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Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand

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Abstract

The vegetation of *Pinus radiata* plantation forests in New Zealand was studied to examine how the indigenous flora has responded to this novel habitat. A chronosequence of stands about 5, 16 and 27 years was assessed in each of four different biogeographic regions to test the effects of several stand and site factors on the succession of vascular understorey plant communities. A total of 202 indigenous and 70 adventive vascular plant species were found across all study areas, with considerable geographic variation among forests in species composition, species richness (range 48–135 species), and the percentage of indigenous species (50–86%). Both richness and cover of adventive species decreased significantly over time, whereas richness and cover of indigenous species was highest in the oldest stands, and overall species richness was lowest at mid-rotation. The guild composition changed from dominance of grasses and forbs in young stands to dominance of ferns and understorey trees in mature stands. These temporal changes were accompanied by a decrease in light-demanding pioneer species and an increase in shade tolerant, later seral species adapted to a forest environment. Measurements of the degree of canopy closure in stands with low or high stocking and modelling of temporal changes of canopy closure indicated that these understorey plant dynamics are influenced by changes in light availability as stands age. Despite the successional changes within forests, geographic variation more strongly influenced understorey communities because stands within a forest area were grouped together in DCA and TWINSPAN analyses, along rainfall and temperature gradients. Although the canopy species of such intensively managed plantation forests is an alien element in the New Zealand flora, the sheltered forest environment of older stands allows the establishment of a mostly indigenous forest understorey community with considerable similarities to indigenous forests located nearby.
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1. Introduction

The loss of natural forests and the consequences for biodiversity are significant global concerns (Wilson, 1988). By contrast, the world-wide area of plantation forests is increasing (FAO, 2001), with uncertain

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outcomes for biodiversity. In many parts of the world, plantation forests involve exotic species. For example, although pines and other *Pinaceae* do not occur naturally in the southern hemisphere south of latitude 2°S (Critchfield and Little, 1966), there are substantial areas of planted pine forests in New Zealand, Australia, Brazil, Chile, and South Africa, with about 1 or 2 million ha in each country (Lavery and Mead, 1998; Le Maitre, 1998). There are concerns about the unsuitability of such exotic plantation forests as habitat for indigenous species (Armstrong and van Hensbergen, 1996; Hartley, 2002), yet others argue that such forests can make a contribution to the conservation of indigenous biodiversity (Allen et al., 1995; Norton, 1998).

The vegetation of the island archipelago of New Zealand literally represents a large-scale field experiment of such interactions of indigenous and adventive plants. Island ecosystems are generally regarded as particularly vulnerable to invasion by exotic species (Elton, 1958; MacArthur and Wilson, 1967; Vitousek et al., 1997), and in fact New Zealand is an extreme case where the number of indigenous vascular plants, approximately 2300 species (with ca. 85% endemics), is nearly matched by the 2100 adventive species (Wardle, 1991; Taylor, 1997; Wilton and Breitwieser, 2000). This is most remarkable because New Zealand lies in an isolated region in the South Pacific and was the last major inhabitable land mass of the world to be colonised by humans only about 800 years ago (Anderson, 1991). Natural forests remain on about 24% of the land area of New Zealand while plantation forests cover about 6% of which 90% are composed of a single species, *Pinus radiata* D. Don (Monterey pine). *P. radiata* occurs naturally only in five small populations in coastal California and two nearby islands, totalling about 7000 ha (Critchfield and Little, 1966; Lavery and Mead, 1998), an area that is exceeded by almost three orders of magnitude in extraterritorial *P. radiata* plantation forests (Lavery and Mead, 1998).

The management of *P. radiata* plantations in New Zealand is usually very intensive (Hammond, 1995). Stands are typically planted at a high stocking of about 750–1500 stems ha^{-1} and are thinned once or twice within 10–15 years to a final stocking of 200–400 stems ha^{-1}. Harvesting typically occurs when stands are about 27 years. Before replanting, herbicides are commonly applied to reduce competition from other vegetation.

Understorey plant assemblages in these pine plantations are highly dynamic and range from surprisingly diverse with many indigenous and adventive species (Allen et al., 1995; Ogden et al., 1997) to virtually non-existent (Henry, 1954; McQueen, 1993). Broadly similar patterns of a variable understorey have been reported for pine plantations in other southern hemisphere countries such as South Africa (Armstrong and van Hensbergen, 1996; Geldenhuys, 1997). To date, there is no clear understanding of the factors responsible for this variability in the understorey composition. Several authors describe the occurrence of strong successional processes (McQueen, 1993; Allen et al., 1995; Ogden et al., 1997), possibly caused by differences in the light availability which is known to be a major direct or indirect factor in forest successions (Connell and Slatyer, 1977; Mitchell et al., 1999; Thysell and Carey, 2001). However, understorey patterns in New Zealand have not been systematically studied on a larger geographic scale, and the impact of changes in canopy density on the understorey succession has not been directly assessed. By contrast, comprehensive studies on the ecology of the understorey vegetation have been carried out in the northern hemisphere (e.g., Hill, 1979a), where conifer stands of low canopy diversity can occur naturally. The successional patterns occurring in such forest cycles are different from so-called 'old-field successions' (Egler, 1954; Bazzaz, 1975; Singleton et al., 2001) because the succession is influenced by the planted trees.

In the present study, we wanted to examine how *P. radiata*, as an exotic canopy species that is taxonomically distant from any indigenous plant in New Zealand, influences the colonisation, understorey succession and diversity of indigenous and adventive vascular plants. In particular, we tested the hypotheses that (1) the succession of the vascular understorey vegetation, and changes in the proportion of indigenous and adventive plant species, are strongly influenced by the development of the *P. radiata* canopy and its effects on understorey light levels and (2) these successional patterns vary among biogeographic regions with climatic differences. To test these hypotheses we examined vegetation plots across four distinct biogeographic regions in young, mid-rotation and

economically mature stands, encompassing different levels of stocking.

2. Methods

2.1. Study areas and climate

Four study regions were chosen to represent a range of geographic and climatic variation (Table 1, Fig. 1). Climate data were obtained from a country-wide database, Bioclim, and individual parameters were modelled according to Leathwick and Stephens (1998). Rotoehu Forest [13.2° mean average temperature (MAT), 1855 mm mean annual rainfall (MAR), 0.35 kPa mean vapour pressure deficit (MVPD)] and Kaingaroa Forest (10.8° MAT, 1475 mm MAR, 0.27 kPa MVPD) are in an area with evenly distributed and relatively high rainfall in an area of the North Island where the majority of New Zealand's plantation forests are located. Kaingaroa forest is situated on the frost-prone interior Volcanic Plateau, whereas Rotoehu Forest is at a lower elevation near the Bay of Plenty coast which has one of the mildest climates in New Zealand. Of the two South Island forests, Hochstetter Forest (9.8° MAT, 2948 mm MAR, 0.20 kPa MVPD) is located near the west coast, an area characterised by high rainfall and relatively low temperatures, whereas Eyrewell Forest (11.3° MAT, 753 mm MAR, 0.39 kPa MVPD) is in one of the driest areas of New Zealand, the Canterbury Plains, with relatively high temperatures and frequent summer droughts. The Canterbury Plains have few remaining areas of natural vegetation and are dominated by pasture lands with low plant biodiversity.

2.2. Study sites and plots

To determine successional changes that occur in the understorey plant community as stands age we

Table 1
Description of study plots and stand characteristics ($n = 3$) in four *P. radiata* plantation forests

Forest	Site class (age and stocking[a])	Stand age (years, in January 1999)	Latitude (south)	Longitude (east)	Altitude (m)	Mean current stocking (stems ha^{-1})	Mean basal area (m^2/ha)	Mean height (m)
Eyrewell	Young	5	43°26′	172°20′	120	930	1.5	3.4
	Mid-rotation 'low'	16	43°26′	172°21′	120	270	19.4	18.0
	Mid-rotation 'high'	16	43°26′	172°21′	120	1080	38.4	17.8
	Mature	26	43°25′	172°24′	90	160	23.2	24.4
Hochstetter	Young	4	42°28′	171°38′	340	810	7.8[b]	9.0[b]
	Mid-rotation 'low'	18	42°25′	171°41′	380	230	14.7	19.7
	Mid-rotation 'high'	18	42°25′	171°41′	380	470	43.9	24.1
	Mature	27	42°33′	171°45′	420	270	33.4	28.5
Rotoehu	Young	5	37°57′	176°32′	245	810	20.3	9.2
	Mid-rotation 'low'	16	37°55′	176°30′	60	250	24.3	27.5
	Mid-rotation 'high'	15	37°55′	176°32′	160	430	38.2	27.2
	Mature	26	37°56′	176°30′	160	170	40.7	33.0
Kaingaroa 1	Young	6	38°39′	176°35′	505	870	9.5	8.3
	Mid-rotation 'low'	16	38°36′	176°36′	400	370	39.8	24.4
	Mid-rotation 'high'	16	38°39′	176°34′	545	560	46.9	23.4
	Mature	28	38°39′	176°35′	565	370	50.3	33.4
Kaingaroa 2	Young	6	38°39′	176°34′	500	870	16.2	8.9
	Mid-rotation 'low'	16	38°36′	176°36′	405	530	48.1	23.6
	Mid-rotation 'high'	16	38°39′	176°33′	550	670	52.9	23.5
	Mature	28	38°40′	176°35′	600	200	31.1	36.0

[a] 'High' and 'low' refers to stands with higher or lower stocking, respectively.
[b] At Hochstetter Forest 'young' basal area and height were measured the following year.
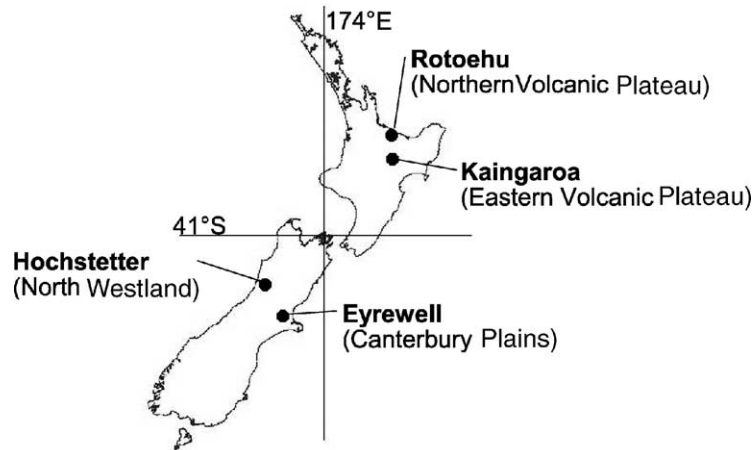
Fig. 1. Map of New Zealand showing location of study areas in *P. radiata* forests in four distinct bioregions, according to McEwen (1987).

selected from each forest three stands that were about 5, 16, and 27 years to reflect young, mid-rotation, and economically mature stands, respectively (Table 1). An additional replicate of 5, 16, and 27 years stands was selected in Kaingaroa Forest. The stand record system maintained by plantation forest owners was used to locate, a priori, stands that met the desired age criteria while being in close proximity and as similar as possible in terms of soil type and previous site management. All plantations were initially established on areas originally covered by natural forests or shrubland. At mid-rotation, two stands were selected from each forest representing higher and lower stockings to assess effects such as differences in light availability on the understorey composition. Paired stands suitable for this high vs. low stocking comparison could be located in each forest, although the exact stocking history varied somewhat among forests (Table 1). In each stand, we established three circular 0.03 ha vegetation reconnaissance plots placed every 40 m along a transect such that they were at least 100 m away from the nearest stand edge. In total we studied 60 plots in 20 stands (Table 1).

2.3. Site characteristics and pine stand parameters

In each vegetation plot, the pine overstory was measured to obtain the current stocking (stems ha^{-1}), diameter at breast height (DBH), tree height (using a Vertex digital hypsometer), the height to which stems had been pruned, the height of the crown containing live foliage (crown height), and mortality. Planting, thinning and pruning history of each stand were obtained from forest owners. The number of rotations ranged from one to three among forests. The effects of this difference are probably small because the species composition of a 3rd rotation stand in the central North Island was found to have changed very little from the 2nd rotation (Allen et al., 1995).

2.4. Canopy closure

The degree of canopy closure was measured in each plot in the mid-rotation stands in each forest by digital image analysis of 13 vertical-view photographs taken with a tripod-mounted digital camera at predefined locations (McElwee, 1999; Knowles et al., 1999). Grey-scale images were cropped to a circle and analysed for the percentage of canopy vs. sky with Foliage^{TM} software (Forest Research Institute, Rotorua). To assess temporal changes in canopy closure retrospectively, current and historical stand data were used to model the degree of canopy closure over time in STANDPAK (Forest Research Institute, 1993) according to Knowles et al. (1999) using function (1)

$$C = \left(a \left(1 - \exp \left(bG \left(1 - c \left(\left(\frac{H_2}{H_1} \right) - 0.4 \right) \right) \right) \right) \right)^{(1-d)}$$

(1)

where C is the percentage canopy closure, G the basal area, H_2 the crown height, H_1 the mean top height, and a–d are the coefficients ($a = 90, b = -0.05, c = 1.2708, d = 0.7984$).

2.5. Understorey vegetation assessment and nomenclature

Vegetation reconnaissance plots were assessed according to the method of Allen (1992), which is similar to Mueller-Dombois and Ellenberg's (1974) relevé method. The vegetation was recorded in each of six vertical tiers: <0.3, 0.3–2, 2–5, 5–12, and >12 m. In each tier, cover classes were assigned for each recorded vascular plant species according to the following classification: <1% cover, 1; 1–5% cover, 2; 5–25%, 3; 25–50%, 4; 50–75%, 5; >75%, 6. Where authorities are not given, species nomenclature follows Brownsey and Smith-Dodsworth (1989) for ferns, Edgar and Connor (2000) for grasses, and Parsons et al. (1998) for all others.

2.6. Life history traits

To enable an examination of plant communities with regard to the life history of the component species each species was categorised according to four different attributes: plant guild, successional stage, shade tolerance, and dispersal mode. Guilds were defined as forbs, grasses, sedges and rushes, ferns and fern allies, shrubs, and trees. To examine successional stage and shade tolerance, each species was categorised as either *pioneer* (colonisers of disturbed open sites, usually shade intolerant), *secondary* species (seral or climax species with an intermediate level of shade tolerance that require canopy gaps to regenerate), or *primary* species (late seral or climax species that are able to germinate and grow in the shade under a closed canopy) based on Allan (1961), Webb et al. (1988), Moles and Drake (1999), Peter Wardle (pers. comm.) and personal experience.

2.7. Data analysis

Summed cover values were calculated according to Allen et al. (1995) as the sum of the cover values of each species in a plot. Relationships of species richness and cover values with stand age and stocking

level were examined by analysis of variance (ANOVA) followed by least significant difference (LSD) tests. These tests were carried out for all species combined as well as for indigenous and adventive species separately. Similar ANOVAs were carried out to determine changes in the cover of particular plant guilds. SAS V. 8 or SYSTAT V. 9 were used to perform ANOVAs and LSD tests (for details see text).

To group vegetation plots we performed detrended correspondence analysis (DCA) (Hill, 1979b) and then qualitatively related compositional patterns to environmental variables. Divisive cluster analysis (TWINSPAN) (Hill, 1979c) was used as another approach to group vegetation plots according to plant compositional patterns. PC-ORD for Windows, V. 4.01 (McCune and Mefford, 1999) was used for DCA and TWINSPAN, using default settings.

3. Results

3.1. Pine stands

The stocking levels encountered ranged from ca. 900 stems ha^{-1} in young stands to ca. 200–400 stems in mature stands (Table 1), reflecting the typical decrease in stocking over time due to thinning by forest managers as well as mortality. Within-forest differences in stocking levels ('low' or 'high') of mid-rotation stands were suitable to assess effects on the understorey vegetation (Table 1). Due to thinning, there was no overall increase in basal area from mid-rotation to mature stands (Table 1). Tree height growth was not noticeably affected by thinning but differed considerably among regions ranging from 24.4 m at Eyrewell to 36.0 m at Kaingaroa 2 in mature stands (Table 1).

3.2. Species richness and geographic variation

We recorded a total of 272 vascular plant species of which 202 species were indigenous (Appendix A). There was considerable variation in total plant species richness among the study areas (Table 2; two-way ANOVA of forest and age factors, forest: MS = 771.7, $F_{4,12} = 7.38, P = 0.003$). Overall, Eyrewell Forest was the least species-rich, with only 48 species, and also had the lowest proportion of indigenous species, whereas Kaingaroa Forest, the most species-rich, had

Table 2
Richness of adventive and indigenous vascular plant species as stand totals of three vegetation plots per stand and total for forests

Forest	Site class (age and stocking[a])	Number of adventive species	Number of indigenous species	Total number of species	Percent indigenous species
Eyrewell	All stands	24	24	48	50
	Young	14	14	28	50
	Mid-rotation 'low'	17	9	26	35
	Mid-rotation 'high'	6	8	14	57
	Mature	14	18	32	56
Hochstetter	All stands	19	87	106	82
	Young	17	40	57	70
	Mid-rotation 'low'	11	39	50	78
	Mid-rotation 'high'	9	49	58	84
	Mature	4	55	59	93
Rotoehu	All stands	36	72	108	67
	Young	31	41	72	57
	Mid-rotation 'low'	18	34	52	65
	Mid-rotation 'high'	11	19	30	63
	Mature	17	44	61	72
Kaingaroa 1	All stands	17	104	121	86
	Young	13	47	60	78
	Mid-rotation 'low'	9	26	35	74
	Mid-rotation 'high'	6	44	50	88
	Mature	7	68	75	91
Kaingaroa 2	All stands	26	109	135	81
	Young	10	46	56	82
	Mid-rotation 'low'	21	34	55	62
	Mid-rotation 'high'	5	36	41	88
	Mature	8	74	82	90
Kaingaroa total		29	132	161	82

[a] 'High' and 'low' refers to stands with higher or lower stocking, respectively.

about three times as many species (Table 2). Variation in species richness among forests was large for indigenous species (two-way ANOVA, MS = 895.4, $F_{4,12} = 11.92, P < 0.001$), but the number of adventive species did not differ as much (Table 2), although differences were significant (two-way ANOVA, MS = 68.8, $F_{4,12} = 3.42, P = 0.044$). For example, Rotoehu Forest had more adventives in each age class than the other forests except for one stand in Kaingaroa 2.

Stands of different ages differed in adventive and indigenous species richness of understorey plants (Fig. 2). With increasing age, there was a decrease in adventive species richness (two-way ANOVA, MS = 101.3, $F_{3,12} = 5.03, P = 0.017$) whereas indigenous species richness was significantly highest in old

stands (two-way ANOVA, MS = 554.3, $F_{3,12} = 7.38, P = 0.005$), but there was no increase from young to mid-rotation stands (Fig. 2). Overall, species richness was lowest at mid-rotation (two-way ANOVA, MS = 551.4, $F_{3,12} = 5.27, P = 0.015$; LSD test, $P < 0.03$) but similar in young and mature stands.

3.3. Understorey cover

Summed cover values, a combined index of the cover values of each species, followed similar patterns as species richness. Across all forests, summed cover values of adventive species significantly decreased with stand age (two-way ANOVA, MS = 3300.2, $F_{3,12} = 5.58, P = 0.012$), whereas those of indigenous species were similar for young and mid-rotation
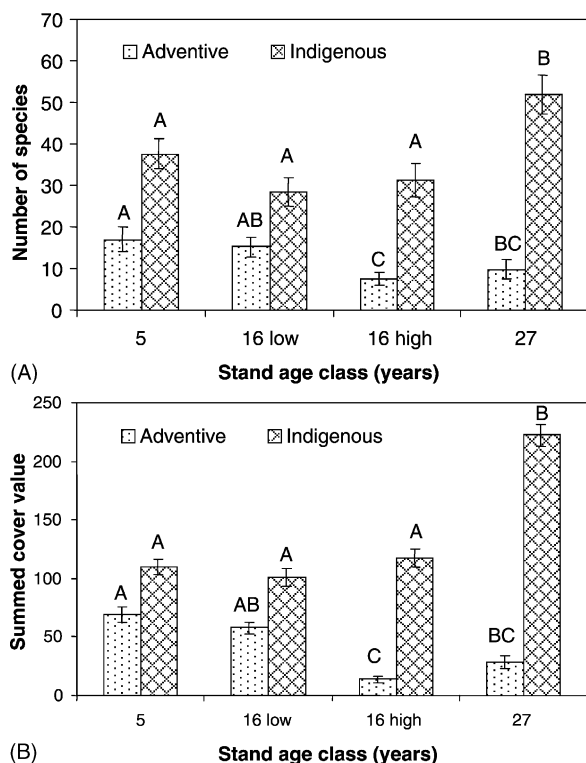
Fig. 2. Number and summed cover values (±S.E.) of adventive and indigenous plant species in *P. radiata* stands approximately 5, 16 and 27 years, based on 60 vegetation reconnaissance plots. Note: 'high' and 'low' refers to the stocking level. Summed cover values according to Allen et al. (1995). Columns with different letters within a time series are significantly different ($P < 0.05$, LSD test following a two-way ANOVA).

stands but increased markedly in mature stands (two-way ANOVA, MS $= 16062.2, F_{3,12} = 15.22, P < 0.001$) (Fig. 2). With few exceptions, the relative increase in indigenous cover with increasing stand age was consistent in each forest. Apart from stand age, the stocking (high vs. low) of mid-rotation stands also influenced the proportion of indigenous plants (see below). Although *P. radiata* was the sole canopy species, very few seedlings or saplings of this species were recorded in the understorey vegetation, but some regeneration was noticed outside our plots in most older stands.

The vegetation density, i.e. cover values, in each height tier varied considerably among forests. Overall, older stands had the highest cover values in the upper tiers and thus were structurally most complex.

However, none of the understorey plants grew into the >12 m tier over the course of the succession to mature stands.

3.4. Vegetation structure: dominant species, guild structure and life history traits

Although many species were shared among forests, only few species were abundant (with a summed cover value of at least 10 in any stand) in several forests (Appendix A). The understorey species with the highest cover values in young plantations were the adventive grass *Anthoxanthum odoratum*, the indigenous grass *Cortaderia fulvida*, and the adventive forb *Lotus pedunculatus* (a nitrogen-fixer which is often undersown in young plantations). In mid-rotation stands, the dominant species were *L. pedunculatus*, the indigenous grass *Microlaena avenacea*, and the indigenous ferns *Pteridium esculentum*, *Dicksonia squarrosa*, and *Histiopteris incisa*. In mature stands, the indigenous tree species *Aristotelia serrata* and *Carpodetus serratus*, and the ferns *D. squarrosa* and *P. esculentum* had the highest cover. Overall there was a change from dominance of grasses and forbs in young stands to dominance of ferns and trees in mature stands (Fig. 3A).

The cover by particular guilds changed with stand age in a similar way to that observed for the dominant species. There appeared to be a decrease in cover of herbs (grasses, forbs and rushes) and an increase of ferns and trees (Fig. 3B) although these changes were only significant for trees, presumably because of the large variation among forests (two-way ANOVAs, results for 'stand age' effects: herbs, MS $= 545.7, F_{3,12} = 1.63, P = 0.24$; shrubs, MS $= 530.7, F_{3,12} = 0.56, P = 0.66$; ferns, MS $= 1059.2, F_{3,12} = 0.89, P = 0.48$; trees, MS $= 677.6, F_{3,12} = 8.57, P = 0.003$). Even where the cover of particular guilds did not change much, there was still a considerable species turnover involving the replacement of many adventive by indigenous species. In many cases, this replacement involved species with different life history traits and habitat requirements. Young stands were largely dominated by pioneer species that invaded the sites disturbed by harvesting and site preparation (Fig. 4). Some pioneer species persisted in the lower tiers in older stands, particularly in canopy gaps such as those created by windthrows. The proportion of
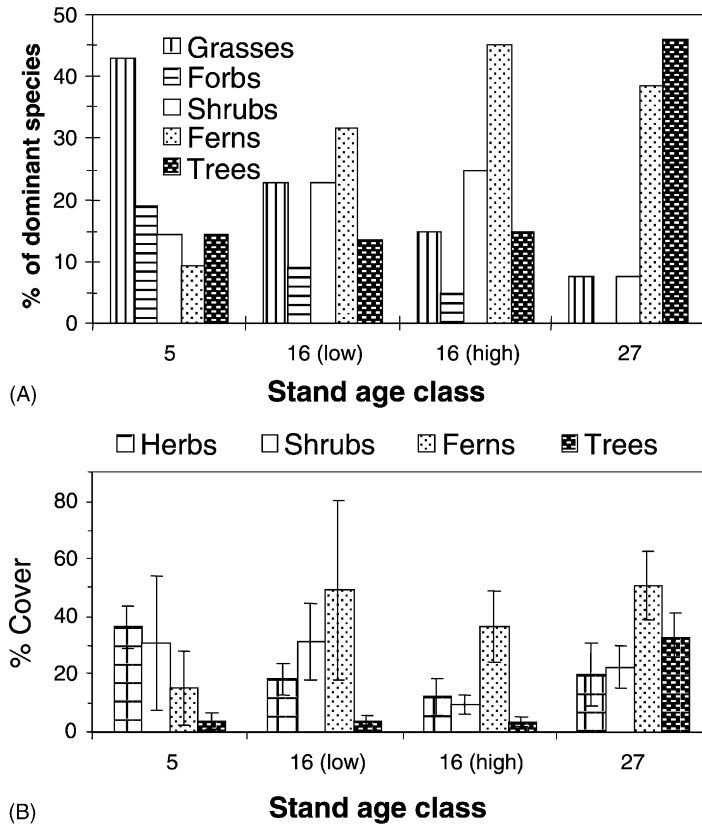
Fig. 3. Vascular plant guilds in the understorey of ca. 5–27 years *P. radiata* stands. (A) Guild distribution of the dominant species (i.e., species that have at least 5% cover). (B) Mean (±S.E.) summed percentage cover of vascular plant guilds of all understorey plants. Note: 'high' and 'low' refers to the stocking levels. 'Herbs' includes forbs, grasses and rushes, and 'shrubs' includes woody lianes.

primary (i.e., shade tolerant) and secondary species with intermediate shade tolerance expanded with increasing stand age (Fig. 4). Differences in stocking also appeared to affect the proportion of pioneer and later seral species as indicated in the differences between mid-rotation stands (Fig. 4). These results suggest that shade from the pine overstory is an important successional factor.

Fig. 4. Mean summed percent cover values of pioneer, primary and secondary species (explanation see Section 2) in the *P. radiata* understorey plotted against tier height by stand age.

Table 3
Degree of canopy closure based on measurements ($n = 3$) in mid-rotation *P. radiata* stands (ca. 16 years) with high or low stocking and model predictions

Forest	Site class (age and stocking)	Stand age (years, in January 1999)	Mean canopy closure (%)	Predicted canopy closure (%)	Residual error (%)
Eyrewell	Mid-rotation 'low'	16	40.1	51.3	11.2
	Mid-rotation 'high'	16	57.7	72.5	14.8
Hochstetter	Mid-rotation 'low'	18	30.5	52.9	22.4
	Mid-rotation 'high'	18	66.9	79.0	12.0
Rotoehu	Mid-rotation 'low'	16	56.0	54.3	−1.7
	Mid-rotation 'high'	15	61.8	69.4	7.6
Kaingaroa 1	Mid-rotation 'low'	16	65.3	72.6	7.3
	Mid-rotation 'high'	16	81.9	76.5	−5.4
Kaingaroa 2	Mid-rotation 'low'	16	79.4	77.9	−1.5
	Mid-rotation 'high'	16	77.8	80.4	2.5
Mean of all forests	Mid-rotation 'low'	16	49.8	61.8	7.5
	Mid-rotation 'high'	16	66.6	75.5	6.3

3.5. Canopy closure measurements and modelling

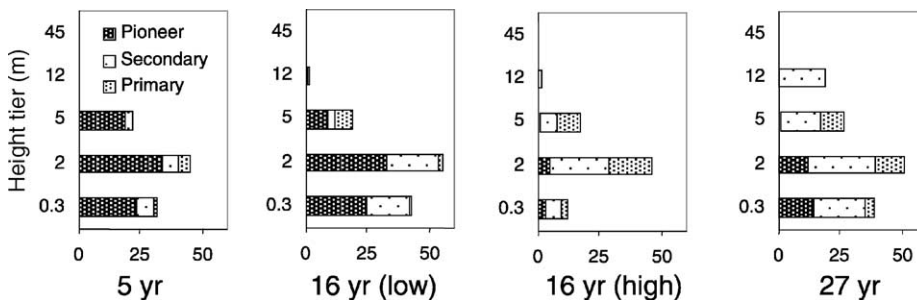The degree of canopy closure in mid-rotation stands reflected within-forest differences in stocking of mid-rotation stands, except for Kaingaroa 2 where plots in stands with high and low stocking were similar (Table 3). Model predictions overall had an average error of about 7% compared with actual canopy closure measurements (Table 3). While model predictions for Rotoehu and Kaingaroa Forests had a small residual error between 1.5 and 7.6%, predictions for Eyrewell and Hochstetter Forests overestimated the degree of canopy closure by over 10%. Models of percentage canopy closure give a good indication of temporal changes in the amount of light available to understorey plants, and how strongly this is affected by thinning operations carried out 5–15 years after planting (Fig. 5). Highly stocked stands can attain between 60 and 80% canopy closure 10 years after planting. Model runs based on the young stands in our study reached theoretical canopy closure values of up to ca. 90%. However, stands usually suffer some mortality over time, which creates canopy gaps, and rarely reach more than 80% canopy closure. The intensity of thinning effects on canopy closure varied among stands (Table 3) depending on the thinning regimes (Fig. 5). In our model runs, thinning had particularly strong effects on canopy closure at Eyr-

ewell (Fig. 5A). Even when current canopy closure values did not differ as much such as at Rotoehu, the model shows that these differences were present throughout most of the stand's history which would have compounded the effects on differences in the amount of light available to understorey plants (Fig. 5B).

3.6. Canopy closure and understorey vegetation at mid-rotation

Eyrewell stands showed the strongest thinning effects on the understorey vegetation. The thinned 16 years Eyrewell stand was about twice as species-rich as the unthinned stand (Table 2) and had over 10 times as much understorey vegetation cover. Overall, higher stocked stands had a lower understorey cover but at the same time a higher proportion of cover from indigenous species (Fig. 2). Correspondingly, stands with higher stocking had significantly fewer adventive species (Table 2, Fig. 2) and a lower adventive cover value (Fig. 2). The higher proportion of indigenous species in stands of higher canopy closure and the observation that such stands also have more later seral and shade-tolerant species (Fig. 4) indicates that the transition from pioneer to later seral species was accelerated in the higher stocked stands.
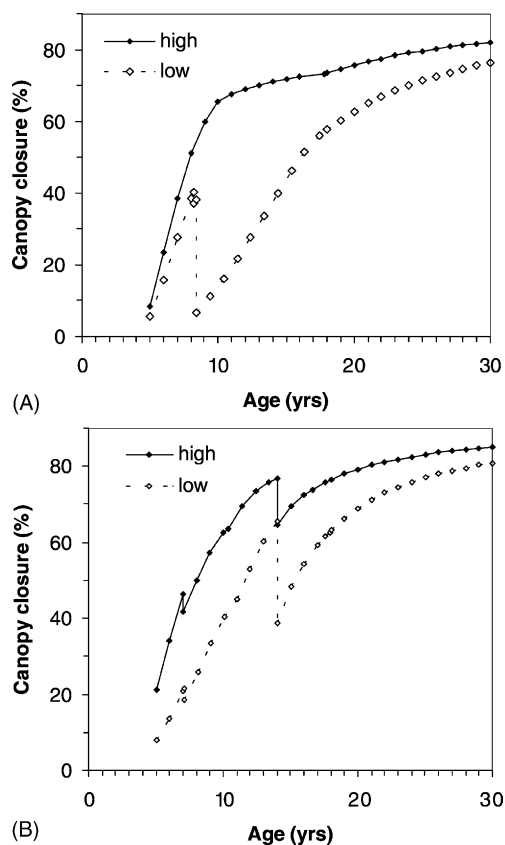
Fig. 5. Modelled relationship between time since planting and canopy closure of nearby *P. radiata* stands that differ in their pruning and thinning history. (A) Eyrewell Forest: 'high' remained at the original stocking of 1250 stems ha^{-1} (sph) whereas 'low' was pruned and thinned to 275 sph (indicated by sharp declines in canopy closure) after 8 years. (B) Rotoehu Forest: 'high' was thinned to 570 sph and later to 330 sph, whereas 'low' was thinned to 450 and 280 sph stems, respectively.

3.7. Understorey community classification and similarity

DCA grouped most stands within a forest together despite the differences in species composition among different age classes (Fig. 6). This indicates that regional differences (among forests) had a greater influence on species composition than temporal variation within forests. On the first axis Eyrewell was clearly separated whereas the other forests were separated along the second axis. Similar results were obtained from TWINSPAN which separated Eyrewell on the first division, and the

remainder of the forests by the 3rd level of division (Fig. 6).

Of the environmental and site variables (see Section 2.1) that could be correlated with these groupings, moisture (rainfall and vapour pressure deficit) distinguished Eyrewell forest from the others and appeared to be the main factor related to the first DCA axis. All forests were sorted by mean temperature along the second DCA axis (Fig. 6). In Hochstetter and, to a lesser extent, Rotoehu and Kaingaroa Forests, there was some tendency for axis 1 to be negatively correlated with stand age. Despite this, it is clear that the species composition of these communities is overall more influenced by geographic and climatic factors than by stand age. Finally, there was a general tendency for increasing among-forest dissimilarity with age (Fig. 6).

4. Discussion

Although plantation forests of *Pinus* species are alien floral elements in southern hemisphere countries, the forests examined in this study had a relatively rich understorey of mostly indigenous plant species. In the 60 plots (totalling 1.8 ha) we surveyed, there were 202 indigenous species, which equates to almost one-tenth of the indigenous vascular plant flora of New Zealand with ca. 2300 species (Taylor, 1997; Wilton and Breitwieser, 2000), as well as 70 adventive species. There was considerable variation in species richness, cover, and 'indigenousness' among and within the forests we studied.

4.1. Geographic variation

Geographic variation strongly influenced the similarity of the understorey plant communities as there was a clear clustering of all stands within forests despite the considerable successional within-forest differences in species and guild composition. This was most apparent in Eyrewell Forest which has a more distinct vegetation, as well as lower species richness and understorey cover than the other forests despite favourable mean air temperatures (the second highest among the four forests). Such low species richness and cover are typical of pine plantations in
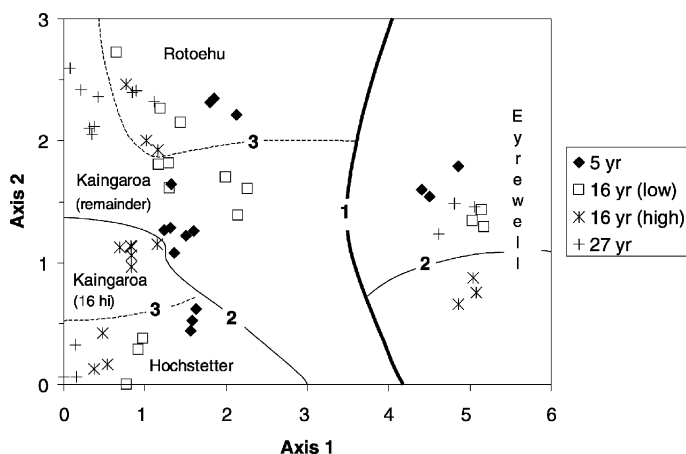
Fig. 6. Plot of first two axes of the DCA of the understorey vegetation of *P. radiata* stands ca. 5–27 years. Dashed lines indicate the first three levels of division of the TWINSPAN analysis which separate the four forests.

the Canterbury Plains (Norton, 1989). This is likely to be due to the frequent drought conditions caused by comparatively low rainfall and high atmospheric moisture deficit at Eyrewell Forest.

Soil and atmospheric moisture deficit (or related parameters) have been found, apart from air temperature, to be primary correlates of plant diversity and composition of forests in New Zealand (Leathwick and Rogers, 1996; Leathwick et al., 1998) and overseas (Richerson and Lum, 1980; Currie and Paquin, 1987; Austin et al., 1996). Furthermore, the scarcity of indigenous vegetation in the Canterbury Plains is likely to cause a shortage of propagules, which would contribute to a low richness. Distance from forest vegetation has been found to restrict colonisation by forest species (Hill, 1979a; Singleton et al., 2001). The other three plantation forests are all located in closer proximity to indigenous forests and have a richer flora. The commonly occurring latitudinal gradient in species richness which has also been reported from New Zealand (see Bellingham et al. (1999) for tree species) was not consistently apparent in our data.

4.2. Successional patterns

Stand age did not greatly affect total species richness but there was a strong effect on the richness of adventive and indigenous species and on the species composition of the understorey vegetation. This was mostly seen in the succession from a community dominated by pioneer species with a large component of adventive herbs and shrubs to a community with abundant ferns and trees and few adventives. Broadly similar changes in guild structure have been reported for other plantation forests (Allen et al., 1995; Ogden et al., 1997) as well as natural primary or secondary forest successions on such substrates in New Zealand (Grubb, 1986; Wardle, 1991; Allen et al., 1992). Despite these common patterns, species composition and temporal sequences generally vary with local climate, grazing pressure and available propagules (Wardle, 1991). Interestingly, ordination grouped the young stands of the different forests closer together than older stands, which reflects the ubiquitous nature of the 'weedy' pioneer species.

Disturbance of forest vegetation by harvesting or thinning can cause an increase in richness or cover of exotic plant species (e.g., Bailey et al., 1998; Thysell and Carey, 2001). However, contrary to northern hemisphere regions where indigenous species typically remain dominant despite such disturbances (e.g., Hill, 1979a; Thomas et al., 1999), adventive pioneer species are often dominant following disturbance in New Zealand, especially in areas that are heavily modified through agriculture and other human activities (Wardle, 1991; Atkinson and

Cameron, 1993). Pioneer species are particularly well-represented among the invasive adventive vascular plants present in New Zealand (Adair, 1995; Williams and West, 2000). All but 6 of the 70 adventive species recorded in the present study were categorised as pioneers, and most of these occurred in young stands (Appendix A). By contrast, the understorey vegetation in older stands had a large proportion of typical indigenous forest species. Similar changes along a successional gradient were observed in another New Zealand plantation forest by Allen et al. (1995) and Ogden et al. (1997).

The understorey composition of older stands showed considerable similarities with that in indigenous forests. For example, about 87% of the indigenous vascular plant species at Eyrewell Forest were shared with a natural *Kunzea ericoides* forest and shrubland, Eyrewell Reserve, in the area (Molloy and Ives, 1972), suggesting that, to a certain degree, *P. radiata* can take the role of *K. ericoides* as a canopy species. Similarly, 48 indigenous species (out of a total of 81–87 such species) were shared between Hochstetter Forest (pine) and a nearby natural *Nothofagus* Forest (Wiser et al., 1998). This relative richness of indigenous species in plantations compares favourably with other intensively managed production ecosystems such as pastoral grasslands in New Zealand, which are inhabited by few, if any, indigenous species (Wardle, 1991).

Based on a comparison of a pine plantation, Kinleith Forest, in the central North Island, New Zealand, with a natural forest nearby, Allen et al. (1995) concluded that while there are strong affinities between the two forests, there were also ''clear floristic differences'' because certain species were missing from the plantation. Interestingly, except for *Metrosideros diffusa*, all other species found to be missing by Allen et al. (1995) (*Prumnopitys ferruginea*, *Beilschmiedia tawa*, *Elaeocarpus dentatus*, *Pseudopanax crassifolius*, *Microlaena avenacea*, and *Hymenophyllum demissum*) occurred in one or both of the North Island plantations we surveyed. This suggests that the differences described by Allen et al. (1995) were due to variation in local species composition, and were not indicative of an inability of such species to inhabit pine plantations. However, it should be noted that many long-lived tree species will not be able to regenerate during the 27-year rotation and their presence will depend on the seed bank or re-colonisation from adjacent areas.

The changes in plant guild patterns we observed in understorey successions in pine plantations are comparable with natural successions in New Zealand. For example, herbs were the initial colonisers of landslide scars in the eastern North Island and these were gradually shaded out by taller species, primarily *K. ericoides* (Smale et al., 1997). Successions from pasture in the same area have also been reported to lead to dominance of *K. ericoides* (Bergin et al., 1995). However, the succession observed in some pine forests appears to progress faster than the natural succession involving *K. ericoides*. On the east coast of the South Island (eastern Otago), the succession from pasture or bare ground through *K. ericoides* proceeds within about 13 years to the stage where open habitat species are shaded out, and after ca. 50 years, most species other than *K. ericoides* are excluded (Allen et al., 1992). Here the establishment of typical forest species appears to depend on the decline of *K. ericoides* (Allen et al., 1992), and may take 200 years or more (Molloy, 1975). This succession is accelerated in areas of New Zealand with higher rainfall, where recruitment of typical forest species can already occur in 20-year old *K. ericoides* stands (Esler and Astridge, 1974; Wardle, 1991). Compared with secondary successions in such habitats, the establishment of shade-tolerant understorey species in pine plantations occurred relatively early, particularly in the more humid environments, apparently due to the quick development of a pine canopy that provides shade. This appears to be particularly noticeable where early stages are dominated by intolerant adventive grasses and forbs as well as the indigenous bracken (*Pteridium esculentum*). In secondary successions in open habitats these species may persist for many years because they have colonised all available habitat and so inhibit the establishment of later seral species (e.g., Bazzaz, 1975; Wardle, 1991). Especially in these situations, a rapidly closing pine canopy appears to facilitate (sensu Egler, 1954) the succession to a forest community by shading out pioneers and by providing the sheltered environment needed by later seral forest species.

The effects of differences in stocking on canopy closure as well as temporal changes of the canopy

are well illustrated by the model predictions for the stands we studied. Model runs show the long-term nature of these changes and help to understand relationships between canopy closure and the development of the understorey vegetation. This is important because the understorey vegetation is likely to respond with some delay to changes in light availability. For example, as the canopy gradually closes, a previously dense understorey will only gradually contract and lose shade-intolerant species. Similarly, the understorey will not immediately respond to an opening of the canopy, for example, after thinning operations. Such lag effects can be better appreciated when canopy closure models are available.

In addition to the successional changes observed along the chronosequence of stands, which can be correlated to the development of a pine canopy, the direct comparison between mid-rotation stands with low and high stocking provides further evidence of a strong canopy influence on the understorey. It could be argued that the observed differences in the understorey vegetation between stands with low and high stocking may be due to other stocking-related factors, such as increased root competition for moisture (e.g., Toumey, 1929). However, this is not likely to be a generally limiting factor for the understorey because most forests (except Eyrewell) are in areas with abundant rainfall that is evenly distributed throughout the year (Whitehead and Kelliher, 1991; Richardson et al., 1996). Light was also found to be the most important limiting factor for the understorey vegetation development in conifer plantations in the United Kingdom, where rainfall is equally abundant (Hill and Jones, 1978; Hill, 1979a).

By contrast, in densely stocked stands in drier areas such as the Canterbury Plains (Eyrewell Forest), soil moisture availability can be a limiting factor for understorey plants. In such dry areas, suppression of the understorey is likely to be exacerbated by the slow decomposition and accumulation of pine needle litter. Extensive litter fall can smother small understorey plants and create an environment not conducive to the establishment of seedlings (Toumey, 1929; Hill, 1979a; Ferris et al., 2000). However, in our study neither shading nor litter fall inhibited understorey growth in areas with higher rainfall, although shading clearly influenced the composition of the understorey (see above). In these areas pine stands still had a substantial undergrowth even near the maximum canopy closure of about 80%. However, beyond this value even shade-tolerant species may be inhibited, as reported from British conifer plantations when relative illumination dropped below 10–20% (Hill, 1979a). A more recent study in Britain also found a negative relationship between understorey cover and canopy cover values (Ferris et al., 2000).

4.3. Conclusions

This study demonstrated that (1) the succession of indigenous and adventive species in the understorey of pine plantations is related to temporal changes in the structure of the pine canopy. Where soil moisture is not limiting, this succession appears to be most strongly influenced by differences in light availability and the differential response of pioneer and later seral species; (2) geographic differences occur in the composition, diversity, and indigenousness of the understorey, and that climatic differences can interact with the influence of differences in stocking and canopy density, particularly where soil moisture is limiting (as in Eyrewell Forest).

The observed successional changes in the understorey vegetation can be summarised in a generalised conceptual model. Following harvesting, these disturbed sites are invaded by exotic and indigenous pioneer plants characterised by good dispersal capabilities, rapid growth and high light requirements. As the stands age and the pines grow, they increasingly shade out this pioneer flora and facilitate the establishment of shade tolerant, mostly indigenous understorey plants. This colonisation is influenced to some degree by the thinning practised in densely planted stands which, in areas where soil moisture is limiting, could otherwise suppress even shade-tolerant understorey species. The sequence of processes in pine plantations has similarities with components of the 'facilitation', 'tolerance' and 'inhibition' models of succession described by Connell and Slatyer (1977). These are variations of the theme that early successional colonising species affect later successional species by modifying the environment. The major difference with these conceptual models is that the pines, the canopy

component of this community, have been planted and have not achieved dominance by natural successional processes.

Were it not for the truncation of this succession through harvesting of the pines and the associated major disturbance of the remainder of the vegetation after about 27 years, such plantations would most likely progress further towards indigenous forest, except perhaps in the drier areas where pine seedlings might be superior competitors with indigenous species (Wardle, 1991). However, with continuing harvesting in an operational plantation forest, rare or threatened species that require a more stable forest environment may not be able to survive in short-rotation plantations, and very few such species have been recorded by us or in previous studies of plantation forest in New Zealand (e.g., Allen et al., 1995; Ogden et al., 1997; but see Gibbs, 1988). One interesting exception is the occurrence at Eyrewell Forest of *Pomaderris phylicifolia*, an indigenous shrub that is rare in the South Island (Speight et al., 1927; Molloy and Ives, 1972).

Tree monocultures such as pine plantations may be used to accelerate the restoration of indigenous forest biodiversity on degraded land, an apparent paradox (Lugo, 1997). The restoration of species-rich indigenous forest communities has also been described for *Pinus kesiya* plantation forests in Thailand (Oberhauser, 1997). This paradox is emphasised in the present study, where the monoculture involves a tree species that has no close relatives in the New Zealand flora. A

study in plantations of *Pinus* spp. and *Eucalyptus saligna* in South Africa also concluded that the identity of the canopy species is of less importance than stand age and site factors (Geldenhuys, 1997). Such findings are critical for our understanding of interactions between adventive and indigenous species, a subject of growing concern as the world's biota are increasingly homogenised. The present study also shows that there is considerable scope for biodiversity conservation in plantation forests, which may be critical in areas where the indigenous forest vegetation has largely been cleared. Such considerations are likely to become more important in future, as conservation efforts increasingly focus on managed landscapes.

Acknowledgements

Appendix A

Plant species recorded in stands in four *P. radiata* plantation forests in New Zealand, and the typical successional stage of occurrence. Values shown are summed cover values from three 0.03 ha plots in each stand (see Section 2 for details). Note: only species with a summed cover value greater than 3 are shown. Low or high tree stocking of 16-year-old stands is indicated by 'lo' and 'hi', respectively.

Guild and species (* indicates adventive species)	Stage (pioneer/ secondary/ primary)	Eyrewell 5 years	Eyrewell 16 years 'lo'	Eyrewell 16 years 'hi'	Eyrewell 27 years	Hochstetter 5 years	Hochstetter 16 years 'lo'	Hochstetter 16 years 'hi'	Hochstetter 27 years	Rotoehu 5 years	Rotoehu 16 years 'lo'	Rotoehu 16 years 'hi'	Rotoehu 27 years	Kaingaroa 1 5 years	Kaingaroa 1 16 years 'lo'	Kaingaroa 1 16 years 'hi'	Kaingaroa 1 27 years	Kaingaroa 2 5 years	Kaingaroa 2 16 years 'lo'	Kaingaroa 2 16 years 'hi'	Kaingaroa 2 27 years
Grasses																					
*Agrostis capillaris**	pi	12	10	1	3	5	3	1		2									2		1
*Agrostis stolonifera**	pi	5	1		2					1											
*Aira caryophyllea**	pi	5																			
*Anthoxanthum odoratum**	pi	12	7		11	1				17	3		3						3		
*Cortaderia selloana**	pi									1			3								
*Dactylis glomerata**	pi																		9		
*Elymus rectisetus**	pi		1		5																
*Holcus lanatus**	pi					6	2	1		6	2	1	1	4	6	4	1	3	7	1	
*Miscanthus nepalensis**	pi									3	1		2								
Cortaderia fulvida	pi											1	2	11	5	4		10		4	2
Deyeuxia avenoides	pi	2			2									3				5			
Dichelachne crinita	pi	3	2		3																
Microlaena avenacea	pr				2				3	2				1		16	3	9		9	1
Microlaena stipoides	se	2			3					3	1			1		1	3	2	5	1	2
Oplismenus imbecillus	se									2	1		13								
Rytidosperma clavatum	pi	6	5		2	1															
Rytidosperma gracile	pi	2		3		3	5	1	3					3				8	3	1	
Rytidosperma unarede	pi	10	10		9																
Forbs																					
*Anagallis arvensis**	pi									4											
*Cerastium glomeratum**	pi										1								3		
*Cirsium arvense**	pi									7	1	2	3	3	3				1		
*Cirsium palustre**	pi					3	1	1	2												
*Cirsium vulgare**	pi	5									1		3	3	3	1	2	3	4		1
*Conyza albida**	pi									8		3		3			3	2	3		1
*Crepis capillaris**	pi	3	2	1	1	3				3	1	2		3		1	1	5	4		
*Digitalis purpurea**	pi					4	1	1		9			1					1			1
*Gnaphalium coarctatum**	pi													2		1					1
*Hieracium lepidulum**	pi		2	1	2																
*Hieracium pilosella**	pi	1	2	2	7																
*Hypochoeris radicata**	pi	3	3		3	2	2	1		4	1			1		2		3	2	2	
*Leucanthemum vulgare**	pi		3	1																	
*Lotus pedunculatus**	pi					14	4			15	7	3	9	1	15				7	2	1
*Lotus suaveolens**	pi									5	2	1									
*Mycelis muralis**	se					2	1	3	1	3	2	1	4	3	5	3	4	5	3	5	5
*Phytolacca octandra**	pi									5			1								
*Plantago lanceolata**	pi	1	3		2						2										
*Rumex acetosella**	pi	3			1					3											
*Senecio bipinnatisectus**	pi									3		3									
*Senecio jacobaea**	pi									5	1	1	3	1	1				3		1
*Sonchus oleraceus**	pi									2	2										

Appendix A. (*Continued*)

Guild and species (* indicates adventive species)	Stage (pioneer/secondary/primary)	Eyrewell 5 years	16 years 'lo'	16 years 'hi'	27 years	Hochstetter 5 years	16 years 'lo'	16 years 'hi'	27 years	Rotoehu 5 years	16 years 'lo'	16 years 'hi'	27 years	Kaingaroa 1 5 years	16 years 'lo'	16 years 'hi'	27 years	Kaingaroa 2 5 years	16 years 'lo'	16 years 'hi'	27 years
Acaena anserinifolia	pi					2				1			3	2	7	3	1	4	1	1	2
Cardamine debilis	pr																		1		3
Chiloglottis cornuta	pr						1	2	3		2			1		1	1	1		1	
Dianella nigra	pi					5	5	2	4	8	5	10	6			1				1	
Dichondra brevifolia	se	1	3	4	3																
Epilobium alsinoides	pi									1				5				3		1	
Epilobium pedunculare	pi						1	3	1								1				
Euchiton audax	pi	2	1		3																
Euchiton gymnocephalum	pi	1								2				3			1	1			
Gastrodia cunninghamii	pr							1						3							
Gastrodia species	pr													1		1		1	1	1	
Geranium potentilloides	pi									3	1			2		1		1	3	1	1
Hydrocotyle dissecta	se					1		1	2				1								
Hydrocotyle microphylla	pi													4				2			
Hydrocotyle moschata	pi													6				4	3		
Lagenifera pumila	pi													2		1	1			1	
Microtis unifolia	pi		2	1	3					2				1				1		1	
Nertera depressa	se					4	9	7	10		2	2		3		2	1	3		1	
Nertera villosa	se						1	4	2					1		3	1	3		3	
Oxalis exilis	se													1			1		1		3
Pseudognaphalium luteoalbum	pi					2				1				3				1			
Ranunculus reflexus	pi										1		2	2	2	4	3	2	4	1	3
Senecio glomeratus	pi	4			1	1															
Senecio hispidulus	pi													3						1	2
Wahlenbergia violacea	pi	2			2					2											
Sedges and rushes																					
*Carex ovalis**	pi					4	1	1													
*Juncus tenuis**	pi													4							
Carex geminata	pi					1	3	6													
Carex solandri	pi										1		2		1				1		1
Carex testacea	pi													1		1			3		3
Carex virgata	pi					1					1		2								
Gahnia procera	se					2			2												
Juncus effusus	pi						5	2													
Lepidosperma australe	pi															1		3			
Uncinia ferruginea	se						4	1													
Uncinia rupestris	se								2					1				5			
Uncinia uncinata	se						1	2	2	2	4		5	4		3	5	3		3	4
Uncinia zotovii	se													2		3				3	
Ferns																					
Asplenium bulbiferum	pr																	2			4
Asplenium flaccidum	pr							1	2									2	1		6
Asplenium polyodon	pr												4			1		2			4
Blechnum discolor	se					4	6	12	7					1		6		2	2	1	3

Blechnum fluviatile	pr							1								1	4		1		6
Blechnum novae-zelandiae	se					1	11	5	4	2	7	4	4	3	6	7	11	2	2	5	11
Blechnum penna-marina	se															1	1		3	2	1
Blechnum procerum	pr							1	4	3						1	1				
Cyathea dealbata	pr									6	16	9	10				6				2
Cyathea medullaris	pr										2		5				1				4
Cyathea smithii	pr							1		2	7						7				12
Dicksonia fibrosa	pr														5	3	7	3	4	3	6
D. squarrosa	pr					12	3	8	15	9	17	22	15	5	4	13	14	4	5	18	17
Diplazium australe	pr									3	1										2
Histiopteris incisa	se					9	8	14	15	2	3		6	2		6	1	1	2	9	3
Hypolepis ambigua	se					4					1							1	2	1	1
Hypolepis distans	se								3	2					8						
Hypolepis rufobarbata	se					4			3								3				1
Paesia scaberula	se					10	12	5	11	1	4	2	14	3	1		4	2	4	12	2
Phymatosorus pustulatus	se								1	2		1						2	1	1	4
Pneumatopteris pennigera	se																		1		4
Polystichum vestitum	se							1		1	2					5			4	3	4
Pteridium esculentum	pi				8	20	38	11	10	1	11	6	13			18	1	6			3
Pteris tremula	pr										1		4						1		
Lianes																					
_Lonicera japonica_*	se									5	24	1	8								
_Rubus fruticosus_*	se							1	1	3	3		8			5				14	
_Rubus laciniatus_*	se	1				2										4					
Clematis forsteri	se									1					1		3				1
Clematis paniculata	pr																2				5
Muehlenbeckia australis	se									1											5
Parsonsia heterophylla	se									1									2		5
Rubus australis	pr							1		3	7										
Rubus cissoides	se							7	2	3	1					3	12	11	9	5	3
Shrubs																					
_Buddleja davidii_*	pi									4						4			4		
_Cytisus scoparius_*	pi	1	17		3															5	
_Erica lusitanica_*	pi															5			3	2	
_Leycesteria formosa_*	pi							36	9	4	1	1		7	8						
_Teline monspessulana_*	se									2	5		4								
_Ulex europaeus_*	pi	7	15		5	6			1							1					1
Brachyglottis repanda	se												2						2		
Carmichaelia australis	pi		5	3	12																
Coprosma "taylorae"	se							3	4	5	14						1	3	4	1	6
Coprosma foetidissima	se									6	9	7									
Coprosma lucida	se									7	5	3	2	3		1		4	2		
Coprosma propinqua	se									2						1			1		
Coprosma rhamnoides	se														3	1	4	6			3
Coprosma robusta	se							1		14	11	14	22		4	5	19	1	1	2	19
Coprosma tenuifolia	pr																1	3	3		5
Cordyline banksii	se							3					6								2

Appendix A. (*Continued*)

Guild and species (* indicates adventive species)	Stage (pioneer/ secondary/ primary)	Eyrewell 5 years	16 years 'lo'	16 years 'hi'	27 years	Hochstetter 5 years	16 years 'lo'	16 years 'hi'	27 years	Rotoehu 5 years	16 years 'lo'	16 years 'hi'	27 years	Kaingaroa 1 5 years	16 years 'lo'	16 years 'hi'	27 years	Kaingaroa 2 5 years	16 years 'lo'	16 years 'hi'	27 years
Coriaria arborea	pi									3		5		1			2				
Cyathodes juniperina	se				4																
Gaultheria antipoda	se					1			1	1	1	1	3	2		4		4	1	2	
Geniostoma ligustrifolium	pr										3	3	12				2				
Hebe salicifolia	pi							2	10												
Hebe stricta	pi									1	4		4				3				1
Leptospermum scoparium	pi									1					3						
Leucopogon fasciculatus	se					1	7	5	4	6	4	3	3	5	10	11	1	4	1	8	1
Myrsine australis	se								1	3	1		2				3				3
Myrsine divaricata	se							1	3												
Olearia avicenniifolia	se						2	6	2												
Olearia ilicifolia	se							1	7												
Trees																					
P. radiata*	pi	17	15	19	23	10	13	13	12	9	13	12	15	19	15	19	15	15	11	17	12
Aristotelia serrata	se	8	11	11	14	1						4	13			5	14	2		2	17
Beilschmiedia tawa	pr												4				4				
Carpodetus serratus	se					1	7	4	15		2			6		4	16			1	11
Cordyline australis	se												4		1			1			
Dacrycarpus dacrydioides	se							1									1				3
Dacrydium cupressinum	se							2	3								6				1
Fuchsia excorticata	se	14	4	1	1					3	1		1			1	2				6
Griselinia littoralis	se	1	2						21							2					
Hedycarya arborea	pr									2			3								
Knightia excelsa	se												2								2
Kunzea ericoides	se	3	4	3	14			1	3	2				3		4	1			1	
Litsea calicaris	se									2			13								
Melicytus ramiflorus	se									2	8	1	7	1			2				4
Metrosideros umbellata	se								4												
Nestegis lanceolata	se															1	2	1			3
Pittosporum tenuifolium	pi														10	3	13				6
Prumnopitys ferruginea	pr						1	1	1								1				3
Prumnopitys taxifolia	se													1			5				
Pseudopanax arboreus	se									6	3	6			4		2				3
Pseudopanax crassifolius	se							1	1					3	1	8	9	4			5
Quintinia serrata	se						3	3	11												
Raukaua simplex	se						1	4													
Weinmannia racemosa	se						1	6	22					4		5	12			1	4

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