UNDERSTOREY SPECIES COMPOSITION PATTERNS IN A *PINUS RADIATA* PLANTATION ON THE CENTRAL NORTH ISLAND VOLCANIC PLATEAU, NEW ZEALAND

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ABSTRACT

Understorey plant species composition of second- and third-rotation *Pinus radiata* D. Don stands was investigated in relation to site variation within three Kinleith Forest compartments varying in time since planting (1, 13, 29 years). Detrended correspondence analysis and detrended canonical correspondence analysis were used to analyse indirect and direct compositional gradients respectively. Within compartments, compositional variation related to topography and soil chemistry, and supported a view that these management units can be inherently variable over short distances. For example, in the 1-year-old compartment *Microlaena stipoides* (Lab.) R.Br. characterised exposed sites low in exchangeable soil cations, *Buddleja davidii* Franch. sites low in soil cations, with *Pneumatopteris pennigera* G.Forst. on sheltered sites, and *Brachyglottis repanda* J.R. et G.Forst. var. *repanda* on sites with high soil cations. Most species recorded in each compartment were indigenous, the proportion increasing with time since planting. The 1-year-old compartment showed some compositional affinities to the pre-planting shrubland, whereas the 29-year-old compartment had stronger affinities with indigenous forest, although it was not a close analogue of a nearby indigenous forest. Species richness was greatest in the 1-year-old compartment and least in the 13-year-old compartment, with the 29-year-old compartment of similar richness to comparatively diverse indigenous forests. This high species richness could be a consequence of repeated disturbance by forestry operations. This study does not support the view that *Pinus radiata* plantations are necessarily "biological deserts".

Keywords: plantation; gradient analysis; correspondence analysis; floristics; biodiversity; volcanic plateau; soils; *Pinus radiata*.

INTRODUCTION

During the last millenium human activity has resulted in grasslands and shrublands replacing forest over much of New Zealand. Against this trend of deforestation, 5% (1.3 million ha) of New Zealand's land surface has been planted in exotic conifers for timber production over the last century. These plantations add a comparatively new, and rapidly expanding, component to the landscape, and can provide a forest environment in areas with little such habitat.

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A common view is that plantations are monocultures and, from an environmental perspective, reflect negatively on forestry as a land use (Whitehead 1982; Perley 1994). Although much of this concern revolves around plantations having a single canopy species, there are other components to diversity, and the few studies describing understorey species composition of such forests report a diverse range of plant species (e.g., Henry 1954; McQueen 1961), including some uncommon ones (e.g., Wilson & Given 1989). Although plantation understoreys can contain a high component of indigenous species, the degree to which this is a unique assemblage of species (as against an analogue of an indigenous forest understorey) is unclear. This has implications for the value of the rapidly expanding plantations as refuges for biological diversity and conservation. Understorey composition is also relevant to forestry, because the distribution of weedy species can influence forest management practices (Allen *et al.* 1995).

Plantation forests provide a useful framework to study compositional variation in vegetation because they contain a mosaic of compartments with a known age and silvicultural treatment, and a single canopy species. In addition, harvesting takes place after a long period (decades) and so provides a temporal dimension in which to observe changing patterns in species composition. This framework has been little utilised in ecological studies, but provides opportunities for quantitative studies of land management impacts on patterns of species diversity (e.g., Swindel *et al.* 1991; Kellner 1993) as well as analyses of emerging theories on plant succession (e.g., Christensen & Peet 1984).

The role of land management in the maintenance of biodiversity is a major issue. Given the limited information available on this aspect of New Zealand's extensive plantations, a project was designed to investigate the influence of plantation management on understorey plant species composition. A second objective was to use these data from an intensively managed system to test hypotheses on vegetation predictability during plant succession, and to contrast these results with more commonly studied natural systems. This paper presents preliminary results from part of Kinleith Forest, within the extensive plantations on the central North Island volcanic plateau, and adds to 1925–26 pre-plantation vegetation descriptions (NZ Forest Products Forests Ltd (Tokoroa) archives) as well as McQueen's (1961) description of *Pinus radiata* forest understorey towards the end of the first rotation. An age sequence (time since planting) of compartments was sampled to reflect a successional sequence after the total removal of a forest canopy (by harvesting). Specifically we (1) describe the compositional patterns within three adjacent *P. radiata* compartments that varied in management history and compartment age, (2) contrast species composition and richness between compartments, and finally (3) compare results with earlier studies as a basis for understanding patterns between successive rotations.

METHODS

Study Area

The study area (approx. 250 ha) was located in the north-eastern portion of Kinleith Forest (Fig. 1), which occupies part of an undulating plateau dissected by small stream channels that result in a relief ranging between 450 and 600 m altitude. Numerous volcanic eruptions have left deposits in this area, most recently the rhyolitic Taupo Tephra deposited c. 1850 years ago (Froggatt & Lowe 1990). Because of the susceptibility of pumice soils to erosion, fluvial

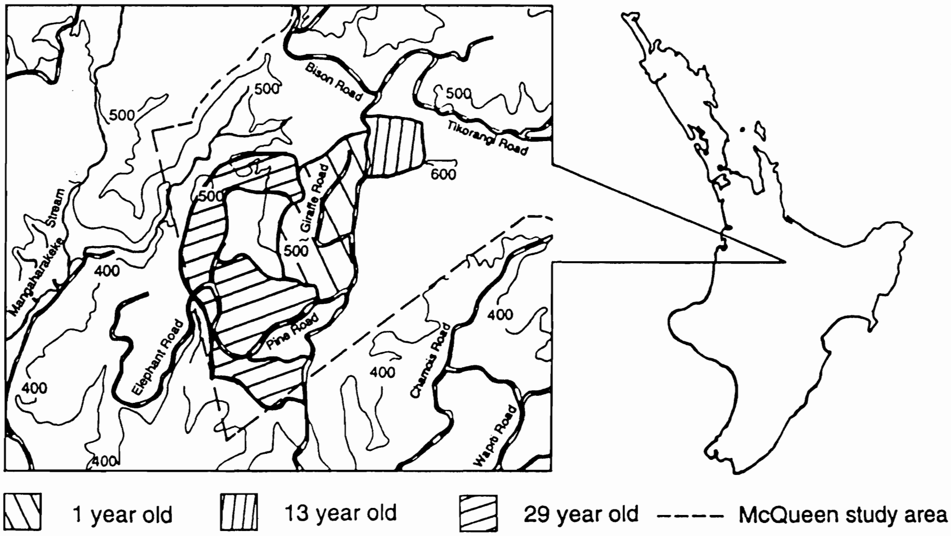

FIG. 1–Location of central North Island study area showing the 1-year-old, 13-year-old, and 29-year-old compartments sampled in Kinleith Forest. Also shown is the approximate boundary of the 34-year-old *Pinus radiata* compartment sampled by McQueen (1961).

processes and forestry operations have modified the distribution of tephra. Soils that have developed are deep, weakly weathered, and usually free-draining because of the coarse texture of Taupo Tephra (Molloy 1988). Climate of the area is cool and humid, with a mean annual rainfall of approx. 1600 mm, and without a pronounced dry period. Mean annual temperature at Kinleith (383 m altitude), some 15 km west of the study area, is 12.2°C, with a February maximum monthly mean of 17.4°C and a July minimum of 6.9°C (New Zealand Meteorological Service 1980).

Before the establishment of *P. radiata* forest the plant cover was seral vegetation typical of the central North Island volcanic plateau (*see* Wardle 1991). Such vegetation increased after volcanic eruptions, and became even more extensive after repeated human-related fires over the last millenium (McGlone 1983). Before planting the study area was mostly mapped as a *Pteridium esculentum** fernland, with a less extensive *Dracophyllum subulatum*-dominated shrub-heath on frost-flats (NZ Forest Products Forests Ltd (Tokoroa) archives). *Pinus radiata* was planted over the whole study area in 1926 and McQueen (1961) described a very different species composition that had developed in these unmanaged, self-thinned stands by the end of the first rotation. Subsequent forest management progressively harvested this first-rotation crop and fragmented the study area into three adjacent compartments (Fig. 1), each with a different management history as follows:

- **1-year-old compartment**: a 100-ha compartment of third-rotation *P. radiata* planted at 666 stems/ha (spacing 5 × 3 m) in the winter of 1991. The previous second-rotation crop had been top-dressed with urea (0.5 tonnes/ha) in 1980 and clearfelled in 1990 (aged 27–

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* Nomenclature follows Cheeseman (1925), Allan (1961), Moore & Edgar (1970), Healy & Edgar (1980), Brownsey *et al.* (1985), Connor & Edgar (1987), and Webb *et al.* (1988) unless otherwise indicated.

28 years), followed by a late-autumn helicopter application of general herbicides in 1991, as well as spot spraying of selected weeds.

- **13-year-old compartment**: a 41-ha compartment planted in 1979. The previous second-rotation crop had been clearfelled in 1979, and the area V-bladed just before planting. The crop had been thinned to waste in 1983 (to 884 stems/ha) and 1990 (to approx. 360 stems/ha). Pruning to 2 m was carried out in 1985 (517 stems/ha), 4 m in 1986 (350 stems/ha), and 6 m in 1987 (260 stems/ha).
- **29-year-old compartment**: a 120-ha compartment planted in 1962–63. This second-rotation crop had been pruned to 6 m and production thinned to approx. 400 stems/ha (1980–83). In 1980 much of this compartment was top-dressed with urea (0.5 tonnes/ha).

Data Collection

In November 1991 and 1992 relevés were subjectively located in each compartment to sample the range of topographic position and slope orientation combinations. Each relevé included a comparatively homogeneous area, generally from 50 to 200 m^2. Understorey vascular plant species present were recorded in height tiers (>12 m tall, 5–12 m, 2–5 m, 0.3–2 m, and <0.3 m) (*see* Allen 1992). The cover of individual species in each tier was estimated using a modified Braun-Blanquet cover-abundance scale (1 = cover <1.0%, 2 = cover 1 to 5%, 3 = 6 to 25%, 4 = 26 to 50%, 5 = 51 to 75%, 6 = >75%) (Mueller-Dombois & Ellenberg 1974). Epiphytic species were recorded by presence separately. In addition, the over-bark diameter (at 1.4 m height) of all *P. radiata* stems was measured within a 0.04-ha circular plot centred on relevés, so that basal area (m^2/ha) and stocking density (stems/ha) could be determined for *P. radiata* stems as an overstorey on each relevé in the 13- and 29-year-old compartments.

Site variables measured for each relevé included aspect and slope and, in combination with latitude, were used to calculate potential solar radiation (*see* Frank & Lee 1966). Subjective indices (1–5) of topographic position and exposure were recorded: topographic position ranged from ridges or hilltops (1) through convex and concave slopes to valley bottoms (5); and exposure ranged from exposed ridge tops (1) to open then sheltered hillsides (5). Six soil samples (approx. 60 mm diameter) from the top 100 mm of mineral soil were collected systematically over each relevé area and composited to form a single sample. Composites were air dried, sieved (<2 mm), and analysed for pH in water, Bray 2 exchangeable cations (calcium, magnesium, potassium; me %) and phosphorus (ppm) as a measure of availability, as well as a measure of total phosphorus (mg %) by ashing (Nicholson 1984).

Data Analysis

For the analysis of compositional patterns the data for each species were transformed into a single importance value for each relevé by weighting its cover in each tier, then summing the cover weights over all tiers. The Braun-Blanquet scale was assigned the following cover weights: "1" was set to 1.0; "2" to 2.0; "3" to 3.0; "4" to 4.0; "5" to 5.0; and "6" to 6.0. Species recorded in the epiphyte tier were given a nominal weight of 0.5. The range of importance values thus derived was 0.5 to 14.0.

Compositional gradients and their relationships with site variables were investigated by detrended correspondence analysis (DCA) and detrended canonical correspondence analysis (DCCA) respectively, using the computer program CANOCO Version 3.10 (ter Braak 1988, 1990). DCA extracts the dominant compositional gradients as axes from a species by relevés data matrix of species importance values, irrespective of site variables, whereas DCCA extracts the dominant gradients as axes given the constraint that they must be orthogonal linear combinations of all the supplied site variables (ter Braak 1988; Palmer 1993). As the number of site variables is decreased the DCCA solution is more constrained (ter Braak 1988). Where only one site variable is used the first DCCA axis is an optimal arrangement of species and stands with respect to that variable alone. The first axis from DCCA is the same as the first axis from canonical correspondence analysis, as detrending only influences the second and subsequent axes (ter Braak 1988). The eigenvalues in DCA and DCCA indicate the amount of variation accounted for by an axis, whereas gradient length represents the amount of species turnover along an axis (ter Braak 1988). A comparison of DCCA and DCA eigenvalues thus indicates compositional variation not accounted for by measured site variables (e.g., Allen & Peet 1990). These ordination methods were run using the default options in the CANOCO algorithm, with detrending by segments (Knox 1989; Økland 1990). Monte Carlo permutation tests within CANOCO were used to assess the significance of DCCA ordination axes (ter Braak 1990). The permutation test randomly links the site variables to the species data, and calculates the first axis eigenvalue. If the actual data have a first axis eigenvalue among the highest 5% of the permutations, then the species are significantly related to the site variables. The second axis can be tested by nominating the first axis stand scores as covariables in a second analysis (ter Braak 1988, 1990). Two-way indicator species analysis using the program TWINSPAN (Hill 1979) was used to classify relevés for defining floristic relationships between groups of plots. The program was run using the default options.

RESULTS

Gradient Structure

For each compartment, DCCA eigenvalues were only marginally lower than the DCA eigenvalues, indicating that the two ordination methods accounted for similar variation (Table 1). This is consistent with the similar gradient lengths generated by the two ordination methods. Spearman's rank correlations showed that for the three *P. radiata* compartments first and second DCA and DCCA axes ordered relevés similarly (Table 1). Overall, the two ordination methods gave similar solutions, but DCCA had the advantage of providing a direct gradient representation.

Monte Carlo permutation tests showed that the first ($p<0.01$) and second ($p<0.01$) DCCA axes of the 1-year-old compartment, as well as the first ($p<0.01$) and second ($p<0.05$) DCCA axes of the 29-year-old compartment, were significantly related to site variables, whereas the tests were not significant for the 13-year-old compartment. When the site variables were reduced to only available-phosphorus for the 13-year-old compartment data, the variable most strongly related to a DCCA axis (the second axis, *see* Fig. 2b), the permutation test showed a significant relationship for the new first axis ($p<0.05$). This suggests that the full analysis of the data from the 13-year-old compartment, by DCCA, was less constrained when all site variables were included.

TABLE 1–Eigenvalues and gradient lengths (SD) for first and second DCA and DCCA axes for ordination of species data from stands selected in three *Pinus radiata* compartments at different times since planting. Also given are Spearman's rank correlations (r_S) of first and second DCA axes stand scores with first and second DCCA axes stand scores (** p<0.01).

Compartment	Axis	Eigenvalues		Gradient length		r_S
		DCA	DCCA	DCA	DCCA	
1 year old	1	0.25	0.22	2.14	1.67	0.90**
	2	0.15	0.12	1.88	1.82	0.78**
13 years old	1	0.27	0.24	2.01	1.71	0.83**
	2	0.16	0.12	1.71	1.40	0.88**
29 years old	1	0.34	0.27	2.37	2.11	0.82**
	2	0.13	0.11	1.88	1.65	0.73**

First axis DCA and DCCA eigenvalues increased with compartment age, whereas there was little variation in second axis eigenvalues (Table 1). First axis DCA and DCCA gradient lengths were greatest for the 29-year-old compartment but, other than for the first DCCA axis, there was not a clear compartment age trend of gradient length. Thus, eigenvalues and gradient lengths partially supported stronger gradient differentiation in the oldest *P. radiata* compartment.

Compositional Gradients and Site Variation

- **1-year-old compartment**: DCCA ordination of relevés from the 1-year-old compartment showed strongest correlations of the two topographically related indices with first axis scores (Fig. 2a). *Morelotia affinis*, *Microlaena stipoides*, and *Pomaderris philicifolia* var. *ericifolia* were characteristic of ridge crest and other exposed sites, with *Lotus* cf. *pedunculatus*, *Lupinus arboreus*, and *Pneumatopteris pennigera* on sheltered, moist sites. The second axis was most strongly correlated (positively) with increasing exchangeable cations (calcium and magnesium) and slope. Species were arranged along this axis in the following order, listed with increasing species scores; *Microlaena stipoides, Buddleja davidii, Rubus fruticosus, Schefflera digitata, Leycesteria formosa, Hebe stricta* var. *stricta, Fuchsia excorticata,* and *Brachyglottis repanda* var. *repanda.* Variation in the composition of this compartment indicates the range of successional pathways that will occur within the compartment.
- **13-year-old compartment**: In contrast to the 1-year-old compartment, the first axis of the DCCA ordination was only weakly related to site variables (Fig. 2b), whereas the Monte Carlo permutation test used above confirmed that the second axis relevé scores increased with decreasing available phosphorus (Fig. 2b). *Schefflera digitata, Fuchsia excorticata, Coprosma grandifolia*, and *Senecio jacobaea* characterised high-phosphorus sites, whereas *Cyathea dealbata, Brachyglottis repanda* var. *repanda*, and *Mycelis muralis* occurred on low-phosphorus sites.
- **29-year-old compartment**: Increasing first axis DCCA relevé scores were most strongly related to decreasing exchangeable calcium and magnesium in the soil (Fig. 2c). Species characteristic of the high cation sites were *Hedycarya arborea, Asplenium bulbiferum* ssp. *bulbiferum*, and *Blechnum chambersii.* A striking feature of the site variable vectors

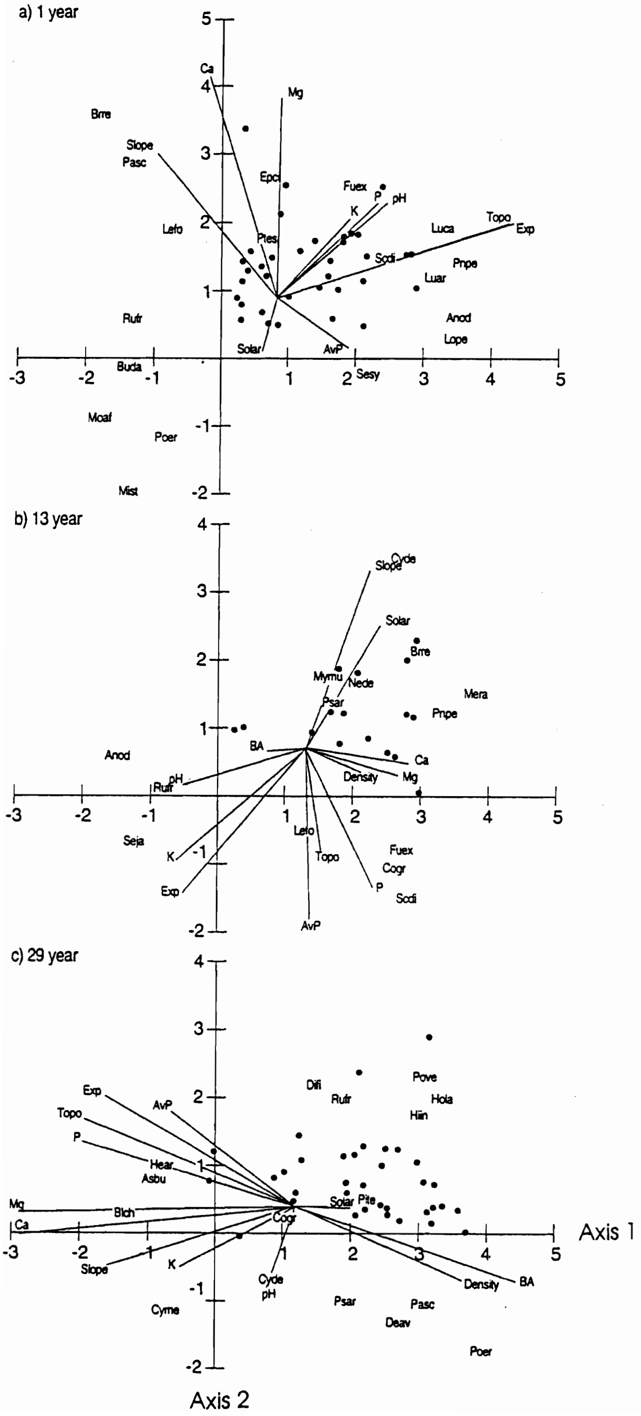

FIG. 2–First and second DCCA axes relevé positions (•) for three *Pinus radiata* compartments: (a) 1 year old; (b) 13 years old; (c) 29 years old. Site variable vectors indicate the direction of maximum change, and their length indicates the strength of site variable correlations with ordination axes. Vectors are shown for pH, Bray 2 exchangeable cations (Ca, Mg, K) and available phosphorus (AvP), total phosphorus by ashing (P), potential solar radiation (solar), topographic (topo) and exposure (exp) indices, slope, *P. radiata* stocking density and basal area (BA). Selected species optimal positions are indicated by acronyms: Anod = *Anthoxanthum odoratum*; Asbu = *Asplenium bulbiferum* ssp. *bulbiferum*; Blch = *Blechnum chambersii*; Brre = *Brachyglottis repanda* var. *repanda*; Cogr = *Coprosma grandifolia*; Cyde = *Cyathea dealbata*; Cyme = *Cyathea medullaris*; Deav = *Deyeuxia avenoides*; Difi = *Dicksonia fibrosa*; Epci = *Epilobium ciliatum*; Fuex = *Fuchsia excorticata*; Hear = *Hedycarya arborea*; Hiin = *Histiopteris incisa*; Hola = *Holcus lanatus*; Lefo = *Leycesteria formosa*; Lope = *Lotus* cf. *pedunculatus*; Luar = *Lupinus arboreus*; Luca = *Luzula campestris*; Mera = *Melicytus ramiflorus*; Mist = *Microlaena stipoides*; Moaf = *Morelotia affinis*; Mymu = *Mycelis muralis*; Nede = *Nertera depressa*; Pasc = *Paesia scaberula*; Pite = *Pittosporum tenuifolium* ssp. *tenuifolium*; Pnpe = *Pneumatopteris pennigera*; Poer = *Pomaderris philicifolia* var *ericifolia*; Pove = *Polystichum vestitum*; Psar = *Pseudopanax arboreus*; Ptes = *Pteridium esculentum*; Rufr = *Rubus fruticosus*; Scdi = *Schefflera digitata*; Seja = *Senecio jacobaea*; Sesy = *Senecio sylvaticus*.

was the decline in basal area and density of *Pinus radiata* from exposed ridge sites to sheltered gully situations, a gradient reflected in both DCCA axes (Fig. 2c). Hence, *Deyeuxia avenoides* and *Pomaderris philicifolia* var. *ericifolia* were species characteristic of ridges under stands of high basal area, with *Hedycarya arborea* and *Dicksonia fibrosa* occurring on sheltered sites with high levels of phosphorus in the soil.

To some degree there was a commonality in the importance of site variables between compartments. For example, compositional relationships with exposure and soil phosphorus were usually found (Fig. 2). For the youngest and oldest compartments, exchangeable calcium and magnesium also related strongly to compositional patterns. This left the question, to what degree are individual species ordered similarly along gradients, with compartment age? DCCA was used to order species along a specified gradient for each compartment age. Exchangeable magnesium was selected as a constraining variable on the first axis because composition of the 29-year-old compartment was the most predictable, and this compartment's first DCCA axis most strongly related to exchangeable magnesium. The DCCA ordination of 29-year-old compartment relevés arranged *Deyeuxia avenoides*, *Pomaderris philicifolia* var. *ericifolia*, *Pittosporum tenuifolium* ssp. *tenuifolium*, *Pteridium esculentum*, *Schefflera digitata*, and *Fuchsia excorticata* along the first axis from low to high exchangeable soil magnesium. Spearman's rank correlation of the 29-year-old compartment's DCCA species scores (those found on >5% of relevés) with those in common with the 1-year-old (58 species) and 13-year-old (51 species) compartments were 0.43 ($p<0.01$) and 0.27 ($p>0.05$) respectively.

The relevés indeed sampled a similar range of site variation in each compartment, except that in the 13-year-old compartment sheltered sites were lacking (Table 2). Because vectors indicate that highest phosphorus levels occurred on topographically sheltered sites (in compartments of all ages; *see* Fig. 2), it is not surprising that the means (and upper limits of the range) of these two variables were lower for the 13-year-old compartment (Table 2). Means for exchangeable cations and soil pH showed little variation with compartment age, although the range was less for cations in the 13-year-old compartment, which may have resulted in the weak correlation of cations with the first DCCA axis (Table 2 and Fig. 2b).

TABLE 2–Mean site variables (with ranges) for relevés sampling three *Pinus radiata* compartments at different times since planting (n = number of relevés).

Site variable	1 year old (n=38)		13 years old (n=16)		29 years old (n=36)	
Slope (degrees)	14	(2–29)	9	(2–24)	13	(2–31)
Potential solar radiation index	252	(176–310)	264	(219–307)	252	(176–312)
Topographic index	3.1	(1–5)	2.6	(1–4)	2.9	(1–5)
Exposure index	2.9	(1–4)	2.2	(1–3)	2.9	(1–5)
Exchangeable Ca (me %)	4.6	(0.7–14.3)	4.5	(1.4–9.0)	4.8	(1.0–19.5)
Exchangeable Mg (me %)	1.1	(0.2–2.5)	1.2	(0.5–2.0)	1.2	(0.2–4.8)
Exchangeable K (me %)	0.7	(0.2–1.6)	0.5	(0.3–0.8)	0.4	(0.1–0.8)
Available P (ppm)	26	(5–140)	18	(11–32)	34	(5–209)
Total P (mg %)	55	(26–123)	45	(21–82)	51	(22–162)
pH	4.5	(4.1–4.9)	4.5	(4.2–4.8)	4.6	(4.0–5.3)
Stocking density (stems/ha)	0		444	(215–818)	378	(43–903)
Basal area (m^2/ha)	0		26	(15–37)	53	(3–110)

Mean stocking of *Pinus radiata* was lower and basal area higher in the 29-year-old compartment than in the 13-year-old compartment. Extremely low basal area on a few of the 29-year-old relevés reflected toppling of *P. radiata* in moist gullies, with highest basal area and stocking tending to occur on ridge sites (Fig. 2c and Table 2).

Floristic Variation with Compartment Age

In total, 147 vascular plant species were encountered on the 90 relevés used in this study. Species richness, as a total number of species recorded for each compartment or as the mean number of species on relevés within each compartment, was greatest in the 1-year-old compartment and least in the 13-year-old compartment (Table 3). In all three compartments most species were indigenous, the proportion increasing with compartment age (from 67% to 82%). Understorey composition was least dissimilar among relevés in the 29-year-old compartment (Table 3), yet this compartment had greatest species turnover along a gradient (Table 1).

TABLE 3–Floristic parameters for relevés sampling three *Pinus radiata* compartments at different times since planting (n = number of relevés).

Floristic parameters	1 year old (n=38)	13 years old (n=16)	29 years old (n=36)
Total number of species	119	64	96
Percentage of species indigenous	67	73	82
Mean number of species per relevé	35	23	25
Mean dissimilarity (%)*	56	56	50

* Using Sorensen's Index for species not in common for all paired combinations of relevés (Mueller-Dombois & Ellenberg 1974).

Approximately 60% of common species (frequency >10%) were found in all three compartments, although very few (e.g., *Pittosporum tenuifolium* ssp. *tenuifolium*) had similar frequency of occurrence and cover across the age sequence (Appendix 1). The 1-year-old compartment was distinguished by a group of largely herbaceous species, only 40% of which were indigenous. Species in this group included *Cirsium arvense, Senecio sylvaticus, S. bipinnatisectus, Sonchus asper,* and *Carduus nutans*, as well as the shrub *Buddleja davidii* (Appendix 1). A small group of species was shared with the 13-year-old compartment (e.g., *Leycesteria formosa* and *Agrostis capillaris*). A consistent trend of declining cover and frequency across the whole age sequence was also shown by a group of species—e.g., *Holcus lanatus*, *Conyza* cf. *albida*, and *Lotus* cf. *pedunculatus*.

In contrast, a trend of increasing cover and frequency across the age sequence was shown by several indigenous sub-canopy shrub species including *Melicytus ramiflorus, Geniostoma rupestre* var. *ligustrifolium*, and *Brachyglottis repanda* var. *repanda*, as well as ferns such as *Cyathea smithii* and (more so in cover than frequency) *Dicksonia squarrosa*. Another group of species was found only in the two older compartments (e.g., *Cyathea medullaris* and *Gaultheria antipoda*), as well as a group found only in the oldest compartment (e.g., *Clematis paniculata* and *Asplenium polyodon*). In fact, all species found only in the two older compartments were comparatively shade-tolerant indigenous lianes, ferns, and sub-canopy shrubs.

Many species did not show a monotonic trend with compartment age, but rather a peak or trough of cover and/or frequency in the 13-year-old compartment. Those exhibiting a trough included *Paesia scaberula* and *Dianella nigra*, but most were actually absent from the 13-year-old compartment. Some of these were species that could also exist under the large statured trees in the 29-year-old compartment because of the open understorey found there (e.g., *Pomaderris philicifolia* var. *ericifolia, Cirsium vulgare,* and *Rytidosperma gracile*), while others with low frequency in the 1-year-old compartment were apparently relicts of the previous rotation (e.g., *Dicksonia fibrosa* and *Asplenium bulbiferum* ssp. *bulbiferum*). Such a pattern may explain the significant correlation of species positions along an exchangeable magnesium gradient in the 29-year-old compartment with the 1-year-old compartment noted earlier. Dominant species with highest frequency and cover in the 13-year-old compartment were the shrubs *Aristotelia serrata* and *Coriaria arborea.* No species were found exclusively in the 13-year-old compartment (Appendix 1).

DISCUSSION

Plant species composition on sites within three Kinleith Forest compartments was strongly related to topographic position, as was reported in the earlier work of McQueen (1961). In the present study, marked differences in soil chemistry over small distances (<50 m) were also strongly related to compositional patterns. Two small-scale patterns were identified: a decline in phosphorus from moist lower slopes to drier ridge crests, and increasing exchangeable soil cations with increasing slope in the 1-year-old and 29-year-old compartments. These results contrasted with regional studies of vegetation pattern in the central North Island which stressed the importance of climatic factors or disturbance (e.g., McKelvey 1963; Leathwick & Mitchell 1992). Contrasting results in part related to the importance of site factors, and the ordering of their importance, varying with the scale of analyses (e.g., Reed *et al.* 1993). However, a feature of such vegetation studies is that contrasting results can also reflect the different sets of site variables measured, and analysed for, in individual studies. A comprehensive comparison of dominant compositional gradients (from DCA) with the most important compositional gradients related to measured site variables (from DCCA) is a useful starting point for addressing the significance of site variables used (Allen *et al.* 1991).

Relevés sampled a similar range of topography within each compartment, and these samples expressed a wide range of soil chemistry conditions. Means and ranges of soil pH and exchangeable cations remained remarkably similar with compartment age (Table 2), suggesting that they had been little modified by different management histories. This was particularly surprising for the 1-year-old compartment because harvesting detritus might have been expected to increase soil nutrient status at a time when nutrient demand from tree growth had been greatly reduced. In addition, mean values for soil cations in the 13-year-old compartment did not appear to have been influenced by V-blading. Such a similarity of selected soil chemistry variables may not occur with the original shrublands, as reforestation with *Pinus radiata* may have modified soil fertility (e.g., McQueen 1961; McIntosh 1980). This may explain some of the compositional differences between pre-planting shrublands and post-reforestation understorey species composition.

There were some floristic links to the pre-planting shrubland. Records of these shrublands in 1925–26 described *Pteridium esculentum* as dominant (up to 1 m tall), with or without varying amounts of *Gaultheria* spp., *Pomaderris philicifolia* var. *ericifolia*, *Poa cita*, and *Leptospermum scoparium* (*see* NZ Forest Products Forests Ltd (Tokoroa) archives). Frost hollows were dominated by *Dracophyllum subulatum, Poa cita*, and *Leptospermum scoparium.* Such a composition is similar to an unplanted shrubland remnant in Kinleith Forest comprehensively described by McQueen (1961). Floristic affinities were greatest between the 1-year-old third-rotation compartment and the pre-planting shrubland where, for example, *Morelotia affinis, Pomaderris philicifolia* var. *ericifolia*, and *Poa cita* remained whereas *Dracophyllum subulatum, Leptospermum scoparium, Lycopodium deuterodensum,* and *Celmisia gracilenta* had been lost (Appendix 1). This loss may be a consequence of altered disturbance regimes (Smale 1989). There also appeared to have been a recent invasion by light-demanding adventive weeds, largely in the 1-year-old compartment, as McQueen (1961), for example, did not record *Leycesteria formosa, Buddleja davidii*, or *Rubus fruticosus.* None of these species had so far invaded a remnant example (40 km to the east) of the infertile frost flat version of the original shrubland (Smale 1990). Maybe such sites are too infertile, although the DCCA ordination of relevés from the 1-year-old compartment showed that *Buddleja davidii* can grow on sites with comparatively low availability of soil cations (Fig. 2a).

Comparison of McQueen's (1961) first-rotation 34-year-old *Pinus radiata* forest with the second rotation 29-year-old compartment sampled in this study allows some conclusions to be drawn about compositional change between rotations. Over 85% of the species listed (with frequency) by McQueen (1961) in the 34-year-old compartment were also recorded in the understorey of the 29-year-old compartment in the present study (Appendix 1). Few major changes in frequency occurred, although marked decreases were shown by *Weinmannia racemosa* and *Pseudopanax arboreus*, while *Geniostoma rupestre* var. *ligustrifolium* increased. Even with more intensive forest management (including thinning and pruning) than at the time of McQueen's (1961) study, further fragmentation of the forest between rotations, and repeated removal of some seed sources and the arrival of others, the development of *Pinus radiata* forest understoreys on the same site appeared to be towards compositionally similar mature forest. Although, McQueen (1973) attributed some understorey differences between nearby 30-year-old *P. radiata* stands to management thinning, this study demonstrated marked compositional variability within compartments, and suggested the site variable effects that may need to be partitioned out to understand the influence of management regimes alone (e.g., thinning or herbicide treatments) on species composition.

Given the high indigenous species component of Kinleith Forest stands, particularly in the 29-year-old compartment, an interesting question is the degree to which the understorey develops to be analogous with that of nearby indigenous forests. To test this, 27 similar relevés sampling indigenous forest understorey (species <12 m tall used) over an elevational range of 400–600 m in Pureora Forest (30 km south-west of the study area) were selected (S. Clegg, unpubl.data). A TWINSPAN classification of a species by relevés data matrix was calculated, with the matrix containing the 37 relevés from the 29-year-old compartment and the 27 relevés from Pureora. This combined data set contained 140 frequent vascular plant species (frequency of occurence >10% in one area), of which 78 were found only in the indigenous forest, 19 only in the 29-year-old pine compartment, and 43 in both. As a consequence, at the first TWINSPAN division all indigenous forest relevés were separated from the 29-year-old pine compartment relevés. Dominants (frequency of occurence >80%)

found only in the indigenous forest were the trees *Prumnopitys ferruginea, Beilschmiedia tawa, Elaeocarpus dentatus,* as well as the shrub *Pseudopanax crassifolius,* and *Microlaena avenacea, Metrosideros diffusa,* and *Hymenophyllum demissum.* Two of the three tree species have large fruits and may be conservatively dispersed. McQueen (1993) considered that tall indigenous tree species do not widely regenerate under *Pinus radiata.* No dominant species were confined to the 29-year-old pine compartment understorey. *Dicksonia squarrosa* and *Schefflera digitata* were dominant species in both types of forest. Broad patterns from the combined dataset suggest that although the 29-year-old pine compartment had strong affinities with the selected indigenous forest, it also had clear floristic differences.

Patterns of species richness (number of species on a plot) after forest clearcutting have been shown variously to increase in the early stages (10 years) of succession (Lugo 1992; Gove *et al.* 1992) or to increase and then decrease (7 years) (Swindel *et al.* 1991). This variability in patterns has parallels with unmanaged forests (e.g., Peet 1992). In the present study species richness was highest immediately after harvesting, was lowest in the 13-year-old compartment, and then appeared to increase towards the end of the rotation. In unmanaged forests Peet (1992) described such a pattern as occurring on favourable sites, where almost any species that arrives grows; competition then removes light-demanding species, followed by an increase in species richness as shade-tolerant species invade. Such a model fits well to the data from Kinleith Forest, with weedy exotic species of disturbed sites contributing to the high species richness in the 1-year-old compartment. These exotic species often have R-selection type traits (*sensu* Grime 1979). It has been argued that species composition in the early stages of succession should be unpredictable after disturbance because there has been little competitive sorting, and that compositional predictability should therefore increase with successional time, resulting in greater compositional similarity of vegetation (Margalef 1963; Christensen & Peet 1984). The increasing eigenvalues with compartment age for first ordination axes and least compositional dissimilarity in the 29-year-old compartment are consistent with this view (Tables 1 and 3).

The understoreys of *Pinus radiata* stands in Kinleith Forest are, in fact, moderately species rich for New Zealand forests. For example, using similar methods, the mean species richness on 250 relevés located in simple mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest in the Harper-Avoca catchment (Canterbury) was 8.9 (range 1–34) (R.B. Allen & K.H. Platt, unpubl. data). Wardle (1984) gave values between 10 and 25 for a mixture of beech forests along elevation and rainfall gradients, whereas in conifer-broadleaved hardwood forest types in central Westland mean species richness values are commonly 20–30 (1087 relevés) (Reif & Allen 1988). The 27 Pureora relevés had a mean species richness of 50 (standard deviation 7.4) (S. Clegg, unpubl. data). Moderate species richness in Kinleith Forest stands may be maintained by the proximity of a range of seed sources (e.g., indigenous forest, agricultural land) and the patchwork nature of plantations. Frequent disturbance by various forestry operations, including harvesting as a catastrophic disturbance, results in a patchwork of compartments at varying stages of development. These compartments result in a diverse range of habitats for species in close proximity. The maintenance of moderate species richness in such a system has parallels with the "intermediate disturbance hypothesis" suggested by Connell (1978), whereby species richness is highest in systems subject to intermediate levels of disturbance. Such a conclusion contrasts markedly with the view that plantation forests are necessarily "biological deserts".

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APPENDIX 1

FREQUENCY AND COVER OF SPECIES

Percentage frequency (Freq) and mean percentage cover (Cov) of species (* denotes adventive species) found on more than 10% of relevés in one of three *Pinus radiata* compartments at different times since planting. Percentage cover for a species on a relevé was the sum of percentage cover in all tiers using the cover-abundance scale mid-points.

Species	1 year old		13 years old		29 years old	
	Freq	Cov	Freq	Cov	Freq	Cov
*Buddleja davidii**	63.2	2.3				
*Cirsium arvensis**	78.9	1.0				
Epilobium alsinoides ssp. *atriplicifolium*	31.6	0.5				
*Senecio sylvaticus**	63.2	0.8				
Morelotia affinis	15.8	0.1				
Gnaphalium audax	31.6	0.2				
*Sonchus asper**	52.6	0.3				
Pseudognaphalium luteo-album	47.4	0.2				
*Senecio bipinnatisectus**	52.6	0.4				
*Carduus nutans**	52.6	0.3				
Gnaphalium sphaericum	15.8	0.1				
*Epilobium ciliatum**	47.4	0.4				
Carex breviculmis	15.8	0.1				
*Rumex acetosella**	13.2	0.4				
Cerastium fontanum ssp. *vulgare**	21.1	0.5				
*Lupinus arboreus**	10.5	0.2				
*Leycesteria formosa**	44.7	0.3	37.5	1.3		
*Agrostis capillaris**	28.9	0.1	31.3	0.2		
*Luzula campestris**	18.4	0.5	6.3	<0.1		
Histiopteris incisa	47.4	0.4			47.2	2.1
Coprosma lucida	2.6	<0.1			19.4	0.1
Dicksonia fibrosa	5.3	0.1			38.9	2.7
Pomaderris philicifolia var. *ericifolia*	39.5	2.4			16.7	0.2
*Cirsium vulgare**	92.1	5.7			22.2	0.1
Rytidosperma gracile	63.2	1.3			22.2	0.2
Asplenium bulbiferum ssp. *bulbiferum*	2.6	<0.1			25.0	1.2
Asplenium flaccidum ssp. *flaccidum*	2.6	<0.1			52.8	0.3
Trichomanes venosum	2.6	<0.1			19.4	0.1
Blechnum fluviatile	2.6	<0.1			19.4	0.2
*Solanum nigrum**	18.4	0.1			2.8	<0.1
Dicksonia squarrosa	78.9	0.7	87.5	12.3	100.0	24.6
Aristotelia serrata	21.1	0.2	100.0	20.3	97.2	11.1
Coprosma robusta	84.2	0.8	100.0	15.7	66.7	4.7
Blechnum sp. "blackspot"	84.2	1.1	100.0	25.7	97.2	25.1
Pneumatopteris pennigera	23.7	0.1	43.8	3.1	55.6	6.8
Dianella nigra	42.1	0.2	6.3	<0.1	47.2	2.0
Geniostoma rupestre var. *ligustrifolium*	10.5	0.1	68.8	1.6	100.0	7.3
Melicytus ramiflorus	26.3	0.1	37.5	0.4	61.1	2.8
*Digitalis purpurea**	36.8	1.9	31.3	0.2	13.9	0.1
Ranunculus reflexus	76.3	1.1	68.8	0.3	55.6	0.7
Lotus cf. *pedunculatus**	50.0	5.3	37.5	3.8	19.4	0.1
Microlaena stipoides	18.4	0.1	6.3	<0.1	38.9	1.6
Brachyglottis repanda var. *repanda*	18.4	0.2	62.5	7.5	63.9	12.1
Cyathea smithii	2.6	<0.1	6.3	<0.1	52.8	2.8

APPENDIX 1 cont.

Species	1 year old		13 years old		29 years old	
	Freq	Cov	Freq	Cov	Freq	Cov
Schefflera digitata	39.5	0.6	37.5	0.5	86.1	17.5
Uncinia uncinata	5.3	<0.1	37.5	0.2	36.1	0.4
Paesia scaberula	28.9	0.3	12.5	0.1	30.6	7.5
Pteridium esculentum	57.9	1.0	50.0	3.1	44.4	0.4
Hebe stricta var. *stricta*	31.6	0.3	43.8	2.2	5.6	0.1
Cortaderia fulvida	81.6	0.8	50.0	3.2	16.7	0.1
Conyza cf. *albida**	97.4	6.4	50.0	0.3	41.7	0.2
*Senecio jacobaea**	42.1	0.2	37.5	1.2	22.2	0.1
*Rubus fruticosus**	68.4	1.0	75.0	5.7	33.3	0.2
Acaena anserinifolia	42.1	0.3	50.0	5.3	41.7	0.3
*Holcus lanatus**	92.1	18.9	81.3	0.4	30.6	0.2
Nertera depressa	31.6	0.3	18.8	0.1	19.4	0.6
*Mycelis muralis**	92.1	3.6	50.0	0.3	44.4	0.2
Deyeuxia avenoides	84.2	10.3	12.5	0.1	16.7	0.1
*Gnaphalium coarctatum**	92.1	8.7	31.3	0.2	22.2	0.1
Fuchsia excorticata	50.0	1.9	68.8	1.8	66.7	8.1
Hydrocotyle moschata	65.8	2.4	6.3	<0.1	11.1	0.1
Pittosporum tenuifolium sp. *tenuifolium*	65.8	1.5	68.8	3.6	61.1	1.8
Stellaria parviflora	44.7	1.9	25.0	0.1	30.6	0.6
*Hypochoeris radicata**	52.6	0.3	25.0	0.1	2.8	<0.1
Coriaria arborea	50.0	0.3	100.0	18.8	5.6	0.4
Chiloglottis cornuta	5.3	<0.1	6.3	<0.1	11.1	0.1
Cyathea dealbata	5.3	<0.1	18.8	1.0	33.3	2.6
Phymatosorus diversifolius	2.6	<0.1	6.3	<0.1	30.6	0.2
Hypolepis rufobarbata	18.4	0.2	6.3	<0.1	8.3	0.1
*Crepis capillaris**	84.2	5.6	18.8	0.1	8.3	<0.1
Coprosma grandifolia	5.3	<0.1	31.3	0.5	27.8	0.2
Senecio minimus	71.1	2.6	12.5	0.1	2.8	<0.1
Polystichum vestitum	10.5	0.1	12.5	0.1	13.9	0.1
Epilobium rotundifolium	31.6	0.2	12.5	0.1	5.6	<0.1
Geranium potentilloides	55.3	0.4	12.5	0.1	5.6	<0.1
Carex geminata	21.1	0.1	12.5	0.1	2.8	<0.1
*Salix cinerea**	28.9	0.2	12.5	0.1	2.8	<0.1
*Anthoxanthum odoratum**	28.9	0.6	31.3	0.2	5.6	<0.1
*Sonchus oleraceus**	31.6	0.2	6.3	<0.1	2.8	<0.1
Pseudopanax arboreus	2.6	<0.1	68.8	4.4	27.8	1.7
Hypolepis ambigua	5.3	<0.1	12.5	1.9	8.3	0.8
*Prunella vulgaris**	15.8	0.1	18.8	0.1	5.6	<0.1
Cyathea medullaris			12.5	0.3	38.9	4.2
Gaultheria antipoda			12.5	0.1	22.2	0.6
Rubus cissoides			25.0	0.4	16.7	0.3
Weinmannia racemosa			18.8	0.1	5.6	0.1
Clematis paniculata					25.0	0.3
Leucopogon fasciculatus					27.8	0.7
Asplenium polyodon					58.3	0.3
Hedycarya arborea					16.7	0.1
Ripogonum scandens					11.1	0.1
Blechnum chambersii					13.9	0.6
Rumohra adiantiformis					13.9	0.1
Hypolepis distans					16.7	1.7