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MORTALITY FUNCTIONS FOR NORTH QUEENSLAND RAIN FORESTS

J. K. Vanclay

Unit of Forestry, Royal Veterinary and Agricultural University, Thorvaldsensvej 57 DK-1871, Frederiksberg, Denmark

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VANCLAY, J.K. 1991. Mortality functions for north Queensland rain forests. Subjective *a priori* grouping of tropical rain forest species for growth prediction may be unreliable because 1) there may be hundreds of species, many comparatively uncommon, the ecology of which may not be well known, 2) species within the same genus may have significantly different growth patterns, and 3) growth rate may not provide a reliable indication of mortality. Growth models can retain the species identity of each simulated tree, but some aggregation is necessary to enable estimation of increment and mortality functions. An objective approach aggregated 100 rain forest tree species into ten groups to enable efficient estimation of mortality functions. This strategy provided better predictions than a previous subjective grouping. Annual survival probabilities were predicted from tree size, stand density and site quality using a logistic equation fitted by maximum likelihood estimation. Additional species with insufficient data for analysis were subjectively assigned to these ten equations. Several strategies were investigated; the best approach for these species seemed to be to employ the equation which served the greatest number of species. The increment pattern did not provide a good basis for assigning such species to equations, and this suggests that different groupings may be necessary to model the various components of tree growth.

Key words: Mortality functions - rain forest - species grouping - prediction - survival

Introduction

The prediction of mortality is essential in growth and yield models for natural forests. It may be acceptable to assume negligible mortality in intensively managed industrial plantations, but such an assumption would be untenable in tropical rain forests.

Many methods for predicting mortality have been developed for even aged monospecific stands, but most are not suited for modelling rain forest stands. Stand density approaches (Reineke 1933, Yoda *et al.* 1963) indicate only the residual stocking and give no indication of survival of individuals. Individual tree competition approaches including threshold increment (Newnham 1964) and limiting competition methods (Mitchell 1969) fail to account for mortality not induced by competition (*e.g.* pests, diseases, cyclones). Hamilton (1974, 1980) proposed the use of logistic functions to predict survival rather than mortality, and Hamilton and Edwards (1976) presented a robust function which predicts survival from tree size and stand density.

A significant correlation often exists between diameter increment during the previous period and survival during the subsequent period, and several

Journal of Tropical Forest Science 4(1): 15 - 36

researchers have employed past diameter increment for predicting survival (Buchman 1979, Ek & Monserud 1979, Hann 1980, Buchman *et al.* 1983, Wan Razali 1988). However, observed diameter increments from the previous period are not generally available from inventory data or for long term predictions. Predicted rather than actual diameter increments could be used, but Monserud (1976) demonstrated that the observed and predicted diameter increments produce different parameter estimates. The correlation between predicted increment and survival is not as strong as for observed increments, and offers little advantage over the basic variables of tree size and stand density.

Tropical rain forests are characterized by large numbers of tree species with diverse growth habits. Although some of these species are widely distributed, others occur infrequently and data from which to develop growth models may be sparse. The rain forests of north Queensland are no exception. Of the 400 tree species recognized on a series of permanent sample plots, the most common 5% of tree species contribute 50% of the available growth data, while the least frequent 50% of species contribute a mere 5% of the data.

This poses unique problems for growth model development. It is impractical to develop mortality functions for each individual tree species, because of the large number of functions that would be required, and the paucity of data for many species inhibits the development of reliable relationships. Thus for efficient estimation of mortality functions, it is desirable to aggregate species into several groups. This reduces the number of functions required to a more manageable number, and avoids the requirement for specific equations for species with few data. Such groupings need not form the basis for growth modelling, as simulation models can retain the individual identity of all species (Vanclay & Preston 1989), but are necessary for the estimation of increment and mortality functions. Ideally, species should be grouped on a priori grounds, and tests performed to justify the validity of such groupings. This may be possible in temperate forests where there are few species and their ecology is well documented, but is unrealistic in tropical moist forests where there are hundreds of species, many of which are not well known. Taxonomy (family or genus) may not provide a good guide to growth habit (Swaine & Whitmore 1988, Vanclay 1991), and other methods based on size at maturity, successional status, *et cetera* may be rather subjective. Mortality may be dependent upon tree size and stand density, so grouping based on average mortality may be specific to the data set used. Not only is it difficult to resolve which species to combine, but it is not clear how many groups are required. Meldahl *et al.* (1985), Leech *et al.* (1991) and Vanclay (1991) have examined procedures to resolve these questions. Meldahl *et al.* (1985) argued that the grouping should reflect the dynamics of growth, and this could be best expressed through the coefficients of a regression equation on diameter increment. They attempted cluster analysis on these coefficients, but found that reasonable results could be obtained only when the regression analysis was constrained to a single explanatory variable. Their best results were obtained using the basal area of trees larger than the current tree as the explanatory variable. Cluster analysis was

weighted by the inverse of the significance level of slope parameter, and provided twenty clusters from 110 species-type equations. The number of data assigned to each cluster varied greatly, and the outcome was subjectively adjusted to provide the final grouping. The adequacy of final groups was tested by fitting a multiparameter linear function and examining the total (across clusters) residual sums of squares, on the assumption that a better grouping would result in a better fit. Whilst the method provide a grouping of similar elements, it did not provide a unique solution.

Leech *et al.* (1991) used a Behrens-Fisher analogue of Hotelling's T^2 to group 27 species for volume equation estimation. They used a polynomial equation to predict tree volume (V) from tree diameter (D) for tree i:

$$V_i = b_{oi} + b_{1i}D + b_{2i}D^2 + \ldots b_{ni}D^n$$

Then, representing the vector of coefficients as

$$u'_i = [b_{oi}, b_{1i}, b_{2i}, \ldots b_{ni}],$$

Hotelling's T^2 between two species i and j can be defined as

$$d_{ij}^2 = (u_i-u_j)'S^{-1}(u_i-u_j)$$

where S^{-1} is the combined covariance matrix of regression coefficients for species i and j. By calculating all possible combinations a symmetric matrix with zero diagonal elements can be formed. Principal coordinate analysis (Gower 1966) was used to group species on the basis of this matrix. Leech *et al.* (1991) concluded that the technique should only be used when the order of the polynomial and the sign of the highest term were the same for each of the two individual species equations. The method was also computationally intensive.

Vanclay (1991) devised an objective means to aggregate 237 species into 41 groups to enable efficient estimation of diameter increment functions for a growth model of tropical rain forest in north Queensland. His approach involved:

- Ranking species in order of increasing number of observations, with the miscellaneous group assigned lowest rank;
- Assigning the species of highest rank the founding species of group 1;
- For each species in decreasing order of rank, conducting pairwise F-tests with all founding species of higher rank. If the incoming species was significantly different ($p<0.01$) from all existing founding species, it became the founding species of a new group. Species not significantly different from all founding species remained ungrouped;
- After identifying all founding species, those species remaining ungrouped were compared, in order of rank, with all existing groups, and grouped with the most similar group. Similarity was determined as that grouping which led to the smallest increase in residual sum squares when the incoming species was amalgamated with the group. These

comparisons were made with the whole group, not just the founding species.

This approach overcomes many of the difficulties associated with the alternatives discussed above, and is computationally efficient. Instead of a comparison of all possible pairs, initial comparisons are made between species with many data, reliable parameter estimates and homogeneous variance. Species with few data are only later compared with one of these major groups. It also avoids Leech's *et al.* (1991) need to arbitrarily select a subset of the more numerous species to define the groups. This selection is by no means intuitive as in Vanclay's (1991) study the species ranked 186 with only 13 observations initiated a new group. This approach provided an objective basis for aggregating species, but there is, unfortunately, no guarantee that the outcome is optimal. However, it provided an efficient, objective and repeatable means to combine many species into a manageable number of groups for modelling the diameter increment of tropical rain forests.

The present study seeks to apply this approach to estimate mortality functions. The basis for grouping is the similarity of regression equations predicting mortality from tree size and stand density. Survival rates cannot be calculated for many species for which no deaths have been observed, and this study also examines strategies for assigning these species to equations.

Data

The present study concerns the tropical rain forests of northeast Queensland. These forests have been managed for conservation and timber production for more than 80 *y* (Just 1991), and prior to their recent inclusion on the World Heritage List, provided a sustained yield of veneer and sawlogs of 60,000 $m^3 y^1$ (Preston & Vanclay 1988). The Queensland Department of Forestry (1983) research programme provided a database of 250 permanent sample plots with a measurement history of up to 40 *y*. These plots sample virgin, logged and silviculturally treated forests.

Permanent sample plots range in size from 0.04 to 0.5 *ha*, and have been frequently remeasured (Vanclay 1990). All trees exceeding 10 *cm* dbh [diameter over bark at breast height (1.3 *m*) or above buttressing] were measured for diameter and assessed for merchantability.

Pairs of remeasurements were selected from the database to attain intervals between remeasurements of approximately five years, which did not span any logging or silvicultural activity. A data file was created for input to the statistical package GLIM (Payne 1986), and contained 70,871 observations of survival derived from 30,523 individual trees (some trees were measured more than twice). The file also contained records of tree species and dbh, and stand and site variables such as stand basal area, site quality and soil type. Site quality for each plot was estimated using Vanclay's (1989b) equation 13. Any plots for which the estimated site quality exceeded the range 0 to 10, or for which the variance of the estimated site quality exceeded 2, were rejected and omitted from the analysis. Reasonable estimates of site quality were obtained for 212 plots, which provided the present database.

Species identity is recorded in the database as a three character mnemonic (the Forest Research Branch code) for the great majority of species, but a few trees of indeterminate identity were identified only as miscellaneous. However, correct species identification is often difficult in these forests, and routine resource inventory procedures record only the standard trade name (SAA 1983), using a subset of the mnemonics known as the Harvesting and Marketing (H&M) code. Although the H&M code retains the correct identity of most species, several members of a genus may share a common code, as may members of more than one genus with similar timber characteristics. There are also additional non-commercial species simply labelled miscellaneous. As the present study was to develop mortality functions to project temporary inventory plots for yield prediction (Vanclay & Preston 1989), it was appropriate to use the H&M codes. Three hundred of the FRB codes in the data were converted into 238 H&M codes for analysis, and the remaining 100 with no H&M equivalent were grouped as miscellaneous.

The resulting data set contained many species with so few observations that meaningful analyses could not be attempted. Thus the data set was partitioned into two parts. The main data set to be used for establishing the mortality models comprised 64,446 observations on the 100 species for which more than five deaths had been recorded in the data. The auxillary data set contained the remainder (6,425) of the observations which would be used to allocate these less common 139 species to the established mortality functions.

Method

The probability that a tree survives may be modelled as a binary response using generalized linear regression fitted by maximum likelihood and adjusted to account for the varying periods of observation. The link function (Aitkin *et al.* 1989) implied is

$$\eta = \text{Log}\left[\frac{p^{1/t}}{1 + p^{1/t}}\right]$$

where n is the linear predictor, t is the number of years between remeasurements and p is the probability of any individual tree surviving for t years. This has the property of mapping p[0,1] onto $(-\infty, \infty)$. GLIM (Payne 1986) enables such generalized linear regression to be performed without explicitly transforming the data, and this enables individual tree observations to be used, with survival coded as a discrete (0,1) variable which has a binomial $b(\eta, p^{1/t})$ distribution.

Various prediction functions were investigated for several species with abundant data. Tree size was found to be the most important variable, and was accommodated in the model using diameter and relative status. Relative status was expressed as the relative position on the cumulative basal area distribution (*i.e.* the biggest tree in the stand has RS=0, and the smallest tree has RS=1). Survival of some species was significantly correlated with site quality and stand basal area, but preliminary trials indicated that the inclusion of these

variables in the model did not improve the final grouping. Although overtopping basal area (*i.e.* basal area per hectare of trees larger than the present tree) was found to be significant in predicting diameter increments (Vanclay 1989b, 1991), it was not significantly correlated with survival. Thus the basis for grouping was the logistic function:

$$P = [1 + e^{-\hat{Y}}]^{-1}$$

where $$\hat{Y} = \beta_o + \beta_1 \text{Log (DBH)} + \beta_2 \text{DBH} + \beta_3 \text{RS}^3 \quad (1)$$

and where P is the annual probability of survival, DBH is diameter (cm dbh), RS is relative status of the tree, calculated as overtopping basal area divided by the total plot basal area (thus 0 implies dominant trees, 1 implies suppressed trees), and β_i are parameters to be estimated. Inclusion of additional variables in the model at this stage provided an inferior grouping. This is consistent with findings by Meldahl *et al.* (1985) that simple models provided a better basis for aggregation.

The following two stage procedure was used to aggregate species into groups for the estimation of equation (1).

- Species were ranked by amount of data (in descending order by number of observed deaths, then by survivals);
- The species of highest rank became the founding species of group 1;
- For each species in decreasing order of rank, pairwise tests were made with one or more founding species of higher rank, using the likelihood ratio test statistic (Aitkin *et al.* 1989):

$$\lambda = -2 \{l(\beta_r) - l(\beta)\} \quad (2)$$

where $l(\beta)$ is the log likelihood and λ has an asymptotic χ^2 distribution if the omitted terms from the model actually have zero regression coefficients. If the incoming species was significantly different ($P<0.01$) from all existing founding species, it became the founding species of a new group. Species which were not significantly different from one or more founding species remained ungrouped at this stage. Thus the first stage identified a subset of species, the founding species, each of which was significantly different from all other species within the subset;

The second stage compared all remaining species (those not in the founding subset) with each of the groups formed by the founding species, and combined these with the most similar group. The ungrouped species were compared in order of rank, and similarity was determined as that grouping which led to the smallest decrease in likelihood when the incoming species was amalgamated with the group. These comparisons were made with the whole group, not just the founding species.

Stage 1 involves many pairwise tests; in the present study about 150 tests were required. Thus the probability of a type 1 error is quite high ($P=1-(1-0.01)^{150} \approx$

0.78).However, stage 1 merely identifies the founding species; the assignment of the remaining species to these groups is performed in stage 2. Meldahl *et al.* (1985) and Leech *et al.* (1991) avoided this large number of tests by using cluster analysis to aggregate species on the basis of individual species regression equations. Whilst this method avoids the problem of the large number of pairwise tests, it creates other problems, and both studies resorted to subjective assignment of species to complete their analyses.

Because some species exhibit non-homogeneous variance, stage 2 may result in the aggregation of species which differ significantly. Consider that a "remaining" species may exhibit a survival pattern similar to but significantly different from one founding species with small variance, whilst another founding species with a different survival pattern may not differ significantly because of its greater variance. Stage 2 will ignore the non-homogeneous variance and group "remaining" species with the most similar founding species irrespective of significance tests (which assume homogeneous variance). Whether or not this is an appropriate strategy is largely a question of personal preference. However, the method remains an objective and repeatable approach.

Following grouping, the inclusion of additional covariates was examined. Site quality (Vanclay 1989b) and stand basal area were significant for some groups, and were included. Thus the final model was:

$$P = [1 + e^{-(\beta_o+\beta_1 Log(DBH)+\beta_2 DBH+\beta_3 RS^3+\beta_4 SQ+\beta_5 BA+\beta_o Log(BA))}]^{-1} \qquad (3)$$

A non-linear response with basal area was detected for two groups. These groups indicated optimum survival at stand basal areas of 16 and 35 $m^2\ ha^1$ for groups 2 and 7 respectively, well within the range observed for the species group (5-55 and 5-86 $m^2\ ha^1$ respectively). For some individual species, stems assessed as unmerchantable had exhibited a lower survival. However, merchantability was found not to have a significant correlation with any of the grouped data. Logging and treatment seemed to have no effect on mortality in the residual stand. Soil type was also examined but contributed no improvement to the model. Some data were drawn from experiments which included planted trees which may not have occurred naturally at that site. However, including a variable to account for these planted stems contributed no significant improvement to the model. It appears that the survival of under-planted stems in the rain forest, after attaining 10 *cm* dbhob, is not greatly different to that of natural regeneration.

Results

Primary grouping

The first stage of the analysis identified ten species, each with significantly ($P<0.01$) different survival patterns, and the second stage aggregated the remaining species to form ten groups (Appendix). The group numbering reflects the amount of data available for the founding species of the group, and

in no way implies any silvicultural preference or average survival rate. The resulting groups reflect similarity of survival pattern (*viz* parameter estimates for Equation 1), and do not necessarily have any other ecological significance. Pioneer and gap colonizing species are not confined to a single group, but occur in several groups (*e.g. Acacia, Alphitonia, Dendrocnide* and *Omalanthus* occur in Groups 1, 4, 5, 6 and 8). Group 1 contains both pioneer and shade tolerant (*e.g. Acacia* and *Myristica*) species. However, this analysis of mortality appeared to differentiate successional status more strongly than did a similar analysis of diameter increment patterns (Vanclay 1991). The analysis also indicates that taxonomy may not provide a rational basis for aggregating species for modelling. For example, *Polyscias murrayi* and *P. australiana* are founding species with significantly different survival patterns ($P<0.01$), and members of the *Elaeocarpus* genus are found in five different groups. Thus it should not be assumed that all species within a rain forest genus exhibit the same growth habits.

Table 1. Comparison with previous grouping

Number of	Deliberate grouping				Average mortality classes			
classes	Source	λ	d.f.	Sig.+	Size	λ	d.f.	Sig.+
1	One equation for all species	+1582	+30	***				
5	Previous groups (Vanclay 1989a)	+1226	+16	***	2.0%	+578	+18	***
10	This study	0	0		1.0%	+433	+3	***
41	Increment groups (Vanclay 1991)	+448	-95	-	0.2%	-89	-96	-
100	One equation for each species	-395	-183	***				

+ *** implies $P<0.001$, - indicates $P>0.5$

The identification of ten groups in stage 1 of the analysis indicates that the five groups previously employed (Vanclay 1989a) are insufficient, and that the 41 groups used for predicting diameter increment (Vanclay 1991) are unnecessary for predicting mortality. This result is confirmed by standard statistical tests. Table 1 reports test statistics (λ from Equation 2 with asymptotic χ^2 distribution) to allow comparisons of various aggregations. These statistics have been summarized by standardizing (Equation 2) the difference in log likelihood from fitting Equation 1 to the present (Appendix) and alternative groupings. Alternatives included five groups used in previous studies (QDF 1985, Vanclay 1989a), the 41 groups used to predict diameter increment (Vanclay 1991), and groups based on average mortality classes (Table 1). Such groups based on average mortality classes of standard width (*e.g.* 1% classes) provided better results than classes of variable width designed to accommodate equal numbers of species or equal amounts of data. Positive test statistics in Table 1 indicate that the present approach was superior to the alternative, whilst negative statistics indicate the alternative provided a better fit.

Table 1 indicates that the present grouping provides a better fit to the mortality data than do the previous five growth groups (QDF 1985,

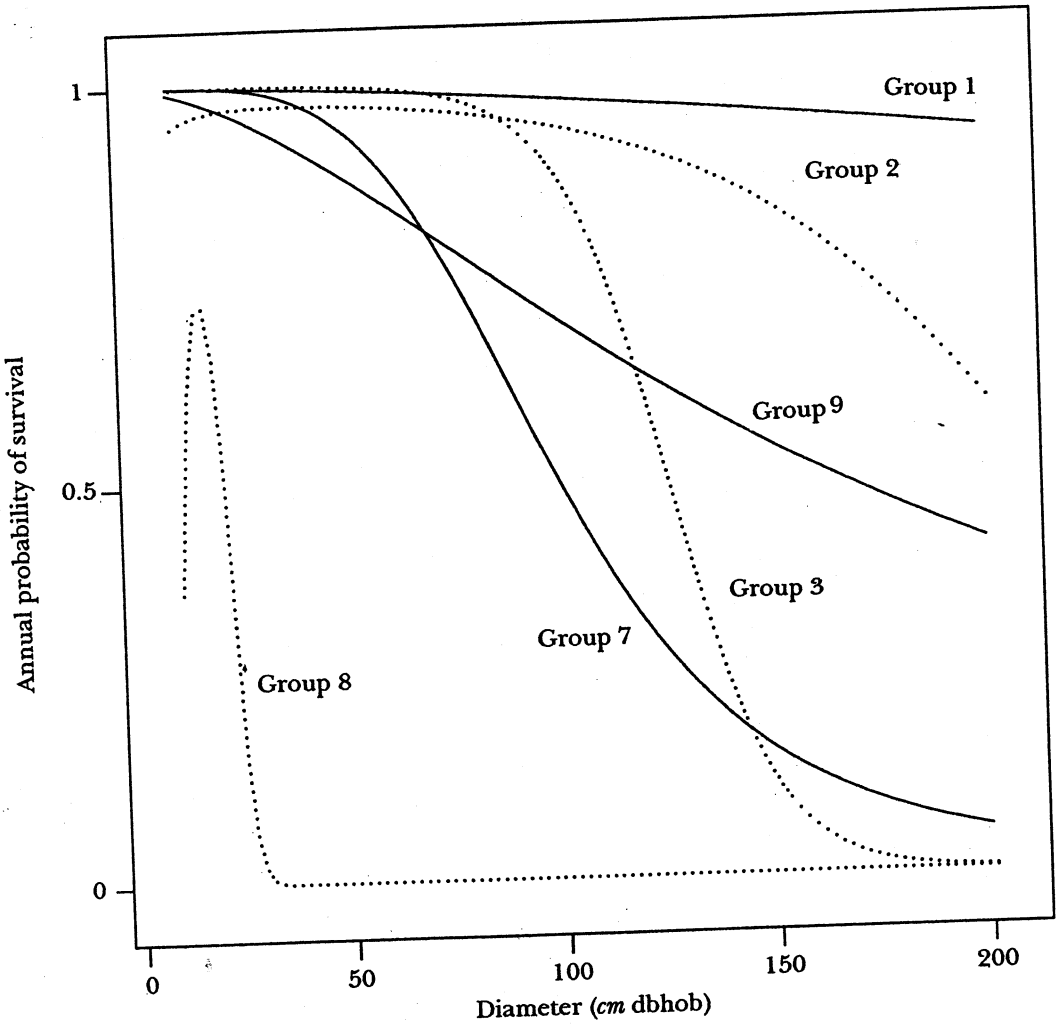

Figure 1. Predicted mortality patterns under typical conditions (RS = 0.5, SQ = 7, BA = 30)

Vanclay 1989a) and the 41 diameter increment groups (Vanclay 1991). Simple aggregations (with the same number of classes) based on average mortality classes performed better than these previous groupings. However, the present classification performed better than the equivalent ten classes based on average mortality, and the 41 average mortality classes were only slightly, but not significantly better than it ($P>0.6$). A comparison with the 100-class model (separate equation for each species) indicated that there is still significant ($P<0.001$) scope for improvement in the model (Equation 1) used for aggregating species.

Figure 1 shows the diversity of mortality patterns predicted for several groups, and Table 2 shows the parameter estimates for Equation 3. All the

parameters are significantly different from zero at P=0.1 or better (most were P<0.001). Five parameters had P>0.05 but were accepted as they were intercepts (β_0, Groups 3 & 4) or described a sensible response with tree size (β_1 & β_2, Groups 2 & 4). It should be noted that the relativities between groups may change for varying site quality and basal area. Survival of some groups is little influenced by site quality and/or basal area, while others are strongly influenced (Figure 2).

Table 2. Parameter estimates for Equation 3

Group	β_0	β_1 Log(D)	β_2D	β_3 RS³	β_4SQ	β_5 BA	β_6 Log(BA)
1	+11.057***	-1.6727***		-2.8801***	+0.1043		
2	- 5.416**	+1.1869	-0.03212		+0.5069***	-0.09605	+1.542**
3	+2.544	+2.1172***	-0.09916***	-3.1237***			
4	+2.015	+2.1021***	-0.02150		+0.0591**		-1.051***
5	+3.621***	+0.6072*	-0.03959**				
6	+4.145***	-0.2236*			+0.0915***		
7	+14.721***	-4.1476***		-4.4682***		-0.05643**	+1.949**
8	-28.648*	+20.7598***	-1.37472**		+0.5304**		-2.843*
9	+8.922***	-1.7353***		-0.5932*			
10	+10.848***	-1.2651***		-2.4067***			

Significance levels *** P<0.001, ** P<0.01, and * P<0.05

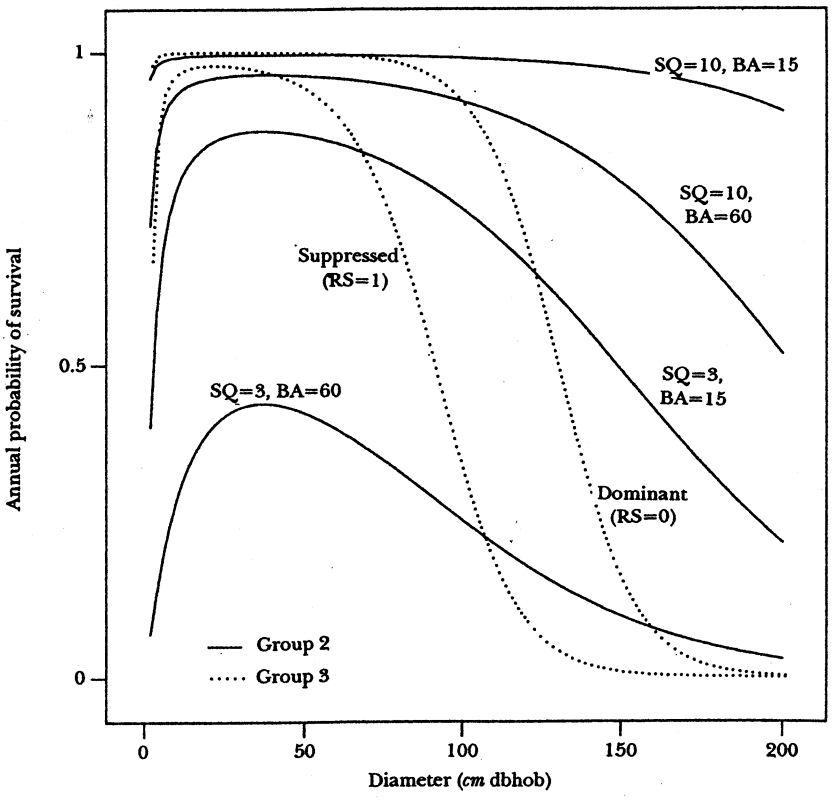

Figure 2. Effect of basal area, site quality and relative dominance on mortality

Secondary grouping

Many species found in these rain forests may not occur on permanent sample plots in sufficient numbers to enable reasonable estimates of mortality to be made, even where the forests are well sampled. These species must still be assigned to equations if the growth of the forest is to be simulated, and some objective procedure for assigning these to prediction equations is desirable. Taxonomy does not provide a reliable guide, and the ecological characteristics of these less common species may not be established. Possible approaches for allocating these species to equations include combining:

- on the basis of its increment group;
- on the basis of its average mortality;
- with the group containing the greatest number of species;
- with the group containing the miscellaneous species; or
- subjectively according to appearance, habit or taxonomy.

Table 3. Mortality pattern and size at maturity

Mortality group	Number of species classified by size at maturity (Stocker 1983)			Total number of species
	Small (<40 *cm* dbh)	Intermediate (40-100 *cm* dbh)	Large (>100 *cm* dbh)	
1	5	24	4	33
5	19	15	0	34
10	2	8	7	17
Others	11	15	0	26
Total species	37	62	11	110*

* based on specific name, not common name, for species classified by Stocker (Appendix)

Where some data are available, an objective approach may be used, but in the absence of any data a subjective decision may need to be made. It has already been shown that taxonomy is not a reliable guide. Neither is the average mortality rate observed in the data of much help (Table 1, Appendix). However, size at maturity (Stocker 1983) does provide a useful indication of the survival pattern (Appendix). Table 3 illustrates how the majority of trees attaining a small size at maturity belong to Group 5, the majority of those attaining intermediate sizes belong to Group 1, and the majority of those attaining large sizes belong to Group 10. Standard statistical tests indicate that this correspondence is highly significant ($\chi^2_6 = 167.1, P<0.001$). Stocker (1983) also indicated the relative growth rates for these species, but no correlation between growth rate and mortality group was evident.

Table 4 illustrates the correspondence between the increment groups (Vanclay 1991) and the mortality groups. The 100 species employed in the preceeding analysis belong to 41 different increment groups, and were grouped into ten mortality groups. If increment group provided a perfect indication of mortality pattern, Table 4 would have only 41 entries. Conversely, the worst case would exhibit 100 entries, and random allocation would result in 83 entries (Table 5). In fact, it contains 84 entries which suggests that incre-

ment pattern provides no indication of the appropriate mortality group. The standard v^2 test cannot be applied to sparse data such as Table 4, but a comparison of the the observed and expected frequency of numbers of species per cell indicates that the difference is not significant and that the diameter increment group provides no guide to the relevant mortality group (Table 5).

Table 4. Comparison between increment and mortality groups

Increment group	Mortality group										Indicated group
	1	2	3	4	5	6	7	8	9	10	
1	MSW										1
2	QMP										1
3			RBN								3
4										QSA	10
5				EVD	CLO		TRQ			NSO	5
6	2					DUB					1
7	2								YEV		1
8	3			STP						STS	1
9	2									KRS	1
10	BRO				CRL						1
11										RDT	10
12					2					2	5
13							LAN				7
14					TST						5
15					NRA					STO	5
16	RLL		KRQ	WES	2		WAL		WHZ		5
17					BOC				IBS		5
18	BSL										1
19					SBS				NKP	5	
20						PKA					6
21	EUQ	WBS		CNN							1
22	HMW							NBD			1
23	SBN					BUA					1
24					2						5
25	2				NLL					CHS	1
26	2				IML					BRC	1
27	ILL				PPW					SSW	1
28					MWN					2	10
29	JHR				WAS						1
30			GPN		BLO				FCH		5
31					COW	MIS					5
32	2										1
33				SST						4	
34	MCB						2				7
35				RAP	BSH				BRY		5
36				RCD		SLQ					4
37					2	BSW	ALB				5
38	CMH				CLL						1
39						ROO					6
40					HAL	TBH					5
41	2			BRP					TYW		1
Total species in group	29	1	3	8	24	8	6	1	6	14	
Average mortality	0.031	0.256	0.038	0.057	0.051	0.076	0.055	0.639	0.089	0.019	

Table 5. Correspondence between increment and mortality groupings

Entries per cell	Expected number	Observed number	Test statistic (χ^2)	Probability
0	327	326	0.00	
1	69	69	0.00	
2+	14	15	0.07	
Sum	410	410	0.07	0.09

This result is somewhat contrary to intuition, as it seems reasonable that growth pattern as represented by diameter increment equations might also indicate something of the mortality pattern. So the possibility of some correspondence will be further investigated. The mortality group indicated by the diameter increment pattern is given in Table 4, and has been calculated as the mortality group most frequently represented within each increment group. Since all species from increment groups 1, 2, 18 and 32 were found to "belong" to mortality group 1, it is reasonable to argue that any other species in these increment groups may also be best assigned to mortality group 1. For increment group 8, three of the five species also belonged to a single group. In contrast, the four species in increment group 5 belonged to four different mortality groups (4, 5, 7 & 10), giving little guide to the most appropriate mortality group. In this case, mortality group 5 may be the best alternative, as 24 of the 100 species examined belonged to that group.

Table 6. Alternative for grouping species with few data

Strategy	139 species (0-4 deaths observed)		83 species (1-4 deaths observed)	
	Predicted deaths	Error sum squares	Predicted deaths	Error sum squares
Optimal (each spp in best group)	202.0	164.5	186.0	164.2
All in Group 1 (most species)	216.0	178.7	183.6	177.4
Implied by size at maturity	253.7	182.4	213.8	180.1
Implied by increment (Table 4)	280.0	189.8	232.3	185.8
All in Group 6 (contains miscellaneous)	523.1	199.9	445.8	192.9
Assigned by average mortality	295.0	210.7	278.3	210.4
Actual deaths	182		182	

Table 6 examines several alternatives for grouping the 139 species with fewer than five observed deaths. The optimal approach was to assign each species to the equation which provided the best prediction (some species were assigned each group, but most species were assigned to Groups 1, 4, 5 and 10), but this approach is not possible for species for which no survival data are available. The increment pattern provided an inferior indication of the appropriate mortality group. A better strategy was to assign all additional species to Group 1, the group containing the greatest number of species. Grouping these species with Group 6 which contains the miscellaneous (unnamed) species resulted in a worse fit, and is not recommended. This also re-enforces the need to correctly identify all trees, even the less common,

rather than to use codes for miscellaneous, *et cetera*. Unless there is some strong reason to assign these species otherwise, it may be most appropriate to group species with no or few growth data to the group which contains the bulk of the species.

Table 7. Comparison of raw data, fitted model and previous model

Size class (*cm* dbh)	Development data			Species with 0-4 deaths			All data			
	Total trees	Observed dead	Predicted dead	Total trees	Observed dead	Predicted dead	Total trees	Observed dead	Predicted dead	Vanclay (1989a)
10-14	24769	1227	1241.1	2340	79	85.0	27109	1306	1326.1	1057.2
15-19	12016	582	550.0	1090	26	35.3	13106	608	585.3	454.6
20-24	7618	286	302.0	654	15	18.4	8272	301	320.4	259.1
25-29	5376	191	195.5	464	9	13.6	5840	200	209.1	166.6
30-34	4116	129	138.2	399	15	11.3	4515	144	149.4	121.5
35-39	3045	100	94.9	280	9	7.9	3325	109	102.8	83.8
40-44	2149	63	70.4	258	7	7.2	2407	70	77.6	58.7
45-49	1675	58	54.4	206	4	5.3	1881	62	59.8	44.5
50-54	1234	47	40.8	165	5	3.4	1399	52	44.3	31.0
55-59	775	37	28.6	153	3	3.4	928	40	32.1	20.3
60-64	484	17	18.3	98	3	2.4	582	20	20.6	12.7
65-69	375	21	13.4	75	1	1.5	450	22	14.9	9.4
70-79	385	12	15.0	106	2	3.1	491	14	18.0	9.4
80-99	222	6	11.8	76	1	2.4	298	7	14.2	5.8
100-119	65	3	3.4	30	1	1.1	95	4	4.6	2.6
120+	65	2	3.8	18	2	0.8	83	4	4.6	15.4
Total	64369	2781	2781.0	6412	182	202.0	70781	2963	2983.8	2352.5

Discussion

Table 7 and Figure 3 compare the observed and predicted deaths. This comparison is based on simple average mortality, taking no account of time period of observation. Good predictions are evident for the smaller tree sizes (to 65 *cm* dbh), but predictions overestimate mortality for larger tree sizes (over 65 *cm* dbh). This discrepancy is due to the assignment of "minor" species with fewer than five observed deaths, which are overestimated (9 deaths predicted, 7 actual), whilst the fitted data provided a good prediction (47 predicted, 44 actual).

Predictions from equations previously developed (Vanclay 1989) underestimate mortality across all sizes except for the largest size class, with an overall bias of about 20%. This may be attributed to the different species composition of the data from which the models were derived. Although the models are similar, the previous model was based on data drawn from only 37 plots, whereas the current model incorporates 212 plots and includes the most recent plot remeasures. The previous database comprised seven virgin and 30 logged plots which had received little disturbance and contained few pioneer and gap colonizing species. The short lived pioneer species *Omalanthus* was absent from that database, and other short lived species were recorded on few plots only (QDF 1983). In contrast, the present database included plots which

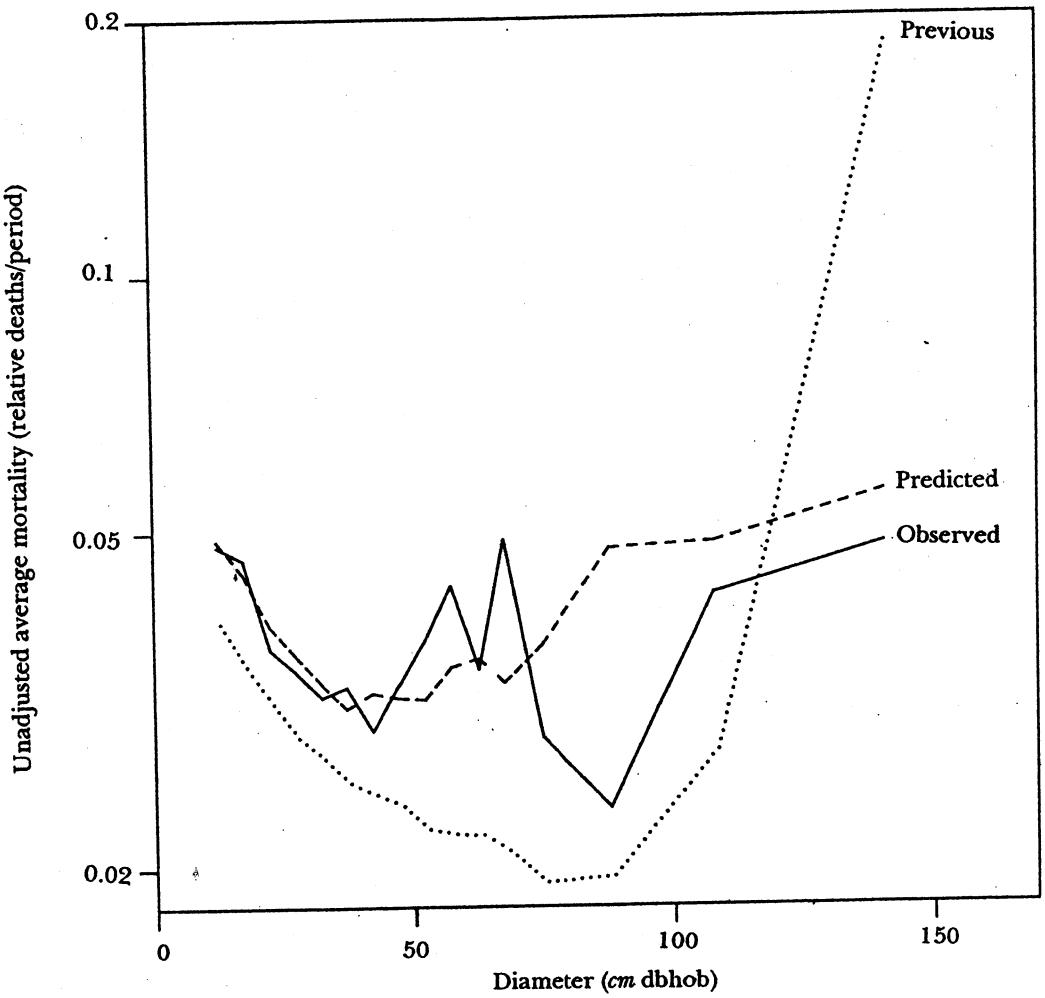

Figure 3. Comparison of observed and predicted mortality

have received a variety of silvicultural treatments, and include plots with low basal areas, considerable disturbance and more short lived and pioneer species.

Application

In many growth models, some aggregation of species is necessary to enable a parsimonious model and ensure sufficient data to enable calibration of diameter increment, mortality and other growth functions. Mos t such models use the same grouping for modelling all growth processes (*e.g.* Buchman 1979, Vanclay 1989a), but the present study suggests that this may be suboptimal, and that it may be preferable to form separate groups for the prediction of the various components.

For many applications in growth and yield modelling it is desirable to retain individual species identities (Vanclay 1989c, Vanclay & Preston 1989), but some amalgamation of species is necessary to provide reliable increment and mortality functions. Look-up tables can be used in growth models to enable any number of species to use a few diameter increment and mortality functions whilst retaining the individual species identities. The present study describes an approach for objectively grouping species for the efficient estimation of regression coefficients. It is not intended that species should be so grouped for all modelling processes, but that the grouping so identified will provide the necessary entries in a look-up table of equation identities for mortality prediction.

Conclusion

Taxonomy does not provide a reliable indication of the growth or survival patterns of forest trees, as trees within the same genus may exhibit significantly different parameters for prediction equations. An aggregation of tree species based on the diameter increment pattern was not significantly correlated with a grouping based on survival. An independent aggregation based on mortality data provided a better model.

Species for which few growth data are available may be best assigned to the group with the greatest number of species for the prediction of mortality. The group containing other "miscellaneous" species may not be the most appropriate for such species, and this emphasizes the need for correct identification of all species.

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Journal of Tropical Forest Science 4(1): 15 - 36

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Appendix - Species Groups

The following species groups reflect similarity of mortality trends, and do not necessarily have any other ecological significance. The group numbering reflects the amount of data available for the founding species of the group, and in no way implies any silvicultural preference or survival rate. In the interests of brevity, varieties and subspecies have been omitted from this list.

The species presented are those actually represented in the data. Some H & M codes are also applied to other species not present in the database.

Size at maturity is based on observations by Stocker (1983) on research plots, where L indicates large (exceeding 100 *cm* dbh), I indicates intermediate, and S indicates small (less than 40 *cm* dbh). For those species not classified by Stocker (1983), the author's own estimate of size at maturity is given in parentheses.

Increment group indicates the aggregation based on diameter increment pattern (Vanclay 1991).

Species assigned to each mortality group

H&M code	Botanical name	Common name	Size at maturity	Increment group	No of deaths	No of survivals	Average mortality
Group 1							
BSL	*Acacia aulacocarpa*	brown salwood	I	18	14	604	0.023
CMH	*Alangium villosum*	canary muskheart	I	38	6	165	0.035
HMW	*Alstonia muellerana*	hard milkwood	I	22	17	542	0.03
SBN	*Archidendron vaillantii*	salmon bean	S	23	5	159	0.03
BRT	*Argyrodendron trifoliolatum*	brown tulip oak	I	32	29	1032	0.027
JHR	*Backhousia bancroftii*	Johnstone River hardwood	L	29	9	245	0.035
BLW	*Beilschmiedia* sp. aff. *B. obtusifolia*	blush walnut	I	26	20	460	0.042
YWN	*Beilschmiedia bancroftii*	yellow walnut	L	25	16	412	0.037
BLW	*Beilschmiedia obtusifolia*	blush walnut	I	26	-	-	0.042
ILL	*Cryptocarya angulata*	ivory laurel	I	27	12	371	0.031
RLL	*Cryptocarya mackinnoniana*	rusty laurel	I	16	28	654	0.041
NSS	*Daphnandra repandula*	sassafras	I	6	51	1609	0.031
BRO	*Darlingia darlingiana*	brown silky oak	I	10	36	1030	0.034
NSS	*Doryphora aromatica*	sassafras	I	6	-	-	0.031
PMH	*Dysoxylum oppositifolium*	pink mahogany	I	9	5	111	0.043
EUQ	*Elaeocarpus eumundi*	Eumundi quandong	S	21	5	155	0.031
BLW	*Endiandra* sp. (AFO 1473, RFK 19)	blush walnut	I	26	-	-	0.042
NRW	*Endiandra cowleyana*	rose walnut	I	9	21	584	0.035
NRW	*Endiandra hypotephra*	rose walnut	S	9	-	-	0.035
NEV	*Euodia vitiflora*	northern evodia	I	7	6	187	0.031
QMP	*Flindersia brayleyana*	Queensland maple	L	2	142	4814	0.029
MSW*	*Flindersia pimenteliana*	maple silkwood	L	1	156	5226	0.029
BWD	*Litsea* sp. (AFO 390, RFK 599)	bollywood	I	7	40	1336	0.029
BWD	*Litsea bindoniana*	bollywood	S	7	-	-	0.029
BWD	*Litsea leefeana*	bollywood	I	7	-	-	0.029
NTG	*Myristica insipida*	nutmeg	I	6	12	357	3033
FSO	*Neorites kevediana*	fishtail silky oak	S	8	6	126	0.045
BLC	*Planchonella xerocarpa*	blush coondoo	I	26	5	127	0.038

Journal of Tropical Forest Science 4(1): 15 - 36

BLA	*Sloanea australis*	blush alder	I	41	20	348	0.054
WCB	*Sloanea langii*	white carabeen	I	32	12	373	0.031
GCB	*Sloanea macbrydei*	grey carabeen	I	8	14	331	0.041
SYN	*Synima cordierorum*	synima	(I)	41	8	187	0.041
RPS	*Syzygium endophloium*	rolypoly satinash	(L)	8	24	656	0.035
RSS	*Syzygium johnsonii*	rose satinash	I	25	8	215	0.036
RPS	*Waterhousea unipunctata*	rolypoly satinash	(L)	8	-	-	0.035
MCB	*Xanthophyllum octandrum*	Macintyre's boxwood	I	34	34	1000	0.033
Group 2							
WBS*	*Polyscias murrayi*	white basswood	S	21	154	448	0.256
Group 3							
RBN*	*Blepharocarya involucrigera*	rose butternut	I	3	146	3815	0.037
GPN	*Diospyros pentamera*	grey persimmon	S	30	6	61	0.09
KRQ	*Elaeocarpus bancroftii*	Kuranda quandong	I	16	6	131	0.044
KRQ	*Elaeocarpus johnsonii*	Kuranda quandong	(I)	16	-	-	0.044
Group 4							
CNN	*Aleurites moluccana*	candlenut	I	21	27	544	0.047
STP	*Canarium australianum*	scrub turpentine	(I)	8	6	143	0.04
STP	*Canarium muelleri*	scrub turpentine	I	8	-	-	0.04
SST	*Dendrocnide photinophylla*	shining-leaved stingingtree	I	33	23	423	0.052
EVD	*Euodia elleryana*	evodia	(I)	5	17	186	0.084
BRP	*Podocarpus elatus*	brown pine	(I)	41	7	161	0.042
BRP	*Podocarpus grayi*	brown pine	(I)	41	-	-	0.042
RAP	*Rapanea achradifolia*	rapanea	S	35	12	120	0.091
WES	*Syzygium wesa*	white Eungella satinash	(L)	16	7	82	0.079
RCD*	*Toona australis*	red cedar	I	36	71	1148	0.058
Group 5							
WAS	*Acronychia acronychioides*	white aspen	S	29	25	438	0.054
WAS	*Acronychia vestita*	white aspen	S	29	-	-	0.054
NRA	*Alphitonia whitei*	red ash	I	15	36	805	0.043
BLO	*Bleasdalea bleasdalei*	blush silky oak	S	30	19	470	0.039
BOC	*Brackenridgea nitida*	brown ochna	S	17	38	633	0.057
CLO	*Carnarvonia araliifolia*	Caledonian oak	I	5	16	469	0.033
PLB	*Chrysophyllum* sp. (AFO 520, RFK 3144)	plum boxwood	I	12	11	217	0.048
PPW	*Cinnamonum laubatii*	pepperwood	I	27	11	155	0.066
NSB	*Citronella smythii*	silky beech	S	24	21	600	0.034
CLL	*Cryptocarya* sp. aff. *C. cinnamomifolia*	cinnamon laurel	S	38	27	442	0.058
CRL	*Cryptocarya* sp. aff. *C. corrugata*	corduroy laurel	I	10	15	178	0.078
CLL	*Cryptocarya cinnamomifolia*	cinnamom laurel	I	38	-	-	0.058
CRL	*Cryptocarya corrugata*	corduroy laurel	I	10	-	-	0.078
NLL	*Cryptocarya hypoglauca*	northern laurel	S	25	30	513	0.055
NLL	*Cryptocarya hypospodia*	northern laurel	S	25	-	-	0.055
NTQ	*Elaeocarpus foveolatus*	northern quandong	I	37	15	185	0.075
NHQ	*Elaeocarpus sericopetalus*	hard quandong	I	37	16	214	0.07
MWN	*Endiandra* sp. aff. *E. muelleri*	rose walnut	I	28	7	183	0.037
COW	*Endiandra dichrophylla*	coach walnut	S	31	20	390	0.049
COW	*Endiandra glauca*	coach walnut	(S)	31	-	-	0.049
COW	*Endiandra montana*	coach walnut	S	31	-	-	0.049
COW	*Endiandra tooram*	coach walnut	S	31	-	-	0.049
TST	*Franciscodendron laurifolium*	tulip sterculia	(I)	14	34	849	0.039
PAL	*Gillbeea adenopetala*	pink alder	I	16	14	176	0.074
BFB	*Irvingbaileya australis*	buff beech	S	24	6	130	0.044

PTM	*Jagera discolor*	pink tamarind	I	16	28	385	0.068
PTM	*Jagera pseudorhus*	pink tamarind	(I)	16	-	-	0.068
KML*	*Mallotus mollissimus*	kamala	(S)	12	58	1018	0.054
KML	*Mallotus philippensis*	kamala	S	12	-	-	0.054
KML	*Mallotus polyadenos*	kamala	S	12	-	-	0.054
WAS	*Medicosma fareana*	white aspen	(S)	29	-	-	0.054
PLB	*Niemeyera chartacea*	plum boxwood	(I)	12	-	-	0.048
BLO	*Opisthiolepis heterophylla*	blush silky oak	I	30	-	-	0.039
SBS	*Polyscias elegans*	silver basswood	S	19	18	359	0.048
HAL	*Pullea stutzeri*	hard alder	I	40	10	118	0.078
IML	*Rhodamnia blairiana*	iron malletwood	S	26	6	135	0.043
IML	*Rhodomnia sessiliflora*	iron malletwood	S	26	-	-	0.043
KML	*Rockinghamia angustifolia*	kamala	S	12	-	-	0.054
PTM	*Sarcotoechia lanceolata*	pink tamarind	(I)	16	-	-	0.068
BSH	*Syzygium cormiflorum*	bumpy satinash	I	35	16	240	0.062
PTM	*Toechima erythrocarpum*	pink tamarind	S	16	-	-	0.068
Group 6							
PKA	*Alphitonia petriei*	pink ash	I	20	56	531	0.095
BUA*	*Apodytes brachystylis*	buff alder	S	23	58	520	0.1
BSW	*Cryptocarya oblata*	bolly silkwood	I	37	10	92	0.098
ROO	*Darlingia ferruginea*	rose silky oak	(I)	39	11	112	0.089
DUB	*Duboisia myoporoides*	duboisia	(S)	6	5	28	0.152
SLQ	*Elaeocarpus grandis*	silver quandong	(I)	36	44	277	0.137
ROO	*Placospermum coriaceum*	rose silky oak	I	39	-	-	0.089
TBH	*Tetrasynandra* sp. aff. *T. laxiflora*	tetra beech	(I)	40	9	123	0.068
TBH	*Tetrasynandra laxiflora*	tetra beech	I	40	-	-	0.068
TBH	*Tetrasynandra pubescens*	tetra beech	S	40	-	-	0.068
MIS	Miscellaneous	miscellaneous	(I)	31	352	4944	0.066
Group 7							
LAN*	*Acronychia acidula*	lemon aspen	S	13	46	915	0.048
PLM	*Archontophoenix alexandrae*	piccabeen palm	(S)	34	9	331	0.026
ROS	*Casuarina torulosa*	rose sheoak	(S)	34	6	15	0.286
TRQ	*Elaeocarpus lagiflorens*	tropical quandong	I	5	41	337	0.108
PLM	*Licuala ramsayi*	licuala palm	S	34	-	-	0.026
PLM	*Normanbya normanbyi*	black palm	S	34	-	-	0.026
WAL	*Polyosma alangiacea*	white alder	I	16	6	131	0.044
ALB	*Prunus turneriana*	almondbark	I	37	10	306	0.032
Group 8							
NBD*	*Omalanthus populifolius*	native bleedingheart	(S)	22	46	26	0.639
Group 9							
BRY	*Brombya platynema*	brombya	(S)	35	30	302	0.09
YEV	*Euodia bonwickii*	yellow evodia	I	7	15	165	0.083
YEV	*Euodia xanthoxyloides*	yellow evodia	S	7	-	-	0.083
IBS*	*Polyscias australiana*	ivory basswood	S	17	44	453	0.089
FCH	*Rhodomyrtus macrocarpa*	finger cherry	S	30	5	57	0.081
WHZ	*Symplocos cochinchinensis*	white hazelwood	(S)	16	14	105	0.118
TYW	*Zanthoxylum veneficum*	thorny yellowwood	I	41	8	105	0.071
Group 10							
NPK	*Agathis atropurpurea*	Queensland kauri pine	L	19	8	601	0.013
NKP	*Agathis microstachya*	Queensland kauri pine	(L)	19	-	-	0.013
NKP	*Agathis robusta*	Queensland kauri pine	L	19	-	-	0.013
RDT	*Argyrodendron* sp. (RFK 2139)	red tulip oak	(L)	11	27	977	0.027
RDT	*Argyrodendron* sp. aff. *A. peralatum*	red tulip oak	(L)	11	-	-	0.027

RDT	*Argyrodendron peralatum*	red tulip oak	L	11	-	-	0.027
BRC	*Canarium baileyanum*	brown cudgerie	I	26	11	404	0.027
NSO*	*Cardwellia sublimis*	northern silky oak	L	5	25	1920	0.013
BBN	*Castanospermum australe*	black bean	L	28	7	235	0.029
STS	*Ceratopetalum succirubrum*	satin sycamore	L	8	28	1204	0.023
FIG	*Ficus* spp.	figwood	(L)	28	8	263	0.03
FIG	*Ficus leptoclada*	figwood	S	28	-	-	0.03
FIG	*Ficus obliqua*	figwood	S	28	-	-	0.03
FIG	*Ficus watkinsiana*	figwood	L	28	-	-	0.03
SSW	*Flindersia acuminata*	silver silkwood	I	27	8	458	0.017
QSA	*Flindersia bourjotiana*	silver ash	I	4	65	3520	0.018
MRB	*Garcinia* sp. aff. *G. hunsteinii*	marblewood	I	12	6	400	0.015
SHT	*Halfordia scleroxyla*	saffronheart	I	12	6	250	0.023
STO	*Oreocallis wickhamii*	satin oak	I	15	5	225	0.022
KRS	*Syzygium kuranda*	Kuranda satinash	I	9	15	1072	0.014
CHS	*Syzygium luehmannii*	cherry satinash	I	25	5	273	0.018

* Founding species of group