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PLANT SPECIES RICHNESS UNDER *PINUS RADIATA* STANDS ON THE CENTRAL NORTH ISLAND VOLCANIC PLATEAU, NEW ZEALAND

Summary: Exotic pine plantations constitute a significant landscape feature in the North Island of New Zealand but their conservation value for native plant species is not often documented. Pine stem density, height and basal area of nine plantations of *Pinus radiata* ranging in age from 6 to 67 years in Kinleith Forest was determined. Pines reached heights of 60m, and stand basal areas up to 183 ± 14 m^{2}ha^{-1}. The abundance of woody shrubs, tree ferns and ground ferns was assessed in each stand. Understorey composition of shrubs and ferns was reflected on the first two axes of DCA ordinations and correlated with the age of the pines. Adventive shrubs predominated in stands < 20 years old. Light-demanding native shrubs with bird dispersed fruits predominated in older stands, with more shade-tolerant species in the oldest site. Species richness increased rapidly in the first 11 years, but thereafter more slowly. Twelve native shrub species and 22 ferns were recorded from the most diverse stands. Richness and species composition were related to stand age, and probably also to topographical heterogeneity and aspect. Tree ferns reached densities of 2000 - 2500 ha^{-1} and basal areas of 20 - 30 m^{2}ha^{-1} in the older stands. Initially the tree fern population was strongly dominated by *Dicksonia squarrosa*, which comprised 84% of individuals overall. Five species were present by 29 years. The faster growing *Cyathea medullaris* and *C. smithii* achieved greater heights than the *Dicksonia* spp., and their relative biomass was greatest in the oldest stands.

Key words: Biodiversity; species richness; *Pinus radiata*; plantations; ground ferns; tree ferns.

Introduction

Exotic tree crops are a feature of the landscape in many countries throughout the world. Frequently such tree plantations are regarded as short-lived low diversity forests, with economic, ammenity and recreational values, but of little relevance in the conservation of native biota. However, in New Zealand it has been recognised that pine plantations sometimes have relatively high plant species richness and value in maintaining populations of native birds (Gibb 1961; Clout & Gaze 1984; Allen *et al*.. 1995b). Pine plantations - mainly *Pinus radiata* - cover about 5% of the New Zealand landscape (Newsome 1987). Plantation forests are particularly extensive on the central North Island Volcanic Plateau, where they have replaced a fire-induced mosaic of indigenous forest, shrubland, heathland and tussock grassland (Ure 1950) either directly, or indirectly following a period during which the land was farmed. The exotic monocultural appearance of these forests has obscured the fact that they harbour a wide range of indigenous plants, birds, and invertebrates. The forest understorey beneath pines commonly comprises native shrub and fern species, many of which also occur in and around canopy gaps in native forest. This assemblage often contains nectar and fruit bearing species which are particularly important for some indigenous birds. Despite some recognition of this link (Clout & Gaze 1984), the sequence of plant species colonisation and the features which control it have received relatively little attention (McQueen 1961; Allen *et al*. 1995b).

Plantation forests provide opportunities for the study of the patterns of vegetation assembly because they comprise a mosaic of areas which differ primarily in known stand age. Other features may also differ between stands, for example topography and soil, thinning regimes or the genetic characteristics of the pines, but with careful site selection many of these confounding variables can be eliminated, or their effects considered in the interpretation of the results.

The aims of our study were: 1) to describe the changes in understorey species composition in progressively older stands of *Pinus radiata*; 2) to quantify the changes in the composition and structure of the tree fern populations in the stands, and 3) to obtain data on tree fern height growth

rates. Here we describe the changes in shrub and fern species composition occurring in stands of different ages.

Nomenclature follows Allan (1961) except where superseded by Connor & Edgar (1987) for indigenous angiosperms and gymnosperms, and Brownsey & Smith-Dodsworth for pteridophytes, except where indicated.

Study area

The study area was located in Kinleith Forest southeast of Tokoroa (Fig. 1). The area is a dissected plateau with the highest points approximately 750m altitude. The substrate is composed of ignimbrites from numerous eruptions, the most recent being the rhyolitic Taupo Tephra, which was deposited c. 232 AD (Sparks *et al*. 1995). The deep deposits of pumice are responsible for the characteristically coarse textured and free draining nature of the soils, which are relatively homogeneous on level surfaces over large areas. The local climate is cool and humid, with a mean annual rainfall of 1600mm. At Kinleith, 383 m altitude, mean monthly maximum temperature is 17.4ºC in February, and the mean July minimum is 6.9ºC (NZ Met. Service 1980). Clear nights with radiation frosts are a feature of the central North Island climate in winter, and the pooling of cold air in basins is thought to be one of the important environmental factors determining plant distribution patterns.
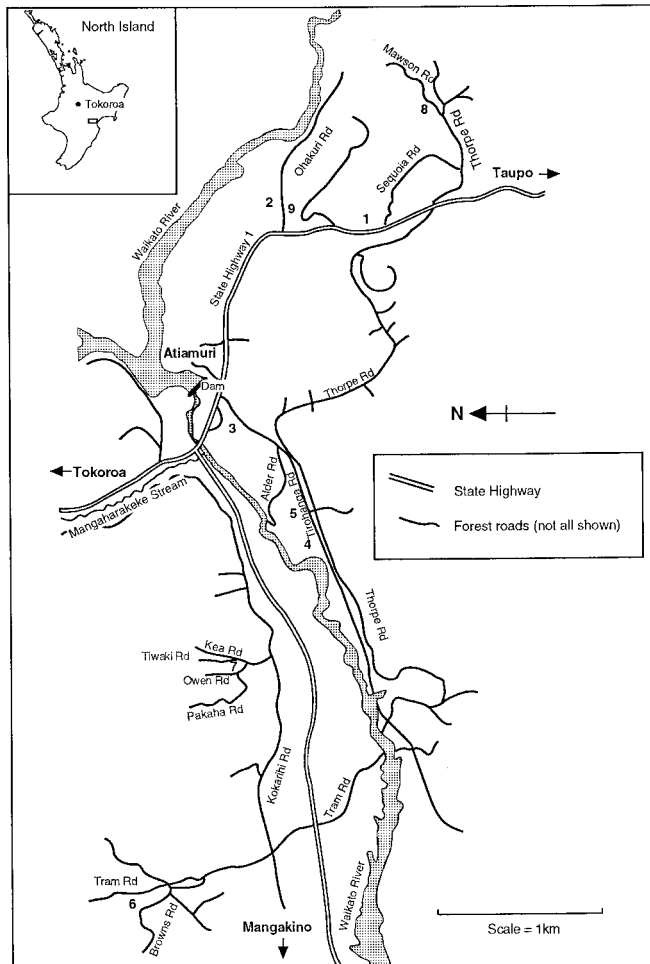

Figure 1: *Map showing site locations and (inset) general location of study area in North Island. Numbers refer to site numbers in Table 1.*

Soils

Vucetich & Wells (1978) describe the soils of most of the study area in relation to land use. A more detailed map was consulted in an unpublished report obtained from Carter Holt Harvey's Kinleith Office.The soils of the nine sites are similar. All are free-draining yellow-brown pumice soils with a silty sand texture derived from the Taupo Tephra. pH is generally in the range 4 - 5 (Allen *et al*. 1995a, Table 2). Sites 1, 2, 6, 7, 8 and 9 belong to the Taupo Series and are developed from rhyolitic airfall tephra. Sites 3, 4 and 5 are on rhyolitic flow tephras of the same age (Atiamuri Series). Site 3 was the only site with large ignimbrite boulders present, and is classified as Whenuaroa sand (re-sorted Taupo Tephra) by Vucetich & Wells (1978). At site 6 the Taupo pumice is thinner and some of the soils are derived from pre-Taupo weathered tephras over ignimbrite (Ngakuru Series) Soil depth is generally related to topographic position. The soils are generally well suited to tree growth, with site indices of 1 in most cases.

Choice of study sites

The nine study sites were chosen on the following criteria: (1) age - we required as even a spread of stand ages as possible, from the oldest to the youngest sites; (2) presence of tree ferns - we sampled areas where tree ferns were relatively abundant; (3) topography - we required level sites, and (4) accessibility - the sites had to be adjacent to formed roads. Because it was difficult to find an adequate spread of stand ages on flat sites the topographic criterion was relaxed and three of the sampled sites were on slopes. Site locations and characteristics are given in Table 1 and Fig. 1.

Limitations of sites

Site age *per se* may not be the important variable controlling understorey composition; age is simply a convenient way of summarising differences in stand structure and resulting environmental features, especially the forest floor light environment. Age is confounded with other variables, in particular the genetic characteristics of the pines, and pruning and thinning treatments. Local features, such as pre-planting vegetation cover, proximity to native forest remnants, and topography influence the likelihood of invasion by native shrubs and may override the influence of stand age. More replication of stands of the same age may amend this problem in future. The Tiwaki Road site was chosen on the understanding that it was planted in 1954, but it subsequently transpired that the central part of the stand (most of the sample) was planted in 1927. Consequently the sample from this stand is heterogeneous.

Methods

At each site a 100m transect was laid out, generally on a north-south bearing from the adjacent road, starting 30m from the stand edge. Points were placed at the start and every 20m along this transect, giving six points. Point-tree distances were used to estimate density, and 24 pine diameters (at 1m height) measured for basal area. At each point a 10 x 10m quadrat was laid out, and the area within this was searched for ground ferns, which were identified and ranked as 1 (rare), 2 (frequent), or 3 (common). Young tree fern sporophytes lacking a trunk (referred to as tree fern seedlings) were included with the ground ferns. Within a similar adjacent area a list was made of all woody shrub species present. Tree ferns were counted, and their heights and

Table 1: *Site characteristics. (1) Site numbers are the order in which they were enumerated. (2) P, pruning. The number of Ps indicates the number of prunings, in sequence to 2m, 4m and 6m height. T, Thinnings. (3) Ai, Atiamuri series; Wn, Whenuaroa series; TpH, Taupo series; NaH, Ngakuru series. Data from soils map of Kinleith Forests provided by Carter Holt Harvey Ltd, Tokoroa. (4) from NZMS 260 Sheets U17 and T17.*

Site name	Site No (1)	Planting date	Age years	Silvicultural treatment (2)	Soil type (3)	Slope aspect	Grid ref.(4)
Tirohanga Rd	4	1988	6	PP	Ai, Wn	Flat	717061
Tirohanga Rd	5	1983	11	PP	Ai, Wn	Flat	724063
Ohakuri Rd	9	1974	20	PPPTT	TpH	Flat	768064
Atiamuri Bridge	3	1970	24	PPPT	Ai, Wn	Flat, rocky	739075
Brown's Rd	6	1965	29	PPP	TpH, NaH	Flat	661088
Mawson Rd	8	1962	32	no record	TpH	25-30º SW	785042
Ohakuri Rd	2	1959	35	PPPT	TpH	Flat	771067
Tiwaki Rd	7	1954	40	T	TpH	15º N & S	698072
		1927	67				
Sequoia Rd	1	1927	67	no record	TpH	15º S	767054

diameters measured, in a strip 5m wide on one or both sides of the 100m transect, depending on tree fern abundance. These results were used to calculate tree fern density, basal area, and volume. To allow comparison with the pines and with other published data, values were expressed per hectare and basal area was calculated from adult tree ferns with diameters measured at 1m height. The absence of secondary thickening in tree ferns means that basal area is not well correlated with plant age or vigour, which is probably better approximated by trunk height. Total (summed) tree fern stem height and volume (stem basal area x height) per hectare were also calculated. Volume was based on juvenile and adult individuals; it is assumed to be proportional to biomass. In addition, tree ferns of species not well represented within the measured strip were searched for outside it, and also measured. These additional data were used only to increase the sample size for population size structures of those species. Tree fern population structure was summarised by dividing the measured individuals into three classes: seedlings lacking a trunk; juveniles with a trunk < 1 m in height, and adults with a trunk > 1 m in height. Dead tree fern trunks were also recorded. Shrub data were recorded as frequency - the number of points out of a maximum of 6 at which the species occurred. An index of ground fern abundance was calculated for each species at each site by summing its abundance ranks across the six quadrats (maximum = 18) and weighting this value by multiplying by the number of quadrats in which the species was found (site frequency). This index consequently has a maximum possible value of 108 for a species classed as common in all six quadrats. Shrub, ground fern and tree fern data were analysed separately using detrended correspondence analysis (DCA) as executed in CANOCO (ter Braak 1988). Polynomial detrending and down-weighting of rare species were employed, otherwise default options were used.

Results

Forest structure

The stands studied varied considerably in the silvicultural treatments to which they had been exposed, and in other respects (Table 1). Consequently, while the intention was to sample a chronosequence, other factors confound the interpretation. With this in mind only broad patterns are described.

Individual pine tree diameters and heights increase with age, while stand densities decline and basal areas increase (Fig. 2). Maximum heights of 60m were measured on fallen trees, apparently reached at 50-60 years . Diameter continues to increase until at least 67 years (the oldest stand in the area), albeit more slowly after c. 40 years (Fig. 2). The exceptionally high density and basal area results from Tiwaki Road (site 7) might be due to having included two differently aged cohorts (40 and 67 years) within the same sample. In the absence of silvicultural thinning, density generally declines through natural mortality as basal area increases.

The oldest sites had tree basal areas in the upper part of the range of those encountered in native podocarp and kauri forests (Lusk & Ogden 1992; Ogden, 1985; Ahmed & Ogden 1991), and maximum heights rarely exceeded by native trees (Table 2). Allen *et al.* (1995a) note that highest basal areas and densities are achieved by *Pinus radiata* on ridge-top sites. In addition to the pines, sites > 30

Table 2: Pine population characteristcs at the different sites. Means ± standard errors.

| Site name	Site No.	Age, yrs	Density, stems ha^{-1}	Basal area, m^2.ha^{-1}	Mean diameter, cm	Modal diameter class/es, cm	Maximum height, m
Tirohanga Rd	4	6	521±50	18±2	21±1	20 < 30	7
Tirohanga Rd	5	11	582±56	49±5	32±1	30 < 40	13
Ohakuri Rd	9	20	377±35	45±4	38±2	20 < 30	25
						40 < 50	
Atiamuri Bridge	3	24	269±23	40±3	42±3	40 < 50	38
Brown's Rd	6	29	475±47	80±8	46±2	40 < 50	43
Mawson Rd	8	32	398±38	61±6	42±2	40 < 50	47
Ohakuri Rd	2	35	274±28	62±6	53±2	50 < 60	52
Tiwaki Rd	7	40/67	564±45	183±14	57±7	20 < 30	59
						80 < 90	
Sequoia Rd	1	67	263±22	91±8	64±4	40 < 50	60
						60 < 70	
						70 < 80	
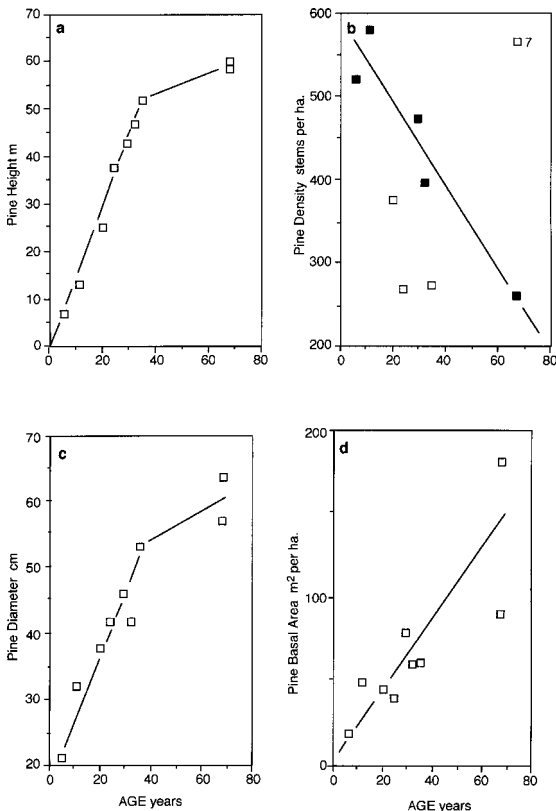
Figure 2: *Relationships between stand age and (a) mean pine tree height m, (b) stand density ha⁻¹ (c) mean tree diameter cm and (d) stand basal area m².ha⁻¹. Curves are fitted by eye. In (b) the line is fitted to unthinned stands only (filled squares) and represents the natural self-thinning trajectory. The exceptional Stand 7 is indicated.*

Figure 3: *Size frequency distributions of pines in each stand (numbers), based on 24 measured diameters per stand. Horizontal axis is in 10 cm diameter classes.*

years old also contained 10 - 30 % basal area of tree ferns and some native shrub species with diameters > 10 cm. Total stand basal areas are thus even greater: 202 and 120 m².ha⁻¹ respectively for stands 7 and 1.

Size frequency distributions (Fig. 3) document the increasing structural complexity of the stands with time. As the modal and maximum size both increase, intraspecific competition between individual trees in the stands causes the spread of sizes to widen. Other structural differences are due to silvicultural treatments (Table 1). In the two oldest stands, the size frequencies indicate the establishment of a second generation of self-sown pines as these stands were opened up by natural mortality of the planted cohort.
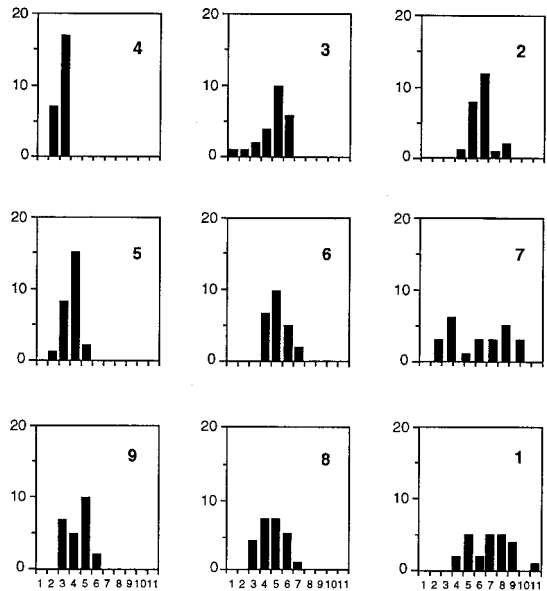
Shrub frequency

Ubiquitous introduced shrubs, especially blackberry (*Rubus fruticosus*), predominate in the two youngest stands (< 20 years) which show the highest similarity in shrub composition as a consequence (Table 3). These introduced shrubs and trees are bird- (*Rubus, Leycesteria*) and wind-dispersed (*Erica, Salix*). Subsequently adventives give way to native species, predominantly *Coprosma robusta, Pittosporum tenuifolium, Fuchsia excorticata* and *Aristotelia serrata*. Of the adventive shrubs, only *Rubus fruticosus* maintains a significant presence in the older pine stands. *Coprosma robusta* was the only species found at all sites, and comprised 21% of the total summed frequencies. The first native species all produce small succulent fruits and are readily dispersed by native and introduced frugivorous birds such as silvereyes (*Zosterops lateralis*) and blackbirds (*Turdus merula*). The two oldest sites (> 40 years) showed an increase in *Brachyglottis repanda* and *Weinmannia racemosa*, and more shade tolerant species such as *Schefflera digitata, Coprosma grandifolia, Pseudopanax arboreus, Melicytus ramiflorus,* and *Geniostoma rupestre*. Most of these species are also bird dispersed, but *Brachyglottis* and *Weinmannia* are wind dispersed.

Except in the youngest stand, the total diversity of native species ranged from 6 to 12 shrub species per 0.06ha sample. The highest diversities were in stands 3 (24 years) and 1 (67 years), which also had higher total abundances, implying greater understorey cover. Comparisons between the younger stands showed a trend of decreasing similarity in composition with increasing stand age, but this was not maintained in the three oldest stands (Table 3).

The first two axes of the stand DCA accounted for c.71% of the total variance (Fig. 4a). Stand

loadings on axis 1 were strongly correlated with age ($y = 6.3595 - 4.4870*\log x$; $r = .8602$, df = 7, P < .01. y = axis 1 loading, x = stand age in years). The logarithmic relationship suggests that species composition changes relatively quickly at first, but thereafter more gradually, corresponding to the shift from mainly adventive to mainly native species after c. 20 years. The transitional 20 year stand (stand 9) was separated on axis 2. This was the only stand thinned twice. (cf McQueen 1973). The species ordination (Fig.4b) emphasises the shift in species
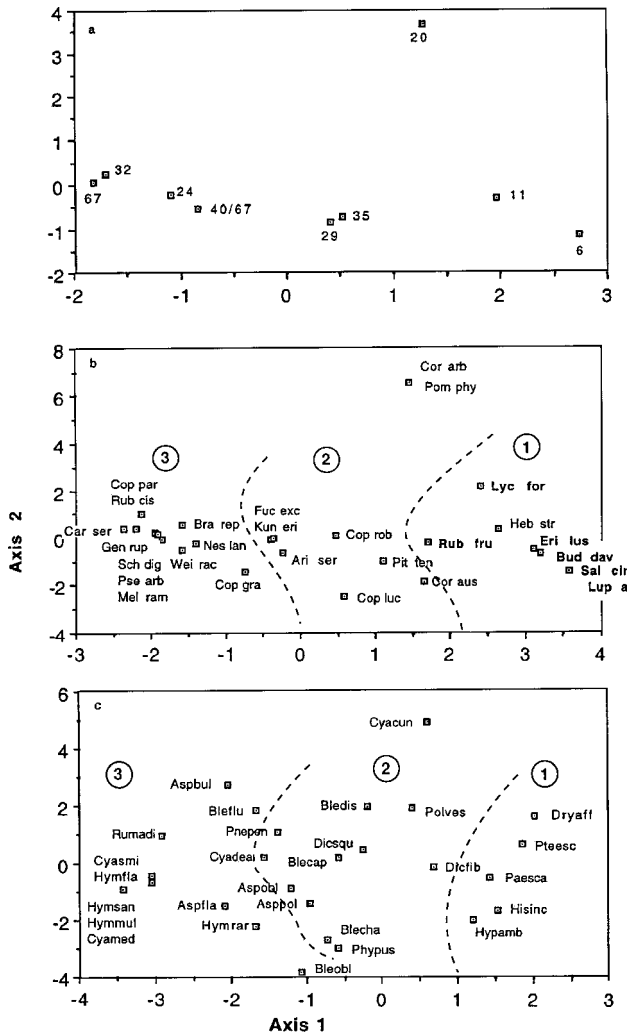

Figure 4: *DCA stand and species ordinations. (a). Stand ordination based on shrub data; stand ages superimposed. (b). Shrub species ordination. Ordination areas: 1, mainly introduced woody weeds; 2, native pioneer shrubs; 3 light requiring native trees and gap colonists. (c). Ground fern species ordination. Ordination areas: 1, colonising rhizomatous species: 2, larger ground ferns and some tree ferns; 3, species requiring more shade and/or moisture (eg filmy ferns). Names are first three letters of generic and specific names; see Tables 3 and 4.*

composition with age, and the isolated occurrence of *Coriaria arborea* and *Pommaderris phylicifolia* in stand 9.

Ground fern abundance

Thirty six species of ground ferns (including seedling tree ferns, and some low epiphytes) and fern-allies were identified, but of these only 6 comprised 75% of the fern ground cover (Table 4). The most abundant species were juveniles of the tree fern *Dicksonia squarrosa,* and *Blechnum capense* (*sensu* Allan 1961). *Pteridium esculentum* was

abundant in the youngest site, and persisted throughout. *Paesia scaberula*, *Pteridium esculentum, Histiopteris incisa* and *Dicksonia fibrosa* seedlings were common in stands 9, 3 and 6 (20 - 30 years). The large ground ferns *Blechnum capense* and *Pneumatopteris pennigera* were particularly abundant on the steep shady slope sampled at site 8. The smaller *Hymenophyllum* spp. and *Trichomanes* spp. were most common in the oldest site (stand 1), where five species were recorded. Fern species abundance and diversity increased in the early stages of forest colonisation (< 20 years), but thereafter showed no clear pattern

Table 3: *Shrub frequency. Values are numbers of points out of six at each site at which the species was recorded. (1) Similarity coefficient: 2w / a + b, where w is the sum of the lowest abundance values for species in common to both stands, and a and b are the respective stand totals.*

	Sites									Overall frequency	%
	4	5	9	3	6	8	2	7	1		
Site age (yr)	6	11	20	24	29	32	35	40/67	67		
Species											
Rubus fruticosus	4	3	1	1			3		1	13	6.0
Buddleja davidii	6	4								10	4.6
Leycesteria formosa	1	3	2							6	2.8
Erica lusitanica	1	1								2	0.9
Salix cinerea	2									2	0.9
Lupinus arboreus	1									1	0.5
Coprosma robusta	4	6	6	6	6	3	6	6	2	45	20.8
Pittosporum tenuifolium	3	1	1		3		6	1	1	16	7.4
Fuchsia excorticata		1	1	2		5	6	1		16	7.4
Aristotelia serrata		1	1	2	6			1	3	14	6.5
Schefflera digitata				2		5		2	5	14	6.5
Brachyglottis repanda			1	2		3	1	1	6	14	6.5
Coprosma grandifolia				1	1		2	6	1	11	5.1
Pseudopanax arboreus				4		1			4	9	4.2
Melicytus ramiflorus				1		2		2	3	8	3.7
Weinmannia racemosa				3				2	2	7	3.2
Geniostoma rupestre				1		1			5	7	3.2
Kunzea ericoides		1		3						4	1.9
Coriaria arborea			4							4	1.9
Cordyline australis	1				1		1			3	1.4
Pommaderis phylicifolia			3							3	1.4
Coprosma sp. (*cf.parviflora*)						2				2	0.9
Hebe stricta		1								1	0.5
Coprosma lucida					1					1	0.5
Rubus cissoides						1				1	0.5
Carmichaelia sp.									1	1	0.5
Nestegis lanceolata				1						1	0.5
Number of species	9	10	9	13	6	9	7	9	12	27	
Number of native spp	3	6	7	12	6	9	6	9	11	21	
Total abundance	23	22	20	29	18	23	25	22	34	216	100
Total native abundance	8	11	17	28	18	23	22	22	33	182	
Adventive abundance	15	11	3	1	0	0	3	0	1	34	
Similarity with next older stand	0.62	0.55	0.41	0.38	0.15	0.37	0.47	0.43			

associated with stand age, although the highest diversity was recorded in the oldest stand. As with the shrubs, stand 3 was notable for its high species diversity. The adjacent stands 2 and 9 had low ground fern diversity. Tree fern seedlings and *Blechnum capense* generally increased in abundance in the older (> 30 year old) stands. All three *Cyathea* species had more juveniles in the oldest stand than elsewhere.

The first two axes of the DCA accounted for c. 75% of the variance, with axis 1 again significantly correlated with stand age (y = -1.8871 + .057441* x; r = .7912; df = 7; P < .02. y = axis 1 loading, x = stand age in years). The first axis of the species ordination (Fig. 4c) separates species typically colonising open sites (eg. *Pteridium esculentum, Paesia scaberula*) from those more characteristic of moist forest interiors (e.g. filmy ferns, *Asplenium bulbiferum*). The larger abundant ground ferns and tree ferns occupy the central region of the ordination space, reflecting their overall abundance throughout the chronosequence.

Table 4: *Ground fern abundance. Numbers in the body of the table are a relative abundance index with a maximum possible value of 108 for any species in any stand (see text). (1)The following species were recorded in one plot only, and have not been included on the table, except in the totals:* Blechnum filiforme, Hymenophyllum demissum, H. dilatatum, H. scabrum, Lastreopsis glabella, Pteris tremulans, Tmesipteris elongatum, Trichomanes venosum, *Unidentified b.* Blechnum *spp. was misrecorded, its true identity is unknown.* Dryopteris affinis *is adventive. (2) Similarity defined as 2w / (a + b), where w is the sum of the lowest values for species in common to both stands, and a and b are the respective stand totals.*

					Sites						
Site age (yr)	4	5	9	3	6	8	2	7	1	Overall frequency	%
	6	11	20	24	29	32	35	40/67	67		
Species (1)											
Dicksonia squarrosa	16	66	60	72	65	72	96	66	90	603	20.3
Blechnum 'capense'		24	50	60	78	102	84	40	90	528	17.7
Paesia scaberula	4	4	90	9	96		60	40	1	304	10.2
Pteridium esculentum	72	28	96	20	30		16	20	9	291	9.8
Asplenium polyodon	2		6	42	25	16	9	66	30	196	6.6
Histiopteris incisa			66	16	78	1	4	1		166	5.6
Pneumatopteris pennigera		4	4	1	30	78	4	1	28	150	5.0
Dicksonia fibrosa		16	30	16	40	12	4	12	4	134	4.5
Cyathea dealbata		9	4	4	4	1	2	15	60	99	3.3
Asplenium flaccidum				30	1	12		25	25	93	3.1
Phymatosorus diversifolius				50	28	1		1	9	89	3.0
Polystichum vestitum		24	16	4	4	12	20		1	81	2.7
Cyathea medullaris									50	50	1.7
Hypolepis ambigua		1	6	4	35		1			47	1.6
Cyathea cunninghamii		20		1						21	0.7
Blechnum fluviatile					4	16				20	0.7
Asplenium bulbiferum subsp. *gracillimum*		1		1	16					18	0.6
Blechnum chambersii			1	9	2	1			1	14	0.5
Cyathea smithii						1		1	12	14	0.5
Hymenophyllum flabellatum							1		9	10	0.3
Hymenophyllum multifidum									9	9	0.3
Hymenophyllum rarum				4		1			1	6	0.2
Blechnum spp.				4						4	0.1
Hymenophyllum sanguinolentum									4	4	0.1
Unidentified a				4						4	0.1
Blechnum discolor		1			1	1				3	0.1
Dryopteris affinis	1	1			1					3	0.1
Rumohra adiantiformis				1		1			1	3	0.1
Asplenium oblongifolium								1	1	2	0.1
Total abundance index	95	201	429	350	524	344	301	289	437	2970	100
Number of species	5	15	12	21	19	17	12	13	22	36	
Similarity with next older stand (2)	.33	.50	.49	.58	.50	.58	.61	.53			

Tree ferns

Tree ferns were prominent in the older stands, with densities of 2000 - 2500 ha.$^{-1}$ and basal areas of 10 - 30 m^2.ha^{-1}. *Dicksonia squarrosa* was the numerical dominant, comprising 84% of all tree ferns (including seedlings) within the sample plots. The other species were ranked as follows: *Dicksonia fibrosa* (7%), *Cyathea dealbata* (4%), *C. medullaris* (3%) and *C. smithii* (2%). Total tree fern basal area and height sum per hectare are highly positively correlated (Fig. 5; Table 5), and both increased rapidly from 20 - 40 years, and thereafter more slowly. Tree fern stem volume is the product of these measures, but is also influenced by species composition, the thick trunks of *D. fibrosa* contributing relatively more than the thin trunks of *D. squarrosa*. The high volume of the oldest stand, where the adult and juvenile tree fern population density is less than in some younger stands, is mainly a consequence of the presence of tall tree ferns, especially *C. medullaris* and *C. smithii*.

Seedlings and juveniles of *Dicksonia squarrosa* were present in the youngest stand (6 years). The juveniles were probably derived vegetatively from trunks not killed by the logging and silvicultural treatments, but the seedlings were probably mostly derived from gametophytes. By eleven years (stand 5) seedlings of *Cyathea dealbata* and *Dicksonia fibrosa* were also present. Seedlings of *Cyathea smithii* and *C. medullaris* were not recorded until 20 years, although by this time juveniles (and even adults of *C. medullaris*) were also present, suggesting that these species also established quite early in the second decade of colonisation. Adults of all five species were present by 29 years (stand 6). *C. medullaris* had no seedlings in the older stands, was totally absent from some stands and usually formed patches, suggesting that conditions for its establishment are less frequent in space and time than is the case for the other species.

Although all species of tree ferns were present from 20 years onwards, their population structures and relative proportions changed. Initially the tree
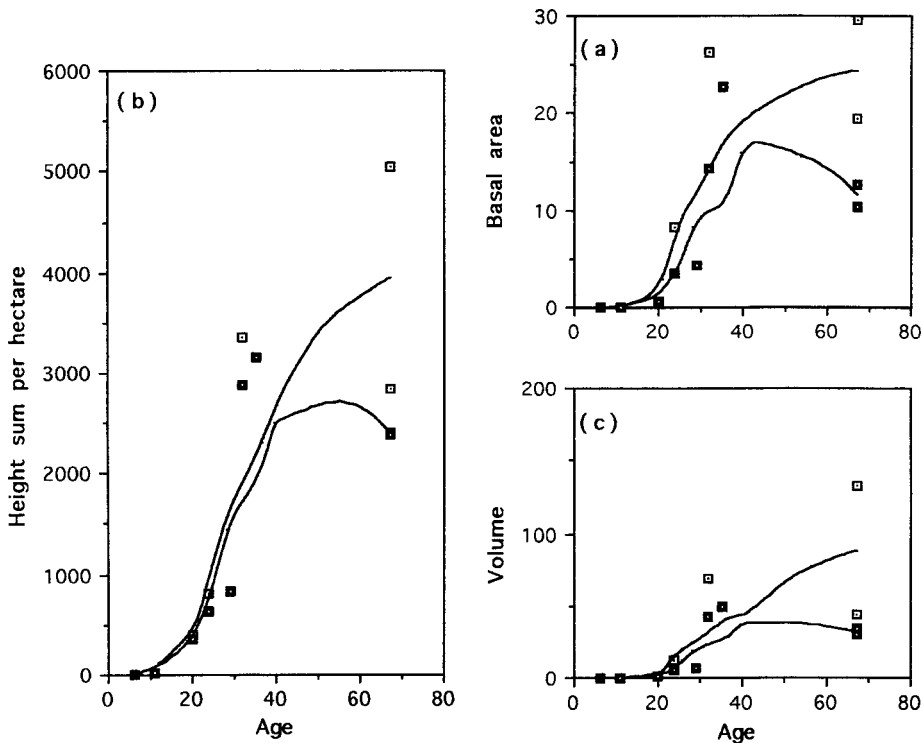

Figure 5: *Trends in (a) tree fern basal area (m^{2}ha^{-1}), (b) height sum (m ha^{-1}), and (c) volume (m^{3}ha^{-1}), with stand age. Trend lines obtained by smoothing: y (smoothed) = ((2y) + Si) / (2 + j), where Si represents the addition of the j values for stands within 10 years of y. Filled squares,* Dicksonia squarrosa*; open squares, all tree fern species combined.*

Table 5: *Tree fern abundance, height and basal area.*

		Sites								
		4	5	9	3	6	8	2	7	1
Site age (yr)		6	11	20	24	29	32	35	40/67	67
Species[1]										
C. dealbata	No.[2]	-	s	+	60	20	80	20	110	170
	Height[3]	-	0	1.3	1.4	1.1	2.3	0.2	3.7	2.6
C. medullaris	No.	-	-	+	-	20	-	-	40	380
	Height	-	-	1.9	-	4.1	-	-	5.4	9.2
C. smithii	No.	-	-	+	s	s +	100	-	s +	90
	Height	-	-	0.2	0	1.9	2.6	-	5.3	8.2
D. fibrosa	No.	-	s	100	140	320	100	40	80	30
	Height	-	0	0.8	2.5	1.4	2.6	0.8	4.7	2.8
D. squarrosa	No.	20	100	880	640	700	1720	2040	1980	940
	Height	0.2	0.8	1.8	2.9	2.8	5.2	4.3	5.1	7.8
Total adult + juvenile. ha^{-1}		20	100	980	840	1060	2000	2100	2210	1610
Total including seedlings.		140	1610	1780	2420	1800	2340	2280	2680	1980
Basal area, m[2].ha^{-1}		0	0	0.7	8.2	4.3	26.3	22.7	19.5	29.5
Height sum, m.ha^{-1}		2	28	394	821	836	3358	3161	2848	5054
Volume, m[3].ha^{-1}		0	0	1	12.8	6.7	68.6	49.8	44.5	132.2

[1] C. = *Cyathea*, D. = *Dicksonia*.
[2] Number of stems (juvenile + adult) – ha[-1]; s: 'seedlings' only present; + indicates present in the stand, but not in the enumerated area.
[3] Trunk height (m) to base of lowest fronds of tallest individual measured in the sample area or in the stand.

fern population was strongly dominated by the two *Dicksonia* species, especially *D. squarrosa*. However, *Cyathea* species were gradually added, and this genus (mainly *C. medullaris*) comprised c. 40% of the juvenile and adult tree ferns in the 67 year stand. Consequently *Dicksonia squarrosa*, although dominant throughout, showed a relative decline in the oldest stands, where *Cyathea medullaris* and *C. smithii* were generally taller than *D. squarrosa*. The shift from a mainly seedling to an adult dominated population stucture is illustrated in Fig. 6.

Ordination of the tree fern data (with each species represented as four categories: seedling, juvenile, adult and dead) accounted for 61% of the variance on axes one and two, with the former again highly correlated with pine age (r = 0.8187; df = 7; P < .01). The species ordination (Fig. 7) shows the change in population structure from right to left across the ordination, coinciding with the changes in composition of the shrub and ground fern understorey illustrated in Fig. 4b and 4c respectively. The separation of the *Cyathea* spp. (especially adult and dead *C. medullaris*) on the second axis could imply that these species are spatially segregated from the *Dicksonia* spp.

The different tree fern species appear to have different height growth rates and maximum sizes (Table 5). This aspect of the results will be presented in more detail in a later paper; here we note that maximum heights and growth rates appear to decline

in the following sequence: *C. medullaris* > *C. smithii* > *D. squarrosa* > *D. fibrosa* > *C. dealbata*. Assuming that they began trunk growth at a pine stand age of 15 years, the *maximum* height growth rate of *C. medullaris* (fastest) and *C. dealbata* (slowest) was about 18 cm. yr^{-1} and 5 cm.yr-1 respectively.

Discussion

Biodiversity is often considered to be an indicator of ecosystem health, stability, and resilience (O'Connor *et al*. 1990), which increases with successional age (Odum 1969). However, ecosystem disturbance, creating new niches for establishment, can also lead to increased biodiversity (Connell 1978). Felling of forest and the planting of a new tree crop is a disturbance which allows the invasion of herbaceous plants and shrubs and can thus locally increase plant diversity. In New Zealand, however, many such invasive plants are adventive, so that the increased species richness may have negative implications for the conservation of the indigenous biota.

Native communities are variously assembled beneath pines through time according to substrate, aspect, topography, distance from seed sources and so on. Allen *et al*. (1995a) ordinated data from plots within three differently aged *Pinus radiata* compartments in Kinleith Forest. In agreement with
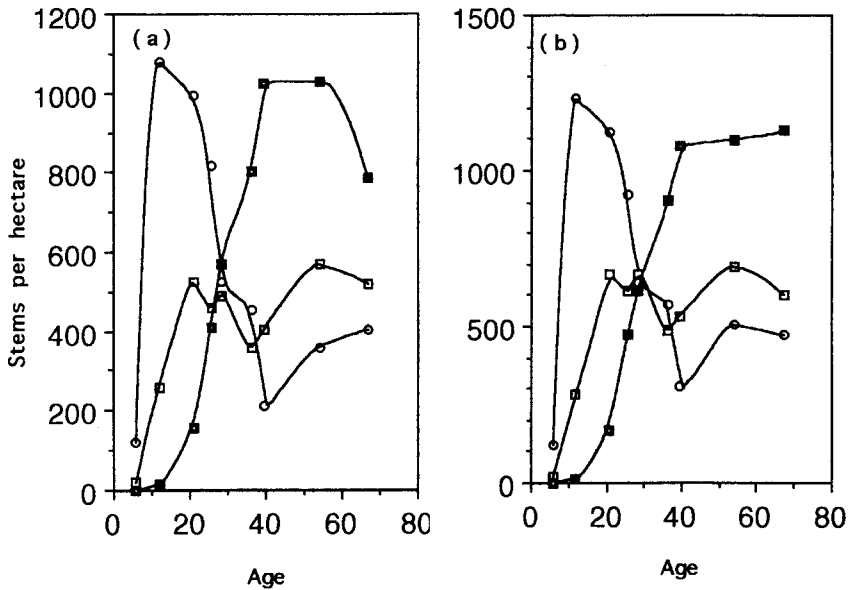
Figure 6: *Changes in population structure of tree ferns with stand age. (a)* Dicksonia squarrosa. *(b) All tree ferns combined. Smoothed as in Figure 5. Open circles, seedlings; open squares, tree ferns < 1m trunk height; filled squares, tree ferns > 1m trunk height.*
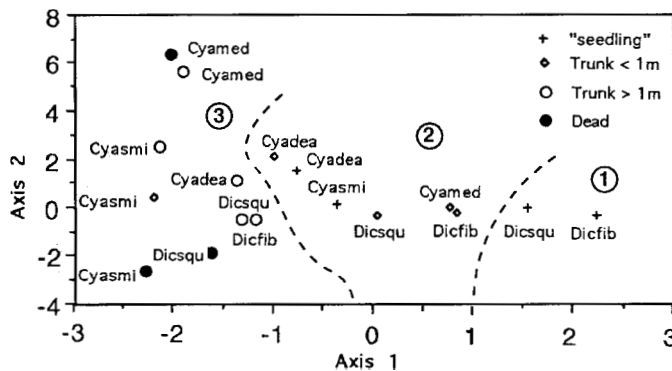

Figure 7: *DCA species ordination for tree fern population data. Abbreviated names are first three letters of generic and specific names. Numbers divide the ordination space into three areas of increasing tree fern and stand age, as in Figure 4b and c.*

earlier studies in the same area by McQueen (1961, 1993), their results indicate the importance of topography, soil nutrients and moisture status in the determination of the invasive vegetation pattern. Because only three stand ages (1, 13 and 29 years) were included in their study the significance of the age trend cannot be assessed with confidence. Likewise, in the current study, because the differently aged plots were not replicated on

different substrates or topographies, the relative importance of these variables cannot be compared with that of age. However, the results agree with the earlier work in that they indicate that site characteristics such as aspect and microtopography are important in determining total plant diversity. For example, site 1 was the oldest stand studied, but it was also south facing and relatively moist. These environmental variables could explain the higher

abundance and diversity of filmy ferns (*Hymenophyllum* spp.) in this site. In contrast, the equally old but mainly north facing Site 7 was noticeably drier, and had a much lower abundance and diversity of ground ferns. Site 3 (aged 24 years) had unexpectedly high shrub and fern diversity. Large boulders in this site created more microtopographical variation than the other stands, with well-lit raised microsites allowing the establishment of wind-dispersed light-demanding species such as *Weinmannia racemosa* and *Kunzea ericoides,* and damp niches favoring the establishment of ferns. These stands indicate that the gradual temporal trends in species recruitment into pine plantations are strongly influenced by site factors other than the age of the pine overstorey.

While the importance of topographic and associated variables is acknowledged, the first axes of the shrub and fern ordinations summarise shifts in composition which are significantly correlated with the age of the pines, indicating that, directly or indirectly, this is an important influence on the species composition of the understorey. The relative proportions of different tree fern species and their population structures and total biomass likewise show a strong relationship with stand age. These results suggest that stand age is the primary control on species richness, with secondary gradients associated with topography and soil type.

Allen *et al.* (1995a) pointed out that invasive adventives often have r-selected traits (*sensu* Grime 1979), and that competitive sorting through time should increase the proportion of longer-lived and shade tolerant native species, and also increase compositional predictability. These two temporal trends can be discerned in the species richness results: an initial invasion of adventives, followed by their reduction and a gradual accretion of native species.

Following site clearance, preparation and planting with pines, the initial invasion phase is dominated by adventive weeds. In addition to the woody species recorded here there are herbaceous species such as *Holcus lanatus*, *Lotus pedunculatus*, *Conyza albida, Circium arvense, Senecio* spp., and *Sonchus asper*. Adventive shrubs and herbs had almost disappeared in stands 20 - 30 years of age, by which time the modal pine diameter class was 40-50cm and stand height was in the range 25 - 45m. Some native shrubs, especially *Coprosma robusta, Pittosporum tenuifolium, Fuchsia excorticata*, and *Aristotelia serrata* are also capable of early invasion. These species may be brought in by birds, but it seems likely that germination from buried dormant seeds also occurs . Likewise, the early arrival of the robust native ferns *Dicksonia squarrosa, Pteridium*

esculentum and *Paesia scaberula* could be from resprouting rhizomes. Unlike the adventives, these early arriving native species generally maintain a presence in older stands.

The second temporal trend was the gradual acquisition of native species as the pines age. Seral native broadleaved species, and more shade-tolerant gap-colonists, become more frequent as the adventive species decline, and are commonest in sites aged from c. 30 to 40 years. Older stands have relatively high shrub and fern richness, a varied tree size structure, abundant tree ferns of several species, and canopy heights and total basal areas comparable to those in native podocarp and kauri forests (Lusk & Ogden 1992; Ahmed & Ogden 1991). Ferns comprise 50 - 70% of all vascular plant species in these stands. Ferns, and probably bryophytes and lichens also, become more important as components of overall species richness with time.

Although management practices to conserve native biodiversity were not included in the aims of this study, the results have implications for them. The New Zealand Government and the forest industry recognised their obligation to conserve indigenous species richness by signing the Convention for Biological Diversity and the New Zealand Forest Accord respectively. Plantation forestry involves the development of a crop and an associated assemblage of adventive and native species which increases in indigenous diversity through time. The latter, however, is largely eliminated when the crop is harvested and the site sprayed with a plant dessicant before re-planting. The level of indigenous plant species richness in planted areas is thus largely a question of the proportion of the landscape maintained as older pine stands or left in indigenous cover. Unless the industry has a conservation policy recognising the significance of older pine stands and/or maintaining pockets of native forest within the managed area, overall native biodiversity becomes largely a function of mean rotation time. Shorter rotations imply a reduction in native plant richness (and its associated fauna) and an increase in the proportion of the landscape in the early stages of succession, dominated by young tree crops and adventive species.

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