Regeneration changes in tree species abundance, diversity and structure in logged and unlogged subtropical rainforest over a thirty six year period

Maina Kariuki [1]*, Robert M. Kooyman [2], R. G. B. Smith [3], Grant Wardell-Johnson [4] and Jerome K. Vanclay [5]

[1] * Corresponding author; Department of Sustainability and Environment, Park and Forests, Level 3, 8 Nicholson Street, PO, Box 500, East Melbourne 3002 Victoria, Australia. Telephone: 61 3 96379809. Email: maina.kariuki@dse.vic.gov.au

Abstract

The long-term effects of logging treatments on rainforest regeneration are difficult to quantify due to compounding interactions between natural dynamics, site characteristics and tree species. The aim of this study was to compare regeneration differences over a 36-year period in stands subjected to various levels of disturbance ranging from natural, through an increasing intensity of individual tree removal to intensive logging. Data for trees ≥ 10 cm diameter at 1.3 m above the ground in subtropical rainforest of north-east New South Wales, Australia were used. Multivariate and univariate analyses showed that regeneration responses were generally correlated with disturbance gradient. In the undisturbed controls there were gradual changes that had no significant effects on tree species richness and diversity, stem density, or diameter distribution. Gradual changes were also observed during the early stages of regeneration following logging. However, in logged sites changes in tree species richness and diversity, stem density and diameter distribution became more rapid with time, and significant changes were observed. This is because changes in logged sites were characterised by periods of distinct floristic assemblages, marked initially by a few species and the most recent assessment revealed species abundance and richness exceeding pre-logging levels. Similar regeneration events across site and disturbance levels resulted in three identifiable stages. In the first stage, lasting about ten years, stem density of abundant shade tolerant trees decreased, with no significant changes in tree species richness. In the second stage, also lasting about ten years, tree species richness and diversity, as well as stem density decreased to minima due to localised species turnover and net mortality. In the third stage, recruitment surpassed mortality and reversed the net loss of both species and stems, as tree species assemblages began to return to pre-disturbance levels. Sites subjected to individual tree selective logging recovered their pre-logging tree species richness and diversity, and stem density within 30 years, but diameter distribution of trees ≥ 40 cm dbh showed low density compared to that observed in the controls. After 35 years, sites subjected to more intensive logging had low species diversity and high densities of both the small sized stems and shade intolerant tree species. More intensively logged sites also had a low density of shade tolerant tree species compared to the controls. This suggests that the restoration of forest structure takes considerably more time than the restoration of tree species richness and abundance following logging in these forests. A high rate of stand basal area growth was observed in moderate tree selection. This indicates high timber production potential at moderate tree selection rates in this type of forest. However, if the stem size distribution of larger trees is to be maintained, a logging cycle with a longer return period than the period covered in this study is necessary.

Key words: Chronological clustering, functional-group compositions, disturbance levels, tree diameter distribution.

1.   Introduction

Post-disturbance regeneration and temporal variation in rainforest ecosystems are complex, and involve a variety of responses including species successional replacement sequences (Hopkins, 1977; Sheil, 2001). Models for species succession, and the underlying processes that involve changes in biomass, species diversity and homeostasis are well documented (see Odum, 1971; Connell and Slatyer, 1977; Brokaw and Busing, 2000). These species succession models have been used to explain changes in rainforest regeneration in gap phases (Denslow, 1987; Webb, 1998; Schnitzer and Carson, 2001), and the interaction of species life cycles and life history traits that promote survival and persistence of species in time and space (Connell and Slatyer, 1977; Pickett et al., 1987; Summerbell, 1991).

Disturbance that creates large canopy gaps in the rainforest disrupt the ecosystem, and initiate a series of distinct species responses (Gomez-Pompa and Vazquez-Yanes, 1981; Olsen, 1989). These responses are described in the intermediate disturbance hypothesis as a succession of rainforest regeneration in which numbers of tree species and stem abundance show a unimodal rise-and-fall over time (Connell, 1978). While the early stages of rainforest regeneration are relatively well understood (Shugart et al., 1980; Denslow, 1995; Magnusson et al., 1999), studies have reached contrasting conclusions on later stages of rainforest regeneration, with some supporting the intermediate disturbance hypothesis (Eggeling, 1947; Sheil, 2001; Sheil and Burslem, 2003), and others not supporting (Hubbell et al., 1999; Molino and Sabatier, 2001). According to Sheil and Burslem (2003), the controversy surrounding the progression of rainforest regeneration lies not only in the refinement of different interpretation and approaches, but also in the different characteristics of study sites. Furthermore, the concept of rainforest stability in later successional stages, including that of intact primary rainforest communities (Whitmore, 1975) is not consistent with the dynamics and behaviour of natural systems (Brokaw and Busing, 2000). In addition, the apparent simplicity of the intermediate disturbance hypothesis is unrepresentative of the involved range of distinct phenomena that can be defined and examined (Brokaw and Busing, 2000; Sheil and Burslem, 2003).

For example, the number of species (species richness) and species commonness or rarity (species relative abundance) in space and time are accepted measures and key indicators of both rainforest community composition and dynamics (Bossel and Krieger, 1994; Philips et al., 1994; Burslem and Whitmore, 1999). The overall measures of species richness and relative abundance coupled with total stand basal area (BA) have been used in assessing long term changes and restoration of pre-logging conditions (Shugart et al., 1980; Horne and Gwalter, 1982; Smith and Nichols, 2005). Accurate descriptions of long term chronological changes in rainforest ecosystems following both natural and anthropogenic disturbances can increase our understanding of how these systems respond to various disturbances (Sheil, 2001).

This study describes both the short and medium term post-disturbance regeneration patterns in rainforest stands subjected to various levels of disturbance ranging from unlogged controls through increasing levels of individual tree selective logging to intensive logging. Changes in tree species richness, stem density and diameter distribution were investigated using data for trees $\geq$ 10 cm diameter at 1.3 m above the ground (dbh). In this study, we consider the following specific questions: (1) can post disturbance regeneration in rainforest be identified by periods of distinct tree species assemblages?; (2) are the regeneration patterns consistent across sites?; (3) how does post disturbance regeneration differ between trees species functional-groups defined by level of shade tolerance?; and (4) are these differences related to the disturbance intensity? We tested the null hypothesis that there was no variation between one set of data and another set collected at a later time. If the probability that the null hypothesis is true was larger than a chosen probability level, then the null hypothesis was accepted and the datasets were fused to create a cluster of samples indicating a period of similar floristic assemblage. The rates and direction of change in stem density, diameter distribution, and stand BA were also investigated across logging intensities.

98 **2.   Methods**
99 *2.1.   Study area*

100 The study area in the subtropical rainforests of north-east New South Wales, Australia lies between
101 latitudes 28° 30' and 28° 45' south, and longitudes 152° 45' and 153° 30' east (Fig. 1). The altitude of
102 the study area ranges from about 210 to 920 metres above sea level. The vegetation is Complex
103 Notophyll Vine forest, the most floristically diverse and structurally complex form of subtropical
104 rainforest in Australia (Hopkins, 1977; Webb et al., 1984). This vegetation type is widely distributed
105 in the region on moist sites with deep, fertile and well-drained red krasnozem soils or ferrosols (Isbell,
106 1998). The geology of the area is related to the Mt. Warning and Focal Peak volcanic series, with
107 basalt as the parent material.

108 Rainfall patterns show a pronounced maximum of about 160 mm per month in late summer (February
109 and March) and a minimum of about 40 mm per month in late winter (August and September). At
110 high altitude this seasonality may be masked by persistent low clouds and fog that can add about 50%
111 of rainfall by way of fog drip (Floyd, 1990). Average annual rainfall ranges from 2500 to 3500 mm
112 and mean monthly temperature ranges from 3-19° C in winter and 15-31° C in summer. The annual
113 mean minimum and maximum are 10.3^O C and 23.6^O C respectively (NSW National Parks & Wildlife
114 Services, 2004).   *{Fig. 1}*

115 *2.1.1.   Study sites*

116 The study sites were determined by the distribution of twenty permanent sample plots (PSPs) covering
117 a total area of approximately 5.4 hectares in four former State Forests. These PSPs were established at
118 different time to address changing circumstances in forestry practices in the region. For example, in
119 the Big Scrub Flora Reserve in the former Whian Whian State Forest (now part of Nightcap National
120 Park), individual tree selective logging started around the turn of 20th Century to mid 1950s when
121 the management of the area changed to that of informal flora reserve (formally declared a
122 Flora Reserve in 1976). According to the Forestry Commission of NSW (1984), the individual tree
123 selective logging moved in stages tapping fresh supplies. For example, as the supply of red cedar
124 (*Toona ciliata* M.Roem.) dwindled, species such as rosewood (*Dysoxylum fraserianum* (A.juss.)
125 Benth.), native teak (*Flindersia australis* R.Br.) and white beech (*Gmelina leichhardtii* F.Muell.) were
126 sought. As these species became harder to find on easier terrain, new technology permitted
127 utilization of a wide range of rainforest species (Horne and Gwalter, 1982; Forestry Commission
128 of NSW, 1984). In 1957 following the termination of repeated individual tree selective logging in the
129 Big Scrub Flora Reserve, three plots each measuring approximately 30 x 25 m were established. These
130 plots were established to monitor forest regeneration and establishment of high value timber species
131 following repeated logging disturbances (Forrest, Unpublshed report).

132 In 1965 in the former Toonumbar and Edinburgh Castle State Forests (Toonumbar National Park)
133 three PSPs each measuring 50 x 40 m were established in each forest. These plots were established to
134 monitor forest regeneration and the establishment of timber species following a single event of
135 individual tree selective logging.

136 Also in 1965 in the former Wiangaree State Forest (Border Ranges National Park), an experiment
137 involving eleven PSPs; three controls and eight silvicultural treatments was established (see Horne and
138 Gwalter, 1982). These treatments had been used to induce regeneration and improve the composition of
139 structurally similar rainforest stands in various parts of the world (Baur, 1961). Plot size ranged from
140 1.42 to 3.89 ha with an average of 2 ha. In each, a central experimental subplot measuring 60.4 x 60.4 m
141 was established. Detailed descriptions of the eight treatments including logging intensity has been
142 provided (Pattemore and Kikkawa, 1974; Horne and Gwalter, 1982; Smith and Nichols, 2005). In this
143 study, treatments were first considered separately, then for further analysis the treatments were reduced
144 into five levels of disturbance based on the percentage overstorey basal area removed (Table 1).

145   *2.2.   Data description*

146   Trees ≥10 cm dbh including those that remained after treatment and those recruited later were
147   measured on several occasions. For example, in the Big Scrub Flora Reserve measurements were
148   carried out in 1957, 1958, 1960, 1962, 1964, 1966, 1968, 1972, 1976, 1979/80, 1988, and 2000/01. In
149   the Toonumbar National Park measurements were carried out in 1966, 1968, 1972, 1976, 1980/81,
150   1987/88, and 2001. In the Border Ranges National Park measurements were carried out in 1965/66,
151   1970, 1971/73 (Pre-exploitation Shelterwood from Nigeria), 1975/76, 1980/81, 1987/88, 1995
152   (controls only), 1999 and 2001. Quality control in 2001 using 5 randomly selected plots revealed
153   previously wrongly identified trees. For example, there were cases where *Polyosma cunninghamii*
154   (Benn) had been confused with *Doryphora sassafras* (Endl), *Guilfoylia monostylis* (Benth, F.Muell)
155   with *Guioa semiglauca* (F.Muell, Radlk) and *Heritiera actinophylla* (Bailey, Kosterm) was not
156   differentiated from *Heritiera trifoliolata* (F.Muell, Kosterm). This necessitated a complete review of
157   field identification to reconcile the previously collected data records with those collected during the
158   2000/01 census. Despite this review and data reconciliation, about 0.4% of stems remained as
159   unidentified mortality (trees that had never been identified before they died). In addition, 0.6% was
160   missing data in trees that had been recorded dead, but were found to be alive during the 2001/01
161   census, and recruited stems that were missed on one or more occasions. Trees in the unidentified
162   mortality were represented by a species category referred to as 'unknowns', so that the effects of
163   change caused by stem recruitment or death could be accounted for during data analyses.

164   *2.3.   Tree species groups*

165   To study rainforest dynamics, woody species are usually categorised into functional-groups, based on life
166   history, light requirement for germination, establishment and growth, and trade-offs between the rate of
167   growth and persistence in the canopy (Swaine and Whitmore, 1988; Kohler and Huth, 1998; Baker et al.,
168   2003). Several classifications are bimodal (see Connell, 1978; Brokaw, 1985; Swaine and Whitmore,
169   1988), while others are more complex with numerous categories (Summerbell, 1991; Condit et al., 1996).
170   In this study, bimodal classification was adequate and tree species were categorised into two main
171   groups; shade intolerant and shade tolerant. Shade intolerant species included pioneers with relatively fast
172   growth rates and short life-spans such as *Acacia melanoxylon* R.Br and *Duboisia myoporoides* R.Br, and
173   early successional species that arrive early, but are persistent and live considerably longer than the
174   pioneers such as *Flindersia schottiana* F.Muell and *Toona ciliata* M.Roem. Members of the shade
175   intolerant group regenerate in disturbed and relatively open sites, and form a minor plant component in
176   mature subtropical rainforests of Australia (Kariuki and Kooyman, 2005). Shade tolerant species
177   included later successional species such as *Dysoxylum mollissimum* Blume S.*lat.* syn. *D. muelleri* Benth
178   and *Neolitsea dealbata* (R.Br) Merr, and mature phase species such as *Caldcluvia paniculosa* (F.Muell)
179   Hoogland, *Heritiera trifoliolata* (F. Muell.) Kosterm and *Geissois benthamii* F.Muell. The shade tolerant
180   group regenerates in shade, and forms the major plant component in mature subtropical rainforests of
181   Australia.

182   *2.4.   Data analysis*

183   Stochastic and small-scale effects that may lead to variations within similarly treated rainforest stands
184   were not addressed in this study (see Queensland Department of Forestry, 1983; Franklin et al., 1997;
185   Hickey and Wilkinson, 1999). This is because analysis of similarity using the number of species and
186   stem abundance recorded during the 2001 census for tree ≥ 10 cm dbh did not show any significant
187   difference between similarly treated plots (Kariuki, 2004). Furthermore, preliminary testing of the null
188   hypothesis at the probability level of $\alpha = 0.01$, 0.05 and 0.1 produced similar clusters in similarly
189   treated plots in each site. Thus, data series from similarly treated plots in a given site; the controls
190   (Border Ranges National Park; site 1), individual tree selective logging in former Toonumbar (site 2)
191   and Edinburgh Castle (site 3), and repeated individual tree selective logging in Big Scrub Flora
192   Reserve (site 4) were combined to effectively create one larger sampling station.

193 We sought to identify when ecological changes at a given plot or sampling station occurred. Thus,
194 matrices of species abundance and the sequence of assessments were analysed using the chronological
195 clustering method in the R-Package (Casgrain and Legendre, 2001b). The appropriate association
196 matrices (*n* x *n*) required by this method were computed using Steinhaus coefficients (S17 in Casgrain
197 and Legendre, 2001a). The Steinhaus coefficients use species abundance data, and reflect similarities
198 in numbers of each species without standardisation (Tuomisto and Ruokolainen, 1993). The
199 chronological clustering method is a time constrained form of agglomerative clustering in which only
200 neighbouring samples can cluster (Legendre and Legendre, 1998). At each step of the intermediate-
201 link linkage agglomerative process, a Mantel test is performed to decide whether fusion of the samples
202 is warranted at a user defined level of significance (see Legendre et al., 1985). The rejection of the null
203 hypothesis was progressively relaxed at four levels of significance ($\alpha = 0.01, 0.05, 0.1, 0.2$). As the
204 level of significance was relaxed finer details were revealed in identifying samples that were
205 significantly different in the data series.

206 Cluster-expansion tests were performed to determine whether a cluster could incorporate samples from
207 adjacent cluster(s) when the structures of the chronological neighbouring clusters were ignored. This
208 ascertained whether the observed pattern of regeneration represents a relatively similar subseries of
209 regeneration events within a continuum, or different and independent regeneration phenomena
210 succeeding one another. A *posteriori* tests were also carried out between non-neighbouring clusters
211 including singletons (aberrant samples significantly different from neighbouring cluster) to determine
212 their relationship.

213 Association matrices (*n* x *n*) with Chord distance coefficients (D03 in Casgrain and Legendre, 2001a)
214 were also computed from the species abundance matrices and sequential assessments. The Chord
215 distance coefficients use species abundance data, and reflect differences in relative proportion of tree
216 species after standardisation by object-vector (Tuomisto and Ruokolainen, 1993). The chronological
217 clustering results from principal coordinate analysis in the R-Package were drawn in the space of the
218 first two principal coordinates to help interpret relationships among clusters, and to evaluate
219 identifiable ecological changes in the regeneration.

220 Changes in tree species diversity in the data series were investigated using the Brillouin diversity
221 index (H_b). The Brillouin statistics were calculated using matrices of species abundance and the
222 sequence of assessments in the PRIMER package (Clarke and Warwick, 1994). These statistics were
223 adequate in this study because they consider density per species as well as the overall density where
224 the randomness of the samples cannot be guaranteed (see Williams et al., 1969). The overall mean
225 diversity statistic for the controls was compared with those obtained in logged sites.

226 Changes in stem density, tree species richness and stand BA for the two main tree species groups were
227 also examined for trends across disturbance levels. Disturbance levels ranged from the controls (0%
228 overstorey stand BA removal) through individual tree selective logging (1-35%), moderate tree
229 selection (36-50%) and repeated individual tree selective logging (estimate 51-65%) to intensive
230 logging (66-80%).

231 To investigate the effect of logging intensity on diameter distribution we examined the number of
232 stems in various dbh classes across treatments. Trees in each assessment were grouped into four
233 diameter classes; (10-19.9), (20-39.9), (40-59.9), and (≥ 60 cm). This ensured a small number of
234 classes with an adequate representation of stems in each. To enhance this approach the rate of change
235 in the number of stems in various diameter classes was investigated by fitting a two-level
236 hierarchical multilevel model in the MLwiN package (Rasbash et al., 1999; Snijders and
237 Bosker, 1999). The rate of change in stem distribution in the hierarchical multilevel model
238 was analysed assuming that one mean function is valid for the subtropical rainforest population, and
239 that, mean functions for single plots vary randomly around the population mean. Accordingly, the
240 functions for rate of change in the number of stems within a given dbh class and plot and stand are
241 assumed to vary randomly around the mean function for the corresponding dbh-class and stand. The

242 natural logarithm of sampled stems rather than the actual counts were used as the dependent
243 variable. Explanatory variables including tree size (dbh classes), logging intensity
244 (disturbance levels), time since disturbance, and the interaction of these variables were tested
245 for significance using both the log likelihood and Wald's tests statistics (Rasbash et al.,
246 1999).

247 **3. Results**

248 A total of 117 species in 45 families were represented in the data series. Families that had the highest
249 number of species included Sapindaceae (19 species), Lauraceae (17), Rutaceae (17), and Myrtaceae
250 (15). Ten species with the highest overall occurrence included shade tolerant species such as
251 *Caldcluvia paniculosa* (2345 occurrences), *Heritiera actinophylla* and *H. trifoliolata* (2815),
252 *Doryphora sassafras* Endl. (1403), *Geissois benthamii* (1161), *Cinnamomum oliverii* F. M. Bailey
253 (923), *Baloghia inophylla* (G. Forst) P. S. Green (909), *Diospyros pentamera* (Woolls & F.Muell) F.
254 Muell (906), *Sloanea woollsii* F. Muell (904), and *Pouteria australis* (syn.*Planchonella australis*) (R.
255 Br) (637). Two pioneer species in the shade intolerant group; *Duboisia myoporoides* (365) and
256 *Polyscias elegans* (337) were the 15th and 16th most frequently encountered species.

257 *3.1. Chronological clustering and clusters arising from the analysis*

258 We present the testing of the null hypothesis at the probability level of $\alpha = 0.2$ (the alpha level that
259 illustrates most breakpoints), which identifies significantly different samples in the data series (Fig. 2).
260 In each series, the cluster-expansion tests revealed that the last cluster was not distinct from the others.
261 This indicates that sample(s) in the last cluster were less similar to one another due to species turnover
262 and recruitment of both, locally new and previously lost species.

263   *{Fig. 2}*

264 The *a posteriori* test results indicate that the chronological clusters depicted in Fig. 2 remain distinct at
265 the probability level of $\alpha = 0.2$, except in the case of the post-exploitation shelterwood (Fig. 2j).
266 However, if a smaller probability level (< 0.2) was used for rejection of sample fusion, then
267 non-neighbouring clusters were not distinct. In post-exploitation shelterwood, the initial assessment
268 carried out before logging, appeared as a singleton (aberrant sample that is significantly different from
269 its neighbouring cluster). However, the singleton is not significantly different compared to the last
270 cluster (P = 0.25), but could not fuse because the samples were not adjacent. This indicates that the
271 last chronological cluster in this data series comprised of tree assemblages with species abundance and
272 richness comparable to pre-logging levels.

273 In the unlogged controls, three clusters were produced (*i*, *ii* and *iii*; Fig. 2a). The cluster expansion
274 results show that the first cluster (*i*) is not distinct and can be expanded to include samples in the
275 second cluster (*ii*) when tested one at a time. Cluster (*ii*) is also not distinct and can be expanded to
276 include samples in cluster (*i*) as well as samples 6 and 7 in cluster (*iii*) when tested one at a time. This
277 indicates that the changes between neighbouring clusters in this series were gradual and that clusters
278 consisted of tree assemblages with relatively similar species abundance and richness.

279 Individual tree selective logging produced two clusters across sites (*i* and *ii*). In all cases, the cluster
280 expansion tests show sharp separation of the first cluster (*i*) from its neighbour. This indicates a
281 distinct tree assemblage in cluster (*i*), due to decrease in both the species abundance, and in richness
282 following logging. Thus, cluster (*i*) cannot be expanded to include samples in cluster (*ii*) when tested
283 one at a time, except in the case of site 3 (Fig. 1d) where cluster (*i*) can only be expanded to include
284 the first sample in cluster (*ii*). These results indicate similar and significant regeneration events across
285 sites associated with individual tree selective logging treatment. However, the regeneration events
286 became evident between 5 and 20 years since logging, indicating that these events could be site
287 specific.

288 The clustering structure for the more intensively logged sites showed distinct differences between
289 clusters. This indicates significant regeneration events in these sites. The cluster-expansion test results
290 indicate distinct floristic assemblages between neighbouring clusters (*i* and *ii*, *ii* and *iii*, and so on).
291 Excluding the last cluster, no other cluster can be expanded to include samples from neighbouring
292 cluster(s), except in the case of the first cluster in the clear cutting treatment from Sabah Malaysia
293 (Fig. 2h), and repeated individual tree selective logging (Fig. 2e) that can only be expanded to include
294 the first sample in the neighbouring cluster.

295 Like the post-exploitation shelterwood (Fig. 2 j), the initial assessment in heavy individual tree
296 selective logging is a singleton (Fig. 2 g). The singletons reflect a similar ecological event resulting
297 from decrease in both the tree density and species richness caused by a high mortality following heavy
298 individual tree selective logging, and the removal of merchantable trees in the post-exploitation
299 shelterwood.

300 Silvicultural improvement from the Democratic Republic of Congo (Fig. 2 k) showed the most recent
301 assessment (2001) as a singleton and an important ecological change between the 1975 and 1976
302 assessments. The singleton indicates missing data, whereby some trees apparently missed in earlier
303 censuses were included as new recruits in the 2001 census. The ecological change (confirmed by
304 cluster-expansion tests) indicates a sharp difference in stem density, and both species abundance and
305 richness before, and after the removal of merchantable stems from the stand.

306 Fig. 2 also shows changes (many gaps) in the majority of the data series corresponding to the period
307 between 1980 and 1988. These changes show when the species abundance and diversity as well as the
308 number of stems decrease to minima, indicating the end of net mortality, and the beginning of net
309 recruitment in trees $\geq$ cm dbh.

310 *3.2.   Regeneration stages*

311 The relationships between species abundance and floristic composition are illustrated in the biplot
312 drawn on equal scale in the reduced space of the first two axes of principal coordinate analysis (Fig.
313 3). The variance accounted for by the two axes (88.3 to 96.7%) is indicative of the similarity of objects
314 in Fig. 3 compared to objects in the multi-dimensional space. The chronological regeneration
315 responses traces a U-shaped redevelopment trend (Fig. 3). Clusters of similar floristic assemblages at
316 the $\alpha = 0.2$ level of significance are delineated for ease of interpretation in this and subsequent
317 sections.   *{Fig. 3}*

318 The general pattern of regeneration illustrated in Fig. 3 shows three identifiable stages. The initial
319 stage of regeneration represents gradual changes between successive assessments (closely grouped
320 samples) with a few exceptions. The exceptions were where induced mortality (poisoning) of stems
321 with no timber values (Fig. 3 i), and removal of merchantable stems (Fig. 3 i, j, k) occurred after the
322 initial assessment. The gradual changes between successive assessments are associated with a
323 decreased stem density, mainly in the abundant shade tolerant species. This caused changes in stem
324 size distribution (Fig. 4), but no discernable change in species richness.   *{Fig. 4}*

325 The second regeneration stage indicates a net loss of species, and a decrease in stem density,
326 culminating in the sites attainment of the lowest values in both characteristics (Fig.3, 4). These results
327 indicate that the vertical axis is significantly associated with changes in species abundance.

328 The reversal in the direction of the biplots marks the beginning of a third stage, which is associated
329 with increased species turnover and a net recruitment of both locally new and previously lost species.
330 This indicates that the first (horizontal) axis in Fig. 3 is significantly related to tree species
331 composition. Thus, the 2001 positions indicate different tree composition between the initial and the
332 2001 assessments (different positions in relation to the first axis), as well as a lack of significant
333 differences in their species abundances (relatively similar positions in relation to the second axis).

334   *3.3.   Changes in species diversity*

335   The controls did not show any significant change in the Brillioun diversity statistic, which ranged
336   between 3.03 and 3.13 with an overall mean of 3.07. In contrast, the overall average Brillioun statistics
337   for the logged sites decreased relative to logging intensity from individual tree selective logging
338   (2.76), moderate tree selection (2.56) and repeated individual tree selective logging (2.52) to intensive
339   logging (2.48). The percentage range between the minimum and maximum number of species (2001)
340   shows a similar trend. In general, the trends of the Brillioun diversity statistics parallel the three
341   regeneration stages defined above.

342   *3.4.   Stem density and stand basal area*

343   Changes in stem density for trees ≥ 10 cm dbh and stand BA contribution for both shade tolerant and
344   intolerant groups are presented in Figure 5. Chi-squared tests on the count of recruited stems indicated
345   that logged sites recruited a higher proportion of both shade tolerant and intolerant species in
346   comparison with the unlogged controls ($P < 0.003$). The densities of both shade tolerant and intolerant
347   species in individual tree selective logging recovered to levels comparable to those of the unlogged
348   controls within 30 years after logging (Fig. 5). Although the density of shade tolerant species in
349   repeated individual tree selective logging had recovered to similar levels, the density of shade
350   intolerant species was high, and comparable to that observed in the intensively logged sites. Both
351   moderate tree selection and intensive logging showed high densities of shade intolerant species, while
352   the densities of the shade tolerant species were lower in comparison with the unlogged controls.

353   *{Fig. 5}.*

354   There was a net increase in the overall stand BA in both logged and unlogged sites. The average
355   contribution of shade intolerant species to the pool of the stand BA for both the unlogged controls and
356   individual tree selective logging was negligible (<2.0%), but increased through moderate tree selection
357   and repeated individual tree selective logging (6.0%) to intensive logging (9.5%). However, the annual
358   rate of stand BA growth for both the shade tolerant and intolerant species showed a switch between
359   moderate tree selection and intensive logging. Thus, average annual rate of stand BA growth increased
360   from the unlogged controls (0.31% and nil) through individual tree selective logging (0.39 and
361   negligible), intensive logging (0.64 and 0.30%) and repeated individual tree selective logging (0.68
362   and 0.35%) to moderate tree selection (0.88 and 0.39%). These indicate poor recruitment and growth
363   of shade intolerant species in less disturbed sites (controls and sites subject to individual tree selective
364   logging), while significant recruitment and growth occurred in both species groups in sites subjected
365   to more intensive logging.

366   *3.5.   Diameter distribution*

367   The trends associated with diameter distribution in the various dbh-classes are shown in Fig. 6. A
368   small intra-plot correlation value of 0.26 (the proportion of the total variance explained by the within
369   plot variance) indicates that the diameter distribution remained relatively similar within a sampling
370   station (plot or amalgamated similarly treated plots in site), but varied considerably between stations.

371   *{Fig. 6}*

372   The parameter estimates shows that the rate of change in diameter distribution is influenced by tree
373   size, level of disturbance, time since the last major disturbance and the interaction between these
374   factors (Table 2). There were no significant changes in diameter distributions in the unlogged controls
375   (Fig. 6). However, the overall linear rate of change in tree diameter distribution across levels of
376   disturbance was significantly different from zero. For example, the number of stems in both the
377   smallest (10-19.9 cm) and largest (over 60 cm) dbh-classes decreased initially, reaching minima
378   between 10 and 20 years, and then increased. A positive quadratic effect with time indicates the
379   overall tendency for the number of stems to increase with time across dbh-classes (Fig. 6). In general,
380   the trends depicted by tree diameter distribution correspond to the defined regeneration stages.

381   *{Tables 1}*

382 **4.** **Discussion**

383 This study has demonstrated that post disturbance regeneration responses in subtropical rainforest of
384 north-east New South Wales, Australia, are correlated with disturbance intensity. The exception was in
385 the case of average annual rate of stand BA growth for both the shade tolerant and intolerant species,
386 which varies depending on the post-logging stage and successional events. Although intensive logging
387 shows high annual growth rates at the tree level (Kariuki et al., 2006), low density of retained large
388 trees, small sized recruited shade tolerant stems and high turnover of recruited shade intolerant trees
389 lowered the overall stand BA contribution in the intensively logged sites. High post logging mortality
390 in the moderately logged sites, especially in heavy tree selection was a transient event, and mortality
391 rapidly returned to lower levels. This is consistent with studies by Nebel et al. (2001) and Smith and
392 Nichols (2005). Thus, despite the initial mortality, moderately logged sites retained a high density of
393 large sized shade tolerant stems. Moderate growth rate in the retained large shade tolerant stems and
394 low turnover in recruited trees resulted in high overall stand BA contribution in both shade tolerant
395 and intolerant species.

396 *4.1.   Regeneration patterns in logged and unlogged sites*

397 The unlogged controls showed limited and gradual changes where the overall rate of change in species
398 abundance and diversity as well as in stem size distribution was not significantly different from zero.
399 However, in the intervening 36 years, there was an overall 8.7% (approximately 0.24% per year)
400 increase in stem density. In addition, the overall stand BA contribution to the BA pool for the shade
401 tolerant species group increased by 10% (0.28% per year). This can be attributed to enhanced
402 recruitment and growth following natural mortality (Fig. 4, 5). It has also been suggested that such
403 changes could result from climatic change over the last 3 decades of the 20th Century, especially
404 changes in solar radiation and increases in both air temperature and atmospheric concentration of
405 carbon dioxide (Lewis et al., 2004). Furthermore, natural unlogged rainforest rather than being a static
406 community is in a process of continuous (albeit sometimes gradual) change (Gomez-Pompa and
407 Vazquez-Yanes 1981). This change includes the slow replacement of the dominant tree species, while
408 maintaining a relatively similar floristic assemblage (Richards, 1952; Schulz, 1960).

409 As would be expected, increased logging intensity was negatively associated with stem densities, and
410 species abundance and richness. This was due to targeted removal of large commercial and non
411 commercial (silvicultural treatments) tree species, and an increased mortality soon after logging. These
412 results are consistent with studies in tropical rainforests (Walters et al., 1982; de Graff, 1986) as well
413 as in other vegetation (Korning and Baslev, 1994). Initial changes in the logged sites for the first five
414 to ten years after logging were gradual, as small changes between successive samples were observed.
415 This was attributed to post-logging mortality leading to decreased stem density of the most abundant
416 species, but without any significant change in species richness. The gradual phase was followed by
417 rapid changes marked with periods of distinct floristic assemblages, and a rate of stem size distribution
418 significantly different from zero. This can be attributed to both local species loss, and gains of
419 previously lost and locally new species. Oliver and Larson (1996) argue that following disturbance in
420 rainforests, the regeneration pattern further affects the arrangement of stand structure, reflecting the
421 impact of the initial disturbance.

422 Species abundance and richness returned to levels similar to those observed in the unlogged controls
423 (pre-logging state) within 30 years of logging, supporting the findings of King and Chapman (1983),
424 and Smith and Nichols (2005). However, apart from the sites subjected to individual tree selective
425 logging, which had recovered their pre-logging species diversity, moderate to intensively logged sites
426 had not recovered to similar levels 36 years after logging (Fig. 5). This is contrary to the findings by
427 Smith and Nichols (2005). Although stem density in the individual tree selective logging have
428 returned to their pre-logging levels, when trees were grouped into dbh-classes, the majority of these
429 stems were in the smaller sized category, and density of the larger stems $\geq$ 40 cm dbh were yet to
430 recover to pre-logging levels (Fig. 4).

431 This study shows that while the overall species abundance and richness, and stem density measures
432 redeveloped rapidly, species diversity and stand structure developed more slowly during regeneration,
433 especially in the more intensively logged stands. Similar findings were reported in a successional
434 study of a rain forest in Mexico (Gomez-Pompa and Vazquez-Yanes, 1981). Thus, the restoration of
435 species abundance and richness to levels similar to that of intact primary forest takes considerably less
436 time than structural and diversity restoration (King and Chapman, 1983; Olsen, 1989; Hubbell and
437 Foster, 1990). This can be further complicated by continuous or repeated disturbances (see Hitimana et
438 al., 2004), as observed in repeated individual tree selective logging.

439 *4.2   Regeneration stages*

440 The regeneration patterns detected in this study indicate three stages across both sites and levels of
441 disturbance. The first stage depicted small changes between successive assessments that lasted for
442 about 10 years (Fig. 3). This was attributed to mortality in species with high frequency, especially the
443 shade tolerant species due to natural causes, in the controls and logging injuries in logged sites (Fig.
444 5a). This mortality decreased stem density with no significant change in species richness, but an
445 observable impact on diameter distributions (Fig. 4). Thus, although logging injuries and hence post
446 logging mortality are common in the frequently encountered tree species (de Graff, 1986; Oavika,
447 2002; Silva et al., 2002), a decrease in the number of stems in these species without substantial change
448 in species abundance reflected very little or gradual change in the floristic assemblage.

449 The second stage also lasted about 10 years. This stage was associated with rapid changes and decline
450 in both stem density and species richness due to continued net mortality and species turnover. Thus,
451 during this stage, the sites registered the lowest values in both the stems ≥10 cm dbh and species
452 richness (Fig. 3, 4). Compared to the 2001 floristic compositions, the lowest values in species richness
453 were positively correlated with levels of disturbance. For example, the floristic assemblage in the
454 unlogged controls registered 12% less species, individual tree selective logging 16 - 28%, moderate
455 and repeated single-tree selection 28% and the intensively logged sites 39 - 46%.

456 Rapid changes were also evident in the third stage of regeneration, which was characterised by
457 increased species turnover and a net increase in recruitment of trees ≥ 10 cm dbh. Recruitment
458 surpassed mortality, and reversed the decreasing trends. An increase in species abundance and
459 richness, as well as stem density in both shade tolerant and intolerant species occurred, particularly in
460 the smallest dbh class (10-19 cm). Successive assessments at this stage included sample(s) that were
461 less similar to one another due to species turnover, recruitment of both locally new and previously lost
462 species, and recovery from past disturbances. The cluster-expansion results showed that the
463 regeneration patterns represent a sub-series of regeneration events within a continuum (Fig. 2).

464 Although natural dynamics in the unlogged controls did not show any significant changes in species
465 diversity, and stem size distribution remained unchanged, the death of a few large stems created
466 canopy gaps. These canopy gaps albeit few, initiated regeneration activities similar to those observed
467 in the logged sites. This could explain the similar regeneration patterns observed in some unlogged
468 rainforest stands (Molino and Sabatier, 2001; Sheil, 2001).

469 *4.3.   Regeneration patterns of tree species functional-groups*

470 The regeneration patterns and trends showed the combined effects of functional group compositions
471 along the disturbance gradient. For example, low disturbance in both unlogged controls and sites
472 subjected to individual tree selective logging created small canopy gaps. The small gaps were quickly
473 reoccupied by the retained stems and advance regeneration with no significant recruitment of shade
474 intolerant species. Similar results and conclusions were reported for a study in a semideciduous
475 tropical forest in Mexico (Dickinson et al., 2000). In our study, stem densities of the shade intolerant
476 species returned to levels comparable to that of the unlogged controls within fifteen years of individual
477 tree selective logging. However, stem densities of the shade tolerant species required about twice as
478 much time to return to similar levels (Fig. 5).

479 Although the density of shade tolerant species in repeated individual tree selective logging has also
480 returned to pre-logging levels, the density of shade intolerant species was high and comparable to that
481 observed in the intensively logged sites. This is not surprising given that repeated individual tree
482 selective logging only targeted large commercial trees for removal without culling the non commercial
483 species including shade intolerant species. Therefore, although individual tree selective logging may
484 mimic natural disturbance, if it is repeated without silvicultural stand improvement or ecological
485 restoration, the proportion of shade intolerant species is likely to increase in comparison with
486 unlogged stands (see also Kariuki and Kooyman, 2005).

487 Moderate tree selection and intensive logging removed more trees than individual tree selective
488 logging. This created large canopy gaps and significantly decreased both stem density and species
489 richness. The large canopy gaps also facilitated significant germination, establishment, and
490 recruitment of both shade tolerant and intolerant species. However, high densities of shade intolerant
491 species and low densities of shade tolerant species in comparison with the unlogged controls
492 accompanied moderate tree selection and intensive logging (Fig.5). This indicates that the large
493 canopy gaps created by moderate and intensive logging facilitated the recruitment of more shade
494 intolerant species at the expense of shade tolerant species. These results support the findings of
495 Hawthorne (1993) on forest regeneration in the Bia South Game Production Reserve Ghana and
496 Dickinson et al. (2000) in semi-deciduous tropical forest in Mexico.

497 The overall average contribution of shade intolerant species to the stand BA pool increased with
498 disturbance intensity, with the converse occurring for shade tolerant species (Fig. 5). The results of
499 this study indicate slow growth, and fewer stems of the shade intolerant species group in less disturbed
500 sites, while both species groups registered increased recruitment of stems and high growth rates in
501 sites subjected to moderate and intensive logging.

502 It appears that logging disturbance produced characteristic changes in the biotic and abiotic
503 environments that not only influence the floristic composition at the onset of regeneration, but also
504 affected later stages (Gomez-Pompa and Vazquez-Yanes, 1981; Webb, 1998; Magnusson et al., 1999).
505 For example, a return to the pre-logging state in logged sites with a high proportion of shade intolerant
506 species is expected to take a relatively long time due to continuing species turnover and secondary
507 treefall disturbances that characterize the dynamics of stands dominated by this species group (see
508 Smith and Nichols, 2005). This process will increase the overall level of mortality for a longer period
509 (Silva et al., 2002). As this trend continues, the proportion of short-lived shade intolerant species ≥ 10
510 cm dbh in logged sites may decrease, as the individuals in this species group are replaced by long-
511 lived shade tolerant tree species (Kariuki and Kooyman, 2005). As a result, the rate of change in
512 species diversity and stand structure will slow as the logged sites gradually approach their pre-logging
513 states.

514 **5.   Conclusions**

515 This study demonstrates that in subtropical rainforests post disturbance regeneration responses are
516 correlated with disturbance gradient. Rainforest tree species-specific levels of shade tolerance during
517 establishment, recruitment and development as well as life history, and trade-offs between rate of growth
518 and persistence in the canopy can be used to explain the observed patterns of regeneration. This is
519 because tree species group (shade tolerant and intolerant) responses relate to the interaction between the
520 regeneration niche and the successional status of the trees. Individual tree selective logging removed only
521 a few large trees and the retained trees together with advance regeneration reoccupied the created gaps
522 that healed quickly without a significant regeneration of shade intolerant species. Thus, sites subjected to
523 this type of treatment appear to have returned to their pre-logging states in all aspects, except stem size
524 distribution. Because of their slow growth, the density of trees ≥ 40 cm dbh was low in comparison with
525 the controls. More intensive logging created large canopy gaps that facilitated regeneration and
526 recruitment of both shade intolerant and tolerant species. Thus, the overall species abundance and
527 richness, as well as stem density in the smaller sized trees were generally higher compared to pre-logging
528 levels. However, the sites had low species diversity and low stem density of shade tolerant species.

529 Conversely, the number of shade intolerant species was high compared to that observed in the controls.
530 This suggests that the restoration of forest structure takes considerably more time than the restoration of
531 tree species abundance and richness following logging in these forests.

532 Post disturbance regeneration events across both sites and levels of disturbance were similar resulting
533 in three identifiable stages; (1) initial period of slight change where the density of the abundant shade
534 tolerant species decline without significant change in species richness, (2) a period where both species
535 and stem density decrease to minima, and (3) a period where the species richness and stem density
536 increased surpassing previous levels.

537 This study also showed that moderate tree selection may facilitate high stand level BA growth rate
538 compared to single-tree selection or intensive logging. This indicates high timber production potential at
539 moderate tree selection in this type of forest. The long time taken for stem size distribution to return to
540 pre-logging levels suggests a need to consider logging cycles with a long return period in these forests.

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719

720 **Figure captions**

721 Fig. 1. Rainforests of north-east New South Wales and the study sites

722 Fig. 2. Chronological clustering showing time series response of changes over 3 decades in permanent
723   sample plots subjected to disturbance levels ranging from natural to intensive logging in
724   subtropical rainforests of north-east New South Wales, Australia. Steinhaus coefficients using
725   association matrices derived from species abundance of repeated sampling are shown. Clusters
726   of consecutive assessments are shown by a thick line segment, cluster expansion tests for α =
727   .2 a thin line segment, singleton (aberrant sample) by a (*), and logging at the plot by a
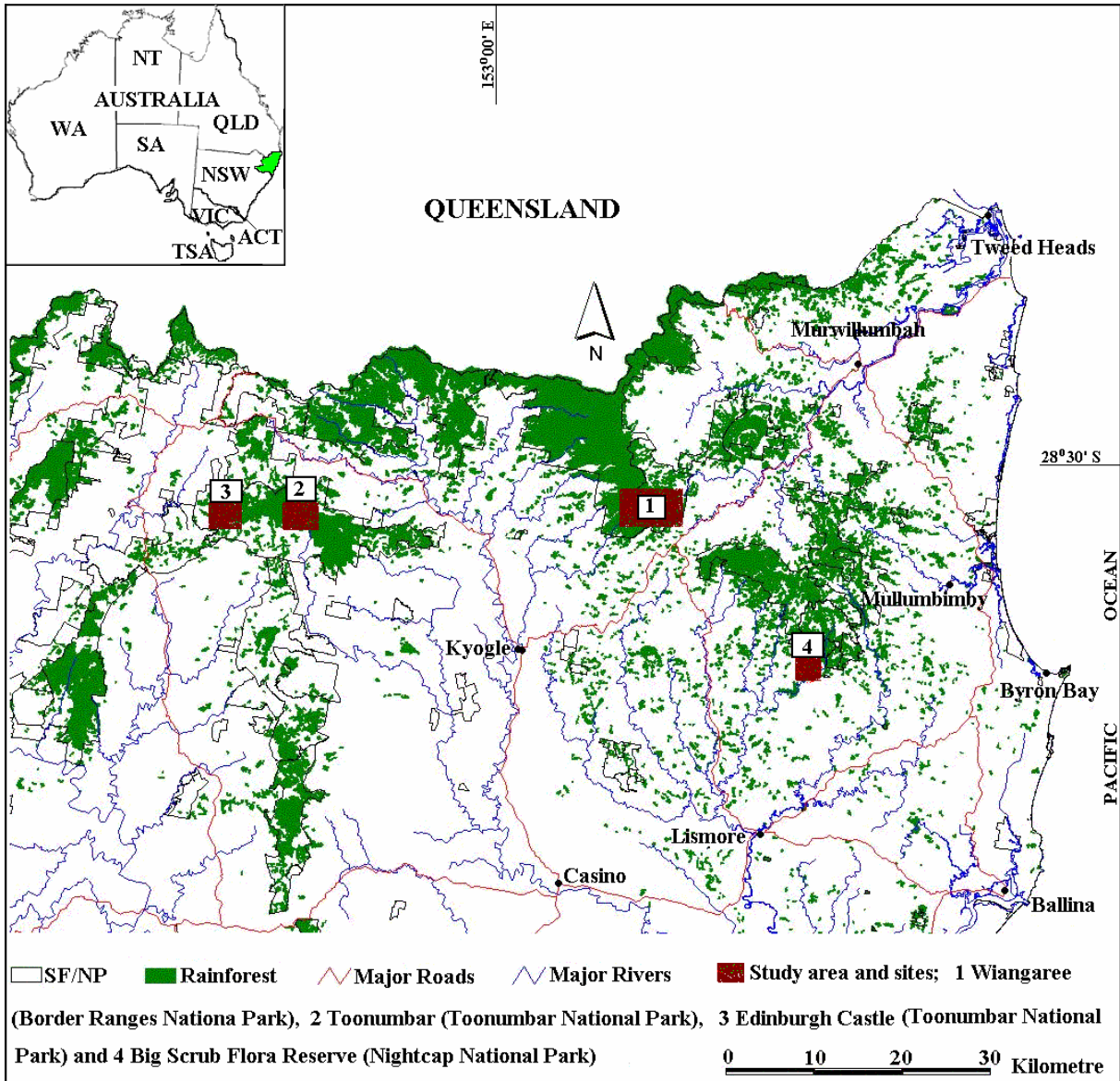728   downwards pointing arrow.

729 Fig. 3. Regeneration changes in subtropical rainforests of north-east New South Wales, Australia.
730   Biplots show the first two axes of principal coordinate analysis using Chord coefficient
731   association matrices derived from species abundances standardised by object vector on
732   repeated sampling in permanent sample plots. Samples with similar species abundance at α =
733   0.2 are enclosed. Treatments: controls 0% basal area removed (a), individual tree selective
734   logging 1-33% in 3 sites; (b c & d), repeated individual tree selective logging estimated
735   51-65% (e), moderate logging 36-50%; tree group selection from Queensland (Australia) 47%
736   (f) and heavy tree selection from New South Wales (Australia) 50% (g), intensive logging 66-
737   80%; clear cut from Sabah Malaysia 70% (h), Pre-exploitation shelterwood from Nigeria 70%
738   (i) Post-exploitation Shelterwood from Trinidad and Guyana 74% (j), Improvement treatment
739   from the Democratic Republic of Congo 71% (k) and logging with enrichment 78% (l).
740   Numbers beside plotted points indicate sampling dates (e.g. 57 represents 1957, 01 represent
741   2001).

742 Fig. 4. Changes in the number of tree stems in various dbh-classes in relation to time in both unlogged
743   and logged stands in subtropical rainforests in north-east New South Wales, Australia.
744   Average percentage of individuals occurring in relation to the maximum observed is shown in
745   parenthesis (logged stands show average since logging). Samples with similar species
746   abundance at α = 0.2 are enclosed. Treatments: controls 0% basal area removed (a),
747   individual tree selective logging 1-33% in 3 sites; (b c & d), repeated individual tree
748   selective logging estimated 50-65% (e), moderate logging 36-50%; tree group selection from
749   Queensland (Australia) 47% (f) and heavy tree selection from New South Wales 50% (g),
750   intensive logging 66-80%; clear cut from Sabah Malaysia 70% (h), Pre-exploitation
751   shelterwood from Nigeria 70% (i) Post-exploitation Shelterwood from Trinidad and Guyana
752   74% (j), Improvement treatment from the Democratic Republic of Congo 71% (k) and logging
753   with enrichment planting 78% (l).

754 Fig. 5. Population dynamics showing the number of stems $\geq$ 10 cm dbh and their basal area
755   contribution on a per hectare basis in shade tolerant (a and c) and shade in tolerant species (b
756   and d) across disturbance intensities in subtropical rainforests of north-east New South Wales,
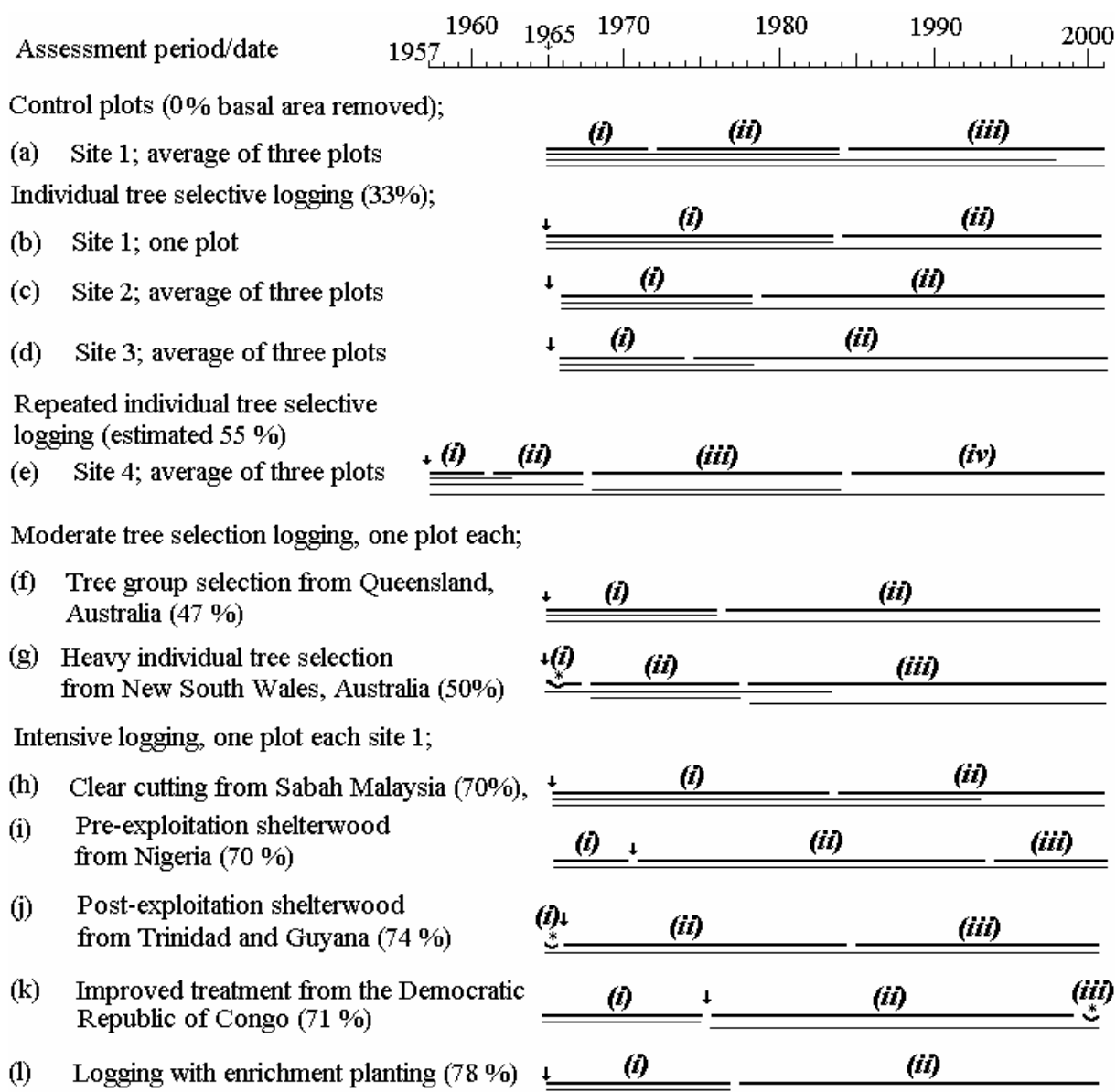
757   Australia. Treatment Treatments: controls 0% basal area removed (disturbance score of 1),
758   individual tree selective logging 1-33% (2), moderate logging 36-50% (3), repeated
759   individual tree selective logging estimated 50-65% (4), intensive logging 66-80% (5).

760   Fig. 6. Estimated log frequencies showing the patterns and trends of changes in number of stems in
761   various diameter classes in relation to time across disturbance intensities in subtropical
762   rainforests of north-east New South Wales, Australia. Disturbance intensity; controls 0% basal
763   area removed (*a*), individual tree selective logging 1-35% (*b*), moderate logging 36-50%
764   (*c*) repeated individual tree selective logging estimated 51 65% (*d*) and intensive logging
765   66-78% (*e*).

Fig. 1.

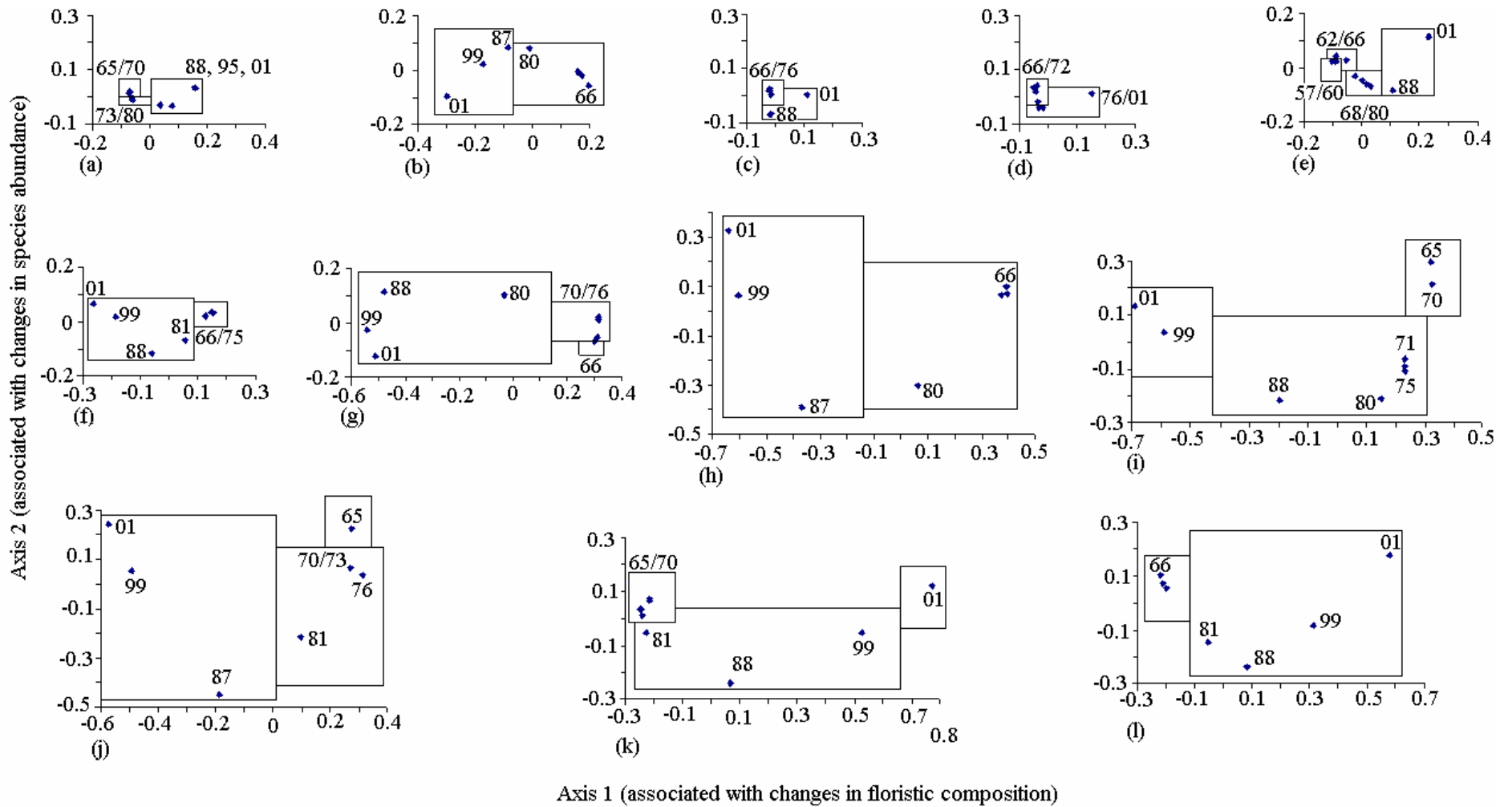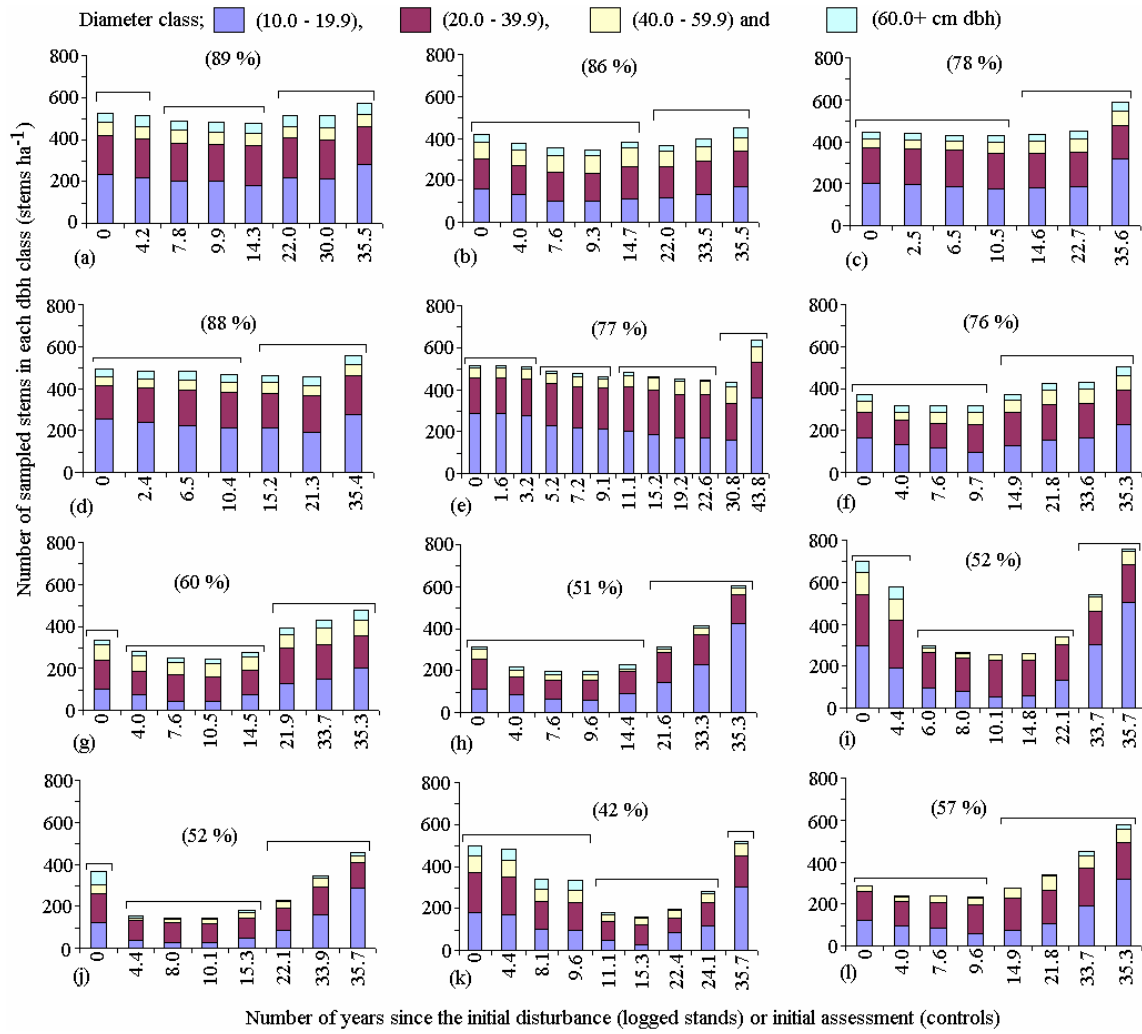Assessment period/date 1957 1960 1965 1970 1980 1990 2000

Control plots (0% basal area removed);

(a) Site 1; average of three plots *(i)* *(ii)* *(iii)*

Individual tree selective logging (33%);

(b) Site 1; one plot *(i)* *(ii)*

(c) Site 2; average of three plots *(i)* *(ii)*

(d) Site 3; average of three plots *(i)* *(ii)*

Repeated individual tree selective logging (estimated 55 %)

(e) Site 4; average of three plots *(i)* *(ii)* *(iii)* *(iv)*

Moderate tree selection logging, one plot each;

(f) Tree group selection from Queensland, Australia (47 %) *(i)* *(ii)*

(g) Heavy individual tree selection from New South Wales, Australia (50%) *(i)* *(ii)* *(iii)*

Intensive logging, one plot each site 1;

(h) Clear cutting from Sabah Malaysia (70%), *(i)* *(ii)*

(i) Pre-exploitation shelterwood from Nigeria (70 %) *(i)* *(ii)* *(iii)*

(j) Post-exploitation shelterwood from Trinidad and Guyana (74 %) *(i)* *(ii)* *(iii)*

(k) Improved treatment from the Democratic Republic of Congo (71 %) *(i)* *(ii)* *(iii)*

(l) Logging with enrichment planting (78 %) *(i)* *(ii)*

768

769 Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Diameter (dbh) class

◆◆◆◆◆◆ (10 - 19.9),

●●●●●● (20 - 30.9),

▲▲▲▲▲▲ (40 - 59.9),

✕✕✕✕✕✕ (≥ 60 cm)

Predicted log frequency

(a)

(b)

(c)

(d)

(e)

8   Time showing the number of years since disturbance (logged) and initial assessment in control sites
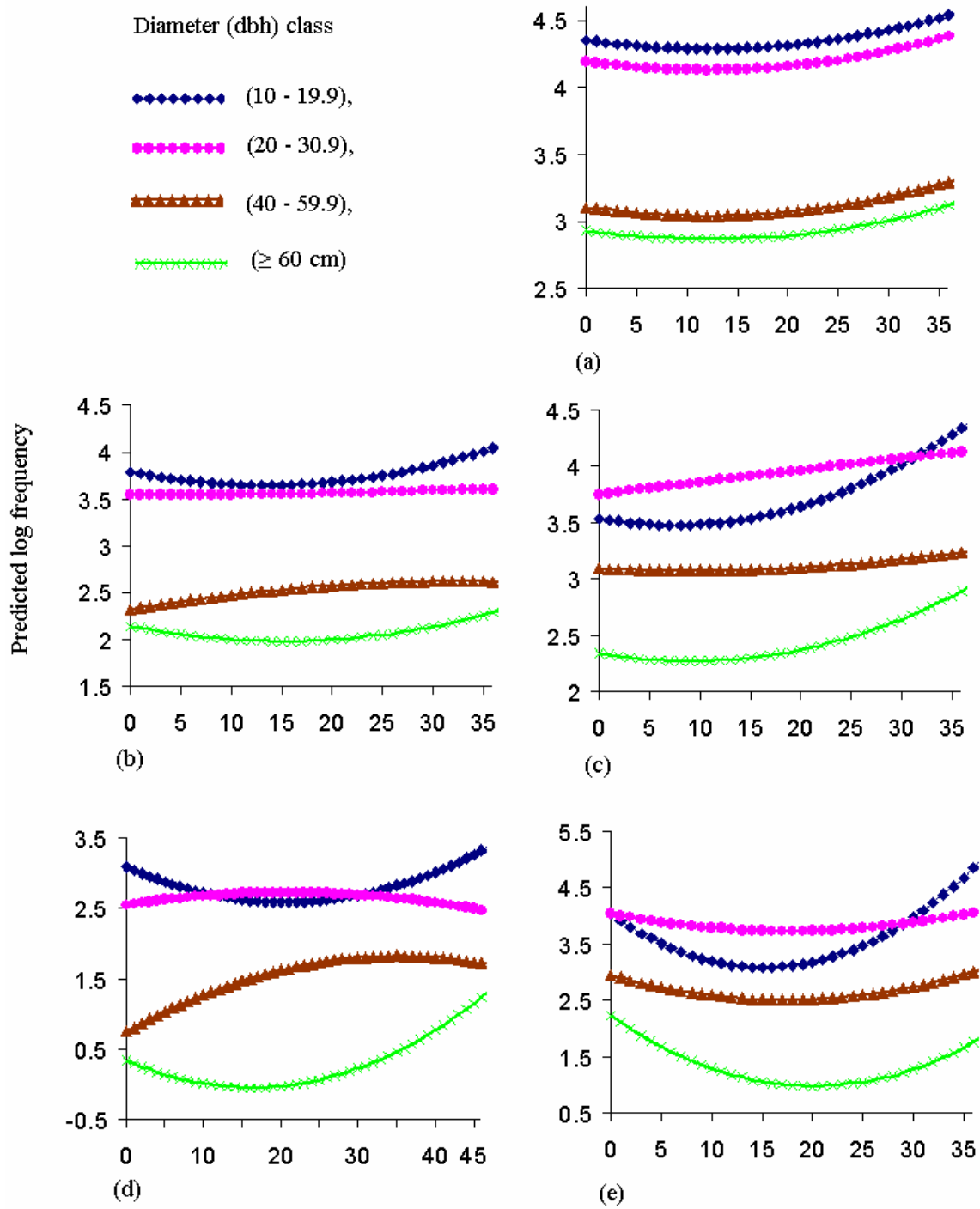
9

10   Fig. 6.

11   *Table 1*.Sites and silvicultural treatments (9 categories) showing logging intensity (based upon
12   the percentage basal area (BA) removed). The BA removed in treatment that occurred in phases
13   such as the Congo treatment refers to the total BA removed.

Site location, treatments description and the percentage BA removed.

Control (0% BA removed) disturbance level score of 1:

Three plots in the Border Ranges National Park (site 1)

Individual tree selective logging (1-35%) with a disturbance level score of 2**:**

One plot in site 1; Individual merchantable stems were logged in 1965 and a nominal 50% canopy cover was retained **(33%)**.

Former Toonumbar State Forest (site 2), three plots: Individual merchantable stems logged in 1965 during a routine timber harvest, and plot established in 1966 **(33%)**.

Former Edinburgh Castle State Forest (site 3), three plots: Individual merchantable stems logged in 1965 during a routine timber harvesting, and plot established in 1966 **(33%)**.

Moderate tree selection in site 1 (36-50%) with a disturbance level score of 3, one plot per treatment:

Group selection from Queensland, Australia; climbers and undergrowth with no timber value were cut and merchantable stems greater than 61 cm dbh except seed trees were logged in 1965 followed by enrichment planting. A regeneration release operation was carried out in 1970 (47% BA removed).

Heavy individual tree selective logging from NSW, Australia; similar to individual tree selective logging above, but with more merchantable stems were removed in 1965 (50%).

Repeated individual tree selection logging at the Big Scrub Flora Reserve in Nightcap National Park

(site 4) with a disturbance level score of 4:

Repeated individual tree selective logging (between 1900s and mid 1950s - approximately 51 to 65% BA removal), three plots established in 1957.

Intensive logging in site 1 (66-80%) with a disturbance level score of 5, one plots per treatment**:**

Clear cut method from Sabah Malaysia; Assessment of regeneration carried out in 1965 followed by removal of merchantable stems (70% BA removed). Regeneration release operation performed in 1970.

Pre-exploitation Shelterwood from Nigeria; Vines were cut and stems with no timber value poisoned in 1965. Merchantable stems were logged 5/6 years later (1970/71 - 70% BA removed).

Post-exploitation Shelterwood from Trinidad & Guyana; Vines were cut in 1965 and logging of all merchantable stems in 1966. Selective poisoning of remaining stems in 1966 formed Shelterwood. Regeneration release operation performed 5 years later (1970 - 74% BA removed).

Improvement treatment from Democratic Republic of the Congo; Vines were cut in 1965 and stems with no timber value poisoned in 1970. All merchantable stems logged 10 years later (1975 - 71% BA removed).

Logging with enrichment planting; All merchantable stems logged in 1965, shelterwood created by selective removal of remaining trees or trees with no timber value, and enrichment planting with valuable faster growing species carried out. Regeneration progressively liberated over a 10-year period (78.4% BA removed).

Table 2. Summary for the hierarchical multilevel model building describing the association of diameter distribution in various dbh classes across logging intensities (control, light selection, moderate, light selection over time and heavy logging) in subtropical rainforests at the north-east NSW Australia. *; P ≤ 0.0001.

Association term or model	-2*loglikelihood (IGLS)= χ^2	Difference in -2*loglikelihood statistic (χ^2)	Degrees of freedom
A baseline variance components model	1919.99		
The dhh classes main effects	1032.19	887.8*	3
Logging intensity main effects	984.74	47.45*	4
Duration (time since logging) main effects	951.64	33.1*	1
Duration squared (quadratic) effects	920.74	30.9*	1
Logging intensity by dbh interaction effects	903.86	16.88*	12
Duration by dbh interaction effects	731.80	172.86*	3
Duration squared by dbh interaction effects	726.77	5.03	3
Logging intensity by duration plus logging intensity by duration squared by interaction effects	684.89	41.88*	8
Logging intensity by duration by dbh plus logging intensity by duration squared by dbh interaction effects	579.27	105.62*	24