of small-scale disturbance and recruitment events. Without age-class structures this can not be confirmed, but the higher rainfall and more equable humidity is probably conducive to continuous population rejuvenation. Kavanagh and Kellman (1986) concluded from size and age class structures of *Tsuga canadensis* that recruitment of stems was more continuous at the species range centre than at the environmental extremes of range. The differences in size class structures of kaikawaka in this study suggest the species is approaching its range limit in the summer-dry western districts.

Seedling microsites

The provision of hospitable conditions for seedling establishment and survival can strongly influence the population dynamics and potential for spread of tall trees. Survival of beech seedlings below dense herbaceous and fern ground cover is especially poor as reported by Kirkland (1961), Franklin (1974), June and Ogden (1975) and Wardle (1984). Other studies have highlighted the preponderance of seedlings on elevated and moist sites e.g. Grant (1963), Franklin (1965), Wardle (1967), Ogden (1971), June and Ogden (1975), June (1982) and Allen (1987b). Deep litter layers are also inhibitory and Kirkland (1961), Franklin (1974) and Wardle (1980b, 1980c) found that recently disturbed mineral soil surfaces favoured beech establishment.

A seedling microhabitat survey was undertaken by the random location of 1.0 m² subplots within 20 m² plots about the boundary zone. The seedling height class was 10-30 cm. The results (Table 3) indicate that the most favourable sites for survival are tree bases, logs and stumps. Bare soil and bryophyte-covered ground, clear of overshading herbs or ferns, are also favoured but litter-covered ground or sites in deep shade are inimical to seedlings. Seedlings on logs have less competition for light from ferns, other herbs and woody plants, and are removed from root competition on the forest floor, while decaying wood and bryophyte cushions provide seedlings with a more reliably moist substrate (June and Ogden, 1975; Wardle, 1980b; Wardle, 1984; Allen, 1987b). Within conifer communities, virtually no seedlings are recorded below dense, lower canopy thickets of *Pseudowintera colorata*, *Coprosma* sp. (t) (Eagle, 1982), and *Rubus* spp. In the central Ruahine Range, Ogden (1971) reported a clumped distribution of adult

Table 3: Total number of seedlings in various microsite classes in 1 m² subplots about the transition zone. N = number of 1 m² plots. n = total number of seedlings.

Location and grid reference (N)	Species	n	Tree bases, stumps and logs	Bare soil	Litter covered ground	Bryophyte covered ground	Herb or fern covered ground
Hihitahi, T21/487811 (50)	Mountain totara	9	5	—	3	1	—
	Kaikawaka	—	—	—	—	—	—
Auahitotara, T21/476883 (50)	Red beech	—	—	—	—	—	—
Ohutu Ridge, U21/759694 (50)	Kaikawaka	44	37	4	—	3	—
Ohutu Ridge U21/757694 (51)	Red beech	35	21	6	3	4	1
Waiokotore Stream, U21/812685 (74)	Kaikawaka	81	73	—	—	8	—
Waiokotore Stream, U21/811683 (104)	Red beech	104	77	14	1	12	—
Ruahine Corner, U21/825700 (50)	Mountain beech	21	8	2	1	9	1

trees "forming loose aggregates on old stumps". The trunk base configurations of many mature trees in conifer stands in the east and single outlier trees of red and mountain beech also indicate the former presence of a log.

Discussion

The conifer-beech boundary on the plateaux of the Moawhango Ecological Region is not correlated with soil, habitat or with altitudinally-controlled climatic gradients. There is thus no discernible environmental barrier to a slow, irregular spread of beech. Holloway (1954), Wardle (1980b, 1980c), June (1982) and Allen (1988) arrived at similar conclusions for several region~ of the South Island.

Several lines of evidence indicate recent expansion of beech at the expense of conifer stands about the boundary. Range expansion occurs in two ways; by slow marginal spread, and by long distance dispersal. Slow marginal spread is by no means universal because large diameter moribund beech trees occur frequently at the boundary. Under favourable conditions, however, a saltatory extension of the boundary occurs at a mean rate of once every 180 years with spot adjustment rates averaging between 5.5 and 8.0 m/century. It is concluded from the frequency of static margins, as inferred from large size trees, and from the results of the seedling microsite survey, that the availability of suitable seedling establishment sites is the most important influence on beech spread.

Windthrow of conifers in upper montane forests of the Ruahine Range has been infrequent in the last five years particularly after Cyclones Bernie and Bola

(pers. obs.), whereas wind thrown beech forests are widespread. This conifer stability is attributable to the narrow foliage profiles and deep-rooting nature of conifers in the well-structured andesitic ash regolith. Given the preponderance of beech seedlings on moist, elevated, well lit sites, lack of canopy windthrow disturbance of conifer stands would act to limit the opportunities for beech invasion.

Baylis (1980) has suggested that the generally slow marginal spread of beech through neighbouring communities is related to the improbability of seedlings forming symbiotic ectotrophic mycorrhizae beyond the rooting zone of parent trees. In this study all the outlier stands examined, including individual trees, were ectomycorrhizal (see also Allen, 1987b). When not associated with a tree, ectotrophic fungi cannot compete with fungi of the saprophytic soil mycota, and are adversely affected by humus and leaf litter toxins (Kendrick, 1985). Ectotrophic fungi may therefore be obligately symbiotic. Naturally dispersed spores would be the only inoculum source for newly established beech seedlings within conifer stands. Given that the andesitic ash soils have accumulated entirely in the post-glacial and that conifer forest has occupied its present sites throughout that period, ectotrophic beech outlier stands which established by long-distance seed dispersal must have become inoculated after establishment. The capricious nature of seedling inoculation may be a serious limitation to beech expansion, particularly in phosphate deficient soils (Baylis, 1980; Allen, 1987b). Cross-infection from *Leptospermum scoparium* as suggested by Baylis (1980) is unlikely as the Waiokotore catchment is above the regional altitudinal limit for the species.

Establishment of an outlier stand in the Moawhango Ecological Region is a rare event, as shown by outlier patterns in the Waiokotore Stream basin. However, seed dispersal should not limit outlier establishment, at least over short distances. Wardle (1970) found that most *Nothofagus solandri* seed fell within 200 m of the parent tree; Allen (1987a) found dispersal of sufficient quantities of silver beech seed for frequent seedling establishment met up to 250 m from the nearest parent tree. This is despite the wings of beech nuts being relatively ineffectual for long-range dispersal. Dispersal at distances of 6-12 km as inferred by Wardle (1980b), June (1982) and Allen (1987a) must be a rare event, promoted by gale force winds and turbulent air movement within mountainous environments. For instance, at Cass, inland Canterbury, leaves and twigs of beech have on occasion been transported over several kilometres (Burrows, 1977).

The combined evidence from the geographic configuration and the dynamics of marginal stands of beech and conifer forest points to a progressive centripetal influx of beech from the surrounding mountains into the plateau conifer stands. What does this contemporary evidence of beech expansion mean to the relative distributions of conifer and beech forest when assessed in a post-glacial time frame? The main body of beech in the Waiokotore basin covers a variable-width, marginal strip up to 1.6 km wide. The position of this boundary in relation to the plateau margin could represent the net result of a post-glacial adjustment of the boundary across the plateau, a process that varied in degree in response to local environments. The rates of 5.5 to 8.0 m/century applied for the 12000-14000 years of forest cover in the post-glacial could account for between 660 and 1120 m of spread. Judging from the width of peripheral beech, the rates of spread have been greatest south of Te Rakanuiakura on sloping surfaces and slowest on level sites just west of Potae where the beech boundary is near the plateau margin (Fig. 6).

The rates of population growth of beech may not have been constant throughout the Holocene. When climatic conditions closely model those of a species' theoretical optimum, enhanced reproductive vigour and colonisation potential results (Lewin, 1985). The extensive red beech forest, Te Rei Bush, on a northern plateau margin at 950 m may have a climate near optimum for the invading species. The net expansion process is probably particularly slow where the invading species approaches an altitudinal or climatic limit, for example on the eastern slopes of Te

Rataunuiakura at 1180 m. Fast rates of range expansion for an invading species would accrue from cyclonic winds producing canopy disturbance and enhanced seed dispersal.

Of considerably wider altitudinal range, and occupying undulating topography, the plateau conifer forests of the Moawhango Ecological Region cannot be considered as just an expanded horizontal equivalent of the narrow treeline belt of montane conifer forest in western Ruahine Range. However, the pollen record from northern and western Ruahine Range (Moar, 1961, 1967) spanning at least the latter half of the Holocene, shows both steady and rapid rises of *Nothofagus*. Whether this population growth has been at the expense of kaikawaka cannot be judged accurately, since kaikawaka pollen is fragile and under-represented in peat bogs (Moar, 1967; Macphail and McQueen, 1983). The narrow treeline belts of conifer forest above extensive red beech may represent a steep-slope enhanced expansion of beech at the expense of conifers during the Holocene; slower rates of long-term adjustment may have operated on the gentle relief of Moawhango plateaux.

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