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LIFE HISTORY DIFFERENCES AND TREE SPECIES COEXISTENCE IN AN OLD-GROWTH NEW ZEALAND RAIN FOREST

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Abstract. We examined stand disturbance history, population structures, spatial relationships of age classes and size classes, and tree growth histories in an old-growth temperate rain forest in southern New Zealand. We aimed to determine the role of juvenile and adult life history differences in promoting coexistence of the four main overstory species (*Nothofagus menziesii*, *Weinmannia racemosa*, *Dacrydium cupressinum*, and *Prumnopitys ferruginea*).

There was no evidence that major compositional shifts were occurring: *N. menziesii*, *D. cupressinum*, and *P. ferruginea* were represented by all-aged populations, indicating continual recruitment of all three species within the 5-ha study area during recent centuries. No age data were obtained for *W. racemosa*, but the diameter distribution of this species was consistent with an all-aged population structure. The temporal distribution of releases in tree ring sequences suggested a history of chronic patchy disturbance during at least the last 400 years.

Ring width sequences were consistent with species differences in growth histories. About half (53%) of *N. menziesii* >20 cm dbh appeared to have reached the canopy in one growth spurt, compared to only 11% of *P. ferruginea*. Many trees of the latter species showed multiple episodes of release and suppression, indicating successive responses to several gap events before reaching the canopy. *D. cupressinum* growth histories were intermediate between these two extremes.

Nearest neighbor age relationships also indicated species differences in regeneration patterns. Neighboring individuals of *N. menziesii* ≥ 10 cm dbh were, on average, significantly more similar in age than random pairs drawn from the age data pool under a bootstrap null model. This pattern is consistent with regeneration of *N. menziesii* in small, even-aged patches, in response to treefall gaps. In contrast, age differences between nearest neighbor pairs of *P. ferruginea* and *D. cupressinum* trees did not deviate significantly from the null model of randomly selected ages, suggesting that establishment and survival were not closely linked to gap formation.

Maximum radial growth rates of *N. menziesii* saplings were nearly 2.5 times those of *D. cupressinum* and *P. ferruginea*. Fast growth of *N. menziesii* beneath treefall gaps may compensate for the greater shade tolerance of *P. ferruginea*, in particular. *D. cupressinum*, although apparently outperformed by one or another of its competitors in both shade and treefall gaps, has a longer life-span than any of the other species. Thus, relatively low recruitment rates may be sufficient to maintain its present abundance. Fewer data were available for *W. racemosa*, but its ability to reproduce vegetatively may be an important factor in its persistence in competition with the other dominants.

Under a disturbance regime dominated by treefall gaps, coexistence of the four dominants appears to be associated with complementary differences in growth rate, shade tolerance, canopy residence time, and facility for vegetative reproduction. Our results serve to emphasize that understanding plant species coexistence may require attention to inter-specific differences in both juvenile and adult life history characteristics.

Key words: bootstrap test; *Dacrydium cupressinum*; disturbance regime; longevity; *Nothofagus menziesii*; null model; *Prumnopitys ferruginea*; radial growth rate; shade tolerance; species coexistence; treefall gap; tree life histories.

INTRODUCTION

Explanations of tree species coexistence in old-growth forests have commonly focused on niche differences that are expressed during the regeneration

phase (Grubb 1977), such as differences in establishment substrate preferences (Nakashizuka 1989, Duncan 1993, Lusk 1995) and differential responses of juveniles to gap-understory light gradients (Ricklefs 1977, Denslow 1980). It has often been postulated that tree life histories are constrained by a trade-off between juvenile survival in shade and growth rates in treefall gaps (Denslow 1980, 1987, Bazzaz 1984, Canham 1989, Poulson and Platt 1989), and such a trade-off

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has been empirically demonstrated for at least one forest community (Kobe et al. 1995). Therefore, the spatial and temporal heterogeneity generated by treefall events is likely to be crucial to the maintenance of species richness in old-growth forests, permitting coexistence of species that perform best on different parts of the understory-gap center gradient, or in gaps of different sizes (Ricklefs 1977, Denslow 1980, 1987, Runkle et al. 1995, Poulson and Platt 1996).

Nevertheless, the concept of regeneration niche alone does not always provide a basis for a convincing explanation of species coexistence. Clark and Clark (1992) failed to find clear evidence of a gap-understory performance trade-off among tree species in a neotropical rain forest. Similarly, Sipe and Bazzaz (1995) reported that growth and survival rankings of three co-occurring *Acer* species were largely invariant along gap-understory gradients in a temperate forest in the eastern United States.

Life history differences expressed during adult stages may also contribute to persistence of species mixtures. For example, differences in life-span can compensate for differences in fecundity or juvenile survivorship (Shmida and Ellner 1984, Veblen 1986, Lertzman 1995). Such mechanisms may be important in the temperate rain forests of New Zealand, where most associations (apart from pure *Nothofagus* forests) contain tree species of widely disparate life-spans (Ogden and Stewart 1995).

In this paper, we address the relevance of both juvenile and adult life history differences to stand dynamics and tree species coexistence in an old-growth temperate rain forest on South Island, New Zealand. We use the term "life history" in a broad sense, including aspects of growth, survivorship, longevity, and size (Huston and Smith 1987, Clark and Clark 1992). New Zealand forests are commonly regarded as consisting of two broad classes or formations: "beech" forests dominated by small-leaved, shade-intolerant *Nothofagus* species, and the wide range of associations referred to as "conifer/broadleaf" forests (P. Wardle 1991). The latter include varied mixtures of angiosperms other than *Nothofagus* (*Beilschmiedia*, *Weinmannia*, *Elaeocarpus*, *Metrosideros*, and *Quintinia* are among the most important genera) and a number of conifers belonging mainly to the family Podocarpaceae. The determinants of landscape partitioning between these two formations are a subject of continuing argument (Leathwick 1995), but *Nothofagus* tends to predominate at high elevations and high latitudes (P. Wardle 1991). In reality, many forests, including the stands that we describe in this paper, contain elements of both formations (see also Stewart 1986).

The overstories of many *Nothofagus* forests are dominated exclusively by one or two species of this genus (J. Wardle 1984), and the regeneration processes of these low-diversity stands are fairly well understood. Most *Nothofagus* forests are subject to periodic cata-

strophic disturbances, but all four New Zealand species of this genus will regenerate by a gap-phase mode in old stands, on sites where there is little competition from other tree species (Ogden et al. 1996). There are fewer certainties about the dynamics of the structurally complex, species-rich conifer/broadleaf forests, but there appear to be broad differences between the regeneration behavior of the (generally emergent) coniferous component and that of the broad-leaved canopy species (Ogden and Stewart 1995). Long-lived conifers such as *Agathis australis* (Araucariaceae), *Dacrydium cupressinum* (Podocarpaceae), and *Prumnopitys taxifolia* (Podocarpaceae) typically have strongly discontinuous age structures in old-growth stands, consistent with regeneration in response to infrequent large-scale disturbance events. In contrast, broad-leaved species such as *Beilschmiedia tawa* (Lauraceae) and *Weinmannia racemosa* (Cunoniaceae) usually have all-sized populations, indicating more continual recruitment. Less still is known about the dynamics of mixed forests containing *Nothofagus*, broad-leaved angiosperms, and conifers. We examined the interaction of these three elements under a disturbance regime dominated by treefall gaps, and evaluated the role of differences in shade tolerance, maximum growth rates, and canopy residence time in the coexistence of four overstory species at our study site.

STUDY SITE

The study was carried out in the Jackson River Valley (44°05' S, 168°40' E) near the west coast of South Island, New Zealand. A superhumid, maritime, cool temperate climate is characteristic of this region. Annual rainfall is ~4500 mm and annual mean temperature is 10.9°C at the nearest climate station at Jackson Bay (New Zealand Meteorological Service 1983). The stands examined were located at ~100 m altitude a.s.l., on a moderately steep (15–30°) south-facing slope, with shallow (25–45 cm) yellow-brown earth soils, developed over schist.

Four species dominated the overstory tiers of the forest, together composing nearly 99% of tree basal area (Table 1). These were, in order of decreasing basal area, *Nothofagus menziesii* (Fagaceae), *Weinmannia racemosa* (Cunoniaceae), *Dacrydium cupressinum* (Podocarpaceae), and *Prumnopitys ferruginea* (Podocarpaceae). Occasional *Podocarpus hallii* (Podocarpaceae) and *Metrosideros umbellata* (Myrtaceae) were also present in the canopy. Common understory species included the small trees and shrubs *Carpodetus serratus* (Escalloniaceae), *Coprosma* spp. (Rubiaceae), *Griselinia littoralis* (Cornaceae), *Pseudopanax* spp. (Araliaceae), the tree fern *Cyathea smithii* (Cyatheaceae), and the crown fern *Blechnum discolor* (Blechnaceae). Nomenclature follows Allan (1961), except for the recent changes suggested by Connor and Edgar (1987).

At the time of sampling (February 1995 and February 1996), a continuous but uneven canopy was pres-

TABLE 1. Height, diameter, mean stem densities (± 1 SD), and basal area data (± 1 SD) for overstory species in an old-growth rain forest, South Island, New Zealand. High SD values in part reflect relatively small size of sample plots (0.177 ha).

Species	Maximum height (m)	Maximum dbh (cm)	No. stems/ha (≥ 10 cm dbh)	Basal area (m ² /ha)
<i>Nothofagus menziesii</i>	28	150	95.0 \pm 98.5	38.5 \pm 34.1
<i>Weinmannia racemosa</i>	23	120	267.5 \pm 170.3	26.1 \pm 17.4
<i>Dacrydium cupressinum</i>	36	140	29.0 \pm 44.9	12.5 \pm 16.2
<i>Prumnopitys ferruginea</i>	28	80	41.8 \pm 51.0	5.0 \pm 6.9
Other trees			11.5 \pm 28.7	1.1 \pm 1.6
Total			444.7 \pm 230.2	55.9 \pm 44.5

ent over most of the study area. Small canopy openings were present throughout the stand, resulting from wind-falls of one to a few trees, or from standing death of canopy individuals. The degree of soil and vegetation development, and the observation that many of the present canopy trees had established on stumps or logs, suggested that there had been no major episodes of slope instability at the study site during recent centuries.

METHODS

The approach

We inferred stand development and disturbance history from population age and size structures and from the temporal distribution of growth releases in tree ring sequences. Individual tree growth histories and age relationships of nearest neighbor trees were then used to infer responses of juveniles to gap and understory environments.

The principal disadvantage of studying forest dynamics by stand history reconstruction is the progressive loss of information from the older periods of stand history (Lorimer 1985). However, this approach offers valuable long-term perspectives on disturbance regimes and stand compositional trends (Henry and Swann 1974, Lorimer 1985).

Population structures

Vegetation was inventoried on 17 parallel transects run approximately perpendicular to the slope contours, spaced 25 m apart. Five circular plots (radius 7.5 m) were centered on sample points sited at random intervals, 20–30 m apart, along each transect. This meant that a total of ~ 1.5 ha was sampled throughout an area of ~ 5 ha. Within each plot, all individuals > 2 m tall of the four common canopy species were counted, and their diameters were measured at breast height (1.4 m). Given that large plots minimize edge effects, our choice of plot size was essentially a trade-off between optimum size (large) for determining species abundances and population structures, and optimum size (small) for sensitivity to fine-scale spatial associations.

Age data were obtained at a randomly chosen subset of 30 of these sample points. Increment cores were extracted from the individual of *Nothofagus menziesii*

≥ 10 cm dbh nearest the sample point, and from its nearest conspecific neighbor ≥ 10 cm dbh. The same procedure was carried out for *Dacrydium cupressinum* and *Prumnopitys ferruginea*. Trees selected for coring were not always within the sample plot. Cores were extracted as close as possible to the ground, usually below 60 cm height. Wherever possible, we took cores from the longest radius, in order to minimize errors due to missing rings (Duncan 1989). In many cases, this required taking more than one core per tree. Some trees were rejected because of extensive heartrot: in cases where we were unable to obtain a core comprising $\geq 60\%$ of the geometric radius, we substituted the next nearest individual ≥ 10 cm dbh for the rotten tree. Rot was more common in *N. menziesii* than in the other species. For cores that fell short of the center, but included $> 60\%$ of the geometric radius, the missing fraction of the tree's growth history was estimated on the basis of mean width of the innermost 50 rings present on the core (Norton et al. 1987). The geometric model of Duncan (1989) was used to estimate the number of rings missing from cores that passed the chronological center, but failed to intersect it. Cores were sanded with successively finer grades of sandpaper, and growth rings were counted using a binocular microscope. We did not cross-date cores. However, other studies have produced very strong evidence of annual ring formation in *D. cupressinum* (Franklin 1969) and *N. menziesii* (Norton 1983). No age data were obtained for *Weinmannia racemosa*, as the growth ring characteristics of this species posed difficulties for interpreting increment cores. Population dynamics of *W. racemosa* were inferred from diameter distributions.

Stand disturbance history

We measured the temporal distribution of growth releases in tree ring sequences as a proxy record of stand disturbance history. Major disturbance events causing widespread overstory mortality throughout the stand should leave evidence in the form of synchronous releases on many of the surviving trees, whereas a history of chronic patchy disturbance should result in more or less random variation in release frequency over time (Lorimer 1985). We defined release as an abrupt

$\geq 100\%$ increase in mean ring width, relative to the previous 10 years' growth, sustained for ≥ 10 yr.

Radial growth rates

Mean radial growth rates were calculated by dividing core length by the number of growth rings. To estimate maximum growth rates attained by juveniles, we measured mean ring width during the decade of fastest radial growth before each tree attained ~ 20 cm dbh. At this diameter, *N. menziesii*, *D. cupressinum*, and *P. ferruginea* usually had attained heights of > 15 m, although some *P. ferruginea* of this size were still overtopped. Measurements were carried out only on cores that included a near-complete ring sequence. We also estimated initial radial growth rates from the first 20 rings present on cores that passed very close to, or included, the chronological center.

Tree growth histories

Species differences in shade tolerance are often reflected in tree ring width sequences. Individuals of shade-tolerant tree species are often overtopped during parts of their early growth history, attaining canopy status through successive responses to several minor openings. Such a growth history will result in a ring sequence containing alternating periods of release (widely spaced rings) and suppression (narrowly spaced rings) during the early stages (Lorimer 1985). In contrast, light-demanding species will not usually show such a pattern, because those juveniles that become suppressed for any length of time usually die (Kobe et al. 1995), and most individuals that attain canopy status do so in one growth spurt after establishing directly beneath an opening.

We reconstructed tree recruitment histories from increment cores by recording the number of cycles of suppression and release that occurred before individuals attained 20 cm dbh, the approximate minimum size of canopy individuals of all three species. These measurements were possible only on cores that contained the complete growth history of the tree, including the chronological center. We applied the same 100% release criterion that was used for investigating stand disturbance history. However, in studying tree growth histories, we recorded only releases from suppression, which we arbitrarily defined as a period of ≥ 10 yr with average ring width of < 0.5 mm. The same suppression threshold was used for all three species, as species differences in shade tolerance are reflected more consistently by differences in survival than by growth at low light levels (Kobe et al. 1995).

Spatial distribution of tree ages

We sought to differentiate between species that had established in small, even-aged patches in treefall gaps and species that had followed a more continuous regeneration pattern (Canham 1989, Veblen 1992). The former pattern may be expected for light-demanding

species, and is likely to result in strong similarities between ages of neighboring trees within an old-growth, all-aged stand (Duncan and Stewart 1991). By contrast, neighboring individuals of shade-tolerant species, whose establishment may be expected to be more continuous in space and time, will not necessarily be of similar ages. To distinguish between these two types of regeneration pattern, we applied a bootstrap test (Efron and Tibshirani 1993) of the null hypothesis that ages of neighboring individuals of a species were independent. For each of the species *N. menziesii*, *D. cupressinum*, and *P. ferruginea*, the mean age difference among 30 nearest neighbor pairs of trees ≥ 10 cm dbh was compared with the mean difference obtained for each of 10^4 null-model data sets (the bootstrap samples), each comprising 30 pairs of values drawn at random and with replacement from the pool of ~ 60 ages for that species. The significance of departure from the null model was calculated as the proportion of null model data sets in which the mean age difference was smaller than the observed mean, multiplying this result by two to effect a two-tailed test. A two-tailed test is appropriate, because a significantly large age difference between neighboring individuals might also be biologically feasible.

Overstory-understory associations

Reciprocal replacement, or cyclical succession, has sometimes been invoked as a mechanism promoting tree species coexistence (Fox 1977). Chi-square tests were used to examine spatial associations between adults and saplings of each of the four dominant species. Two-way contingency tables were assembled using presence-absence data from the 84 sampling plots (see *Methods*, *Population structures*). A separate table was created for each overstory-understory combination, where overstory individuals were defined as those with stems ≥ 25 cm dbh and understory individuals were those with stems < 10 cm dbh. A significantly high value for χ^2 (departure from the null hypothesis of independence) was interpreted as evidence for association of an understory species with an overstory one (Lusk and Ogden 1992).

RESULTS

Population structures

Each species was represented by an all-sized population. Diameter distributions of all species included abundant saplings, generally with declining numbers of individuals in successively larger diameter classes (Fig. 1). Deviations from this trend were minor, resulting in highly significant fits ($P < 0.0001$) of all four species to the power function model $y = y_0 x^{-b}$, which has been shown to adequately describe population structures resulting from a history of continual recruitment (Hett and Loucks 1976). *Nothofagus menziesii* and *Dacrydium cupressinum* had relatively flat

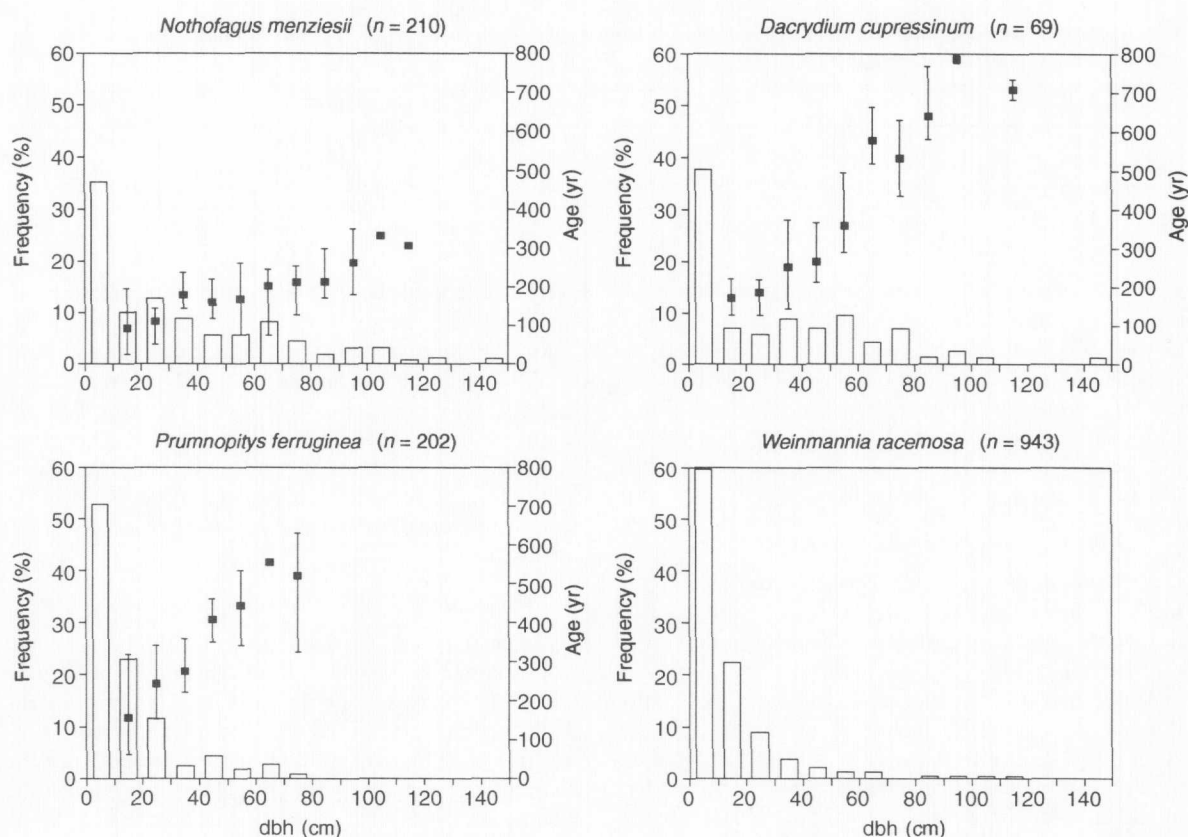


FIG. 1. Diameter frequency distributions of four dominant tree species in an old-growth rain forest on South Island, New Zealand. The x-axis shows midpoints of dbh classes. The squares and vertical lines show means and absolute ranges for tree ages (right-hand y-axes) in each diameter class, for each species except *Weinmannia racemosa*.

diameter distributions (Fig. 1), both with ~45% of their stems in the smallest two size classes (0–20 cm dbh). *Prumnopitys ferruginea* and *Weinmannia racemosa* had steeper distributions, with stems <20 cm dbh accounting for 76% and 81%, respectively, of their populations. Age–diameter relationships were highly significant for all species (Table 2), and mean ages in successive diameter classes were, for the most part, progressively older (Fig. 1). No age data were collected from *W. racemosa*, but the diameter distribution of this species is also consistent with an all-aged population structure.

Tree growth rates and longevity

There were substantial species differences in radial growth rates and longevity. Although *N. menziesii* and *D. cupressinum* attained similar maximum diameters of 140–150 cm, the former grew, on average, >2.5 times faster than the latter (Table 3) and was much shorter lived (Fig. 1). Many *D. cupressinum* individuals were aged at >700 yr old (maximum 785 yr), whereas no *N. menziesii* were found to be older than ~355 yr. Extensive heartrot prevented age determination of the largest individuals of both these species (Fig. 1). Extrapolation of age–diameter relationships (Table 2) in-

dicates that maximum ages of ≥ 950 yr are probable in *D. cupressinum*, but that very few *N. menziesii* are likely to exceed 350 yr of age. Mean growth rates of *P. ferruginea* were only slightly lower than those in *D. cupressinum* (Table 3). However, *P. ferruginea* did not exceed 80 cm dbh (Fig. 1), as a result of its shorter life-span, with few individuals exceeding 500 yr (maximum 640 yr) of age.

Maximum growth rates during sapling and small-tree stages (<20 cm dbh) were also much faster in *N. menziesii* than in the two conifers, which had very similar values (Table 3). Initial growth for all three species averaged about half of the mean rate for the whole life of the trees, but it was somewhat less variable in *P. ferruginea* than in *N. menziesii* and *D. cupressinum* (Table 3). However, without detailed information on the locations of juveniles in relation to canopy openings, it is unclear whether this indicates that *P. ferruginea* seedlings established in a narrower range of light environments than did the other two species, or whether *P. ferruginea* is simply less responsive to light intensity.

Stand disturbance history

Growth releases occurred throughout the 400-yr period examined, with $\leq 7\%$ of trees showing release in

TABLE 2. Regression equations for estimating age (y) from diameter at breast height (x) for dominant species in an old-growth rain forest, South Island, New Zealand. $P < 0.0001$ for all species.

Species	N	dbh range (cm)	Equation	R ²
<i>N. menziesii</i>	63	12.0–134.0	$y = 70.56 + 1.90x$	0.52
<i>D. cupressinum</i>	56	10.5–111.0	$y = 68.00 + 6.37x$	0.85
<i>P. ferruginea</i>	56	10.0–79.5	$y = 76.14 + 6.81x$	0.76

any 5-yr period (Fig. 2). This is consistent with a history of sporadic, localized disturbances, such as falls of one or a few canopy trees, with no evidence for episodes of massive overstory mortality. Although a few ring sequences extended back as far as the 13th to 14th centuries, we considered that the sample size before about AD 1600 ($n < 20$) was not sufficient to justify inclusion in the chronology.

Species-specific radial growth histories

Nothofagus menziesii, *D. cupressinum*, and *P. ferruginea* showed marked differences in growth histories, with significant differences in mean numbers of post-establishment releases (Table 3).

About half (53%) of the *N. menziesii* population showed no post-establishment release before attaining 20 cm dbh, and no individual was found to have experienced more than one release (Table 3). About half of the individuals of this species that successfully acceded to the overstory, therefore, apparently did so in one growth spurt: none survived multiple cycles of suppression and release. This suggests that, although saplings of *N. menziesii* have some capacity to survive beneath the canopy, recruitment of new or pre-existing seedlings in treefall gaps was very important for the regeneration of this species in this stand.

Most *D. cupressinum* (81%) showed postestablishment release before attaining 20 cm dbh (Table 3). Only one individual showed two successive episodes of release from suppression. Initial growth rates were highly variable, so it is difficult to generalize about early growth environments. However, the release data indicate that *D. cupressinum* saplings usually underwent a

period of growth beneath overtopping vegetation before attaining canopy status.

Most *P. ferruginea* (89%) showed at least one post-establishment release, and many (44%) had two or three releases before attaining 20 cm dbh (average 1.50 releases per tree; Table 3). Recruitment of *P. ferruginea* to the canopy, therefore, often involved a sequence of alternating episodes of release and suppression in response to formation and closure of a series of canopy openings.

Age differences between conspecific neighbors

Mean distances between nearest neighbors ranged from 4.0 m in *W. racemosa* to 11.6 m in *D. cupressinum* (Table 4). Nearest neighbor pairs of *N. menziesii* trees ≥ 10 cm dbh were, on average, significantly more similar in age than were random pairs selected from the *N. menziesii* age data pool (Fig. 3a). This implies the existence of a mosaic of even-aged patches in the *N. menziesii* tree population. Nearest neighbor pairs of *D. cupressinum* trees were, on average, slightly more similar in age than expected under the bootstrap null model, but not significantly so (Fig. 3b). The mean age difference between nearest neighbor pairs of *P. ferruginea* was very similar to the mean age difference among bootstrap samples (Fig. 3c), implying an essentially random spatial arrangement of tree ages within the stand for this species.

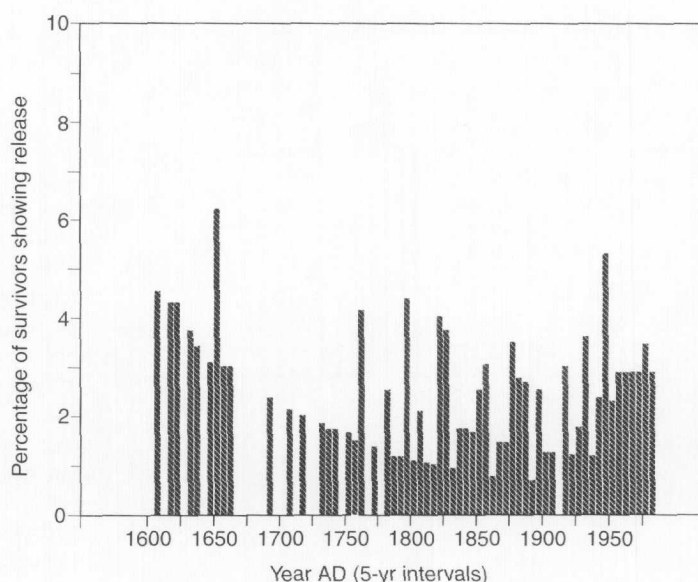
Overstory-understory associations

There was little evidence of strong negative or positive associations of juveniles with canopy individuals of the same, or other, species (Table 5). Two out of 16

TABLE 3. Radial growth of three dominant tree species in an old-growth rain forest, South Island, New Zealand, from measurements on increment cores. Means followed by the same letter are not significantly different at $P < 0.05$. Overall growth rates were calculated for the whole life of the tree, in individuals ≥ 10 cm dbh.

Measure	<i>Nothofagus menziesii</i>	<i>Dacrydium cupressinum</i>	<i>Prumnopitys ferruginea</i>
Overall growth rate, $\bar{X} \pm 1$ SD (mm/yr)	1.68 \pm 0.72 [N = 63]	0.64 \pm 0.18 [N = 56]	0.53 \pm 0.16 [N = 58]
Mean dbh (cm) of sampled trees	57.9	50.0	27.6
Growth during 1st 20 years, $\bar{X} \pm$ cv (mm/yr)	0.77 \pm 69% [N = 17]	0.31 ^a \pm 71% [N = 16]	0.30 ^a \pm 51% [N = 18]
Growth (mm/yr) during decade of fastest growth before reaching 20 cm dbh; $\bar{X} \pm 1$ SD	2.55 \pm 0.95 [N = 17]	1.11 ^a \pm 0.33 [N = 16]	1.12 ^a \pm 0.27 [N = 19]
No. releases before attaining 20 cm dbh; \bar{X} (range)	0.47 (0–1) [N = 19]	0.88 (0–2) [N = 16]	1.50 (0–3) [N = 18]

FIG. 2. Temporal distribution of growth releases since AD 1600 in an old-growth rain forest on South Island, New Zealand, from trees alive in February 1995 (all species combined). Data are the percentage of trees alive during each 5-yr interval that show release during that period. Release is defined here as an abrupt $>100\%$ increase in ring width sustained over ≥ 10 yr. Sample size increases from 20 trees in the year AD 1600 to 173 trees after AD 1600.



tests showed associations with significance levels of $P < 0.05$: understory *N. menziesii* were negatively associated with overstory *D. cupressinum* and positively associated with overstory *W. racemosa* (Table 5). A binomial test indicates that the probability of obtaining two significant results (i.e., $P < 0.05$) out of 16 tests by chance alone is $120(0.95)^{14}(0.05)^2 = 0.146$ (non-significant overall). Therefore, these results do not provide convincing evidence of deviations from randomness in associations between overstory and understory elements.

DISCUSSION

Regeneration patterns

All four dominants had population structures indicative of continual recruitment within the study area during recent centuries (Fig. 1). However, spatial distributions of tree ages and tree growth histories suggest species differences in regeneration behavior, stemming from differences in growth rate and in the capacity of juveniles to survive suppression.

The closely matched ages of nearest neighbor adults of *Nothofagus menziesii* (Fig. 3a) indicate a population consisting of small, even-aged patches. This is consistent with recruitment of new or pre-established seed-

lings (rather than suppressed saplings) in treefall gaps, resulting in a narrow age range within each patch (Duncan and Stewart 1991). A good correspondence with the tree growth history data (Table 3) is apparent, both lines of evidence suggesting that treefall gaps are important for the establishment and survival of *N. menziesii*.

In contrast to *N. menziesii*, *Prumnopitys ferruginea* showed no suggestion of deviation from a random spatial arrangement of tree ages (Fig. 3c). This implies that establishment and survival in this species were essentially independent of gap formation. Again, there is close agreement with the growth history data, which suggest that juveniles of *P. ferruginea* often spent long periods beneath the canopy, undergoing multiple episodes of release and suppression before attaining overstory status (Table 3).

Growth history data for *Dacrydium cupressinum* suggest that juveniles usually experienced an early period of growth under canopy, but that few individuals survived repeated cycles of release and suppression to the extent observed for *P. ferruginea*. *D. cupressinum* showed only a weak, nonsignificant tendency for nearest neighbors to be more similar in age than would be expected by chance (Fig. 3b), suggesting, on face value, that recruitment was not closely linked to canopy gap formation. Thus, the overall impression is that establishment and survival of juveniles were less dependent on gaps in *D. cupressinum* than in *N. menziesii*, but more dependent than in *P. ferruginea*. Studies in other forests also indicate that *D. cupressinum* saplings are less tolerant of shade than those of *P. ferruginea* (Beveridge 1983, Lusk and Ogden 1992, Duncan 1993).

Although there are no major inconsistencies between the evidence from our various lines of investigation, the poor age correspondence between nearest neighbors

TABLE 4. Distances between conspecific nearest neighbor pairs ≥ 10 cm dbh in an old-growth rain forest, South Island, New Zealand. $N = 30$ pairs for each species.

Species	Mean distance (m)	Range (m)
<i>N. menziesii</i>	5.7	0.8–15.0
<i>D. cupressinum</i>	11.6	3.4–22.5
<i>P. ferruginea</i>	8.5	2.5–16.1
<i>W. racemosa</i>	4.0	1.4–7.5

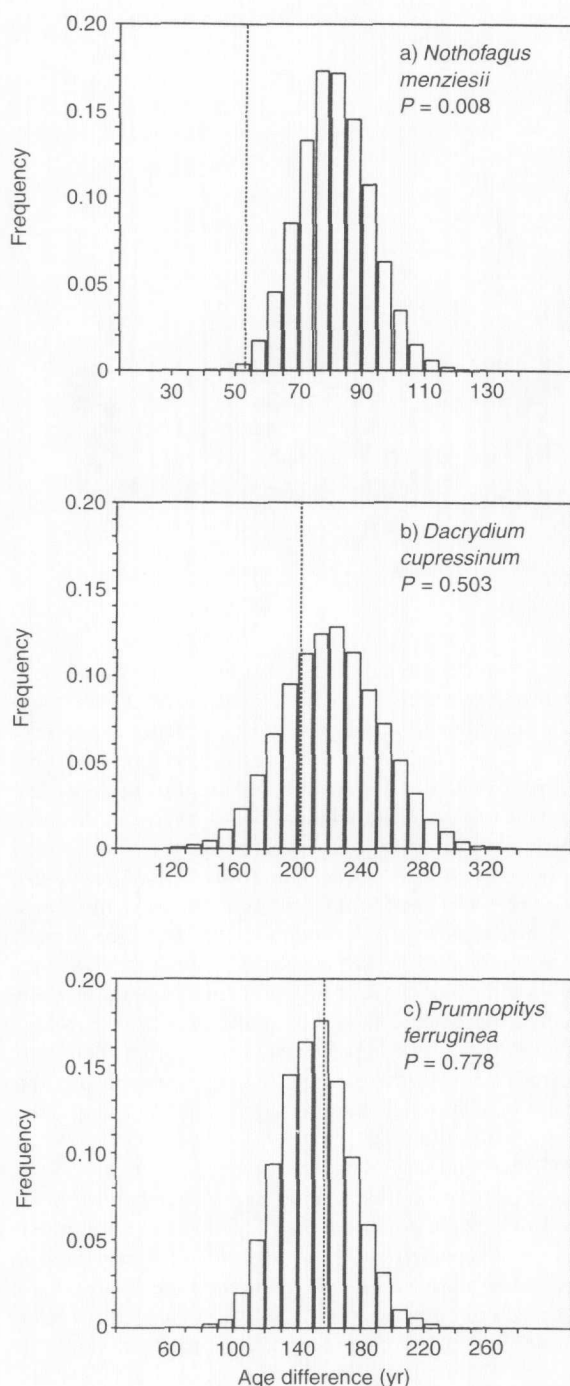


FIG. 3. Mean observed age difference between neighboring conspecific trees ≥ 10 cm dbh (dotted line), compared with null frequency distribution of mean age differences for 10^4 bootstrap data sets, each consisting of 30 random pairs drawn from the pool of observed ages. The P value (two-tailed) indicates significance of difference between means of observed and random age differences. (a) *Nothofagus menziesii*, (b) *Dacrydium cupressinum*, (c) *Prumnopitys ferruginea*.

in *D. cupressinum* contrasts with most previous findings on the regeneration ecology of this species (Beveridge 1973, 1983, Lusk and Ogden 1992, Duncan 1993), and an alternative interpretation of the result may be worthy of consideration. Although we assumed that a lack of correlation between the ages of neighboring trees would indicate that recruitment was essentially independent of canopy gap formation, a non-significant result would also be expected if only one individual of a given species were recruited in most gaps. This latter interpretation seems plausible for *D. cupressinum*, because stems ≥ 10 cm dbh of this species were present at lower densities than those of any of the other overstory dominants. The likelihood of this scenario could be assessed in more depth by comparing mean gap diameters with the mean distance between neighboring pairs of *D. cupressinum*. Although we collected no data on gap sizes in our stand, some useful comparisons can be made using data from other old-growth forests with similar canopy heights. Data in Ogden et al. (1991) indicate a mean gap diameter of ~ 9.3 m in a montane conifer/broadleaf forest, and Stewart et al. (1991) reported a mean of 10.9 m for *Nothofagus fusca*-*N. menziesii* stands, both of these figures falling slightly short of the mean distance between neighboring pairs of *D. cupressinum* in our stand (Table 4). Thus, there is some evidence to support our alternative interpretation of the poor age correspondence between neighboring pairs of *D. cupressinum* trees: in many cases, they are spaced too far apart to have been recruited in the same canopy gap.

Because no increment cores were obtained from *Weinmannia racemosa*, there are no data on tree ages or growth histories for this species. Studies of other old-growth forests throughout New Zealand have often reported all-sized (Stewart and Veblen 1982) or all-aged (Lusk and Ogden 1992) populations of *W. racemosa*. Establishment of small-seeded *W. racemosa* in old-growth forests may be limited as much by availability of suitable elevated substrates as by the occurrence of canopy gaps: several studies have shown that *W. racemosa* seedlings are highly associated with fallen logs, tip-up mounds, and tree fern trunks (Stewart and Veblen 1982, Stewart 1986, Lusk and Ogden 1992).

Life history differences and species coexistence

The population structures observed suggest that no appreciable shifts in species composition were occurring, and that the stand had not been massively disturbed for ≥ 800 yr. Release data (Fig. 2) and age relationships of nearest neighbor *N. menziesii* trees (Fig. 3) are consistent with a history of sporadic, localized disturbances. A recent landslide scar was found on a slope adjacent to our study site, implying that slope instability does periodically cause larger scale and more severe disturbances in this area. Nevertheless, our data suggest that stable coexistence of the four overstory dominants may occur at stand scale in the absence

TABLE 5. Overstory-understory associations of four tree species in an old-growth rain forest, South Island, New Zealand, showing direction of association (+, positive; -, negative) and its significance (*P*) from a chi-square test.

Understory	Overstory			
	<i>Nothofagus menziesii</i>	<i>Dacrydium cupressinum</i>	<i>Prumnopitys ferruginea</i>	<i>Weinmannia racemosa</i>
<i>Nothofagus menziesii</i>	(-) $\chi^2 = 0.409$ <i>P</i> = 0.522	(-) $\chi^2 = 5.161$ <i>P</i> = 0.023	(-) $\chi^2 = 0.147$ <i>P</i> = 0.701	(+) $\chi^2 = 4.812$ <i>P</i> = 0.028
<i>Dacrydium cupressinum</i>	(+) $\chi^2 = 0.077$ <i>P</i> = 0.782	(-) $\chi^2 = 1.975$ <i>P</i> = 0.160	(-) $\chi^2 = 3.552$ <i>P</i> = 0.059	(+) $\chi^2 = 0.152$ <i>P</i> = 0.697
<i>Prumnopitys ferruginea</i>	(+) $\chi^2 = 1.017$ <i>P</i> = 0.313	(-) $\chi^2 = 0.034$ <i>P</i> = 0.854	(+) $\chi^2 = 0.540$ <i>P</i> = 0.463	(-) $\chi^2 = 0.008$ <i>P</i> = 0.930
<i>Weinmannia racemosa</i>	(+) $\chi^2 = 1.730$ <i>P</i> = 0.188	(+) $\chi^2 = 0.534$ <i>P</i> = 0.465	(+) $\chi^2 = 0.257$ <i>P</i> = 0.612	(+) $\chi^2 = 2.388$ <i>P</i> = 0.122

of such events. Both differential responses of juveniles to gap-understory gradients and differences in canopy residence time appear to be involved in maintaining the balance between the dominants.

Our evidence of responses to gap and understory environments is indirect, and does not permit detailed comparisons of species performance along the understory-gap center gradient. For example, responses to gap margin environments cannot be inferred from our data. Nevertheless, our growth history and nearest neighbor age data are consistent with a shade tolerance hierarchy, in descending order: *P. ferruginea* > *D. cupressinum* > *N. menziesii*. On the other hand, maximum juvenile growth rates of *N. menziesii* were well over twice those of *D. cupressinum* and *P. ferruginea* (Table 3), implying that the advantage of the podocarps in the shade may be offset by much faster growth of new *N. menziesii* recruits beneath canopy openings. Although we only measured radial growth rates, which are of little direct relevance to plant competition, data from other studies confirm that height growth is also much faster in *Nothofagus* spp. than in podocarps (Wardle 1991: Table 14.8). Thus, although subcanopy individuals of *P. ferruginea*, in particular, are likely to be present prior to the formation of canopy openings, neutralization of this advantage by rapid growth beneath gaps probably favors the persistence of *N. menziesii* in the stand.

Juveniles of *N. menziesii* and *P. ferruginea* have sharply differentiated responses to gap and understory environments; therefore, shifting advantage beneath a spatially and temporally heterogeneous canopy may be a sufficient explanation of their coexistence in this forest. However, such a mechanism is unlikely to explain the persistence of *D. cupressinum*, which appears to be considerably outperformed by one or another of its competitors, both in the shade and beneath gaps. The release data indicate that *D. cupressinum* is at a notable disadvantage to *P. ferruginea* in the shade (Table 3), and closely matched juvenile maximum growth rates

in these two species (Table 3) suggest that there is no reversal of competitive advantage beneath treefall gaps. Canopy recruitment rates of *D. cupressinum* are, therefore, likely to be lower overall than those of the other dominants, consistent with the lower densities of saplings and small trees relative to the those of *N. menziesii* and *P. ferruginea* (Fig. 1).

However, the longevity advantage of *D. cupressinum* must be weighed against the apparently greater competitiveness of the juveniles of its associates. The role of great longevity in the persistence of *D. cupressinum* in the stand is highlighted by estimation of maximum overstory residence time (maximum total age minus estimated age at canopy accession). Extrapolation of age-diameter relationships (Table 2) suggests maximum ages of ~960 yr in *D. cupressinum*. If we assume canopy accession at ~20 cm dbh and subtract average age at this diameter (195 yr) from the maximum total age estimate, a maximum overstory residence time of ~765 yr is suggested. Equivalent calculations for *N. menziesii* and *P. ferruginea* give maximum overstory residence times of ~247 and ~428 yr, respectively. The rank order of species longevities that we observed is confirmed by previous work from other forests, which reports maximum figures of 650–1170 yr for *D. cupressinum*, 500–770 yr for *P. ferruginea*, and 350–600 yr for *N. menziesii* (June 1983, J. Wardle 1984, Six Dijkstra et al. 1985, Stewart and Rose 1990, Lusk and Ogden 1992). The very slow turnover of the *D. cupressinum* overstory population that is evident from our longevity data means that only modest recruitment rates would be required to maintain its present abundance. Such occasional recruitment could occur in localized patches where *P. ferruginea* and *N. menziesii* juveniles are stochastically absent during periods favorable for survival and growth of *D. cupressinum*, or under a limited range of light and/or substrate conditions (not quantified by this study) in which *D. cupressinum* juveniles might enjoy competitive superiority.

Although wood strength and decay resistance are the fundamental determinants of tree longevity (Loehle 1988), the status of *D. cupressinum* as an emergent may also contribute to its canopy residence time advantage over its associates. Mature *D. cupressinum* cannot be overtopped and suppressed by other species. Furthermore, species height differences will undoubtedly affect probabilities of secondary mortality during treefalls. The fall of an emergent *D. cupressinum* invariably destroys or severely damages several other overstory or subcanopy trees (e.g., Ogden et al. 1991), but adult *D. cupressinum* are very unlikely to be knocked down by species that attain lower stature.

For practical reasons, fewer data were obtained for *Weinmannia racemosa* than for the other dominant species at the study site (see *Methods*). Therefore, any analysis of the maintenance of the balance between *W. racemosa* and its associates must necessarily be more speculative. Data from other studies show that *W. racemosa* grows faster than *D. cupressinum* and *P. ferruginea* (Lusk and Ogden 1992), but at only about half the rate of *N. menziesii* (Stewart 1986). The maximum longevity of individual stems of *W. racemosa* is much less than that of most podocarps, and is broadly similar to that of *N. menziesii* (Lusk and Ogden 1992). However, *W. racemosa* is the only one of the four dominant species known to frequently reproduce by vegetative means (Wardle 1991), and this trait may bestow an advantage in pre-emption of treefall gaps. We collected no data on the incidence of vegetative reproduction in the stands described in this paper. However, data from a North Island old-growth conifer/broadleaf forest (Lusk, unpublished data) indicate that >10% of "dead" *W. racemosa* canopy stems (including standing dead, snapped, and toppled individuals) either resprouted or were survived by pre-existing basal shoots. Small stems of *W. racemosa* usually greatly outnumber those of *N. menziesii* in closed-canopy mixed stands, suggesting greater shade tolerance in the former species (J. Wardle 1984). Several papers have reported evidence for reciprocal replacement between *W. racemosa* and podocarp species in conifer/broad-leaved forests, the former capturing gaps formed by podocarp windfalls, and the latter, in turn, regenerating beneath thinning crowns of old *W. racemosa* (Beveridge 1973, Norton 1991, Lusk and Ogden 1992). However, overstory-understory associations (Table 5) revealed no evidence of this pattern in the mixed stands examined in the present study.

Although longevity differences contributed to a coexistence that showed a high degree of stability at the spatial and temporal scales examined in our study, life-span is also an important factor in the persistence of patently non-equilibrium species mixtures in New Zealand forests (Ogden and Stewart 1985). In lowland conifer/broadleaf forests (i.e., without *Nothofagus*), regeneration of emergent conifers such as *Agathis australis*, *Dacrydium cupressinum*, and *Prumnopitys taxifolia* is

associated primarily with coarse-scale disturbances, although such species also appear to respond to more localized openings on sites where harsh climatic or edaphic conditions reduce competition from associated angiosperms (Ogden and Stewart 1995). On mesic sites with mild temperatures, broad-leaved angiosperms dominate recruitment in both understory and small gap environments in old-growth stands (Dawson and Sneddon 1969, Smale and Kimberley 1983). However, the life-span of the emergent conifers is about twice that of their broad-leaved associates, with some species attaining ages >1000 yr (Lusk and Ogden 1992). As a result, although they are typically represented by declining populations in old stands, the conifers are rarely completely eliminated, even on sites where stand-destroying disturbances are very infrequent (Ogden and Stewart 1995). Thus, it is evident that both disturbance regimes and the population dynamics of *D. cupressinum* at our site differ appreciably from those reported from conifer/broadleaf forests in northern New Zealand (Dawson and Sneddon 1969, Beveridge 1973, 1983, Lusk and Ogden 1992). The absence of the most shade-tolerant angiosperms of the conifer/broadleaf forests (especially *Beilschmiedia* spp.) is probably an important factor in the ability of *D. cupressinum* to regenerate without major disturbance at our site.

Population structures reported from mixtures of *Nothofagus* species suggest that *N. menziesii* is the least light-demanding New Zealand representative of this genus (J. Wardle 1984, Stewart and Rose 1990). However, we found evidence that *N. menziesii* was less capable of surviving suppression than were *D. cupressinum* and *P. ferruginea* (Fig. 3, Table 3), two of the most widely distributed dominants of conifer/broadleaf forests throughout the country. This lends support to the view that *Nothofagus* species, as a group, are less shade-tolerant than most overstory dominants of the conifer/broadleaf forests, which tend to occupy the most favorable sites for plant growth in New Zealand (J. Wardle 1984).

Given the individualistic nature of plant species' physiological responses to environmental gradients such as temperature and rainfall (Austin and Smith 1989), the competitive balance between species will vary along such gradients (e.g., Kobe 1996). Although the four dominant species at our site co-occur widely throughout cool, humid districts of New Zealand (J. Wardle 1984, P. Wardle 1991), stable coexistence at stand scales may, therefore, be restricted to a subset of their total range overlap. Spatial and temporal variation in disturbance regimes will presumably also affect the competitive balance between the study species (cf. Poulson and Platt 1996).

Our results serve to emphasize that understanding the coexistence of tree species may require attention to both juvenile and adult life history differences. Although some studies have produced strong evidence of shifting advantage along gap-understory gradients,

large differences in canopy residence time may, in addition, permit the persistence of species whose juveniles perform relatively poorly, both under canopy and in treefall gaps. Like some previous authors (Veblen 1986, Stewart and Rose 1990, Lertzman 1995, Ogden and Stewart 1995), we conclude that taking life-span differences into account can permit an enhanced understanding of both equilibrium and non-equilibrium stand-scale coexistence.

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