

MULTIVARIATE ANALYSES OF FORESTS DOMINATED BY *AGATHIS AUSTRALIS* SALISB., IN NEWZEALAND

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Abstract

Multivariate analyses of 25 mature *Agathis australis* (kauri) stands extending from Te Pahi to Kati-kati are presented. Four groups of Kauri-*Nothofagus truncata*, Kauri-*Beilschmiedia tarairi*, *Dysoxylum spectabile*, Kauri-*Ilex brexioides*, *Ackama rosaefolia* and Kauri-*Oleria rani*, *Phyllocladus trichomanoides* may be recognised. In most stands however, the overlapping species distribution indicated the relative homogenous nature of the various Kauri forests. Similarities between canopy and understorey classification/ ordination imply that canopy and understorey species are correlated in their occurrence. Stand groupings obtained by multivariate analyses showed distinct relationship to soils group. Higher values (basal area and density) of Kauri were recorded on soils derived from predominantly igneous rocks. The relationship between multivariate results and overall community and topographical attributes were assessed. Density values and slope showed a significant correlation with ordination axes.

Introduction

The principal aim of classification or ordination is to summarise quantitative ecological data and indicate the relationships between groups of attributes or stands. The merits and demerits of both forms of analysis has been discussed by McIntosh (1967). However, approaches emphasising relative discontinuity (classification) and relative continuity (ordination) may be regarded as complementary serving different needs rather than antagonistic (Orloci, 1975; Whittaker, 1956).

Cockayne (1928) considered *Agathis australis* Salisb., forests as one association which he classified into various sub-associations. On the basis of relative abundance of physiognomically dominant trees, a provisional classification of indigenous forests of the North Island was presented by Mckelvey & Nicholls (1957) and Nicholls (1976). This classification was subjective and included most of the logged or highly disturbed kauri forests. According to Cockayne (1908) the New Zealand kauri forest, with its huge coniferous emergents and a diverse angiosperm understorey, is a type of association rarely replicated elsewhere in the world. Sale (1978) stated that within New Zealand every area of Kauri forest is unique in its species composition. Informations on Kauri have been gathered by Ecroyd (1982). Though Kauri is one of the most important endemic trees of New Zealand, no extensive quantitative work has yet been published on mature Kauri forest. The aim of this study was to present the multivariate analysis of mature Kauri forest,

based on geographically comprehensive sampling and detailed objective methods. Nomenclature follows Allan (1961). Species abbreviation are given in appendix I.

Methods

The Kauri-dominated stands studied (lat. $34^{\circ}28'$ to $37^{\circ}36'$) ranged in elevation from 150 to 800 m, with relatively flat to steep slopes facing various directions. Location and grid references of sites are presented in Fig. 1 and Table 1.

The Point Centred Quarter Method was used to sample the stands (Cottom & Curtis, 1956). In most stands 20 points were sampled at intervals of 25 m between points. Except in a few cases, sampling was restricted to areas which showed no signs of human disturbance.

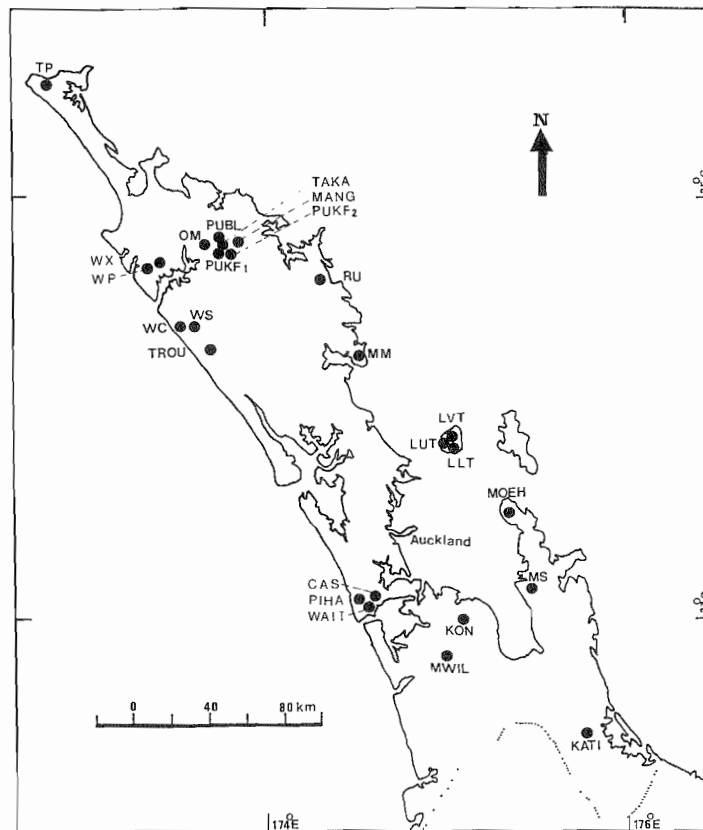


Fig. 1. Locations of sampling sites and distribution of *Agathis australis* (after Ecroyd 1982). For Key to code see Table 1. Dotted line show the southern most limit of the species.

Table 1. Site Characteristics.

Stand No.	Locations	Code	Latitude S	Longitude E	Approximate Grids	Altitude (m)	Slope	Aspect
1.	<i>Te Paki Coastal Park</i>	TP	34° 28	172° 46	25-26/45-46	220	24	W
2.	<i>Omahuta Sanctuary</i>	OM	35° 15	173° 37	13-14/54-55	150	12	Flat
<i>Puketi State Forest</i>								
3.	Te Harua Stream	PUKFL	35° 16	173° 44	23-24/51-52	305	35	N
4.	Onekura Bluff	PUBL	35° 11	173° 45	26-27/60-61	305	30	N
5.	Loop Track	PUKF ₂	35° 15	173° 44	26-27/52-53	274	31	NE
6.	Takapau Track	TAKA	35° 13	173° 45	24-25/55-56	252	19	
7.	<i>Manginangina Scenic Reserve</i>	MANG	35° 12	173° 48	30-31/59-60	274	24	E
8.	<i>Russell State Forest</i>	RU	35° 23	174° 15	75-76/3839	221	26	SW
<i>Warawara State Forest</i>								
9.	Ridge Site	WX	35° 22	173° 17	78-79/37-38	468	32	N
10.	Plateau Site	WP	35° 23	173° 17	79-80/35-36	358	28	N
<i>Waipoua State Forest</i>								
11.	Waipoua Sanctuary	WS	35° 29	173° 34	09-10/04-05	145	19	SW
12.	Waipoua Coastal	WC	35° 37	173° 29	07-08/98-99	244	21	SW
13.	<i>Trounson Kauri Park</i>	TROU	35° 43	173° 38	15-16/95-96	175	19	N
14.	<i>Mount Manaia</i>	MM	35° 49	174° 31	02-03/85-86	320	31	E
<i>Little Barrier Island</i>								
15.	Upper Thumb Track	LUT	36° 12	175° 04	35-36/75-76	335	32	S
16.	Lower Thumb Track	LLT	36° 13	175° 04	35-36/75-76	213	26	NE
17.	Valley Track	LVT	36° 13	175° 04	35-36/75-76	243	34	S
18.	<i>Te-Moehau</i>	MOEH	36° 31	175° 24	90-91/01-02	450	29	NW
19.	<i>Manaia Sanctuary</i>	MS	36° 52	175° 32	03/04/55-56	350	30	NW
<i>Waitakere Ranges</i>								
20.	Cascade Kauri Park	CAS	36° 53	174° 33	03-04/55-56	240	35	EW
21.	Piha	PIHA	36° 58	174° 30	03-04/46-47	274	29	NW
22.	Huia	WAIT	36° 58	174° 34	09-10/446-47	274	31	NW
<i>Hunua Range</i>								
23.	Konini Forks	KON	37° 04	175° 08	70-71/35-36	335	30	NE
24.	Mount William	MWIL	37° 13	175° 02	90-91/41-42	350	26	N
25.	<i>Katikati State Forest</i>	KATI	37° 36	175° 52	62-63/97-98	350	30	NW

The frequency data on the understorey species (< 10 cm dbh) was obtained from a plot with a 2 1/2 m radius centred around each sampling point. Phytosociological attributes (Frequency, density and basal area) were calculated following Mueller & Ellenberg (1974). Since a better understanding of the vegetation may be obtained when the parameters of

canopy layer and understorey data are employed, density and basal area data of canopy layer and frequency data of understorey layer were used in multivariate analyses.

A computer programme, CONDENSE (Singer & Gauch, 1979) was used to convert the raw data (basal area $m^2 ha^{-1}$, stem density ha^{-1} and frequency) in the matrix into a standard format acceptable to both classification and ordination programme. Then TWINS-SPAN (a two way indicator species analysis for classification programme) and DECORANA (deterended correspondence analysis for ordination programme) were applied to standardised data obtained by CONDENSE. Details are given in the manuals (Hill, 1979 a & b). Multivariate analysis was performed at the stand level and not at the species level, since species ordination obtained by DECORANA have been found to be generally less satisfactory than those obtained from stands (Hill & Gauch, 1980).

Kauri was not included in the TWINS-SPAN (basal area analysis only) because it has a very high basal area in all stands and its inclusion would 'homogenise' the pattern between stands and would have blocked the recognition of differences revealed by other species. Running TWINS-SPAN with Kauri basal area gave evidence for this opinion.

Various soil groups were plotted on ordination diagrams to find some possible relation between stand and soil groups. Soil informations were obtained from Burt (1963). Correlation coefficients were calculated to describe the relationship between overall community and topography with respect to two ordination axes.

Results

1. *Basal area ($m^2 ha^{-1}$ for trees > 10 cm dbh):* The results of stand and species classification using TWINS-SPAN are given in Table 2. The values of pseudospecies, ranked on a scale from 1 to 5. The resulting dendrogram, along with the 'indicator species' (species which are strongly preferential to one or other side of the axis) which characterise the divisions, is given in Fig. 2. The stand ordination produced by DECORANA is given in Fig. 3. Axis-1 accounted for 54% and axis-2 for 31% of the total variance. TWINS-SPAN (Fig. 2) shows six groups while DECORANA (Fig. 3A) indicates four groups.

2. *Density (stem ha^{-1} > 10 cm dbh):* Stand density results (Table 3) were derived using TWINS-SPAN in a similar manner to the basal area analysis. Pseudospecies in this case ranged from 1-6. The classification and ordination results are presented in Figs. 4 and 5, respectively.

In the density ordination, axis-1 accounted for 46% of the variance while axis-3 for 18% of the variance. In this ordination the stand distribution on axes 1 and 2 was difficult to interpret though these axes described slightly higher (67%) variance. However, the stand

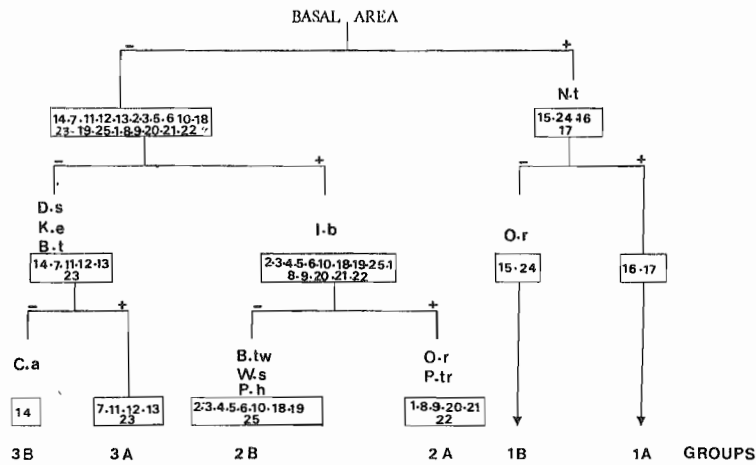


Fig. 2. Twinspan classification diagram based on basal area data (excluding Kauri) indicating indicator species in each group. The numbers in the boxes are the stands (Table 1) in each group after division. For Key to abbreviation see appendix 1.

groupings indicated in the classification were more apparent on axes 1 and 3. Both TWINSPAN and DECORANA analyses produced six groups.

3. *Frequency (percentage frequency < 10 cm dbh)*: The data table for the frequency analysis containing 112 species is given in Ahmed (1984). The resulting diagram and ordination are presented in Figs. 6 and 7. Axis-1 accounted for 41% and axis-2 for 37% of the variance. Classification (Fig. 6) and ordination (Fig. 7A) diagrams show 5 and 3 groups, respectively.

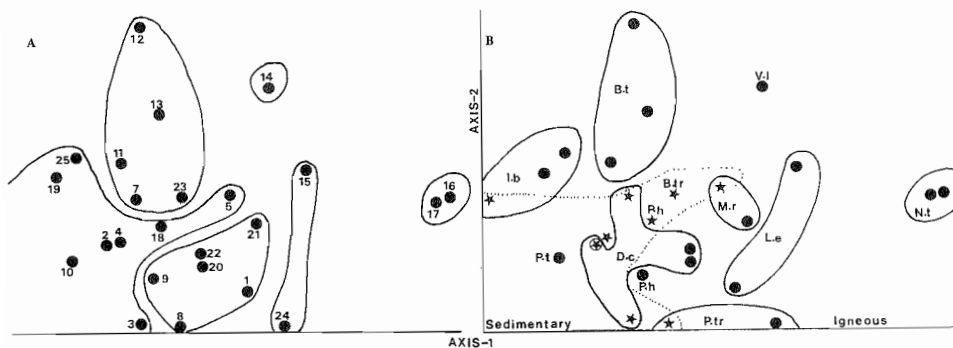


Fig. 3A. Stand position on two dimensional stand ordination of basal area data (Decorana). Groups are those indicated by Twinspan.

B. Grouping on the basis of species distribution having highest relative basal area value in a stand. Broken line separates two predominant soil groups. (See also Key to 7c).

Table 2. Basal Area Classification Matrix.

Site Code:	MM	MANG	WS	WC	TROU	KON	OM	PUKF ¹	PUBL	PUKF ²	TAKA	WP	MOEH	MS	KART	TP	RU	WX	CAS	PIHA	WAIT	LUT	WMIT	LTF	LVF	1st Div	2nd Div	3rd Div	Species Classification					
Stands —	1 4	1 7 1	1 2 3	1 1 2	1 2 3	2 3	2 3	4 3	4 5	5 6	6 0	1 8	1 9	1 5	2 1	1 8	9 0	2 1	2 0	2 1	2 2	2 2	1 2	1 4	1 6	1 7								
Species:																																		
1	Ackama rosaeifolia	1	2	1	1	1	1	2	1	1	3				1															0	0	0		
5	Cyathodes fasciculata		1	1				1						1			1	1	1	1	1									0	0	0		
6	Dacrydium cupressinum	1	3	0	0	2	3	3	1	2	3		1	2	1	2	1	2	1	3	1									0	0	0		
7	Dacrydium kirkii							2						1																0	0	0		
10	Elaeocarpus dentatus		1	1	1	1	1	1	1	1	1		1	1	1		1	1	1	1	1	1								0	0	0		
13	Ilex brexioides		1		1		1		4	3	1	5	3		1	1	1	1	1	1	1									0	0	0		
16	Libocedrus plumosa							1			1	1		1			1	1	1	1	1									0	0	0		
21	Nestegis montana		1						1		1	1		1			1	1	1	1	1									0	0	0		
23	Olearia furfuracea		1		1		1	1			1	1		1			1	1	1	1	1									0	0	0		
25	Phyllocladus glaucus							1		1							1														0	0	0	
29	Podocarpus hallii		1	1	1	2	1	2	1	1	2	3	4					3													0	0	0	
30	Podocarpus totara	1	1	2		1	1	1	3	4		3	1	3	1	3	1	1	2												0	0	0	
33	Quintinia serrata	1			1	1	1	1	2	1				1			1	1	1	1	1										0	0	0	
35	Persoonia tobu							1									1	1	1	1	1										0	0	0	
36	Weinmannia sp.		1	1	1	1	1	1	2	3	3	2																				0	0	0
3	Betischmedia tarairi		2	3	4	4		1		1			1																			0	0	1
4	Coprosma arborea		2					1						1	1	1	1	1	1	1	1											0	0	1
8	Dracophyllum hybrid		1	1																												0	0	1
9	Dysoxylum spectabile	1	1	1	3	1								1																		0	0	1
12	Hoheria populnea	1																														0	0	1

4	<i>Beilschmiedia tarairi</i>	6	6	6	3	3	3	1	2	2	0	1	1
6	<i>Cyathodes fasciculata</i>	2	2	1	1	1	1	1	1	1	0	1	1
9	<i>Dracophyllum</i> hybrid	2	2		1	4	1				2	0	1
16	<i>Leptospermum ericoides</i>	1	2		2	6	4	6	5	4	5	6	1
19	<i>Metrosideros robusta</i>	1			2		3	1	4	2	4	1	0
21	<i>Nestegis lanceolata</i>	2		1			1	2	3	2	1	4	1
25	<i>Olearia rami</i>	3		1	1	1	3	4	4	1	3	5	6
26	<i>Phyllocladus glaucus</i>		2	1			4						1
32	<i>Pseudopanax arboreus</i>	2	1		4	3	1	4	2	1			1
5	<i>Coprosma arborea</i>			1			1	4	3	2	2	6	1
13	<i>Hoheria populnea</i>								3		5	1	0
17	<i>Libocedrus plumosa</i>						1	2	1	4			1
23	<i>Nothofagus truncata</i>										4		1
35	<i>Sophora microphylla</i>								5	2	6		1
38	<i>Vitex lucens</i>	2									4	1	0
28	<i>Pittosporum tenuifolium</i>	2	2	2	2		2		1	1		2	4
36	<i>Personia toru</i>	1	2				1		1	2			1
15	<i>Knightsia emeisa</i>	4	3	2	2	1	5	1	2	5	4	5	4
20	<i>Myrsine australis</i>	1	4	3			3	1	2	3	2	1	2
27	<i>Phyllocladus trichomanoides</i>	3	2	3	5		4	3	1		2	6	5
Stand	1st Division	0	0	0	0	0	0	0	0	0	0	1	1
Classi-	2nd Division	0	0	1	1	1	1	1	1	1	1	1	1
fication	3rd Division	0	0	0	0	0	1	1	1	1	1	0	0
Groups		6	5	4	3	2	1						

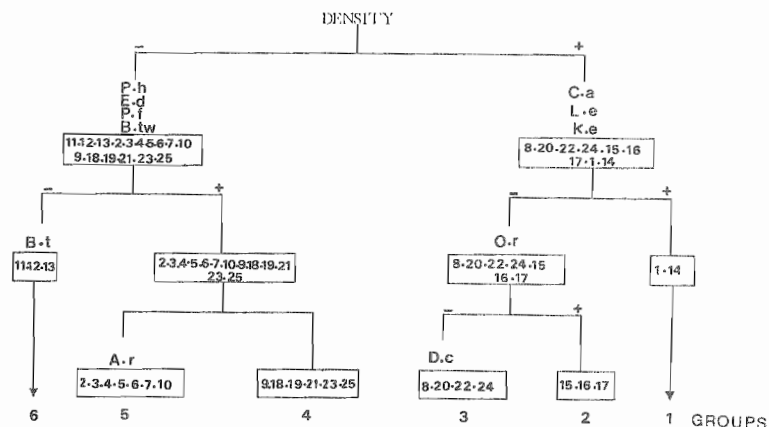


Fig. 4. Dendrogram produced by Twinspan analysis of the density for the 25 stands. The species on which the division was made were indicated. The number in the boxes are the same stands as described in Table 1. For Key to abbreviations refer to appendix 1.

Discussion

A feature of both classifications is that they arrange the final groupings in the order they would be on the first axis of a reciprocal averaging (RA) type of ordination (DECORANA). If we consider only 'constant groups' — those stands which appeared together in all classification diagrams — the ordering of these stands appears to reflect changes in species composition, total density, basal area and species diversity. This is suggestive of a gradient of relative stand maturity. Stands 16 and 17 from Little Barrier Island have low species diversity and high values for species thought to be indicative of recent disturbance (eg., *Leptospermum ericoides*). *Nothofagus truncata*, the characteristic species of these stands, favours cooler southern slopes and is also probably indicative of a past disturbance (Macdonald, 1984). This group is distinct in all classification and ordination diagrams. At the other side (stands 11, 12 and 13) Waipoua and Trounson are larger basal area Kauri forests with a well developed sub-canopy of *Beilschmiedia tarairi* and *Dysoxylum spectabile*, and abundant seedlings of canopy and sub-canopy species. The presence of scattered (but relatively large) individuals of *Knightia excelsa* is an interesting feature of these forests.

The central group (constant stands 2, 3, 4, 5, 6, 7 and 10) showed different indicator species in the two canopy classifications, but they always clustered in a group. Except for stand No. 10 all other stands came from the same vicinity (Puketi, Omahuta and Manginangina). In the basal area classification *Ixerba brexioides* appears to be a prominent species of this group, while in the density classification it was *Ackama rosaefolia*. Though classification analysis grouped these stands together, ordination appeared to indicate two neighbouring groups. From this it was assumed that the only difference between them is

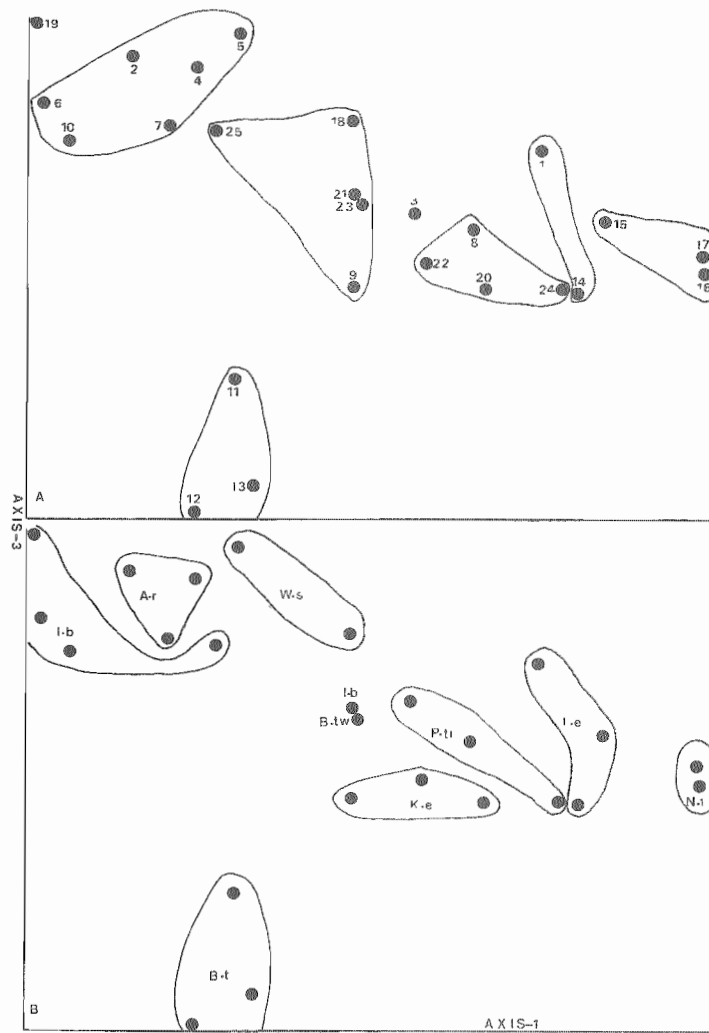


Fig. 5A. Stand position on two dimensional stand density data ordination (Decorana). Groups are those defined by Twinspan.

B. Species distribution on the basis of highest relative density. Species shown are co-dominant with kauri.

quantitative composition. Furthermore, both groups showed similar understorey species distribution.

The fourth group (stands, 8, 20 and 22) had *Olearia rani* and *Phyllocladus trichomanoides* as indicator species. This group was merged with stands 11, 12 and 13 in the understorey classification, which also showed *Phyllocladus trichomanoides* as an indicator species.

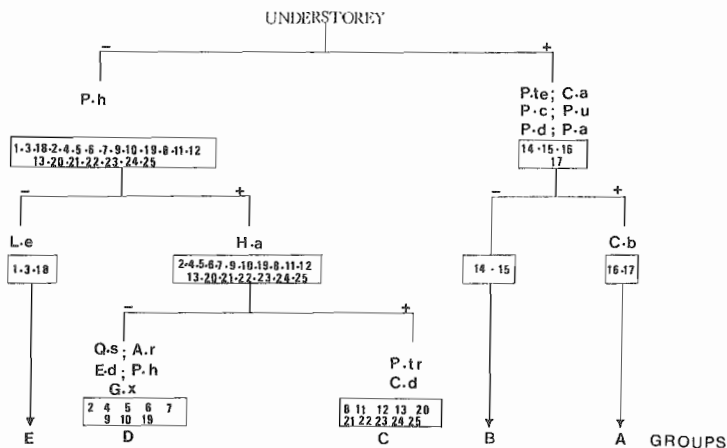


Fig. 6. Twinspan classification of the frequency of understorey species (< 10 cm dbh) for 25 stands.

In most cases groupings based on either one of the two co-dominant species (Fig. 8) overlapped with groupings based on the first co-dominant species suggesting that continuous relationships exist between the groups. This indicated the relatively homogenous nature of the various stands studied. On the basis of characteristic species it can be assumed that, while it may be possible to recognise various Kauri dominated associations in various habitats, all classification groups were an abstraction from a continuous sequence of relationships.

Detailed description of the undergrowth was not the main objective of the present study and percentage frequency is not the best approach for comparative vegetation description. However, understorey stands showed different dominant species, clustering of stands in some groups was the same as in the density and basal area classifications. It was also evident that some stands (1, 3, 17, 25, 12 and 13) had abundant species or seedlings (< 10 cm dbh) of canopy trees (Fig. 7B). Moreover, common tree species, such as *Coprosma arborea*, *Ackama rosaefolia*, *Elaeocarpus dentatus* and *Podocarpus hallii* appeared as indicator species in both the understorey and the canopy classifications. These results indicate a strong relationship between the canopy and its associated understorey.

The density and basal area ordinations were quite similar (Figs. 3 and 5). The first axis of the ordinations (accounts for the maximum variance) highlights the stand sequence similarities. In general, the clustering and arrangement of stands on axis 1 of the understorey ordination, agreed with the canopy ordination implying that understorey and canopy species are correlated in their occurrence.

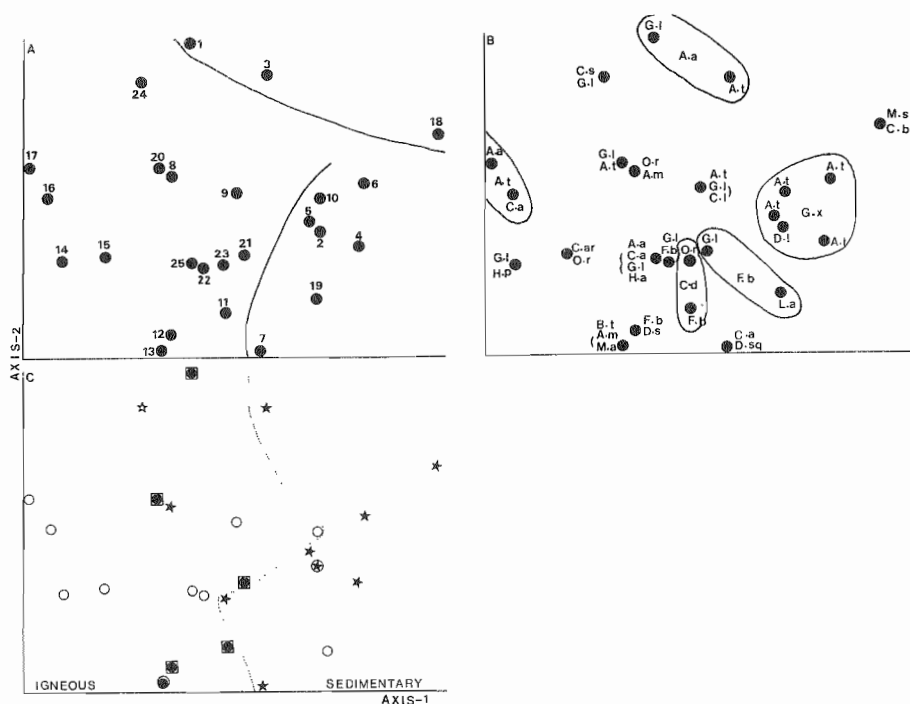


Fig. 7A. Stand position on two dimensional stand frequency data ordination (Decorana). Groups are those defined by classification.

B. Species distribution on the basis of highest frequency attained in a stand. Species shown in a centre of a group is the common dominant of the group, while those others are co-dominant. Species have similar values if bracketed.

C. Distribution of predominant lithology and soil series.

sedimentary soils — Hukerenui-Rangiora	⊗
— Te Ranga-Marua	★
igneous soils — Te Kie-Awapuka	○
— Waimatenui and Waitakere	■
— Rangiuru Tutamoe	●
— Hamilton and Naikē	☆

Kauri is found frequently on soils derived from both sedimentary and igneous rocks (Clayton-Greene, 1978). Eight stands were on steep-land soils (Te Ranga Marua series) of Yellow Brown Earth derived from sedimentary rocks. In most of the stands sampled, soils derived from the igneous rocks were of two main types.

1. On soils derived from Waimatenui and Waitakere Series the stem density was not much different from that of the sedimentary soil (103 ha^{-1}) but the basal area was higher ($59.6 \text{ m}^2 \text{ ha}^{-1}$).

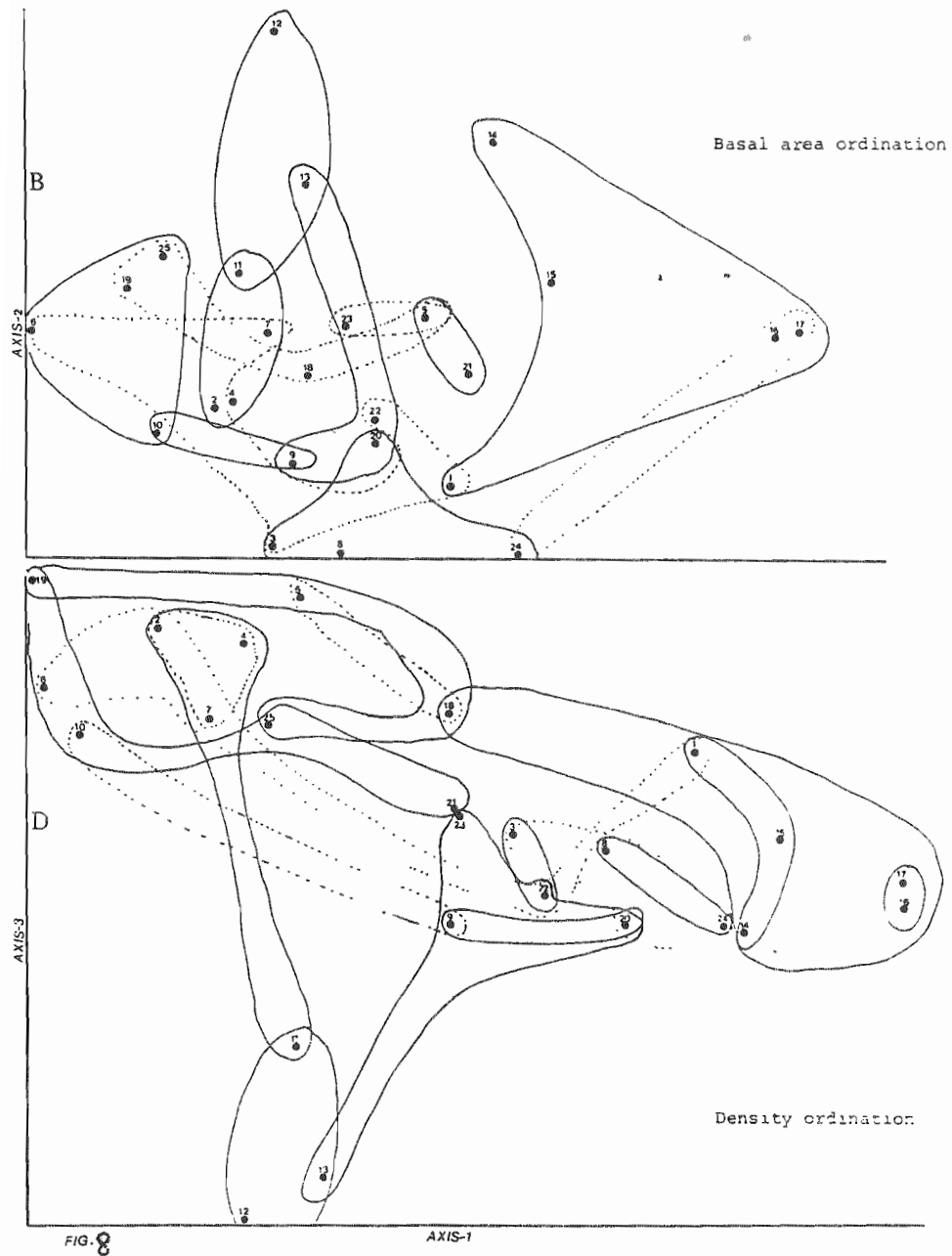


Fig. 8. Grouping on the basis of at least one species in common between the first two co-dominant (on the basis of importance values) species of the stand.

2. On the soil series Te Kie-Awapuka (a related steep-land soil) the average density was greater (147 ha^{-1}) but the basal area was similar to that on the Te Ranga-Marua series ($54.7 \text{ m}^2 \text{ ha}^{-1}$).

Consequently, on an overall basis both basal area and density values of Kauri were higher on soils predominately derived from igneous rocks.

Although no distinct grouping was evident from soil type or geology, in the classification diagrams groups A, B (understorey), groups 1, 2, 6 (density) and groups 1A, 3B (basal area) were associated with soils derived from igneous rocks. Sedimentary soils were predominantly found in groups 5 of the density classification diagram only, while all other groups showed no clear correlation. However, the understorey ordination separates the two main soil types on the first axis. Figure 7C shows that soils derived from sedimentary rocks occupy the right side of the ordination while stands found on soils derived from igneous rocks are grouped on the left. In the basal area ordination (Fig. 3B) all stands from sedimentary soils tended to group from the middle to the left side of the ordination. *Nothofagus truncata*, *Beilschmiedia tarairi*, *Coprosma arborea* and *Corokia buddleioides* were found as co-dominant and indicator species on igneous soils (brown granular clay and loam) while *Acama rosaefolia* was the indicator species of groups 5 and D (density and understorey respectively) recorded on sedimentary soils (yellow brown earths). However, in general, the floristic composition, indicator species and stand groupings showed no distinct relationship to soil groups.

Table 4 describes the relationships between the overall community and topography with respect to two ordination axes. Overall density showed a significant correlation with both axes while Kauri density was significantly related to axes-1 of both canopy ordination. Basal area was highly variable among the stands and showed no correlation in most cases (only weakly with the second axis of the basal area ordination). This is of some in-

Table 4. Correlation between various stand and the stand loading on the axes of ordination.

Attributes	Basal area $\text{m}^2 \text{ ha}^{-1}$ ordination		Density ha^{-1} ordination	
	Axis 1	Axis 2	Axis 1	Axis 3
Stand density ha^{-1}	P < .1	P < .05	P < .05	P < .02
Kauri density ha^{-1}	P < .02	NS	P < .001	NS
Stand basal area $\text{m}^2 \text{ ha}^{-1}$	NS	P < .02	NS	NS
Kauri basal area $\text{m}^2 \text{ ha}^{-1}$	NS	NS	NS	NS
Altitude (m)	NS	NS	NS	NS
Degree of slope	NS	P < .05	P < .05	NS

terests as Kauri itself was not included in this ordination because as mentioned earlier inclusion of Kauri was thought to homogenise the results. Though altitude and species distribution were not clearly correlated for most species, some general trends were noted. *Beilschmiedia tarairi* and *Rhopalostylis sapida* were recorded only on moderate slopes from 150 to 250 m. *Ackama rosaefolia* occurs up to 300 m, while *Ixerba brexioides* is associated with Kauri from 250 to 450 m. Therefore, it is likely that the different species associated with Kauri are related to rainfall and altitude. Some of these co-dominant species may reflect the moisture conditions of the site. Furthermore, slope, elevation and soil texture are all intercorelated (Marks & Harcombe, 1981) therefore the independent effect of any one of these variables may be weak.

The above discussion and relative homogeneous nature between both canopy and understorey classification/ordination give additional support to the Cockayne's (1928) opinion, therefore all Kauri forests should be regarded as one 'Kauri type'.

Acknowledgements

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Appendix. 1

SPECIES ABBREVIATIONS

A.a	<i>Agathis australis</i>	A.m	<i>Alseuosmia macrophylla</i>
A.r	<i>Ackama rosaefolia</i>	A.t	<i>Astelia trinervia</i>
B.t	<i>Beilschmiedia tarairi</i>	B.tw	<i>Beilschmiedia tawa</i>
C.a	<i>Coprosma australis</i>	C.ar	<i>Coprosma arborea</i>
C.b	<i>Corokia buddleioides</i>	C.d	<i>Cyathea dealbata</i>
C.l	<i>Coprosma lucida</i>	C.s	<i>Coprosma spathulata</i>
D.c	<i>Dacrydium cupresinum</i>	D.l	<i>Dicksonia lanata</i>
D.s	<i>Dysoxylum spectabile</i>	D.sq.	<i>Dicksonia squarrosa</i>
E.d	<i>Elaeocarous dentatus</i>		
F.b	<i>Freycinetia banksii</i>	G.x	<i>Gahnia xanthocarpa</i>
G.l	<i>Geniostoma ligustrifolium</i>	H.p	<i>Hoheria populnea</i>
H.a	<i>Hedycarya arborea</i>		
I.b	<i>Ixerba brexioides</i>	L.e	<i>Leptospermum ericoides</i>
K.e	<i>Knightsia excelsa</i>	M.s	<i>Myrsine salicina</i>
L.a	<i>Lygodium articulatum</i>		
M.a	<i>Myrsine australis</i>	P.c	<i>Pittosporum cornifolium</i>
M.r	<i>Metrosideros robusta</i>	P.f	<i>Podocarpus ferrugineus</i>
N.t	<i>Nothofagus truncata</i>	P.t	<i>Podocarpus totara</i>
O.r	<i>Olearia rani</i>	P.tr	<i>Phyllocladus trichomanoides</i>
P.a	<i>Pseudopanax arboreus</i>		
P.d	<i>Pseudopanax discolor</i>		
P.h	<i>Podocarpus hallii</i>		
P.tc	<i>Pittosporum tenuifolium</i>		
P.u	<i>Pittosporum umbellatum</i>		
Q.s	<i>Quintinia serrata</i>		
V.l	<i>Vitex lucens</i>		
W.s	<i>Weinmannia sp.</i>		