

Stand Development in the Red/Silver Beech and Mixed Beech Forests of North Westland

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CONTENTS

1.	Introduction	5
2.	Background	5
3.	Objectives	5
4.	Methods	6
	<i>4.1 Forest structure and regeneration</i>	6
	<i>4.2 Species regeneration ecology</i>	6
	<i>4.3 Influence of natural disturbances on regeneration</i>	6
5.	Results	7
	<i>5.1 Forest structure and regeneration</i>	7
	<i>5.2 Species regeneration ecology</i>	9
	<i>5.3 Influence of natural disturbances on regeneration</i>	11
6.	Conclusions	13
7.	Acknowledgements	14
8.	References	14

1. Introduction

The most widespread beech forests in the north-west of the South Island are those dominated by red (*Nothofagus fusca*) and silver (*N. menziesii*) beech. The stand structure and regeneration dynamics of red/silver beech forest in the Maruia Valley, South Island, has been investigated by the Native Plants and Animals Division, Manaaki Whenua-Landcare Research (previously Forest Research Institute), since 1986/87. In 1990/91 the work was extended to the more complex mixed-beech forests of north Westland.

This report summarises significant findings from the research covered in the appended manuscripts but gives special emphasis to research results that have not yet been published.

2. Background

Forests dominated by one or more beech species are an important component of about two-thirds of our remaining c. 6 million ha of indigenous forest. These forests are of vital importance for watershed protection, wildlife habitat, and a variety of other functions, and some of them are likely to be the focus of sustained-yield forest management. Surprisingly, there are numerous gaps in our ecological knowledge of these forests.

Forest ecologists are interested in regeneration processes because they indicate how present forest structures have arisen and how these might change in response to natural or man-made perturbations. Conservationists need to understand the natural cycles of forest mortality and replacement so that they can devise management strategies to cope with such diverse impacts as browsing by introduced animals and episodic forest dieback. The forester must understand the natural regeneration processes since these form the basis of classical silviculture and are vital for any sustained-yield management.

3. Objectives

- To investigate the stand structure and regeneration dynamics of red and silver beech in mixed stands.
- To use ecological information to predict the likely influence of natural phenomena and management practices.

More specific objectives were to:

- Determine the size and age structure of the forest and how it reflects regeneration patterns.

- Assess differences in the regeneration ecology of the two species.
- Determine what natural disturbances (e.g., windstorms, disease, insect outbreaks, drought) influence regeneration patterns and how frequently disturbances occur.
- Assess the patterns and importance of gap-phase replacement in beech forests containing a mixture of beech species.

4. Methods

4.1 FOREST STRUCTURE AND REGENERATION

Two stands (0.48 ha and 0.3 ha) were destructively sampled to reconstruct patterns of forest development over the last 300-400 years (for specific methodology see Stewart & Rose 1990). In addition, all trees ≥ 5 cm dbh were tagged in four large reference stands (c. 1 ha) and remeasured annually to monitor recruitment and mortality.

4.2 SPECIES REGENERATION ECOLOGY

Fifteen seed traps were set out in three of the reference stands to collect and monitor seedfall at monthly intervals. Approximately 1% of the area of each of these reference stands was sampled by systematically located and permanently marked 0.3 m radius circular seedling plots. All seedlings in each seedling plot were counted in height classes annually to monitor recruitment and mortality.

Height-growth rates were compared by determination of ages and annual diameter increments at several heights for pairs of red and silver beech stems that had responded to similar disturbances (Runkle & Stewart 1989). In addition, the diameter-growth rates for the tallest trees in 150 'canopy gaps' (see section 4.3) were determined to examine the effect of position within the gap on the likely success of gap capture (Runkle *et al.* 1990, Runkle *et al.* in press.)

4.3 INFLUENCE OF NATURAL DISTURBANCES ON REGENERATION

Regeneration processes in openings in the forest canopy caused by disturbances ('canopy gaps') were surveyed over tens of hectares in three different areas (Station Creek, Fergies Bush, Rough Creek) to determine species responses in canopy gaps of different sizes and ages. Permanently marked canopy gaps (50 in each of the three areas) sampled initially in 1987/88 were remeasured in 1992/93 to determine patterns of expansion and closure and associated species responses (for more specific sampling methodology see Stewart *et al.* 1991).

The patterns and importance of gap-phase replacement in mixed-beech forests, were assessed on elevational transects from the Rahu Saddle on the western boundary of the Maruia Valley (c. 550 m) to treeline (c. 1200 m). At 50-m intervals point-centred quarter (PCQ) plots were located to sample forest composition. To characterise canopy composition, the distance to and diameter of the nearest canopy tree ($>2/3$ average canopy height) in each quarter were measured. Subcanopy composition was similarly sampled by PCQ plots for the nearest trees in each quarter that were $<2/3$ average canopy height but 1.4 m tall. At each PCQ plot, altitude, slope, aspect, and average canopy height were also recorded.

All gapmakers (trees >20 cm dbh that had died and caused the formation of a canopy opening) that occurred within 3 m either side of the transect were sampled. Gapmakers were classified as branch break, dead standing (recently dead and generally >15 m tall), snap (crown broken off), or uproot. The species, diameter, height or length, direction of fall, and decay class (based on a 3-point scale, after Stewart & Rose 1990) of each gapmaker were recorded.

The number of saplings (1.4 m tall and <5 cm dbh) and the diameter of all stems 5 cm dbh were recorded by tree species in the 3-m radius plot centred on the gapmaker. The tallest tree $<2/3$ canopy height in each plot was deemed the 'potential successor' to the canopy and its height was measured.

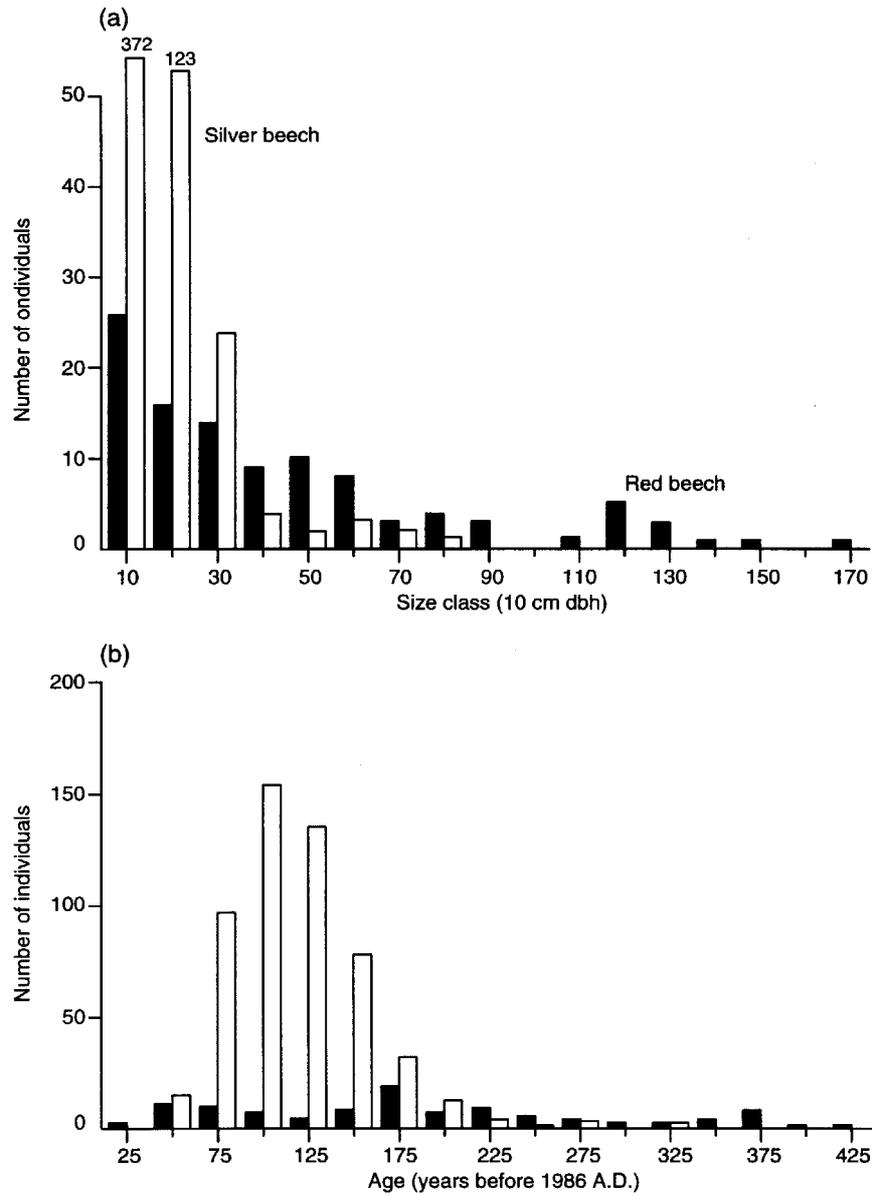
If the transect passed through areas of canopy opening the line intercepts of 'expanded gap' and 'canopy gap' (*sensu* Runkle 1982) were recorded. The frequency of occurrence of gaps in each forest type was determined by comparing the number of gaps to the total length of transect sampled for each forest type. The portions of forest in expanded gap and canopy gap were investigated in relation to elevation, slope, and forest type.

5. Results

5.1 FOREST STRUCTURE AND REGENERATION

The most striking feature of red/silver beech forests was the canopy dominance by red beech. Silver beech was less conspicuous in the canopy but it numerically dominated the lower tiers, often forming a dense sapling layer in the understorey of the forest (Fig. 1a). The numerical dominance of silver beech, especially of small stems, led many ecologists in the past to conclude that silver beech was replacing old red beech.

FIG 1. (A) DIAMETER AND (B) AGE-CLASS FREQUENCY DISTRIBUTIONS FOR RED (105 STEMS) AND SILVER (531 STEMS) BEECH IN AN OLD-GROWTH RED/SILVER BEECH FOREST, MARUIA VALLEY (AFTER STEWART & ROSE 1990).



The presence of red beech of all sizes (Fig. 1a) suggested frequent and sporadic regeneration, which was also indicated by a range of tree ages up to c. 400 years (Fig. 1b). The high numbers of small silver beech and progressively declining numbers in larger size classes (Fig. 1a) suggested a more continuous regeneration pattern, with many young trees and progressively fewer old trees. However, tree ages show that very few young trees were present - most were 75-150 years old (Fig. 1b). A steep decline in the age class distribution of silver beech after 125 years suggested that many of the individuals that survive to this age do not reach the main canopy.

Mortality was similar for all years from 1986 to 1992, i.e., 1-1.5% of stems > 5 cm dbh died per annum. Death by suppression of small diameter stems (5-15 cm dbh) was the most common cause of mortality, affecting silver beech at Station Creek and red beech at Pell Stream. A few canopy-sized red beech that had suffered heavy infestation with the scale insect *Inglisia* in 1990/91 also died.

5.2 SPECIES REGENERATION ECOLOGY

Differences in the life-history characteristics of the two beech species influence regeneration success. These characteristics include seed production and viability, shade tolerance, seedling and tree mortality patterns, longevity, and height-growth rate.

Red beech produces massive amounts of seed every few years, resulting in large populations of small seedlings in the forest understorey. After minimal seedfall (often <200 seeds/m²) in 1988 and 1989, a major seeding year for red beech occurred in 1990. At Station Creek and Rough Creek c. 7000 seeds/m² (70 million/ha) fell, of which c. 75% was viable. Red beech seedfall at Pell Stream was slightly lower at 5000 seeds/m². Silver beech seeded less heavily (1000-2500 seeds/m²) and fewer seeds were viable (c. 35-45%). Low seed production for both species occurred for the 2 years after the heavy seedfall in 1990.

Numbers of red beech seedlings in the forest understorey changed dramatically after the 1990 seedfall. From 1986 to 1990, numbers of seedlings of red beech <15 cm tall varied from 25 000 - 130 000/ha at Station Creek and 200 000 - 500 000/ha at Pell Stream. As a result of the heavy seedfall in 1990, however, numbers of red beech seedlings <15 cm tall increased dramatically (up to 400 000/ha and 2 500 000/ha at Station Creek and Pell Stream). At Rough Creek, where fern understoreys dominated, numbers of seedlings <15 cm remained fairly static from 1986 to 1991 (15 000 - 20 000/ha). Taller seedlings (16-45 cm) were not abundant in any area (<25 000/ha), and seedlings >45 cm were common only at Rough Creek (3 000 to 5 000/ha).

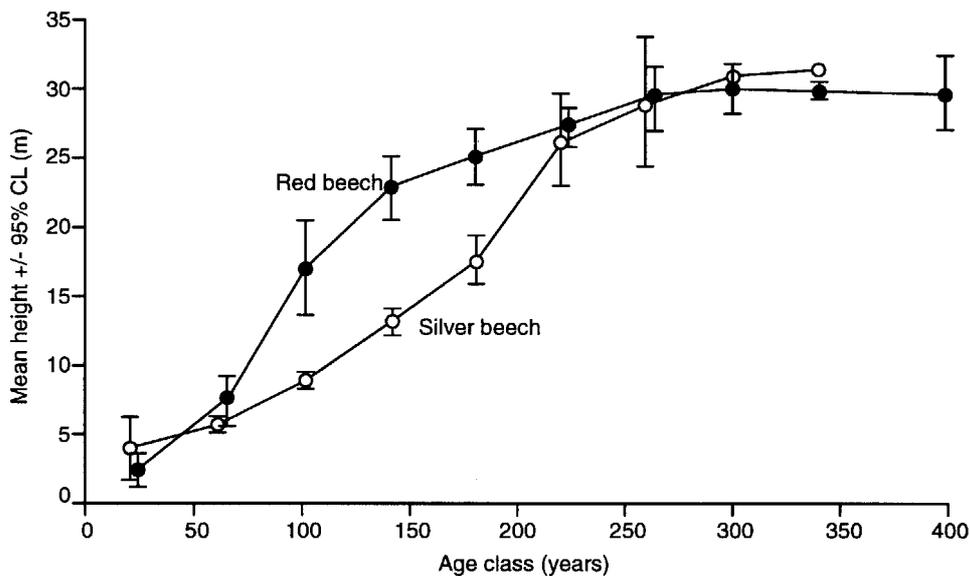
Silver beech seedlings <15 cm were less abundant than those of red beech, although they also increased after the heavy seedfall in 1990 at both Station Creek and Pell Stream (3 000 to 30 000/ha and 35 000 to 350 000/ha, respectively). Numbers at Rough Creek were consistently low (500 - 1500/ha). Numbers of seedlings 16-45 cm were variable but generally <3000-4000 in all three areas.

Very few of the tens of thousands of small seedlings attained sapling size, indicating heavy mortality, especially for red beech. After the large increases in seedling numbers in 1990, mortality of seedlings of both species <15 cm tall between 1991 and 1992 was high, e.g., c. 25% of red and silver beech seedlings present in 1991 had died by 1992 at Station Creek. Tall seedlings (>15 cm) and saplings (1.4 m) of both species were almost always confined to openings in the canopy, although saplings and small trees of silver beech occurred where openings have since closed.

Logs, tree stumps or tree tip-up mounds were important elevated sites for seedling establishment and survival, especially for red beech, and seedlings of both species were generally more abundant here than on the forest floor. Often 50-75% of all seedlings of both species occurred on these substrates, which covered only about one-third of the forest floor. Mortality of seedlings was high under the forest canopy, especially for red beech, although it appeared to be lower on elevated sites.

The two beech species also grew at different rates. For example, the light-demanding red beech took only c. 100-120 years to reach the canopy at 18-20 m whereas, on average, it took c. 180-200 years for the more shade-tolerant silver beech to attain the same height (Fig. 2). On many sites, red beech established many decades after silver beech but outgrew it to attain the canopy first (Runkle & Stewart 1989).

FIG. 2. AVERAGE HEIGHT GROWTH OF RED AND SILVER BEECH TREES OF DIFFERENT AGE CLASSES IN A STAND IN THE MARUIA VALLEY (AFTER STEWART & ROSE 1990).



The analysis of the effects of gap position revealed that both species had marginally significant faster height-growth rates on the sunnier, south side of canopy gaps. There were, however, no significant differences in species locations within the gaps.

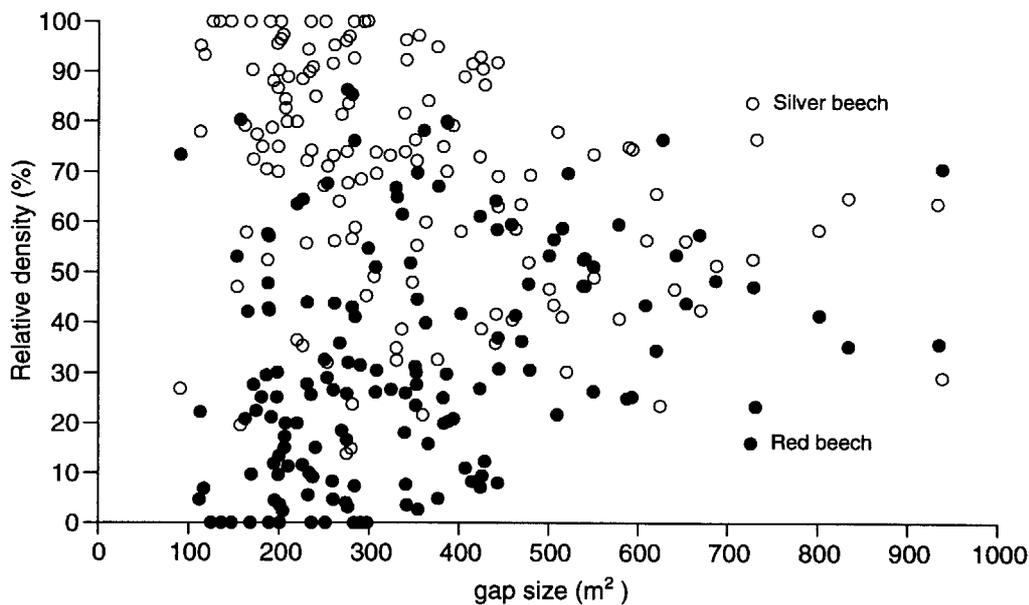
5.3 INFLUENCE OF NATURAL DISTURBANCES ON REGENERATION

Disturbances such as windstorms break branches, topple trees, or snap the boles of unthrifty or dead trees to produce gaps of various sizes in the forest canopy. These gaps are sites for regeneration and are essential if either of the beech species is to reach canopy stature.

Our 1987 survey of 150 such gaps identified the following:

- The sizes of gaps and the way in which they were formed varied because of differences in the history of disturbances between localities.
- Most seedlings and saplings that successfully regenerated in gaps were present when the gaps were formed.
- Saplings and small trees of silver beech occurred both under the closed forest canopy and in gaps; those of red beech primarily occurred in gaps.
- Silver beech outnumbered red beech in gaps of all sizes, especially in small gaps (<400 m², Fig. 3). However, the abundance of a species in the subcanopy did not necessarily reflect its potential to capture a canopy gap. Differences in growth and survival were ultimately more important (see Fig. 2).
- At least five periods of above-average treefall gap formation (identified by dating growth releases in surviving trees) were identified in the Maruia Valley over the last 100 years. Three of these were related to historically recorded gales in the region and two to drought-induced dieback and subsequent death attributable to attack by pinhole borer beetles.

FIG. 3. RELATIVE DENSITY OF RED AND SILVER BEECH IN 150 CANOPY GAPS OF VARIOUS SIZES FOR THREE LOCALITIES IN THE MARUIA VALLEY (AFTER FOREST RESEARCH INSTITUTE 1992).



The 1992/93 resurvey of the same 150 gaps identified the following:

- Gaps <400 m² were most often filled by growth of lateral branches from adjacent canopy trees rather than by upward growth of understorey trees.
- Closure by lateral crown expansion was rapid, especially in small gaps or long narrow gaps, e.g., at Rough Creek canopy gaps >200 m² were closing at the rate of 29 m² per year. Also, rates of lateral crown expansion were faster in larger gaps than in small gaps, e.g., at Station Creek canopy gaps <50 m² were closing on average at 4 m² per year while those 50-100 m² averaged 7 m².
- Rates of gap formation and closure varied because of differences in the history of disturbances between localities, e.g., over an area of 10.5 ha at Station Creek where frequent single treefalls caused small gap formation, 420 m² of gap area closed from 1987 to 1992 and 670 m² of new gaps formed. At Fergies Bush (6 ha) where heavy mortality of red beech canopy dominants had occurred in the mid 1970s, canopy gap area measured in 1987 had increased a further 10% by 1992.
- Many of the tallest trees in each gap that were identified in 1987 as having the potential to capture the gap ('potential successors') were damaged or killed by gales between 1987 and 1992. This provides further evidence that the abundance of a species in the undisturbed forest subcanopy does not necessarily reflect its potential to capture a canopy gap.

In mixed-beech forests the sizes of gaps and the area of forest in gaps varies because of differences in the type of gap formation (bolesnap, uproot, death standing, or branch break) and species of gapmaker. At Rahu Saddle, five forest types related to increasing altitude and slope were identified - mountain beech, mixed (red/mountain/silver) beech, red/silver beech, mountain/silver beech, and silver beech. Snapping of the bole was the principal type of gap formation for all forest types, although dead standing trees were also important in mountain and mountain/silver beech forest, and uprooting in red/silver and silver beech forest. In mountain beech forest trees frequently died standing (one gap on average every 27 m) resulting in 9.5% of the forest area in canopy gaps, but because of minimal disturbance to surrounding trees most gaps were small (mean expanded gap width = 9.3 m; Table 1). The total area of gaps in red/silver beech forest was similar (9%) but there were fewer, larger gaps (mean expanded gap width = 13.3 m) due to the impact of large uprooted red beech.

TABLE 1. CANOPY GAP CHARACTERISTICS OF FOREST TYPES AT RAHU SADDLE (STEWART UNPUBLISHED DATA).

FOREST TYPE	NO. METRES PER GAP ⁺	% EXPANDED GAP (EG) [*]	% CANOPY GAP (CG) [*]	MEAN EG WIDTH	MEAN CG WIDTH
mountain beech	27.2	22.6	9.5	9.3	3.9
mixed beech	70.8	18.9	8.3	10.9	4.8
red/silver beech	44.1	27.4	9.0	13.3	4.4
mountain/silver beech	43.1	22.7	10.3	8.8	4.0
silver beech	36.7	30.7	11.6	10.5	4.0

⁺ Average distance between gaps

^{*} As a fraction of transect length for each forest type

6. Conclusions

The population dynamics and disturbance history of red/silver beech stands suggest that red and silver beech coexist by way of different life-history strategies, where silver beech has low juvenile mortality, and red beech has greater longevity and adult survivorship. Even though silver beech saplings and small trees may be more abundant in the understorey than red beech, red beech survivors reach the canopy first because they grow faster in canopy openings.

Although forests sampled at the three localities were broadly similar in canopy composition, the response of red and silver beech to gap formation varied according to seemingly minor differences in forest structure and disturbance history. Gaps were formed by a variety of different disturbances and at different rates, thus providing different opportunities for regeneration. Therefore different changes in the relative abundance of *N. fusca* and *N. menziesii* were occurring at the three localities. Any interpretation of regeneration response to gap parameters such as size and age therefore needs to take into account differences in disturbance history between sites.

Differences in disturbance history between localities also influence rates of gap closure because of the effects of competing understorey vegetation and the influence of microtopography (i.e., elevated sites) on tree establishment, growth, and survival. Because rates of gap closure are used to estimate forest turnover times, meaningful comparisons of disturbance regimes for different forest types can only be made if this intersite variability is addressed.

Various aspects of gap-phase regeneration in red/silver beech forests have implications for forest managers. The species responses to gaps of various sizes and ages can be manipulated for sustained-yield management of 'near natural' stands. Coupe sizes of <400 m² would be too small for either species to

regenerate because adjacent canopy trees would quickly fill the available space. In large gaps red beech saplings (and mountain beech in mixed stands) would be at a competitive advantage for height growth over silver beech, so that silver beech would form a smaller proportion of the dominant canopy trees than if a smaller coupe size were chosen.

Our enhanced understanding of regeneration processes in relatively undisturbed old-growth stands and the natural cycles of dieback and recovery caused by drought and insect attack could help explain patterns of beech forest dieback in other areas on the DOC estate.

7. Acknowledgements

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