

MODELLING GROWTH, RECRUITMENTS AND MORTALITY TO DESCRIBE AND SIMULATE DYNAMICS OF SUBTROPICAL RAINFORESTS FOLLOWING DIFFERENT LEVELS OF DISTURBANCE

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ABSTRACT. The capacity of rainforests to recover from logging disturbance is difficult to model due to the compounding interactions between long-term disturbance effects, natural dynamics, site characteristics and tree species regeneration strategies. The aim of this study was to develop a quantitative model using over three decades of data from stands subjected to various levels of disturbance ranging from natural, through increasing intensities of tree removal to intensive logging. Data for trees ≥ 10 cm diameter at 1.3 m above the ground (dbh) in subtropical rainforest of north-east New South Wales, Australia were used. Botanical identity of trees at species level, species-specific shade tolerance and size at maturity were used to classify 117 species into five groups. These groups include the emergent and shade tolerant main canopy species, shade tolerant mid canopy species, shade tolerant understorey species, moderate shade tolerant species, and shade intolerant tree species. Multilevel nonlinear regression was used to estimate growth, recruitment and mortality parameters, based on the assumption of variations in tree species performance at both the plot and tree levels. The species group, tree size and competition from larger trees accounted for most variation at the tree level. Significant stand level variables included topography (elevation, slope and aspect), stand basal area, and time since the disturbance. The final model is a classical matrix management-oriented model with an ecological basis and maximum size-dependent parameters of ingrowth and outgrowth. The model provides a tool to simulate stand performance after logging and to assess silvicultural prescriptions before they are applied.

Simulations with estimated parameters indicate that moderate harvesting (47% overstorey basal area (BA) removal) in a checkerboard of logged and unlogged patches (group selection) on a 120-year cycle could enable sustainable timber production without compromising the ecological integrity in these rainforests. This is due to reduced logging damage in group selection, which also released retained stems and facilitated recruitment of both shade tolerant and intolerant trees. Single-tree selection (35% BA removal) created small canopy gaps that resulted in low recruitment, a slight increase in the growth of retained stems and recovery time of 150 years. Intensive single-tree selection (50% BA removal) resulted in high logging damage that increased recovery time to 180 years. Intensive logging (65-80% BA removal) decreased the stem density and created larger canopy gaps allowing for high growth rates and recruitment of both shade tolerant and intolerant trees. However, few retained stems and high mortality of recruits, increased the recovery time to 180-220 years. Pre-harvest climber cutting coupled with poisoning of non-timber species followed by logging could allow harvesting on a 300-year cycle. Shorter logging cycles may lead to changes in species composition as well as in the forest structure.

Keywords: Growth categories, multinomial, two stage recruitment, silvicultural treatment.

1 INTRODUCTION

Rainforest is a potentially renewable resource with the resilient ability to recover from disturbance, through regeneration, succession and recovery processes, if there are no significant changes in the abiotic environment and sufficient and proximate seed sources remain (see Connell and Slatyer 1977, Summerbell 1991, Denslow 1995). The renewable characteristic is thus obvious, but its sustainability depends on the management applied to the forest (Favrichon 1998). This management is often based on timber production, which plays an important role in many national economies. Management for timber production may involve culling of non commercial species to improve the growth of retained trees destined as the future timber crop (de Graff 1986). Information about diameter distribution and species composition, which are often inferred through modelling studies (Shugart and West 1981), are fundamental for understanding rainforest resilience and dynamics.

While modelling of rainforest dynamics has progressed significantly in the recent past, quantitative studies of forest dynamics are often hindered by the heterogeneity and complexity of these forests and the lack of long-term experimental data (Vanclay 1990, 1991, 1994a, Alder 1995, 1996, Gourlet-Fleury and Houllier 2000). Heterogeneity and complexity are manifest in the species and life form richness of these forests, which may vary significantly in space and time. These forests are known to be highly diverse with a multitude of species, many of which are rare and represented by only a few individuals (Vanclay 1994b, Favrichon 1998, Sheil *et al.* 2006). These species may exhibit contrasting behaviours, life-cycles, and life-histories and hence different pathways of replacement after major disturbance (Noble and Slatyer 1980, Oldeman and Van Dik 1989, Gourlet-Fleury and Houllier 2000, Nebel *et al.* 2001, Smith *et al.* 2005).

Timber production from rainforests has ceased in much of the developed world, precipitating a shift in research focus and funding to other more active sectors of forestry. As a consequence many long-term experimental plots in rainforests have been neglected and do not receive the attention they warrant. Indeed, there are few experimental stations able to research the impact of forest management on rainforest growth (Favrichon 1998). Revisiting and reviving these neglected long-term experimental research sites can help to increase our understanding of rainforest dynamics. This is necessary to guide ecologically-sound management systems that provide harvests as well as biodiversity conservation (Sayer and Wegge 1992, Stork *et al.* 1997, Seydack 2000).

The data used in this study are heterogeneous, with variability contributed by the wide range of tree species, plot sizes (750 to 3648 m²), elevation (210 to 920 m above sea level), measurement intervals and logging regimes, the majority of which were not replicated. Furthermore, repeated observations on the same tree or plot are correlated because they contain a common contribution from the same tree or plot. Although the heterogeneity and correlations presented some challenges, the dataset remains one of the most comprehensive in existence. The aim of this study was to develop a growth model for uneven-aged mixed-species rainforest stands based on over three decades of data from stands subjected to various silvicultural regimes reflecting different logging intensities. The model is based on three components:

- (1) Botanical identity of trees was determined to species level, and the species-specific level of shade tolerance, regeneration strategy and size at maturity were used to classify trees into five groups of ecologically similar species (Alder and Synnott 1992).

- (2) The spatial heterogeneity of ecological conditions was represented using simple environmental information such as altitude, aspect, slope, topographical position in relation to the top and bottom of the ridge, and disturbance level (Vanclay 1989b, Vanclay 1992).

- (3) Tree and plot level variables were examined simultaneously to account for rainforest trees behaviour and performance in natural (unlogged) and logged stands during 35-44 years of regeneration and beyond.

The model uses the relatively stable state of the average unlogged stands (control) as a reference for sustainability, and simulates stand dynamics after silvicultural treatments reflective of various disturbance regimes (see Favrichon 1998).

2. STUDY AREA AND METHODS

2.1. The study area. The study area (previously State Forest managed under the New South Wales (NSW) Forestry Act of 1916, now as National Park under the National Parks and Wildlife Act of 1974) is located in north-east NSW, Australia. The area lies between latitudes 28° 30' and 28° 45' south, and between longitudes 152° 45' and 153° 30' east, and ranges in altitude from about 210 to 920 meters above sea level (masl). The vegetation is Complex Notophyll Vine forest, which is widely distributed in the region on moist sites with deep, fertile and well-drained red krasnozom soils or ferrosols (Isbell 1998).

Rainfall patterns show a pronounced maximum of about 160 mm per month in late summer (February and March) and a minimum of about 40 mm per month in late winter (August and September). Rainfall in the

area can be as high as 4000 mm on the Nightcap Ranges, close to one of the study sites (Big Scrub Flora Reserve). Average monthly temperature ranges from 3-19°C in winter and 15-31°C in summer and annual mean minimum and maximum are 10.3°C and 23.6°C respectively (NSW National Parks & Wildlife Services 2004).

2.1.1. The study sites and treatments. The study sites were determined by the distribution of 20 permanent sample plots (PSPs) and three temporary plots covering a total area of approximately six hectares among four former State Forests. In 1957 three plots each measuring approximately 30m × 25m were established within the Big Scrub Flora Reserve in the former Whian Whian State Forest (now part of Nightcap National Park). In 1965, six PSPs each measuring 50m × 40m were established in the former Toonumbar and Edinburgh Castle State Forests (now Toonumbar National Park). In the former Wiangaree State Forest (now Border Ranges National Park), an experiment involving eleven plots; three controls and eight silvicultural treatments was established in 1965. Plot sizes ranged from 1.42ha to 3.89ha with an average of two hectares. In each, a central experimental subplot measuring 60.4m × 60.4m with a 40m buffer strip was established. Burgess *et al.* (1975), Horne and Gwalter (1982), Pattemore and Kikkawa (1974) and Smith *et al.* (2005) provide detailed descriptions of the Border Ranges experiment, and offer analyses complementary to the present study. A brief summary of the plots and their treatments (percentage overstorey basal area (BA) removed) reveals:

- Control (no logging); three PSPs (Border Ranges National Park) and three temporary control plots (each measuring 40m × 50m in Toonumbar National Park).
- Single-tree (light) selection logging of merchantable stems (35% BA removal):
 - One PSP (Border Ranges National Park) logged in 1965 with a nominal 50% canopy cover retention.
 - Three PSPs (former Toonumbar State Forest) established in 1966 following routine single-tree selection logging in 1965.
 - Three PSPs (former Edinburgh Castle State) established in 1966 following routine single-tree selection logging in 1965.
- Moderate selection (47 - 50% BA removal), Border Ranges National Parks:
 - Queensland group selection (one PSP): climbers and undergrowth were cut and merchantable stems >61cm dbh (except seed trees) were logged in a checkerboard of logged and unlogged patches (group selection) in 1965 (47% BA removal) with enrichment planting where necessary. Further treatment to release regeneration was carried out in 1970.
 - NSW heavy tree selection logging (one PSP): similar to light logging, but more merchantable stems were removed in 1965 (50% BA removal).
- Repeated single-tree selection (three PSPs, Big Scrub Flora Reserve): area revisited more than once (51-65% estimated assuming 35% initial BA removal and less for revisits).
- Intensive logging (Border Ranges National Parks):
 - Sabah (Malaysia) clear cutting method (one PSP): presence of regeneration assessed in 1965 followed by over 70% BA removal. Regeneration release operation performed five years later (1970).
 - Nigeria pre-exploitation shelterwood (one PSP): vines were cut and stems with no timber value poisoned in 1965. Merchantable stems were logged 5/6 years later in 1970/71 (total BA removed 70%).
 - Trinidad & Guyana post-exploitation shelterwood (one PSP): vines were cut in 1965 and logging of all merchantable stems in 1966. Selective poisoning of remaining stems in 1966 formed Shelterwood (74% BA removal). Regeneration release operation performed 5 years later in 1970.
 - Democratic Republic of the Congo silvicultural improvement treatment (one PSP): Vines were cut in 1965, stems with no timber value poisoned in 1970 and merchantable stems were logged in 1975 (total BA removed 71%).
 - Logging with enrichment planting (one PSP): merchantable stems logged in 1965, shelterwood created by selective removal of remaining trees or trees with no timber value (78% BA removal) and enrichment planting with valuable faster growing species with regeneration progressively liberated over a 10-year period.

2.2. Data description. A total of 4067 individual trees ≥10cm dbh in 20 PSPs were identified to species, tagged and assessed between 1 and 12 times, giving a total of 19303 individual measurements. Forests NSW, Land Management and Technical Services Division (and its predecessors) collected most of the data during 1957, 1958, 1960, 1962, 1964, 1965/66, 1968, 1970-1973, 1975/76, 1980/81, 1987/88, 1995 (controls only) and

1999. All plots were reassessed in 2000/01 by the first and second authors. Quality controls in five of the PSPs revealed that 4 to 33% of the trees had been wrongly identified in earlier assessments (see Kariuki *et al.* 2006a). This necessitated a complete review of field identification to reconcile the previously collected data records with those collected during the 2000/01 census. Despite this comprehensive review and data reconciliation, about 0.4% of stems remained as unidentified mortality and 0.6% as missing data in trees that were previously assumed dead, and those missed on one or more occasions. Although the latter were identified to species and majority matched with previous dbh measurements using both species name and sequence of tagging, a few could not be reconciled because they had no tags or matching dbh records. These few were assumed to be ingrowth that had been missed during previous measurements. However, some of the larger trees could have been trees that survived poisoning treatments. In addition, ladder-based measurements revealed that many estimates of diameter above buttresses (dab) were inaccurate, especially amongst those made during the first three assessments. To calculate plot basal areas, anomalous or missing diameters were estimated by interpolating a constant rate of growth between reliable measurements. These estimates were combined with other data to calculate stand basal area and trees competition indices, but were not used in estimating parameters describing tree growth.

2.2.1. Environmental data. During the 2001 census, stand characteristics including slope (degrees), aspect (degrees) and relative topographic position in relation to the top (crest) and bottom of the ridge (without considering the distance) were assessed from the centre of the plot (see Kariuki *et al.* 2006b). Altitude was deduced from the topographic maps of the area and categorised into three classes; low (210-399), mid (400-699) and high (≥ 700 masl). The treatments were classified into five disturbance levels based on the percentage overstorey BA removed. The disturbance levels include the control (0% BA removal), single-tree selection logging (1-35%), moderate tree selection logging (36-50%), repeated single-tree selection (51-65%) and intensive logging (66-80%). In addition, both slope and aspect were used simultaneously to find the stand orientation in reference to north-south (northness) and east-west (eastness). Northness was estimated as sine (slope) multiplied by cosine (aspect) and eastness as sine (slope) multiplied by sine (aspect). This would theoretically assign a score of 1 to north and east facing cliffs, -1 to south and west facing cliffs, and 0 to flat ground.

2.2.2 Species groups. Taxonomic identity to species level, mature size, and species ecological affiliation in relation to level of shade tolerance were used in reducing the floristic diversity into five groups of ecologically similar species (Kooyman 1996, Favrichon 1998, Kohler *et al.* 2000).

- Group 1. This includes the few emergent tree species that are tall with crowns that extend beyond the main forest canopy at maturity (e.g. *Araucaria cunninghamii* Aiton ex D.Don, and *Ficus* species) plus the shade tolerant average to tall sized trees whose crowns form the main forest canopy such as *Heritiera trifoliolata* (F.Muell) Kosterm, *H. actinophylla* (Bailey) Kosterm and *Sloanea australis* (Benth) F.Muell.
- Group two comprises shade tolerant mid-canopy tree species with crowns that tend to form the middle strata e.g. *Acronychia pubescens* (F.M.Bailey), *Akania bidwillii* (Hogg) Mabb and *Zanthoxylum brachyacanthum* F.Muell).
- Group three comprises shade tolerant understorey tree species, mainly small trees and shrubs whose crowns are below those of other species mentioned above e.g. *Actephila lindleyi* (Steud.) Airy Shaw, *Denhamia celastroides* (F.Muell.) Jessup and *Wilkiea huegeliana* (Tul.) A.DC.
- Group four encompasses moderate shade tolerant and persistent tree species including *Toona ciliata* M.Roem, *Flindersia schottiana* F.Muell and *Cryptocarya triplinervis* R.Br.
- Group five includes shade intolerant tree species such as *Acacia melanoxylon* R.Br., *Dendrocnide excelsa* (Wedd.) Chew and *Polyscias elegans* (C.More and F.Muell.) Harms.

2.3. Data structure, manipulation and analysis. Negative diameter growth was observed in some trees during some growing periods. This may be attributed to measurements errors, senescence (Dickinson *et al.* 2000) or unfavourable growing condition such as drought (Dawkins 1956). Negative and zero diameter increments are common growth phenomena in rainforest trees and were not removed or corrected in this study.

We used periodical annual increments in diameter as the primary description of growth. This was calculated as $\Delta D = (D_1 - D_0) / (t_1 - t_0)$ where ΔD is annual periodic stem diameter growth (cm), D_1 and t_1 , and D_0 and t_0 are stem diameter and time (years) at the end, and at the beginning of the growing period respectively.

Due to some long growing periods (8 years or more from 1980), the tree average periodic annual diameter growth was assumed to have occurred at the middle of the growing period. Therefore, all new recruits had

their dbh estimated at the middle of the period preceding their initial assessments. Thus, growth, recruitment and mortality were assumed to be influenced by the stand conditions at the middle of each growing period. The annualised periodic increment was used as the basic time unit for our growth model. This was adequate to address the question of changes and facilitated estimation of models parameters in a resolution not provided by the available data. The resolution allowed us to represent temporal changes in other processes such as recruitment and mortality on an annual basis.

The annualised periodic diameter increment data were ordered into various hierarchical levels with individual periodic measurements in the lower level, through individual trees that were grouped into an upper hierarchy at stand level. Annual growth in tree diameter was then analysed using a single mean function for the subtropical rainforest population, assuming that the mean functions at any given level vary randomly around the population mean. Accordingly, the functions for annual growth responses within a given tree, and a tree within a stand were assumed to vary randomly around the mean function for the corresponding tree and stand (Goldstein 1995). Multilevel mixed modelling approach was used. This approach applied random parameters at each of the hierarchical levels (stand, tree and measurement levels) facilitating the analysis of growth at these levels simultaneously and permitting the autocorrelation associated with repeated measurement data (see Lappi and Bailey 1988). This method assists in understanding random parameters (random effects) and in determining whether a proportion of variation in these parameters is dependent on site characteristics at the plot level or tree variables at the tree and measurement levels (fixed effects). Fixed effects were attributed to explanatory variables given in Table 1.

Table 1. Explanatory variables used in fitting annual growth, recruitment and mortality models for subtropical rainforests in north-east NSW, Australia.

| | Variable | Description | Coding/use |
|--------------------|-------------------------|---|--|
| Tree level | Species groups | Emergent and shade tolerant main canopy trees (1) Shade tolerant mid canopy (2) Shade tolerant understorey trees (3) Moderate shade tolerant and persistent species (4) Shade intolerant pioneers (5) | Each species estimated separately in growth equation, but represented as binary coding (dummy variables; 1 and 0) in a single equation for recruitment and mortality |
| | Tree size (dbh) | Tree diameter at 1.3 m above ground level for growth and dbh-classes in mortality; (10-19.9), (20-39.9), (40-59.9) and (\geq 60cm) | Dbh (cm) centred at the species means (values minus the overall mean) for growth, and as dummy dbh-class variables for mortality estimation |
| Plot level | Tree competition | Basal area of trees greater than the subject tree | m ² ha ⁻¹ centred at stand mean |
| | Two largest dbh classes | Number of the last two largest dbh classes (40-59.9 and over 60cm) five and ten years previously. | Number used in recruitment estimation |
| | Altitude | Low (200-400), mid (401-700) and high altitude (over 700m) | Three categories using dummy variables |
| | Topography | Relative positions in respect to the crest and bottom of the ridge without consideration of distance; upper slope, mid slope, lower slope & creek/gully. | Four categories using dummy variables |
| | Disturbance levels | Percentage of the stand basal area removed (bar); Controls no logging (0%), single-tree selection (light) logging (1-35%), moderate selection (36-50%), repeated single-tree selection logging (51-65%) and intensive logging (66-80% bar). | Five categories using dummy variables to represent each category in a single equation |
| | Northness | North-south orientation | -1.0 – 1.0 centred at the stand mean with 0 for flat sites |
| | Eastness | East-west orientation | -1.0 – 1.0 centred at the stand mean with 0 for flat sites |
| | Stand basal area | Stand basal area (BA) per hectare | m ² ha ⁻¹ centred at stand mean |
| Time since logging | Inverse of time (years) | Number centred at the mean | |

Plot level variables included northness, eastness, altitude, topographic positions, basal area, disturbance levels and inverse of time since logging (logged stands). Variables at the tree level included species group while at measurement level there were tree diameter and basal area for all trees greater than the subject tree (Table 1). In order to incorporate both the quantities and qualitative data during parameter estimations, categorised data such as altitude, topographic positions and disturbance levels were expressed in binary form (1 and 0).

Data exploration ignored the hierarchical structure in the data and regressions were initially carried out using the SPSS package (SPSS Inc. 1999). This approach identified potentially important explanatory variables that provided the basis for more complex and sophisticated multilevel models using stepwise regression procedure with a hypothesis test at each iteration in the MLwiN software (Rasbash *et al.* 1999, Snijders and Bosker 1999). The criterion for adopting and retaining any explanatory variable in the models was based on two components; statistical significance and biological interpretation.

2.4. Growth estimation and model specifications. A log-transformation of the dependent variable (annual diameter growth) plus 0.5 (an offset to accommodate negative growth including measurement errors) was initially used as the response variable. The following equation was fitted using each species dataset in the multilevel mixed model in MLwiN 1.1 software (Rasbash *et al.* 1999, Snijders and Bosker 1999):

$$\ln(G_{ijk} + 0.5) = \beta_0 + \beta_1 \ln(D_{ijk}) + \beta_2 D_{ijk}^2 + \beta_3 E_{ijk} + \beta_4 C_{ijk} + \mu_k + \nu_{jk} + \varepsilon_{ijk} \quad (1)$$

where G_{ijk} is the i^{th} annual diameter growth of the j^{th} tree in the k^{th} stand, D is dbh, E a combined estimate for environmental factors, C is a measure of competition using variables such as BA, BAL and inverse of time since logging (Table 1), and μ and ν are the respective random effects of a stand, and a tree within a stand, and ε is the residual error term for annual diameter growth for a tree within a stand. Each of μ , ν , and ε has mean zero, and its own variance.

The -2log-likelihood statistic for the mixed model (1) was used to test significance of model fit (Rasbash *et al.* 1999). Using equation (1), the explained variance R^2 at the plot level ranged from 49 to 88% (Kariuki *et al.* 2006b). However, simulations done using the estimates derived from this equation were found to underestimate the annual growth when extrapolated beyond the range of the available data. This was attributed to this equation's tendency to underestimate the mean annual growth rates. Attempts to remove the influence of negative growth in trees through the use of longer growing period failed to improve the simulation results. Thus, a method where annual growth response was classified into five growth alternatives for each species group was considered, as described below.

2.4.1. Multilevel logistic regression. In general, tree growth varies in space and time depending on the prevailing climatic conditions and the growing stage of the subject trees (Dawkins 1956, Dickinson *et al.* 2000). Estimates of the mean annual diameter increment in rainforests vary from 0.1 to 0.5cm per year with the majority of trees tending towards the lower value (e.g. Horne and Gwalter 1982, Korning and Baslev 1994, Favrichon 1998, Finegan *et al.* 1999). Using these estimates as a guide, five annual growth categorical responses were considered; negative and nil (non-performers), below average (0.01-0.1), average (0.11-0.5), above average (0.51-1.0) and excellent growth (over 1.0cm yr⁻¹). Due to acute under-representation in excellent and above average growth categories in species groups 1 and 4, both growth categories were merged. For similar reasons, average, above average and excellent growth categories were merged in both species groups 2 and 3 (Table 2).

Diggle *et al.* (1994) advocates use of the logit for modelling correlated data. A logit is the natural log of the odds, and odds is the ratio of the probability of the annual growth category of interest to the probability of an annual growth category chosen as the reference. A multinomial logit model is an extension of binary logistic model to several response categories such as the defined growth alternatives. In this study the models were not interpreted in terms of odds ratios, but in terms of the estimated probabilities of response categories.

Suppose that in any given tree species group, y_{ijk} is the i^{th} categorical growth response in the j^{th} tree in the k^{th} plot and the growth response has m annual growth alternatives. We denote the probability of a tree exhibiting annual growth alternative s by $\pi^s = \Pr(y = s)$. We take the m^{th} growth response (i.e. the response with largest π) as a reference category. The multinomial logit model estimates a set of $m - 1$ equations contrasting each of the remaining growth categories with the reference category. The multinomial logistic regression model is:

$$\ln\left(\frac{\pi_{ijk}^s}{\pi_{ijk}^m}\right) = \beta_0^s + \beta_1^s x_{ijk}^1 + \dots + \beta_n^s x_{ijk}^n + \mu_k^s + \varepsilon_{ijk}^s \quad (2)$$

where x_{ijk}^r is the r^{th} explanatory variable associated with the i^{th} growth alternative in the j^{th} tree in k^{th} plot, μ_k^s is a plot- k specific random effect for contrast s , and ε_{ijk}^s is a random error term (assumed to be *iid*). The residual variance can be partitioned into components corresponding to each hierarchical level. The residual variance between plots (stands) is σ^2_{uk} and between individual trees within a given plot is $\sigma^2_{\varepsilon_{ijk}}$. The same explanatory variables appear in each of the $m - 1$ contrasts and hence, the random effects may be correlated across the contrasts, with a variance-covariance matrix Ω_v .

Table 2. Five growth categories describing annual diameter growth for various tree species groups in subtropical rainforests north-east NSW, Australia. First line in each cell shows the number of cases, second line percentages in parentheses and third line the annual growth rate in cm per year.

| Species | Non-performers; Nil growth (Category 1) | Below average growth; 0.01-0.10cm yr ⁻¹ (2) | Average growth 0.11-0.50cm yr ⁻¹ (3) | Above average growth 0.51-10.0cm yr ⁻¹ (4) | Excellent growth over 1.0cm yr ⁻¹ (5) | Total |
|--|---|--|---|---|--|---------------------------|
| Emergent and shade tolerant canopy trees (Group 1) | 2013 (16.0) 0.0 | 4993 (40.0) 0.096 | 3586 (29.0) 0.326 | 1863 (15.0) 0.860 | - | 12455 (100.0) 0.261 |
| Shade tolerant mid canopy trees (2) | 240 (18.6) 0.0 | 653 (50.5) 0.089 | 399 (30.9) 0.405 | - | - | 1292 (100.0) 0.170 |
| Shade tolerant understorey trees (3) | 162 (23.5) 0.0 | 377 (54.7) 0.077 | 150 (21.8) 0.379 | - | - | 689 (100.0) 0.125 |
| Moderate shade tolerant trees (4) | 21 (6.8) 0.0 | 161 (52.0) 0.098 | 95 (30.6) 0.301 | 33 (10.6) 1.019 | - | 310 (100.0) 0.250 |
| Shade intolerant trees (5), | 130 (11.8) 0.0 | 264 (23.9) 0.097 | 265 (23.9) 0.329 | 220 (19.9) 0.719 | 226 (20.5) 1.649 | 1105 (100.0) 0.582 |
| Total for all species groups | 2566 (16.2) 0.0 | 6448 (40.7) 0.094 | 4495 (28.4) 0.334 | 2116 (13.3) 0.848 | 226 (1.4) 1.649 | 15851 (100.0) 0.270 |

The estimated form of model (2) may be rearranged to give the estimated probability associated with the annual growth outcome of interest:

$$\hat{\pi}_{ijk}^s = \hat{\pi}_{ijk}^m \exp(\hat{\beta}_0^s + \hat{\beta}_1^s x_{ijk}^1 + \dots + \hat{\beta}_n^s x_{ijk}^n + \hat{\mu}_k^s) \quad (3)$$

Summing over $s = 1, \dots, m$, we obtain,

$$\begin{aligned} \sum_{s=1}^m \hat{\pi}_{ijk}^s &= \hat{\pi}_{ijk}^m + \sum_{s=1}^{m-1} \hat{\pi}_{ijk}^m \exp(\hat{\beta}_0^s + \hat{\beta}_1^s x_{ijk}^1 + \dots + \hat{\beta}_n^s x_{ijk}^n + \hat{\mu}_k^s) \equiv 1 \\ &= \hat{\pi}_{ijk}^m (1 + \sum_{s=1}^{m-1} \hat{\pi}_{ijk}^m \exp(\hat{\beta}_0^s + \hat{\beta}_1^s x_{ijk}^1 + \dots + \hat{\beta}_n^s x_{ijk}^n + \hat{\mu}_k^s)) \end{aligned} \quad (4)$$

Hence,

$$\hat{\pi}_{ijk}^m = \frac{1}{1 + \sum_{s=1}^{m-1} \hat{\pi}_{ijk}^m \exp(\hat{\beta}_0^s + \hat{\beta}_1^s x_{ijk}^1 + \dots + \hat{\beta}_n^s x_{ijk}^n + \hat{\mu}_k^s)} \quad (5)$$

so that from (4) and (5) we obtain:

$$\hat{\pi}_{ijk}^s = \frac{\exp(\hat{\beta}_0^s + \hat{\beta}_1^s x_{ijk}^1 + \dots + \hat{\beta}_n^s x_{ijk}^n + \hat{\mu}_k^s)}{1 + \sum_{s=1}^{m-1} \hat{\pi}_{ijk}^m \exp(\hat{\beta}_0^s + \hat{\beta}_1^s x_{ijk}^1 + \dots + \hat{\beta}_n^s x_{ijk}^n + \hat{\mu}_k^s)} \quad (6)$$

During the logistic regressions centering of variables was necessary to avoid numerical problems (Franklin *et al.* 2001). A two-level hierarchical and unordered categorical response multinomial logit model was fitted to each species group dataset using the MLwiN 2.0 package. To assess whether the model distribution assumption is adequate in terms of the growth model datasets, extra-multinomial variation was tested by allowing the variance-covariance of the error terms to be different from the unit matrix, but constraining error variances, and covariances (correlations) to be equal (Yang *et al.* 2001).

2.4.2. Significance tests and model fit. A likelihood ratio test is typically used to determine the necessity of fixed and random effects for mixed effects models that assume the lowest error (ϵ_{ijk}) is normally distributed (Pinheiro and Bates 2000). While the likelihood ratio test is applicable to equation (1), it cannot be applied in multilevel binary (e.g. recruitment and mortality) or multinomial response (growth) models that use quasi-likelihood to estimate the parameter, because there is no true likelihood available (Rice 2001, Rose *et al.* 2006). Therefore, inference was restricted to the use of parameter estimates and the log likelihood values are not reported. The significance of independent variables was tested using simple Wald tests (Rasbash *et al.* 1999).

2.5. Recruitment and mortality. Binary logistic regression has statistical efficiency to analyse correlated data from repeated measurements in both mortality and recruitment (Liang and Zeger 1986, Gordon 2004). This method deals with correlated data when the data are binary (i.e., alive or dead) or counts (numbers of recruited trees), that are modelled assuming Binomial and Poisson distributions (Agresti 1990, Gordon 2004).

2.5.1 Recruitment. Tree stems were categorised arbitrarily into four dbh classes; (10-19.9, 20-39.9, 40-59.9 and ≥ 60 cm) where recruitment was assumed to occur into the smallest diameter class only. The problems of different plot sizes and time intervals between measurements were addressed by creating an offset variable using time interval (years) multiplied by the plot area (hectares). Recruitment could not be fitted satisfactorily with a Poisson or Binomial model, because of the sporadic and over-dispersed nature of recruitment. A two stage approach provided a more satisfactory solution (Vanclay 1994a).

In the first stage we fitted a 2-level hierarchical logistic regression model using presence and absence of recruitment between measurements and all species groups in a single equation to estimate the annual probability of recruitment. In this stage, the following multilevel (2-level) mixed Binomial regression model with log-link was used to estimate the annual probability of recruitment.

$$\ln(\pi^{rec}_{ij}) = \beta_0 + \beta_1 ssp2_{ij} + \dots + \beta_4 ssp5_{ij} + \beta_5 disturb_{ij} + \mu_j \quad (7)$$

where π^{rec}_{ij} is the estimated overall probability of recruitment for the j^{th} plot in the i^{th} year of measurement, β_0 is a constant that also account for the probability of recruitment in the controls as well as for species group 1, $ssp2_{ij}$ represent species group 2, $ssp5_{ij}$ group 5 and etc., $disturb_{ij}$ is the i^{th} level of disturbance in the j^{th} plot and μ_j is a plot specific random effect (assumed to follow a normal distribution with mean zero and variance σ^2_{u0}). The residual variance can be partitioned into components corresponding to level 2 ($\sigma^2_{u_j}$) and level 1 ($\sigma^2_{e_{ij}}$) variances.

Using the number of recruits when recruitment occurred, the following 2-level Poisson regression model was then used to determine the number of trees recruited in one hectare annually.

$$\ln(regen_{ij}) = \beta_0 + \beta_1 spp_{ij} + \dots + \beta_4 spp_{ij} + \beta_5 dbhcl_{ij}^5 + \beta_6 dbhcl_{ij}^{10} + \mu_j \quad (8)$$

where $regen_{ij}$ is the overall number of trees recruited in one hectare in a year whenever recruitment occurred in the j^{th} plot, $dbhcl_{ij}^5$ the number of stems in the i^{th} dbh-class in the j^{th} plot five years previously, $dbhcl_{ij}^{10}$ the number of stems in i^{th} dbh-class in the j^{th} plot ten years previously and other terms as defined above.

2.5.2. Mortality estimation. To cater for the death of trees not identified to species, large trees (≥ 60 cm dbh) were ascribed to species groups 1 and 4, while small tree (< 60 cm dbh) were ascribed to all 5 species groups depending on the densities of the species group. The issue of sparse data was addressed through the use the four dbh classes defined above and combining all species in the same equation. Mortality was estimated as an annualised rate assuming the first-order kinetics in accordance with the methods given by Sheil (1995)

$$M = 1 - [1 - (N_0 - N_1) / N_0]^{1/t} \quad (9)$$

where M is the annual mortality, N_0 and N_1 are population counts at the beginning and at the end of each growth period, the term $(N_0 - N_1)/N_0$ is the proportion of the population that died during a given growth period and t is the time interval. Assuming variations at the measurement period and plot level, the probability of death in various dbh classes was investigated through a 2-level hierarchical model using the following logistic regression in MLwiN software.

$$\ln(\pi_{ij}^m) = \beta_0 + \beta_1 spp_{ij} + \dots + \beta_4 spp_{ij} + \beta_5 disturb_{ij} + \beta_6 dbhcl_{ij} + \mu_j \quad (10)$$

where π_{ij}^m is the overall annual probability of death for a tree in the j^{th} plot in the i^{th} year, $dbhcl_{ij}$ is the i^{th} dbh-class in the j^{th} plot and other terms as defined above.

3 SIMULATION OF FOREST DYNAMICS

Parameter estimates of recruitment, growth and mortality were used together with the initial plot records to simulate and predict changes in both logged and unlogged stands using the Simile visual modelling environment version 3.2 (Muetzelfeldt and Massheder 2003). Implementing the rainforest dynamics in the Simile modelling environment sought to at least visually verify whether our predicted estimates are compatible with field observations of rainforest dynamics. We expected that the control plots should exhibit small changes with no significant effects (relatively stable behaviour), and that treated plots should depict initial changes with significant effects, but they should with time converge towards the relatively stable state as the stands recover from logging. The relatively stable state should be independent of the initial stand conditions and the overall changes in relation to species density and composition, stand BA, and tree diameter distribution are expected to remain relatively unchanged over time (see Buongiorno and Michie 1980).

3.1. Growth simulations. There was evidence that the data used in the models development were collected when the stand BA and species richness in both the control and logged sites were generally increasing (Kariuki *et al.* 2006b). While this is expected in the logged plots, it was unexpected in the unlogged controls. Increase in these two parameters in the unlogged control may indicate some previous natural disturbance where large trees died creating room for more stems and species. However, over a large area or in the scale of decades, it is realistic to expect convergence to a relatively stable state in both stand BA and species richness (see Favrichon 1998).

In order to obtain satisfactory long-term forest behaviour and to account for logging disturbance effects, it was necessary to introduce some regulation of the parameters in the models (see Favrichon 1998). These conditions were introduced by defining the expected relationship between parameters and some measured variables. For example, tree growth in general starts slowly, increases to a maximum, and then decreases towards nil growth as the tree tends toward its maximum diameter. Thus, the choice of parameter to be regulated at the tree level (diameter) and stand level (ingrowth and outgrowth), and the choice of regulatory variables (growth categories) affect not only the simulated growth of trees, but also the behaviour of the model as a whole. For instance, these conditions could affect the attainment of the maximum tree diameter and the speed of convergence to either maximum tree diameter or oscillation about the stable state (see Favrichon 1998).

A modifier function for tree growth was introduced during simulation as a residual of the observed tree diameter in relation to the maximum diameter recorded or defined for each species group (1-dbh/dbh_{max}). If the observed dbh_{max} for a tree species group was within a given dbh class (see Table 1), the end point of that class was chosen as the dbh_{max}. This modifier function allows increasingly smaller proportions of trees to grow at the highest designated growth alternative for a species group and when the maximum diameter is attained, the trees become non-performers.

3.2. Recruitment and mortality simulations. Recruitment and mortality data are censored because observations can only be made if a recruit survived until the next assessment. Any tree that was recruited (reached 10cm dbh) and died wholly within a single growing period (evident as dead, standing stems measuring about 10cm) was not included in this study. However, as stand becomes more crowded, mortality should increase particularly in species group 5, and recruitment should decrease in all species groups. Because these scenarios were not captured in our data, it was necessary to introduce them as modifier

functions during simulation, especially beyond the range of the available data, so that the model, at least in theory reproduces what the forest is doing now and in the simulated future.

Other scenarios were constrained by carefully choosing the transformations of variables used in the model. For instance, time since logging was included in the models as the inverse of $(1 + \text{time since logging})$ to ensure that the effect of disturbance decreases with time since logging (Vanclay 1990). In addition, when the overall trees density reaches 75% that of an average unlogged stand the mortality of non-performers and the simulated overall mortality in species group 5 was increased by 3%. When the overall trees density exceeded that observed in the control, the simulated mortality of non-performers in species groups 1 - 4 was also increased by 3%.

The probabilities associated with growth and mortality of a tree should sum to unity (1). For a living tree in the i^{th} diameter class at time t , there are several possibilities such that, at time $t + 1$ the tree may:

- stay alive in the i^{th} class and not grow at all (non-performer),
- stay alive in the i^{th} class and grow slowly (accumulating the probability of moving to class $i+1$; that is, grow slowly every year increasing the chance to move into the next larger class),
- stay alive and grow into the $(i+1)^{\text{th}}$ class (either through a single annual growth increment, or accumulated probabilities),
- die (either through a single probability of mortality, or through accumulated probability).

The following conceptual-model diagram for the rainforest dynamics shows the relationship between recruitment, growth and mortality models on one hand and stand environmental variables and the characteristics of simulated rainforest stand on the other (Figure 1).

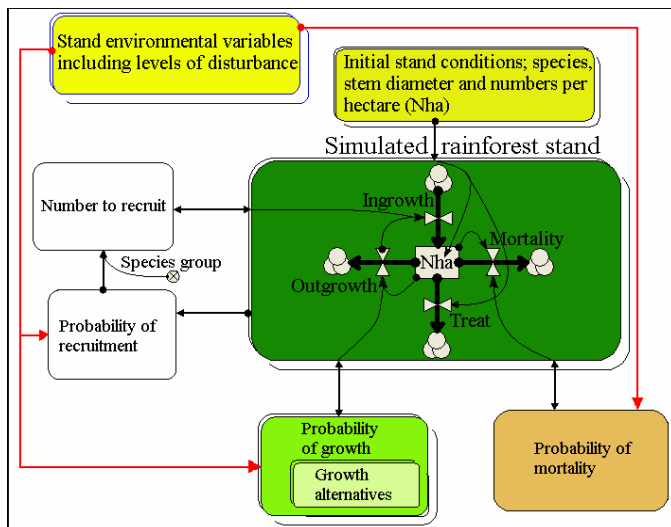


Figure 1. Conceptual-model diagram for a simulated subtropical rainforest stand in north-east NSW, Australia representing the rainforest dynamics showing the effects of the environmental variables and that of the simulated rainforest stand on the probabilities of recruitment, growth and mortality, and the number of recruited trees. The treat represents the silvicultural treatments where tree harvesting was carried out after the initial stand assessment and identifies the trees that were removed. Species group identifies the relevant tree species group to be recruited into the simulated stand.

The model was designed to have a time step of one year and size classes of 2cm dbh. This choice of time step and size class ensured that no tree could be expected to move more than one dbh class in a year.

Recruits were introduced as a vector R_{t+1} whenever recruitment occurred. $R_{t+1} = (\text{regen}_{1,t+1}, \text{regen}_{2,t+1}, \dots, \text{regen}_{5,t+1})$ where *regen* represents the number of recruits entering the smallest diameter class (10-19cm) and subscripts 1, 2, ..., 5 represent the species groups and $t + 1$ is a one year time step. However, it was necessary to introduce a negative density dependence modifier during long simulations beyond the range of the data (Wright 2002). This modifier constrained recruitment so that it was set to decreased to zero when the simulated density of a species group exceeded the observed average in unlogged stand by 10%.

A series of simulations were initiated using the initial plot records and were compared with subsequent plot reassessments, and with other records of the dynamics of these forests. A further series of simulations were carried out to simulate a range of logging regimes and investigate the time of recovery from logging disturbance for BA, diameter distribution, species groups and overall species density.

4 RESULTS

4.1. Growth models. Statistical analysis revealed that all explanatory variables (Table 1) were significantly associated with diameter growth of subtropical rainforest trees. However, due to correlation among these variables, when used simultaneously some were rendered non-significant and removed from the final models. Summary statistics associated with growth parameter estimates are given in Appendix I. The relationship between the coefficients produced by the multinomial logit and the odds ratios produced by logistic [logits are natural log of odds, and probabilities are $\text{odds}/(1+\text{odds})$] was used to interpret the effects of variables on the associated probabilities in terms of discrete change in the probabilities (see Agresti 1990).

4.1.1 Discrete changes in the probabilities. To interpret the growth model coefficients, the discrete changes in the probabilities associated with changing explanatory variables from 0 to 1 for dummies and plus or minus one standard deviation from the mean for continuous variables, keeping all the other variables at their sample means were calculated (see Agresti 1990). For example, at the means, the probabilities for an average tree in species group 1 to exhibit no growth, below average growth, average growth or above average growth alternatives over the study period were, 24.7, 21.0, 26.7 and 27.6% respectively (Table 3). When an average tree is subjected to high competition (mean plus one standard deviation of basal area greater than the subject tree; BAL), the probability of non-performers jumps from 24.7 to 57.5%, and while that of below average growth remained unchanged at 21.0%, that of both average and above average growth alternatives decreased from 26.7 to 12.3 and 27.6 to 9.2% respectively (Table 3).

The results of this study show the importance of competition from large trees for the shade tolerant and moderate shade tolerant species (groups 1 to 4) where trees are more likely to grow slowly under high competition. For example, under high competition, the probabilities for species groups not to grow and to grow at below average rates increased from their means with values ranging from 93 to 188.6% while the probability of average and above average growth alternatives decreased with values ranging from 42 to 85.6%.

However, when an average shade intolerant tree species (group 5) is subjected to high competition, the respective probability of above average and excellence growth is increased by 42 and 4%, while the probabilities of lower growth rates decreased with values ranging from 9 to 31% from their means. This indicates that where stand conditions are not limiting to high growth rates for example, in canopy openings and in logged sites, species group 5 grow without suffering any competition, but where conditions are limiting an increase in competition decreases growth performance.

When the stand basal area (BA) is increased from the means to mean plus one standard deviation (keeping everything else at the means), the probability of shade tolerant trees species (groups 1 to 4) not to grow decreases with values ranging from 62% to 86%, but increases more than 500% in the case of the shade intolerant species. Increase in the likelihood for the shade intolerant species to exhibit slow growth alternatives or to become non-performers in a stand with high basal area indicates the failure of this species to perform well in unlogged stands without canopy opening where trees are poorly illuminated. Decreased likelihood for the shade tolerant species to become non-performer with increase in stand BA indicates these species ability to grow under shade.

Increase in diameter of an average rainforest trees was associated with a decreased likelihood for the tree to grow at faster growth rates and increased likelihood not to grow, except in the case of the shade tolerant understorey. Diameter increase of an average shade tolerant understorey was associated with an increased likelihood for this species group to exhibit maximum growth alternative and decreased likelihood to grow at below average alternatives. This indicates vigorous regeneration and establishment of the shade tolerant understorey species below the forest canopy.

Our results show that different variables are important in different species groups. In general, BAL, stand BA and tree size showed the decreasing order of importance for these variables in the growth of rainforests trees. Other variables showed further decreasing effects with northness showing the least effect (Table 3).

Comparing the covariance matrix between different growth alternatives revealed that the random effects were correlated across annual tree growth alternatives in species groups 1, 2 and 3, but not in species group 4 or 5 (Appendix 1). This indicates that there were unobserved plot level factors that affected more than one annual growth alternatives in species groups 1, 2 and 3.

Table 3. Discrete change in the probabilities of growth categories in response to changing explanatory variables, for various species groups of subtropical rainforest trees in north-east NSW, Australia. The species groups (in parenthesis) include emergent and shade tolerant canopy trees (group 1), shade tolerant mid canopy trees (2), shade tolerant understorey trees (3), moderate shade tolerant and persistent trees (4) and shade tolerant pioneers (5).

| | Non-performers (%) | Below average growth (%) | Average growth (%) | Above average growth (%) | Excellent growth (%) |
|---|--|--|--|--|------------------------------|
| Actual | 16.2 (1) 18.6 (2) 23.5 (3) 6.8 (4) 11.8 (5) | 40.0 (1) 50.5 (2) 54.7 (3) 51.9 (4) 23.9 (5) | 28.8 (1) 30.9 (2) 21.8 (3) 30.6 (4) 24.0 (5) | 15.0 (1) - - 10.6 (4) 19.9 (5) | - - - - 20.5 (5) |
| At the means | 24.7 (1) 22.9 (2) 33.0 (3) 21.6 (4) 14.3 (5) | 21.0 (1) 25.0 (2) 29.3 (3) 20.8(4) 15.8(5) | 26.7 (1) 52.1 (2) 37.7 (3) 21.9 (4) 15.3 (5) | 27.6 (1) - - 35.7 (4) 24.0 (5) | - - - - 30.1 (5) |
| Mean dbh plus one standard deviation | 28.5 (1) 29.4 (3) 23.1 (4) 26.1 (5) | 20.1 (1) 28.2 (3) 21.0 (4) 18.2 (5) | 24.4 (1) 42.4 (3) 18.1 (4) 21.6 (5) | 27.0 (1) - 37.8 (4) 17.7 (5) | - - - 16.3 (5) |
| Mean basal area plus one standard deviation | 8.5 (1) 3.1 (2) 9.9 (3) 8.1 (4) 94.8 (5) | 14.7 (1) 8.5 (2) 19.2 (3) 13.3 (4) 5.1 (5) | 33.6 (1) 88.4 (2) 70.9 (3) 35.2 (4) 0.07 (5) | 43.1 (1) - - 43.4 (4) 0.04 (5) | - - - - 0.0 (5) |
| Mean basal area greater than tree (BAL) plus one standard deviation | 57.5 (1) 66.1 (2) 63.7 (3) 45.7 (4) 9.8 (5) | 21.0 (1) 26.4 (2) 26.3 (3) 26.1 (4) 14.4 (5) | 12.3 (1) 7.5 (2) 10.1 (3) 7.5 (4) 10.5 (5) | 9.2 (1) - - 20.7 (4) 34.1 (5) | - - - - 31.2 (5) |
| Mean Northness plus one standard deviation | 25.4 (1) 24.7 (2) 34.4 (3) 14.5 (5) | 21.0 (1) 25.4 (2) 28.9 (3) 16.2 (5) | 26.1 (1) 49.9.0 (2) 36.7 (3) 15.8 (5) | 27.5 (1) - - 24.7 (5) | - - - 28.8 (5) |
| Single-tree selection logging | 21.4 (1) 23.5 (4) 12.9 (5) | 20.1 (1) 22.0 (4) 14.9 (5) | 32.4 (1) 19.9 (4) 15.0 (5) | 25.3 (1) 34.6 (4) 20.5 (5) | - - 36.7 (5) |
| Moderate to high selection logging | 24.4 (1) 20.4 (4) 13.2 (5) | 21.4 (1) 20.6 (4) 15.2 (5) | 29.0 (1) 30.0 (4) 14.8 (5) | 25.1 (1) 29.1 (4) 22.4 (5) | - - 34.3 (5) |
| Intensive logging | 23.3 (1) 23.2 (4) 13.8 (5) | 21.3 (1) 21.2 (4) 14.3 (5) | 30.4 (1) 26.4 (4) 13.2 (5) | 25.0 (1) 29.2 (4) 20.5 (5) | - - 38.2 (5) |
| Mean 1/(time since logging) minus one standard deviation | 23.9 (1) 14.3 (5) | 19.9 (1) 15.8 (5) | 24.6 (1) 15.2 (5) | 31.5 (1) 23.9 (5) | - 30.7 (5) |
| Mean 1/(time since logging) plus one standard deviation | 24.1 (1) 14.3 (5) | 20.2 (1) 15.8 (5) | 25.2 (1) 15.2 (5) | 30.5 (1) 23.9 (5) | - 30.7 (5) |
| Mid altitude | 28.8 (1) 28.0 (2) | 21.5 (1) 27.1 (2) | 22.8 (1) 44.9 (2) | 26.9 (1) - | - - |
| High altitude | 25.7 (1) 29.0 (2) | 22.1 (1) 28.3 (2) | 26.5 (1) 42.6 (2) | 25.6 (1) - | - - |
| Topographic position; | | | | | |
| Mid slope | 14.8 (5) | 16.2 (5) | 14.5 (5) | 26.8 (5) | 27.6 (5) |
| Lower slope | 14.4 (5) | 16.0 (5) | 15.0 (5) | 24.6 (5) | 30.0 (5) |
| Creek/gully | 14.2(5) | 16.5 (5) | 16.5 (5) | 26.8 (5) | 26.1 (5) |

4.2. Probability of tree species recruitment. The summary statistics for the mean annual probability of recruitment in various tree species groups are presented in Table 4. The fixed part of the model shows that species group 5 was significantly more likely to recruit in any given year compared to other species groups, but species group 1. Conversely, species groups 2, 3 and 4 in order of decreasing magnitude were significantly less likely to recruit in any given year compared to species group 1. The probability of recruitment appears to increase in concert with disturbance level from natural through increasing levels of tree selection to intensive logging. While the effect of single-tree selection logging was not significant, there was evidence of increased likelihood for recruitment in moderate tree selection ($P = 0.065$) and both repeated single-tree selection and intensive logging showed significantly increasing likelihood of recruitment compared to natural disturbance. The random part of the model did not show any significant unexplained variations at the plot level, but at the measurement level. Testing for extra binomial variation by allowing the parameter of level-1 variance to be estimated from the data, revealed extra-binomial variations associated with over-dispersion in the recruitment data.

Table 4. Parameter estimates, their standard errors and Wald tests of significance (* significant at the 95% confidence level) for the binary logistic model, estimating the probability of recruitment in various species groups in subtropical rainforests north-east NSW, Australia.

| Variable description | Coefficients (SE) | Z | P> Z |
|---|--------------------|-----------|--------|
| Fixed Part: | | | |
| Constant | -0.70094 (0.26937) | -2.60215* | 0.93% |
| Shade tolerant mid canopy trees (group 2) | -0.51673 (0.22306) | -2.31655* | 2.05% |
| Shade tolerant understorey trees (3) | -0.87978 (0.23503) | -3.74327* | 0.02% |
| Moderate shade tolerant and persistent trees (4) | -1.13412 (0.25954) | -4.36973* | 0% |
| Shade intolerant pioneer trees (5) | -0.38656 (0.23585) | -1.63901 | 10.12% |
| Single-tree selection (light) logging | 0.35704 (0.27794) | 1.28459 | 19.89% |
| Moderate to heavy trees selection logging | 0.71991 (0.38934) | 1.84905 | 6.45% |
| Repeated single-tree selection | 1.12329 (0.33701) | 3.33311* | 0.09% |
| Intensive logging | 1.32726 (0.30717) | 4.32093* | 0% |
| Random part (Residual variance): Level 2 (plots) $\sigma^2_{u_j}$ | 0.08017 (0.62840) | 0.12758 | 89.85% |
| Level 1 (period) $\sigma^2_{e_{ij}}$ | 3.81539 (0.21774) | 17.52269* | 0% |

4.2.1 The number of recruited trees. The summary statistics for the mean annual number of trees recruited in various species groups in one hectare are presented in Table 5. The fixed part of the model shows that the number of trees recruited annually in species group 5 is less, but not significantly so compared to species group 1. Conversely, the number of trees recruited in species groups 2, 3 and 4 (in order of decreasing magnitude) were significantly less than in species group 1. The density of stems ≥ 40 cm dbh five years previously had strong increasing effects, while the density of the same stems ten years previously had strong decreasing effects on the number of recruited trees. The random part of the model did not show any significant unexplained variation at the plot level, but at the measurement level. There was extra-Poisson variation associated with over-dispersion in the data.

Table 5. Parameter estimates, their standard errors and Wald tests of significance (* significant at the 95% confidence level.) for a Poisson regression model estimating the mean annual number of trees recruited in various species groups in a hectare of subtropical rainforests north-east NSW, Australia.

| Variable description | | Coefficients (SE) | Z | P> Z |
|--|--------------------------------------|--------------------|-----------|--------|
| Fixed Part | | | | |
| Constant | | 1.92926 (0.23900) | 8.07222* | 0% |
| Shade tolerant mid canopy trees (group 2) | | -0.65517 (0.22521) | -2.90915* | 0.36% |
| Shade tolerant understorey trees (3) | | -1.68796 (0.37861) | -4.45831* | 0% |
| Moderate shade tolerant and persistent trees (4) | | -2.21378 (0.61209) | -3.61676* | 0.03% |
| Shade intolerant pioneer trees (5) | | -0.22340 (0.20092) | -1.11189 | 26.62% |
| Density of trees 40-60cm dbh, 5 years previously | | 0.07769 (0.02515) | 3.08907* | 0.20% |
| Density of trees ≥60cm dbh 5, years previously | | 0.21203 (0.05904) | 3.59123* | 0.03% |
| Density of trees 40-60cm dbh, 10 yrs previously | | -0.09764 (0.03031) | 3.22138* | 0.13% |
| Density of trees ≥60cm dbh, 10 years previously | | -0.22088 (0.05481) | 4.02992 * | 0% |
| Random part | Level 2 (plots) $\sigma^2_{u_j}$ | 0.01109 (0.04278) | 0.25923 | 79.55% |
| (Residual variance) | Level 1 (period) $\sigma^2_{e_{ij}}$ | 11.00914 (1.17865) | 9.34047* | 0% |

4.3. Mortality. The summary statistics for the mean annual mortality rates during the study period are presented in Table 6. The fixed part of the model show that the mean annual probability of a tree dying was dependent on the tree species group, logging intensity and tree size. Trees in species groups 2, 3, 4 and 5 had higher rates of dying each year compared to species group 1. Compared to natural disturbance, intensive logging was associated with significant increase in the mean annual mortality rates, but increasing levels of tree selection logging were not significant. The results show that the probability of death decreases in concert with tree size. The random part of the model shows evidence of unexplained variations at the plot level (P = 0.064). In addition, there was extra-Binomial variation associated with under-dispersion exhibited by the data.

Table 6. Parameter estimates, their standard errors and Wald tests of significance (* significant at the 95% confidence level) for a binary logistic model, estimating the mean annual probability of a tree dying in various species groups in a subtropical rainforests north-east NSW, Australia.

| Variable description | | Coefficients (SE) | Z | P> Z |
|--|--------------------------------------|--------------------|------------|--------|
| Fixed Part | | | | |
| Constant | | -4.72969 (0.20705) | -22.84323* | 0% |
| Shade tolerant mid canopy trees (group 2) | | -1.49887 (0.15387) | -9.74115* | 0% |
| Shade tolerant understorey trees (3) | | -1.83714 (0.21082) | -8.71426* | 0% |
| Moderate shade tolerant and persistent trees (4) | | -3.27143 (0.51073) | -6.40540* | 0% |
| Shade intolerant pioneer trees (5) | | -0.42683 (0.11904) | -3.61598* | 0.03% |
| Single-tree selection (light) logging | | -0.05165 (0.25418) | -0.20320 | 83.90% |
| Moderate to heavy trees selection logging | | 0.47711 (0.31076) | 1.53530 | 12.47% |
| Repeated Single-tree selection logging | | -0.20318 (0.33754) | -0.60194 | 54.72% |
| Intensive logging | | 0.84216 (0.24187) | 3.48187* | 0.05% |
| DBH class (20-39cm) | | -0.20223 (0.10212) | -1.98032* | 4.77% |
| DBH class (40-59cm) | | -0.8998 (0.23878) | -3.76832* | 0.02% |
| DBH class (≥ 60cm) | | -1.09441 (0.39052) | -2.80244 * | 0.51% |
| Random part (Residual variance) | Level 2 (plots) $\sigma^2_{u_j}$ | 0.08060 (0.04353) | 1.85160 | 6.41% |
| | Level 1 (period) $\sigma^2_{e_{ij}}$ | 0.63620 (0.02391) | 26.60811* | 0.0% |

4.4. Rainforest dynamic simulations. The pre-logging assessments were not available for all plots and involved only trees ≥ 20cm dbh. Because this study involved trees ≥ 10cm dbh, the pre-logging records were not used, rather the controls status were considered appropriate benchmark for pre-logging stand characteristics. However, simulation results of the rainforest dynamics using each of the initial control measurement separately showed differences in stand BA and density with the former ranging from 53 to 73 m² ha⁻¹ and the latter from 470 to 580 stems ha⁻¹. This was associated with stochastic and small-scale effects in the rainforest due to different stand characteristics such as northness, topographic position and local natural disturbance (see e.g. Clough 1979, Golden 1979, Horne and Gwalter 1982). When the initial measurements in the three permanent control plots were merged and the average standardised on hectare basis, and then used to simulate the dynamics of an unlogged stand, tree size distribution and overall stem densities were decisive

stand characteristics that remained steady during the simulation. The basal area increased by 15% before converging at 60 m² ha⁻¹. This increase could be associated with the defined dbh_{max} (see section 3.1; Growth simulations) to which the model is sensitive and was higher than the recorded value in species groups 2-5. The 15% increase in BA was considered acceptable and measurements from the initial controls were combined with those of the three temporal control plots and standardized on a hectare basis to provide a reference with which to compare the logged sites. The initial basal area was used as the lower limit for a typical unlogged stand.

Figure 2 shows the predicted changes in stand BA, tree size distribution, stem density per species group and overall stem density in an average unlogged control and stands subjected to single-tree selection and selected stands subjected to single-tree selections (Border Ranges, Toonumbar and Edinburgh Castle sites), and repeated single-tree selections (Big Scrub Flora Reserve). The results show the deterministic evolution of an average unlogged stand and the effects of single-tree selection and repeated single-tree selection logging without the related stochastic nature of the forest dynamics during a simulation of 300 years. The initial BA in the logged stand at both the Border ranges and Edinburgh Castle sites was similar to that of an average control, but both the Toonumbar and the Big Scrub Flora Reserve sites had less. The recovery time (time the stand characteristics in a logged stand take to resemble that of an average unlogged control) for BA in both the Toonumbar and the Big Scrub Flora Reserve sites is estimated at 30 and 150 years respectively. The recovery time for the two larger dbh classes in Border Ranges, Edinburgh Castle, Toonumbar and Big Scrub Flora Reserve are 20, 30, 50 and 100 years respectively. The recovery time scale for the two smaller dbh classes is similar to that of stem densities at 90, 100, 150 and 180 years in Edinburgh Castle, Toonumbar, Border Ranges and Big Scrub Flora Reserve respectively.

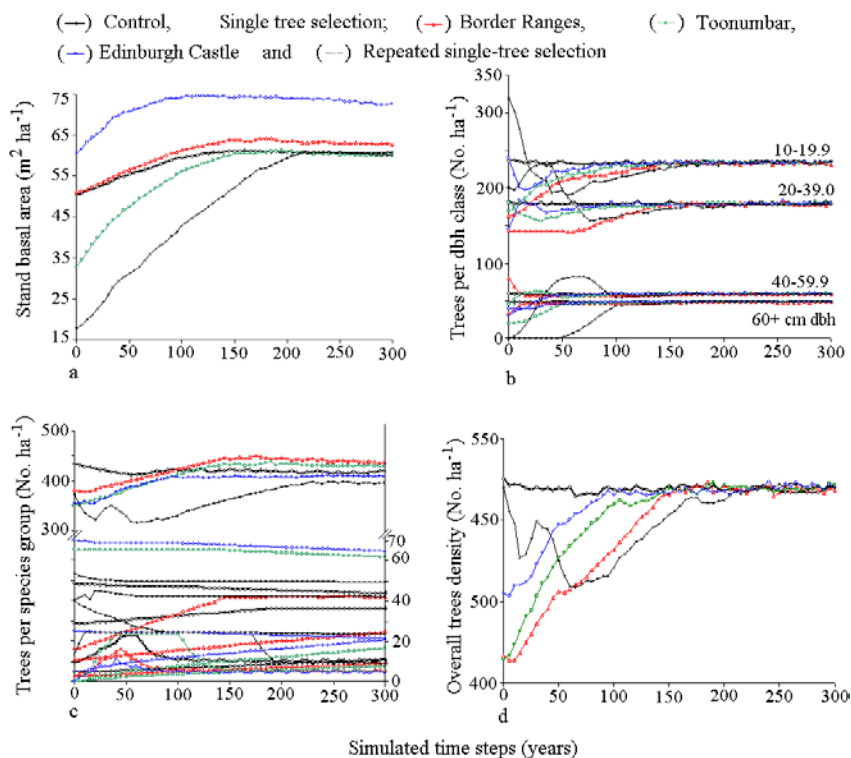


Figure 2. Predicted changes in an average unlogged control and stands subjected to single-tree selection, and repeated single-tree selection logging in subtropical rainforests north-east NSW, Australia. Stand basal area in m² ha⁻¹ (a), diameter distribution in various dbh-classes (b), stem density per species group (number of trees per species group) in order of abundance; emergent and shade tolerant main canopy, shade tolerant mid canopy (left hand side scale), shade tolerant understorey and moderate shade tolerant with shade intolerant pioneers alternating in abundance with one or more of the last 3 species groups, see scale on the right (c), and overall stem density (d).

Although selected stands in both the Edinburgh Castle and Toonumbar sites exhibited a rapid recovery following single-tree selection, other stands with similar treatment in the vicinity showed a recovery time of 100 to 240 years. This indicates that recovery following similar silvicultural treatment may vary from one

stand to another. This difference may be attributed to different site characteristics among other factors. However, the recovery times shown in Figure 2 for both Edinburgh Castle and Toonumbar stands should be interpreted cautiously as there was evidence of plot boundaries clearance. This plot boundary clearance and evidence of stumps near the boundaries could have implications for tree growth and stand dynamics within the main plot area, even though directional felling would have directed damage away from the plot.

Figure 3 illustrates the predicted changes in stands subjected to increasing levels of disturbance, including the unlogged control, Queensland group selection (Vanclay 1989a), NSW heavy tree selection, Sabah clear cutting and logging with enrichment planting. These series of simulations with increasing levels of disturbance show that stands converge to a relatively steady state after 80 to 220 years. For example, BA recovered to levels similar to that observed in the control plots after 80, 110, 115 and 120 years for Queensland group selection, heavy tree selection, logging with enrichment planting and Sabah clear cutting respectively. The recovery time for the two larger dbh classes in Queensland group selection is less than 100 years and there were no differences between the other treatments where recovery is achieved in less than 150 years. The recovery time for the two smaller dbh classes were longer in comparison with larger dbh classes ranging from 120 years (Queensland group selection) through 180 years (both heavy selection and Sabah clear cutting) to 220 years (logging with enrichment planting).

(—) Unlogged control, (—) Queensland group selection, (—) Nsw heavy selection,
 (—) Sabsh clear cutting method and (—) Logging with enrichment planting

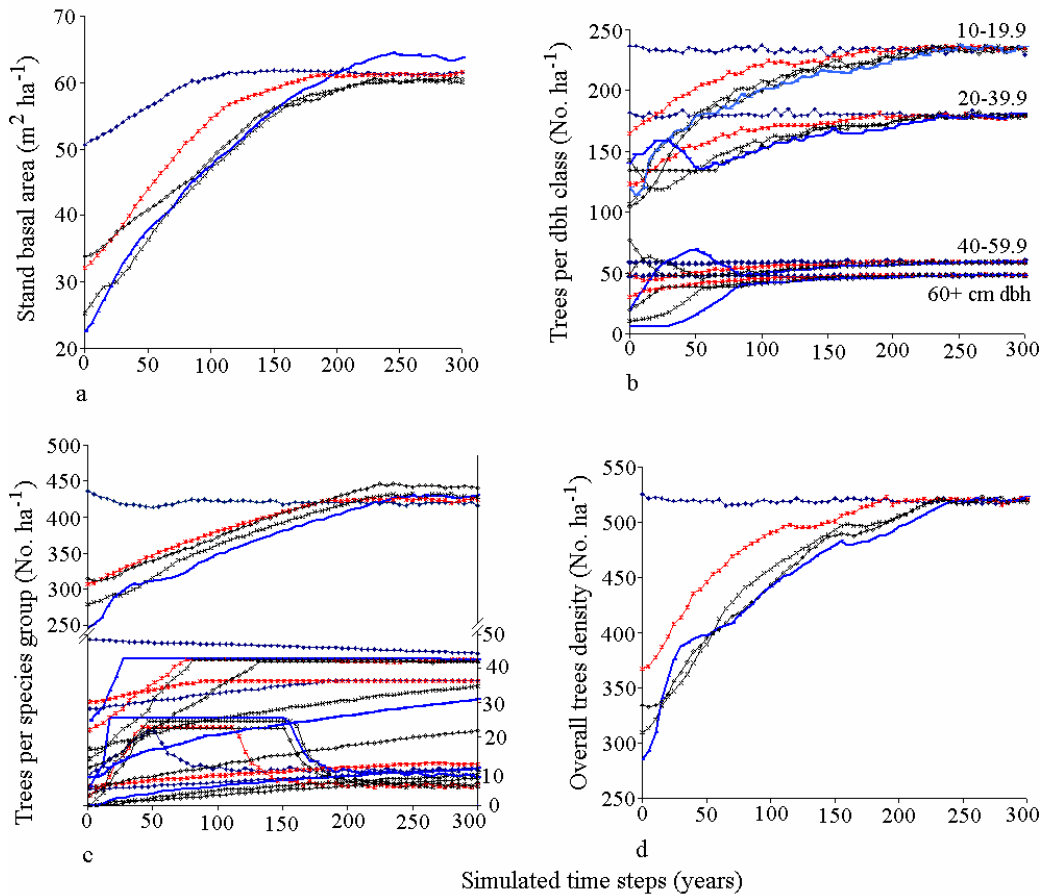


Figure 3. Predicted changes in an average unlogged control and stands subjected to increasing logging intensity in subtropical rainforests north-east NSW, Australia. Stand basal area in $m^2 ha^{-1}$ (a), stem diameter distribution in various dbh-classes (b); 10 – 19.9, 20 – 39.9, 40 – 59.9 and ≥ 60 cm dbh, stem density per species group (number of trees in each species group) in order of abundance; emergent and shade tolerant main canopy (left hand side scale), shade tolerant mid canopy, shade tolerant understorey and moderate shade tolerant with shade intolerant pioneers alternating in abundance with one or more of the last 3 species, see scale on the right (c), and overall stem density (d).

Enrichment planting can hasten rainforest recovery processes. This is evident in stand BA, stem density of species group 1 and that of the overall species, especially during the early stages of recovery. However, this advantage gradually disappears as the two smaller dbh classes continue to adjust due to high mortality and replacement of the large proportion of shade intolerant with shade tolerant species. The high mortality that followed heavy tree selection logging is also evident and this slowed the regeneration processes of the stand for the recovery time scale to resemble that of higher logging intensities.

Some plots received pre-harvest treatment (climber cutting and poisoning of non-commercial trees) before timber harvesting of commercial trees. These treatments included pre-exploitation shelterwood, post-exploitation shelterwood and silvicultural improvement treatment. The changes predicted in these stands are presented in Figure 4. The destruction of the non-merchantable trees is evident in the data as species from the mid canopy, understoreys, moderate shade tolerant species and pioneers were virtually eliminated. The respective time of recovery associated with these treatments in respect to basal area ranged from 145 through 175 to 190 years, while the time to recover a similar size structure to that of an average control is about 290 to 300 years (Figure 4). The modifying constraints in the models are apparent in stem density per species in species groups 2 to 5.

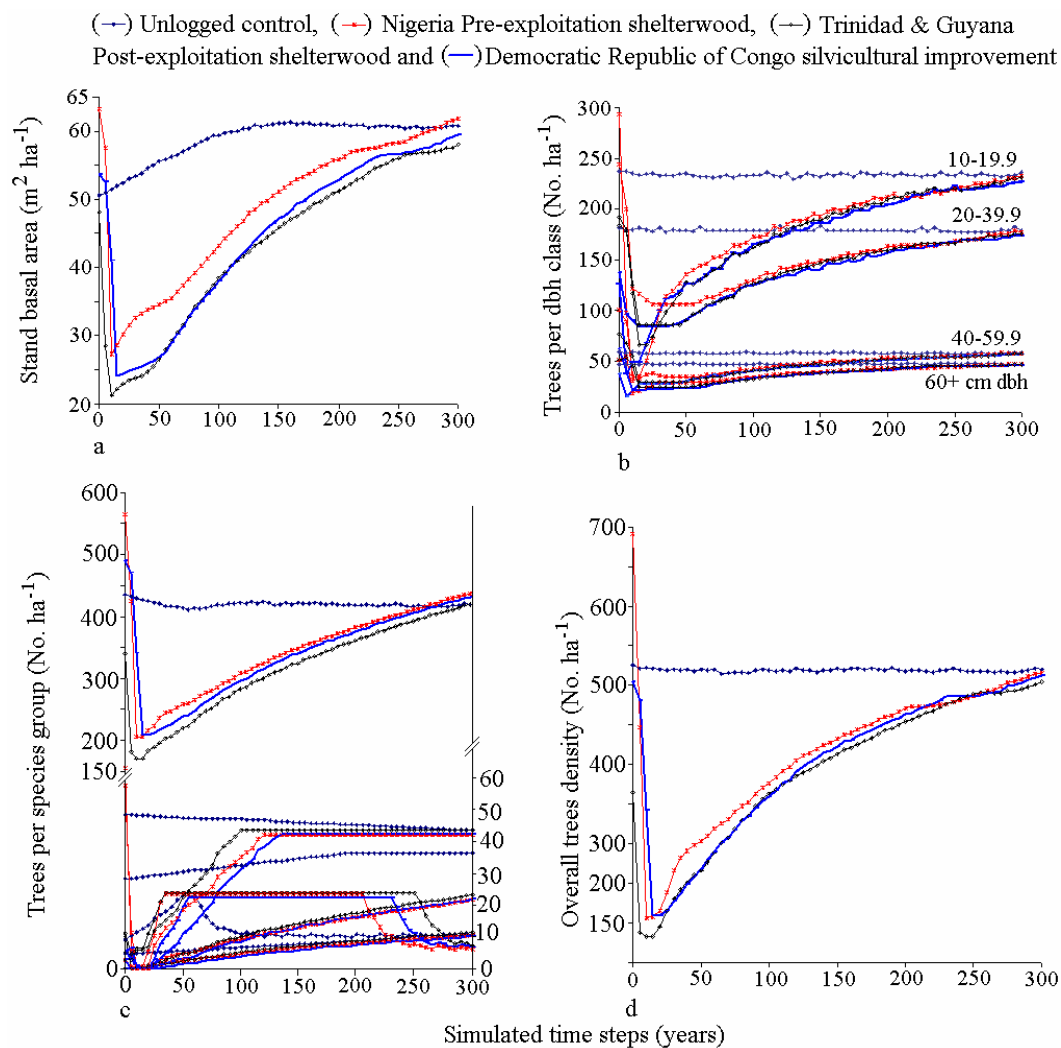


Figure 4. Predicted changes in an average unlogged control and stands logged after some initial climber cutting in subtropical rainforests north-east NSW, Australia. Stand basal area in $m^2 ha^{-1}$ (a), stem diameter distribution in various dbh-classes (b); 10 – 19.9, 20 – 39.9, 40 – 59.9 and ≥ 60 cm dbh, stem density per species group (number of trees in each species group) in order of abundance; emergent and shade tolerant main canopy (left hand side scale), shade tolerant mid canopy, shade tolerant understorey and moderate shade tolerant with shade intolerant pioneers alternating in abundance with one or more of the last 3 species groups, see scale on the right (c) and overall stem density (d).

5 DISCUSSION

5.1. Rainforest dynamic (recruitment, growth and mortality) estimates. We used rainforest trees identity to species level, mature size, and species ecological affiliation in relation to level of shade tolerance in categorizing 117 species into 5 groups of ecologically similar species (see also Finegan *et al.* 1999, Kohler *et al.* 2000). The rainforest responses depicted in this study reflect the reality that performance of an individual tree and that of the forest community in general, are highly variable in space and time and may differ greatly from the overall average. Rainforest tree species-specific level of shade tolerance during recruitment, establishment and development, tree size and competition (BAL) were used to explain the observed rainforest responses at the tree level. Site characteristics including stand BA, altitude, slope and orientation in relation to north and east, topography, disturbance intensity and time since the disturbance affected stand-level responses (see Appendix I; Tables 3, 4, 5, 6). The multilevel mixed models accommodated tree and plot level variations allowing the development of dynamic parameters that described the average annual changes and behaviour of both the logged and unlogged subtropical rainforest stands.

The recruitment, growth and mortality parameter estimates in this study indicate that the subtropical rainforest dynamic responses reflect the combined functions of the functional-group composition and environmental gradients supporting the findings of various studies in the rainforests (Brokaw 1985, Denslow 1987, Brokaw and Busing 2000, Kariuki *et al.* 2006b). This contrasts with the findings of Gourlet-Fleury and Houllier (2000), who worked on long-term experimental plots in the Paracou experimental station in French Guiana where site information did not improve their growth parameter estimates. This is probably because their modelling structure and hence method of analysis did not specifically seek to address variations at the plot and tree levels. Detailed description of subtropical rainforest tree growth responses in relation to environmental gradients are given in Kariuki *et al.* (2006b).

Logging reduced both stem density and competition and increased the availability of resources for the retained stems. Accordingly, the results of this study show that annual growth rates in all species groups increased from the unlogged control through increasing levels of tree selection to intensive logging. While the likelihood of annual recruitment was positively correlated with logging intensity (Table 4), the number of recruited trees was dependent on species and density of large tree $\geq 40\text{cm dbh}$ five to ten years previously (Table 5). Because the trees $\geq 40\text{cm dbh}$ constitute the overstorey forest canopy (Horne and Gwalter 1982), the results indicate that five years was the time lag between canopy opening, germination, establishment and recruitment into the 10cm dbh threshold. This study showed that tree species and size as well as logging intensity were important factors in the mortality of trees in the subtropical rainforest stands.

The general post-disturbance regeneration responses within the range of our data both in natural unlogged and logged stands resemble that of other uneven-aged mixed-species forests (Vanclay 1987, 1989a, Alder and Synnott 1992, Vanclay 1994a, Favrichon 1998, Finegan and Camacho 1999, Finegan *et al.* 1999). A test of significance between the observed and predicted changes in stand BA, tree size distribution in various species group and overall stem densities did not show any significant difference at the 5% level of confidence. However, there was a tendency to overestimate both the stand BA and overall stem densities, especially in the intensively logged sites during the first five to 30 years and to underestimate during the last ten-year period of the 44-year history of regeneration. The tendency to overestimate could be attributable to mortality, which was negatively correlated with tree size. The tendency for decreased mortality in large tree is evident in the data, especially in trees $\geq 60\text{cm dbh}$ where data were scarce. This problem was also encountered by Clark and Clark (1998). According to Favrichon (1998), poor estimates of mortality in the largest diameter classes could have a strong effect on the model behaviour. However, the model is stable and the convergence to a steady state in all the four stand characteristics is plausible.

5.2. Simulation of forest dynamics. The concern of the forest manager focuses particularly on changes of the stand characteristics after silvicultural treatment and the ability of the forest to recover the initial natural state (Favrichon 1998). The described models were used to simulate various disturbances ranging from single-tree selection (35% overstorey basal area removal) through increasing intensities of tree selection (36-65%) to intensive logging (66-80%), see Figures 2, 3 and 4. The models were also used to evaluate the ecological sustainability of silvicultural prescriptions, and to investigate the ability of logged sites to return to a relatively steady state in terms of stand BA, tree size distribution, and overall stem density. The expected recovery time scale was evaluated at two levels to allow for comparison with work done earlier using some of the data (see Horne and Gwalter 1982). The first level addresses the recovery of overstorey basal area for trees $\geq 40\text{cm dbh}$ and the second level addresses the return to the relatively steady state in terms other stand characteristics, especially trees $< 40\text{cm dbh}$, stem size distribution, stem density in species groups and the overall stem density (ecological recovery).

For example, the recovery time for the overstorey (trees ≥ 40 cm dbh) basal area and tree size distribution following single-tree selection logging appeared to be between 20 and 50 years (Fig. 2). Although this values compares favourably with the 30 to 60 years predicted by Horne and Gwalter (1982), there was evidence of some stands that may take up to 100 years to recover from such treatment. Furthermore, the recovery of the pre-logging basal area and tree size distribution of the overstorey species could be misleading because the diameter distribution of trees ≥ 40 cm dbh showed low density compared to that observed in the controls (Kariuki *et al.* 2006a). The time it takes the overall stem density and the smaller sized trees to recover to the original size structure (90-150 years) could be the best indicator of ecological recovery (Fig. 2). This interval allows for species densities to readjust and for slow growing shade tolerant species to increase in size and hence the stand structure to revert to pre-logging conditions. However, the responses attributed to single-tree selection logging can vary greatly (90-240 years) indicating that silvicultural treatments should be tailored to specific site and stand conditions.

Increasing logging intensity from single-tree selection (35% overstorey basal area removal) to the Queensland group selection (47%) may reduce the ecological recovery time from 150 to 120 years (Fig. 3). These results are consistent with the findings of Dickinson *et al.* (2000) that sites subjected to single-tree selection appear to take a longer time to recover due to both low recruitment and growth rates compared to sites subjected to a relatively intensive logging where high recruitment and growth rates were observed. Furthermore, the ecological damage from single-tree selection may be greater in retained stems, as was observed in the case of NSW heavy tree selection compared to group selection (see also Kariuki *et al.* 2006a). This also slowed the recovery processes in single-tree selection compared to Queensland group selection (Fig. 3). Because there was no study on logging damage, it may not be possible from the data to clearly separate out the logging intensity effect from the two types of tree selection methods. Suffice to say that single-tree selection method created small and scattered canopy gaps that did not influence recruitment or growth response significantly.

Logging decreased the number of stems retained in the stand reducing competition and allowing post disturbance recruitment and growth responses to be positively correlated with logging intensity and time since the last major disturbance. Group selection (moderate tree selection) not only created larger canopy gaps facilitating for significant recruitment, but also retained a modest number of relatively large shade tolerant trees that afforded significant growth responses after logging. According to Kariuki *et al.* (2006a) moderate growth of the retained large shade tolerant trees and low turnover in recruited trees resulted in high overall stand level BA contribution in both shade tolerant and intolerant species in the group selection method.

Increasing logging intensity from the group selection to heavy tree selection logging (50% overstorey BA removal) did not reduce the recovery time scale further, but increased it to about 180 years. This was attributed mainly to both high logging damage and mortality following this type of logging. Similar recovery times were also predicted for repeated single-tree selection logging (55% overstorey BA removal) and Sabah clear cutting (70%), see Figures 2 and 3. Further increases in logging intensity (logging with enrichment planting; 78%) increased the recovery time to 220 years, despite some benefits from enrichment planting during the early stages of regeneration (Fig. 3). The results of this study suggest that the overall stand behaviour and performance for both shade tolerant and intolerant species varied depending not only on the post-logging conditions and stage of regeneration, but also on successional events. Thus, although intensively logged sites were associated with high annual growth rates at the tree level (Kariuki *et al.* 2006b), low density of retained large shade tolerant stems and high mortality in recruited trees appear to have combined and increased the overall time scale for the intensively logged stands to recover.

The use of initial stand characteristics and silvicultural harvesting prescriptions scheduled for later dates showed the potential for this type of modelling approach to evaluate effects of silvicultural prescriptions before they are applied in the field (Fig. 4). For example, the recovery time scales for pre- and post-exploitation shelterwood as well as silvicultural improvement were estimated between 290 and 300 years. The difference could be attributed partly to levels of disturbance and time lag before logging as recovery time increased in concert with these two variables. However, compared to treatments where equivalent basal area was removed, the results for pre-exploitation shelterwood as well as that of silvicultural improvement treatment suggest that later logging may have set the plots back in recovery time scale. This is probably because the regenerated stems that followed the initial climber cutting and thinning of non-commercial trees were crushed during later logging. In addition, a very high density of very thin saplings some of which remain upright through the support of neighbouring trees and climbers was observed in the pre-exploitation shelterwood. In post-exploitation shelterwood where logging occurred a year after the climber cutting, the long recover time scale could be attributed to plot variations, as this plot is astride a gully with a creek head and steep slopes where soil slips, and increased mortality are more likely. Moreover, stands located in creek/gully sites could also be associated with lower growth rate (Kariuki *et al.* 2006b) and this could increase the recovery time.

From these results, it appears that the pre-disturbance stand BA is achieved fast before the overall tree size distribution, which is attained much later in the regeneration. The convergence to a steady state in the tree size distribution for trees $\geq 10\text{cm dbh}$ is also thought to mark the convergence between this component and the regenerating trees $< 10\text{cm dbh}$ in terms of floristic composition. The recovery time associated with this convergence could be taken as the ecological recovery time scale that would allow sustainable forestry in this type of forest.

However, the ecological recovery time scales shown in our simulation models should be considered only as indicative guides, due to the long projection period where conditions are likely to change. Moreover, there is considerable variation in species growth rates due to changes in species light requirement during ontogeny (Clark and Clark 1992, 1999). For example, Kariuki *et al.* (2006b) observed that small trees $< 67\text{cm}$ in the emergent and shade tolerant main canopy trees group associated with the northern aspect recorded higher growth rates compared to trees on flat terrain and those in southern facing sites. This demonstrates that the saplings of this species group can respond to increase in canopy illumination to reach the forest canopy. As the saplings increase in size they will be exposed to increasing levels of illumination leading to increased growth rates (Clark and Clark 1992, Hawthorne 1995, Thomas and Bazzaz 1999). In addition, climatic changes could enhance both recruitment and the overall increase in tree densities. For example, Lewis *et al.* (2004), while using 50 long-term plots across unlogged mature stage in South American tropical forests observed that growth and recruitment were increasing across these forests during the last 3 decades of the 20th Century. They attributed the increased growth and recruitment mainly to change in solar radiation, and increase in both air temperatures and atmospheric concentration of carbon dioxide over the recent decade. These conditions are likely to reduce the recovery time scale depicted in our simulations.

If our interpretation of tree and plot level ecological variations is correct, then it may be argued that a strategy that specifically seeks to account for these variations (using analyses such as the approach used here) provides a more realistic framework for analysis, interpretation and modelling stand dynamics than one where these variations are ignored or averaged. Moreover, our results correspond to expectations as shade tolerant and moderate shade tolerant species showed decreased growth rates when subjected to competition, while pioneers showed very fast diameter increment in large canopy openings caused by logging disturbance. In addition, mid canopy and understorey tree species were associated with the lowest rates of annual diameter increments (see also Kariuki *et al.* 2006b).

6 CONCLUSION

This model was developed using data spanning 35-44 years in the rainforests of north-east NSW, Australia. To capture variations due to species, the botanical identity of trees to species level, tree size at maturity and species-specific shade tolerance were required, and provided the basis for trees classification into five groups of ecologically similar species. The modelling structure for each species group dataset was hierarchical and multilevel to take into account variations in growth at the plot and tree levels. The final model is a classical matrix model with maximum size-dependent parameters of ingrowth and outgrowths.

This study has shown that growth and yield projections for uneven aged mixed-species rainforests can be modelled using an approach that accounts for both the plot and tree level variations. Simulations with the model indicate that a moderate tree selection could be sustained if 47% of the overstorey stand BA was removed once every 120 years in a checkerboard of logged and unlogged patches. Simulations show that single-tree selection (35%) could be conducted every 150 years and that intensive logging (50-80%) could be undertaken every 180 – 220 years, depending on the intensity of logging. The model indicates that shorter logging cycles will alter the structure and floristic composition of the forest, reducing the incidence of shade tolerant species and favouring shade intolerant species.

However, there are some indications that the mortality model may underestimate the death rate amongst larger trees, with diameters exceeding 60cm dbh. The model is also sensitive to the natural maxima of stem density per species and tree size. These variables were judiciously selected for the model to perform well beyond the range of available data.

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APPENDIX I

Parameter estimates from hierarchical 2-level multinomial logistic models for subtropical rainforest trees in north-east New South Wales, Australia. First line; shows estimates associated with no growth (growth category 1), second; average growth (3) third; above average growth (4) and fourth excellent growth (5). Wald tests; * significant at the 95% confidence level.

Emergent and shade tolerant canopy trees (group 1)

| Explanatory variable | Growth category | Coefficient | Standard error | Z-score | P> Z |
|---|-----------------|-------------|----------------|----------|------|
| Constants | 1 | 0.1233 | 0.0541 | 2.279* | 2% |
| | 3 | 0.3018 | 0.06965 | 4.333* | 0% |
| | 4 | -0.01835 | 0.05285 | -0.347 | 73% |
| Diameter (cm units) | 1 | 0.003742 | 0.0001585 | 23.609* | 0% |
| | 3 | -0.0009304 | 0.000159 | -5.852* | 0% |
| | 4 | 0.0004308 | 0.0001592 | 2.706 * | 1% |
| Basal area | 1 | -0.01356 | 0.0005478 | -24.754* | 0% |
| | 3 | 0.01118 | 0.0006341 | 17.631* | 0% |
| | 4 | 0.01527 | 0.0006418 | 23.792* | 0% |
| Basal area greater than the subject tree | 1 | 0.01845 | 0.0003967 | 46.509* | 0% |
| | 3 | -0.01684 | 0.000398 | -42.312* | 0% |
| | 4 | -0.02396 | 0.0003985 | -60.125* | 0% |
| 1/(Time since logging) | 1 | -0.01943 | 0.02819 | -0.689 | 49% |
| | 3 | 0.02702 | 0.02887 | 0.936 | 35% |
| | 4 | -0.1875 | 0.02908 | 6.448* | 0% |
| Single-tree selection logging | 1 | 0.1392 | 0.02317 | 16.918* | 0% |
| | 3 | -0.201 | 0.02907 | -6.914* | 0% |
| | 4 | 0.0799 | 0.03034 | 2.633* | 1% |
| Moderate to heavy tree selection logging | 1 | 0.0289 | 0.04311 | 0.670 | 50% |
| | 3 | -0.06751 | 0.05585 | -1.209 | 23% |
| | 4 | 0.1102 | 0.04246 | 2.595* | 1% |
| Intensive logging | 1 | 0.06975 | 0.02071 | 3.368* | 0% |
| | 3 | -0.1179 | 0.02732 | -4.381* | 0% |
| | 4 | 0.1091 | 0.02647 | 4.122* | 0% |
| Northness | 1 | -0.06943 | 0.02386 | -2.910* | 0% |
| | 3 | 0.06293 | 0.03085 | 2.040* | 4% |
| | 4 | 0.01397 | 0.02327 | 0.060 | 95% |
| Mid altitude | 1 | -0.1281 | 0.06122 | -2.092* | 4% |
| | 3 | 0.1834 | 0.07857 | 2.334* | 2% |
| | 4 | 0.05001 | 0.06192 | 0.808 | 42% |
| High altitude | 1 | 0.009912 | 0.05061 | 0.196 | 84% |
| | 3 | 0.05667 | 0.06505 | 0.871 | 38% |
| | 4 | 0.1233 | 0.04885 | 2.524* | 1% |
| Random effects or residual variance at plot level | 1 | 0.002685 | 0.0009123 | 2.943* | 0% |
| | 3 | 0.004616 | 0.001523 | 3.031* | 0% |
| | 4 | 0.002477 | 0.0008567 | 2.891 * | 0% |
| Testing correlated random effects across each contrasts | 3/1 | -0.003415 | 0.001132 | -3.017* | 0% |
| | 4/1 | -0.001631 | 0.0007258 | -2.247 * | 2% |
| | 4/3 | 0.001235 | 0.000854 | 1.446* | 15% |
| Shade tolerant mid canopy trees (group 2), | | | | | |
| Constants | 1 | 0.2732 | 0.06005 | 4.550* | 0% |
| | 3 | 0.06026 | 0.06348 | 0.949 | 34% |
| Basal area | 1 | -0.01728 | 0.001896 | -9.114* | 0% |
| | 3 | 0.0307 | 0.00193 | 15.908* | 0% |
| Basal area greater than the subject tree | 1 | 0.02103 | 0.001555 | 13.524* | 0% |
| | 3 | -0.04164 | 0.001557 | -26.744* | 0% |

| | | | | | |
|---|-----------------------|-----------|----------|----------|------|
| Northness | 1 | -0.1322 | 0.04028 | -3.282* | 0% |
| | 3 | 0.1292 | 0.04317 | 2.993* | 0% |
| Mid altitude | 1 | -0.1196 | 0.07144 | -1.674 | 9% |
| | 3 | 0.2311 | 0.07573 | 3.052* | 0% |
| High altitude | 1 | -0.115 | 0.06612 | -1.739 | 8% |
| | 3 | 0.3245 | 0.07011 | 4.628 * | 0% |
| Random effects or residual variance at plot level | 1 | 0.006142 | 0.002647 | 2.320 * | 2% |
| | 3 | 0.00734 | 0.003011 | 3.438* | 0% |
| Testing correlated random effects across each contrasts | 3/1 | -0.006163 | 0.002463 | -2.502* | 1% |
| Shade tolerant understorey trees (group 3) | | | | | |
| Constant | 1 | 0.2288 | 0.02441 | 9.373* | 0% |
| | 3 | 0.2221 | 0.02853 | 7.785* | 0% |
| Diameter | 1 | -0.004279 | 0.003727 | -1.148 | 25% |
| | 3 | 0.009303 | 0.003773 | 2.466* | 1% |
| Basal area | 1 | -0.01461 | 0.002633 | -5.549* | 0% |
| | 3 | 0.01986 | 0.002755 | 7.209* | 0% |
| Basal area greater than the subject | 1 | 0.01538 | 0.002166 | 7.001* | 0% |
| | 3 | -0.02421 | 0.002185 | -11.080* | 0% |
| Northness | 1 | -0.1087 | 0.04626 | -2.350* | 2% |
| | 3 | 0.02488 | 0.05392 | 0.461 | 64% |
| Random effects or residual variance at plot level | 1 | 0.006035 | 0.003403 | 1.773 | 8% |
| | 3 | 0.00969 | 0.004758 | 2.037* | 4% |
| Testing correlated random effects across each contrasts | 3/1 | -0.00708 | 0.003381 | -2.094* | 4% |
| Moderate shade tolerant and persistent trees (group 4) | | | | | |
| Constant | 1 | 0.06542 | 0.0273 | 2.396* | 2% |
| | 3 | 0.4101 | 0.04158 | 9.863* | 0% |
| | 4 | 0.04284 | 0.0273 | 1.569 | 12% |
| Diameter | 1 | 0.001444 | 0.00154 | 0.934 | 35% |
| | 3 | -0.005765 | 0.001681 | -3.430* | 0% |
| | 4 | 0.001373 | 0.00154 | 0.892 | 37% |
| Basal area | 1 | -0.01024 | 0.003573 | -2.866* | 0% |
| | 3 | 0.01753 | 0.003841 | 4.564* | 0% |
| | 4 | 0.01224 | 0.003573 | 3.426* | 0% |
| Basal area greater than the subject | 1 | 0.01097 | 0.002612 | 4.200* | 0% |
| | 3 | -0.02745 | 0.002675 | -10.262* | 0% |
| | 4 | -0.01621 | 0.002612 | -6.206* | 0% |
| Single-tree selection logging | 1 | -0.02402 | 0.09098 | -0.246 | 81% |
| | 3 | 0.1521 | 0.1111 | 1.370 | 17% |
| | 4 | 0.08694 | 0.09098 | 0.956 | 34% |
| Moderate to heavy tree selection logging | 1 | 0.05101 | 0.06861 | 0.743 | 46% |
| | 3 | -0.3259 | 0.09055 | -3.600* | 0% |
| | 4 | 0.1939 | 0.06861 | 2.826* | 0% |
| Intensive logging | 1 | -0.0533 | 0.07118 | -0.749 | 45% |
| | 3 | -0.1696 | 0.08981 | -1.889 | 6% |
| | 4 | 0.2187 | 0.07118 | 3.072* | 0% |
| Random effects or residual variance at plot level | 1 | 0 | 0 | 0 | None |
| | 3 | 0.005301 | 0.004094 | 1.294 | 20% |
| | 4 | 0 | 0 | 0 | None |
| Covariance matrix between different growth categories at plot level | All growth categories | 0 | 0 | 0 | None |
| Shade tolerant pioneers species (group 5) | | | | | |
| Constant | 1 | -0.2832 | 0.0486 | -5.827* | 0% |
| | 3 | 0.03477 | 0.07242 | 0.480 | 63% |
| | 4 | 0.5698 | 0.0486 | 11.724* | 0% |
| | 5 | 1.045 | 0.0486 | 21.502* | 0% |

| | | | | | |
|---|-----------------------|-----------|----------|----------|------|
| Diameter | 1 | 0.01594 | 0.001342 | 11.878* | 0% |
| | 3 | 0.007124 | 0.001377 | 5.174* | 0% |
| | 4 | -0.01524 | 0.001342 | -11.356* | 0% |
| | 5 | -0.02659 | 0.001342 | -19.814* | 0% |
| Basal area | 1 | 0.06921 | 0.1481 | 0.467 | 64% |
| | 3 | -0.09918 | 0.1625 | -0.610 | 54% |
| | 4 | -0.1238 | 0.1481 | -0.834 | 40% |
| | 5 | -0.3275 | 0.1481 | -2.211* | 3% |
| Basal area greater than subject | 1 | -0.007877 | 0.002022 | -3.896* | 0% |
| | 3 | -0.007775 | 0.002484 | -3.130* | 0% |
| | 4 | 0.01224 | 0.002022 | 6.053* | 0% |
| | 5 | 0.003161 | 0.002022 | 1.563 | 12% |
| Northness | 1 | 0.03748 | 0.04542 | 0.825 | 41% |
| | 3 | -0.04408 | 0.06978 | -0.671 | 50% |
| | 4 | -0.03789 | 0.04542 | -0.632 | 53% |
| | 5 | 0.3264 | 0.04542 | 7.186* | 0% |
| Single-tree selection logging | 1 | 0.04779 | 0.04319 | 1.107 | 27% |
| | 3 | -0.03955 | 0.08377 | -0.472 | 64% |
| | 4 | 0.09987 | 0.04319 | 2.312* | 2% |
| | 5 | -0.2388 | 0.04319 | -5.529* | 0% |
| Moderate to heavy tree selection logging | 1 | 0.04467 | 0.03926 | 1.138 | 26% |
| | 3 | -0.006568 | 0.07366 | -0.089 | 93% |
| | 4 | 0.02684 | 0.03926 | 0.684 | 49% |
| | 5 | -0.155 | 0.03926 | -3.948* | 0% |
| Intensive logging | 1 | -0.06811 | 0.05324 | -1.279 | 20% |
| | 3 | 0.04661 | 0.1017 | 0.458 | 65% |
| | 4 | 0.0555 | 0.05324 | 1.042 | 30% |
| | 5 | -0.3238 | 0.05324 | -6.082* | 0% |
| 1/(Time since logging) | 1 | 0.002357 | 0.001149 | 2.051* | 4% |
| | 3 | 0.00396 | 0.001211 | 3.270* | 0% |
| | 4 | 0.0009754 | 0.001149 | 0.849 | 40% |
| | 5 | -0.004136 | 0.001149 | -3.600* | 0% |
| Mid slope topographic position | 1 | -0.0109 | 0.03489 | -0.312 | 75% |
| | 3 | 0.07555 | 0.06624 | 1.141 | 25% |
| | 4 | -0.08785 | 0.03489 | -2.518* | 1% |
| | 5 | 0.1297 | 0.03489 | 3.717* | 0% |
| Lower slope topographic position | 1 | 0.00572 | 0.04168 | 0.137 | 89% |
| | 3 | 0.02937 | 0.089 | 0.33 | 74% |
| | 4 | -0.01436 | 0.04168 | -0.345 | 73% |
| | 5 | 0.03186 | 0.04168 | 0.764 | 44% |
| Creek/gully topographic position | 1 | 0.04732 | 0.04381 | 1.080 | 28% |
| | 3 | -0.03373 | 0.1037 | -0.325 | 74% |
| | 4 | -0.0712 | 0.04381 | -1.625 | 10% |
| | 5 | 0.1992 | 0.04381 | 4.547* | 0% |
| Random effects or residual variance at plot level | 1 | 0 | 0 | 0 | None |
| | 3 | 0.007027 | 0.003427 | 2.050* | 4% |
| | 4 | 0 | 0 | 0 | None |
| | 5 | 0 | 0 | 0 | None |
| Testing correlated random effects across each contrasts | all growth categories | 0 | 0 | 0 | None |