COMMUNITY MATRIX MODEL PREDICTIONs 0F
FUTURE FOREST COMPOSITION AT RUSSELL
STATE FOREST

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SUMMARY: The data of Lloyd (1971) on the 'chosen tree' and 'chosen seedlings' in 5607 4 x 4 m plots in Russell forest are analysed using a simple transition matrix model. The most realistic analysis predicts little change in relative species composition, other than a slight increase in the softwoods. The virtue of the approach lies more in the questions it raises than in the predictions obtained. Before such models can be applied satisfactorily in New Zealand basic data on seedling survival, tree growth rates and average life spans are required for most indigenous species.

KEYWORDS: Mathematical models; transition matrix; indigenous forest; forest composition; population dynamics; kauri; Agathis australis; Araucariaceae; Russell State Forest; Northland.

INTRODUCTION

The life history of an individual tree, or the structure of a tree population, can be conceived as comprising a series of stages (e.g. seedling, saplings, poles, mature trees etc.). One way of studying population growth is to measure the contribution which any such stage makes to any other stage over unit time. Such a model, predicting future 'stage structure' and the direction and rate of change is the 'Leslie matrix' model (Leslie, 1945). In matrix notation it may be stated as:

$$n_t + 1 = Mn_t \qquad (1)$$

where n_t is a column vector (n_{t0}, n_{t1} n_{t2} . . . . . . n_{ts}) representing the structure at time t of a population divided into s stages. The Leslie matrix, M, is a square transition matrix of order s, describing the changes in the population structure over unit time. The elements of the matrix are probabilities of individuals remaining in their current stage or moving to another, normally the next, stage in the life cycle. This model is described in detail by Enright and Ogden (1979) and there are several examples of its application to plant populations in the literature (Namkoon and Roberds, 1974; Sarukhan and Gadgil, 1974; Hartshorn, 1975; Werner and Caswell, 1977; Bullock, 1980). In New Zealand the model has been applied to red beech *(Nothofagus lusca)* populations by Enright and Ogden (1979), and to mangrove *(Avicennia marina)* populations by Burns (1982).

The multi-species community model discussed here takes the same form as equation (1), but with the rows and columns of the transition matrix (M) referring not to different stages in a population, but to different species in a community. Thus the matrix defines the probability of any tree species being replaced by an individual of its own kind, or by another species. The column vector (n_t) represents the initial species composition (%) of the stand being studied. In this model there is no net change in the total population size of all species, but the proportional representation of species may vary. Its application was described in more detail by Enright and Ogden (1979).

The probability values in the Leslie (single species) matrix are calculated from birth rate (seed input), mortality and growth rate data, using a standard life-table approach. No such guide-lines are available for calculating the replacement probabilities in the community (multi-species) matrix.

Stephens and Waggoner (1970) collected data on the dominant species in a given plot at time t and again ten years later (t_1). Using information from it large number of such plots (n = 327), the change in dominance over time was calculated as a simple proportion. Thus, for example, of the original number of plots dominated by species X after 10 years, 0.82 of these plots were still dominated by species X, whilst 0.18 had become dominated by some other species. These values define for species X of probability of self-replacement or site loss to other species respectively.

Horn (1975) and Fox (1977) used a different approach, basing replacement' (or transition)

probabilities on the proportional representation of saplings beneath mature trees. For example, among a total of 837 saplings found beneath mature gray birch *(Betula populifolia)* trees scattered throughout his study area, Horn found no gray birch saplings, 142 red maples *(Acer rabrum)* and 25 beeches *(Fagus grandifolia)*. Hence the probability that a given gray birch will be replaced by another gray birch is given by 0/837 = 0, by a red maple, 142/837 = 0.17 (17%), and by beech, 25/837 = 0.03 (3%) (Horn 1975, p. 198).

Enright and Ogden (1979) calculated replacement probabilities from the measured (or estimated) mortality rates of the mature trees and the proportions of saplings of various species present in sub-plots and considered capable of capturing the released sites.

In this paper the data of Lloyd (1971) from Russell forest are analysed using Horns (1975) simple methodology. My aim is to illustrate the potential of the community matrix model for the prediction of future composition in New Zealand forest.

STUDY AREA

Russell forest is located on the east coast of Northland to the south of Bay of Islands (Latitude, 35° 24'S; Longitude, 174° 16'E). It comprises an area of regenerating kauri *(Agathis australis)* and podocarps, extending over 11,000 ha. Elevation ranges from c. 60 m to a high point at 408 m. The topography is highly dissected and valley slopes are frequently steep.

Logging for kauri, and later for podocarps, began in the area in the 1850s and some selective logging of 'second growth' kauri continues today. Some parts of the forest were logged several times, but large scale operations ceased in the 1950s. Less than 180 ha remain in a virgin condition.

The basal area (stems> 5 cm dbh) of the plots studied was generally in the range 10-50 m² ha⁻¹. In the undisturbed mature kauri forest basal area is c. 75-80 m² ha⁻¹ (M. Ahmed, pers. comm.; Halkett, 1983). Densities generally range from c. 200 to c. 2500 with an overall mean of 896 ± 115 stems >5 cm dbh ha⁻¹ (mean and standard error).

METHODS

The data set

Lloyd's field work at Russell forest commenced in 1959. The forest was traversed in 32 miles (51 km) of permanently pegged belt transects running 'across the lay of the land' and covering about 1 % of the total forest area. 'Seedlings' were recorded on one side only of the transect centre-line in contiguous 10 x 10 link (c. 2 x 2 m) units. 'Trees' were record-

ed in an area defined by two contiguous seedling units and an equivalent area on the opposite side of the transect line. Thus the 'tree unit' area was 20 x 20 links (c. 4 x 4 m). Seedlings were defined as individuals of canopy species up to 3 it (1 m) in height, all larger individuals being categorised as 'trees'. Trees were further divided into 'saplings' (1-2 m height), 'established saplings' (2 m height to 10 cm dbh), 'poles' (10-30 cm dbh) and mature trees (> 30 cm dbh). In each 2 x 2 m seedling unit the seedling considered best established or most likely to survive was recorded. In each 4 x 4 m tree unit the tree (frequently a sapling or pole) considered best established or having the best chance of ultimately achieving dominance was recorded. In both cases only 'approved species' were recorded. As these comprise the majority of all canopy species this is not a serious deficit.

Thus in each tree unit, the fittest canopy tree and two choices of fittest seedling were made. These data are summarised in Table 1, which shows for each chosen tree, the number of occasions on which each species was the chosen seedling in one or both of the associated seedling plots. Thus the table summarises data from 5607 tree plots and twice this number of seedling plots([1]).

These data are readily transformed into a transition probability matrix by expressing each element as a proportion of its row total. For example, of the 928 chosen seedlings recorded in plots where kauri was the 'chosen tree', 237 were kauri, 134 were kohekohe *(Dysoxylum spectabile)* etc., giving replacement probabilities of 237/928 = 0.255 and 134/928 = 0.144, respectively.

The initial species composition (ISC) based on mature trees, is defined in Table 2. Further unpublished data from Lloyd (1971) are used and discussed where appropriate.

Limitations of the data

The method of field sampling and the subsequent collation of the data into one table (Table 4), results in information from different forest types being amalgamated. For example, kauri occurs predominantly on upper slopes and ridges, with hardwoods in the gullies. It is conceivable that no change in the overall percentage of kauri could arise as a consequence of increases in some areas and decreases in others. Thus, the model is gross, reflecting the overall average behaviour of species in a large and topographically diverse area.

It should be noted also that only 63 % of all

([1]) Not all demarked plots contained a seedling and/or a tree.

TABLE 1. *Number of seedlings chosen as most likely to succeed in plots dominated (or potentially dominated) by different canopy tree species. From Lloyd* (1971). *For explanations see text.*

Canopy tree species (species code)	Seedling most likely to succeed									
	KAU	KOH	MIR	REW	RIM	TAN	TAR	TAW	TOT	Totals
Agathis australis (KAU)	237	134	14	32	36	116	204	19	136	928
Dysoxylum spectabile (KOH)	24	2053	32	179	9	58	681	33	100	3169
Podocarpus ferrugineus (MIR)	11	70	4	5	1	4	44	4	11	154
Knightia excelsa (REW)	20	460	14	67	4	56	183	18	53	857
Dacrydium cupressinum (RIM)	54	106	6	27	5	41	74	5	43	361
Phyllocladus trichomanoides (TAN)	324	256	19	67	49	122	270	30	246	1392
Beilschmiedia tarairi (TAR)	48	1751	34	172	14	102	717	44	147	3029
Beilschmiedia tawa (TAW)	8	386	15	27	1	24	119	23	29	632
Podocarpus totara (TOT)	42	282	9	37	9	45	152	31	67	674
Totals:	768	5507	147	613	128	568	2444	207	832	11214

TABLE 2. *Initial Species Composition* (ISC) *at Russell State Forest. The first column gives the average number of stems> 30 cm dbh ha^{-1} for each chosen species (based on 1228 trees; Lloyd, 1971). The second and third columns give the same data expressed as percentages. All figures rounded off to whole numbers.*

Name (species code)		stems ha^{-1}	ISC (%) including 'others'	ISC (%) excluding 'others'
Agathis australis	(KAU)	7	11	12
Dysoxylum spectabile	(KOH)	11	18	19
Podocarpus ferrugineus	(MIR)	1	2	2
Knightia excelsa	(REW)	3	5	5
Dacrydium cupressinum	(RIM)	2	3	3
Phyllocladus trichomanoides	(TAN)	5	8	9
Beilschmiedia tarairi	(TAR)	19	31	33
Beilschmiedia tawa	(TAW)	4	7	7
Podocarpus totara	(TOT)	6	10	10
Others	(OTH)	3	5	(exclude)
Totals		61	100	100

Note: Others include: *Elaeocarpus dentatus, Podocarpus dacrydioides, Podocarpus spicatus* and *Vitex lucens.*

TABLE 3. *Survival and longevity data for the different species. Species codes as given in Tables* 1 *and* 2.

Species code	Survival	Estimated longevity (years)
KAU	0.075	600
KOH	0.013	300
MIR	0.040	500
REW	0.032	250
RIM	0.119	600
TAN	0.062	500
TAR	0.052	400
TAW	0.142	400
TOT	0.055	600
OTH	0.230	500

Note: Survival was calculated as the ratio of the number of stems ≥ 30 cm dbh to the number of seedlings ≤1 m high (Table 3, p21 of Lloyd 1971 ; adjusted for sample sizes).

plots contained trees of the chosen species. In particular there were extensive areas of kanuka *(Leptospermum ericoides)* scrub. Such 'empty' plots have been excluded, so that the analyses performed here relate only to the more established phase of the secondary growth and to the less disturbed forest.

The essentially subjective nature of the choice of most successful tree and seedling must be kept in mind. Moreover, because saplings have been included in the most successful tree class, there remains the possibility that differences in species composition and abundance between age cohorts (i.e. successional trends) have been masked. For these reasons, Lloyd (1971) cautions against the use of his data for ecological studies. However, the exceptionally large quantity of data collected must reduce bias and increase confidence in the transition probabilites.

The 'second-best' seedlings and trees were also recorded in each plot. Although these additional data do not otherwise concern us here, the close agreement between the first- and second-choice data sets strongly implies that that the first-choice reflects overall abundance.

Analysis methods

Two analyses were performed. In both cases a square transition matrix derived from Table 1 was post-multiplied by a column vector of the initial special composition (ISC) from Table 2. The procedure is explained in text-books on matrix algebra and in Williams (1979). The whole analysis was performed on a pocket Hewlett-Packard 33E calculator, and later checked using the BASIC program employed by Enright and Ogden (1979).

In the first analysis (Matrix 1), the transition matrix was derived directly from Table 1 (by dividing each element by its row total). The ISC used excluded relatively uncommon species (column 3, Table 2).

In the second analysis (Matrix 2; Table 4) the transition matrix was extended to include a row and column for 'other' species, and all probabilities recalculated accordingly. These new probabilities were then further adjusted by multiplying them by a factor reflecting the species' probability of survival to 30 cm dbh (Table 3).

In both analyses, a 'stable stage distribution'-in which species proportions do not change with time--was obtained. However, because the generations of trees are not synchronous and species have different longevities this was weighted by the average longevity of each species to obtain a final stable stage composition (SSC) (Horn, 1975). The average longevity data employed (Table 3) are approximations based mainly on my own experience in examining increment cores and cross-sections from all species except kohekohe and miro *(Podocarpus ferrugineus).* Maximum longevity data are available for some species in the literature (e.g. Hinds & Reid, 1957; Herbert, 1980; Katz, 1980). For the initial purposes of the model it is necessary only that the figures reflect the relative life spans of the species. Thus I assume that, for every generation of kauri, there will be 2.0 generations of kohekohe, 2.4 generations of rewa rewa *(Knightia excelsa),* and 1.2 generations of miro. This means that sites occupied by kohekohe and rewarewa become available for 'capture' by the same or other species twice as often as kauri sites.

RESULTS

Analysis 1

The predicted future composition based on the relative abundance of seedlings beneath (or in close proximity to) selected dominants (Table 1) is given in Table 5. Further multiplications did not significantly alter the distribution obtained at t_3, which was consequently multiplied by longevity to produce the stable stage composition (SSC).

TABLE 4. *Transition probability matrix* 2. *Species codes as given* in *Tables* 1 *and* 2.
Seedling replacement

Tree	KAU	KOH	MIR	REW	RIM	TAN	TAR	TAW	TOT	OTH
KAU	.330	.032	.010	.019	.080	.134	.197	.050	.139	.009
KOH	.020	.304	.015	.065	.012	.041	.403	.053	.063	.024
MIR	.135	.149	.026	.026	.019	.041	.374	.093	.099	.038
REW	.050	.201	.019	.072	.016	.116	.319	.086	.098	.023
RIM	.241	.082	.014	.051	.035	.151	.229	.042	.141	.014
TAN	.316	.045	.010	.028	.076	.098	.183	.056	.176	.012
TAR	.037	.232	.014	.056	.017	.064	.380	.064	.082	.054
TAW	.030	.251	.030	.043	.006	.075	.310	.164	.080	.011
TOT	.108	.181	.019	.022	.012	.096	.228	.083	.107	.179
OTH	.073	.181	0.19	.022	.012	.096	.228	.083	.107	.179

Note: The main diagonal of the matrix represents the probability of self-replacement by any species. The rows represent the probability of a tree of any species losing its site, while the columns represent the probability of site capture by the seedlings.

These results predict changes in the composition of the canopy at Russell forest. They suggest increases in kohekohe and decreases in tarairi *(Beilschmiedia taraid),* and all softwood (coniferous) species. However, although a distinct shift to kohekohe dominance is predicted, it should be noted that the overall shift in composition is not great: the rank order of species abundance is almost unchanged between the ISC species rankings and those finally predicted in the SSC ($r_s = 0.94$; $p < 0.001$).

The time-scale of the model can be gauged by the average longevity of all species ($\overline{x} = 460$ years). If some allowance (100 years say) is made for the current age of existing canopy trees, all other things being equal, the model predicts some shifts in canopy dominance during the next 360 years followed by more gradual changes occurring as stability is approached at c. 1200 years in the future. Of course, all other things are unlikely to remain equal over such long periods of time!

Analysis 2

The above analysis took no account of seedling survival to maturity, except in-so-far-as the seedling rated as having the greatest chance of survival in the plot was chosen. The data appeared to be weight-ed strongly in favour of abundant seedlings. In the second analysis transition probabilities were weighted in proportion to the seedling's changes of reaching maturity (Table 3). When the resultant transition matrix (Table 4) was post-multiplied by the ISC vector (Column 2, Table 2) almost no change in composition occurred. stability was achieved in one or two generations (Table 6).

This result implies that, given current seedling densities and the estimated survival rates, the current canopy composition at Russell forest will be reproduced indefinitely. However, if account is taken of the supposedly different logevities of the species some minor shifts are indicated: kauri and totara *(Podocarpus to tara)* show modest increases, while kohekohe and tarairi have slight decreases. Again, the overall species rankings are little changed, and the maximum change in relative density predicted is only c. 4 %.

DISCUSSION

The difference between the results for matrix 1 and matrix 2 illustrate how simplistic conclusions about future composition, based solely on seedling abundance, can be misleading. The second analysis, making allowance for seedling and sapling mortality,

TABLE 5. *Predicted future composition using matrix* 1. *Proportions are rounded off to the nearest whole number. Species codes are given in Tables* 1 *and* 2. *The transition matrix was derived directly from Table* 1 *by dividing each element by its row total.*

Species code	ISC	T1	T2	T3	SSC
KAU	12	7	5	3	5
KOH	19	48	53	58	49
MIR	2	1	1	1	1
REW	5	5	5	5	4
RIM	3	1	1	1	2
TAN	9	5	3	3	4
TAR	33	22	22	22	25
TAW	7	2	1	1	1
TOT	10	7	7	5	9

Note: ISC = Initial species composition (%). Tl, T2, T3 are predicted species compositions after 1, 2 and 3 time periods respectively. SSC = stable species composition obtained by multiplying T3 by the species longevities.

TABLE 6. *Predicted future composition using matrix* 2 *(Table* 4). *Proportions are rounded off to the nearest whole number. Species codes are given in Tables* 1 *and* 2.

Species codes	ISC	Tl	T2	SSC
KAU	11	10	10	14
KOH	18	18	19	14
MIR	2	2	2	2
REW	5	5	5	2
RIM	3	3	3	4
TAN	8	8	8	9
TAR	31	31	32	30
TAW	7	8	8	7
TOT	10	10	10	14
OTH	5	4	4	4

Note: See notes on Table 5. Stability was reached at T2 which was then multiplied by longevity to get the final stable species composition.

probably provides a more accurate prediction. The coincidence between the ISC and the composition predicted after only one time period in this analysis implies that the elements of the transition matrix are biologically realistic. The minor changes predicted are due almost entirely to differential longevity of different species, emphasising the need for better data on this subject.

In common with other models, the main virtue of the transition matrix approach lies in the way in which it directs the investigator towards precise questions. Thus, in the example discussed, it is apparent that more data on seedling survivorship and tree longevity are required. The predictions obtained by the technique must be regarded only as possibilities, to be confirmed or rejected by alternative approaches. The modest increase predicted for the hardwoods at Russell forest is in agreement with Lloyd's (1971) conclusions, and seems reasonable in view of the selective logging of kauri in the past. Note also that forest basal area is generally well below that for mature kauri forest, implying that some changes in forest structure will occur while the current kauri crop matures.

The great utility of the transition matrix model, is that its parameters can be readily varied to model specified situations. Thus, it is a simple matter to examine the effects of increasing the longevity of kauri, or to model an increase in grazing pressure reducing the survivorship of kohekohe seedlings.

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