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Diameter growth performance varies with species functional-group and habitat characteristics in subtropical rainforests

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Abstract

We examined tree diameter growth in 20 plots subjected to various disturbance intensities (natural, low, moderate and intensive logging) in a bid to understand the general tree growth responses in relation to habitat characteristics in subtropical rainforests of north-eastern New South Wales, Australia. Species-specific regeneration strategy, maximum size and level of shade tolerance were used to classify species into 5 groups; emergent and shade tolerant main canopy (group 1), shade tolerant mid canopy (2), shade tolerant understoreys (3), moderate shade tolerant (4), and shade intolerant (5) tree species. Data series for trees ≥ 10 cm diameter at 1.3 m above the ground level (dbh) providing observations spanning over 36-years were used in multilevel regression analyses. The results showed that spatial and temporal effects in tree growth at the stand-level are a combination of the differences between species functional-group compositions and environmental gradients. High growth responses were observed in the shade intolerant species while increasing level of shade tolerance and decreasing maximum size decreased trees growth rates. Tree growth increased with altitude on a large scale across regions, and with disturbance intensity on a small scale at the plot (stand) level. Increase in northness (south through flat to north facing sites) increased growth in species group 1 for trees < 67 cm dbh, but beyond this dbh threshold the opposite was true. These showed that saplings of species group 1 may require increased illumination to reach the forest canopy, but once in the canopy, low soil water availability may be limiting to tree growth in the north facing sites. Decrease in northness was associated with increased growth in species group 2 indicating that reduced illumination and improved soil moisture in the south facing sites were conducive for maximum growth in this species group. Maximum growth potential in species group 4 and 5 increased with decrease in eastness, suggesting that the increased afternoon solar radiation and temperature were conducive for high growth rates in these species. Although topographic gradient may determine the spatial and temporal variations in tree growth where growth appeared to increase from the crest down the slope into the creek, its effects on soil fertility and water availability, and interactions between these and other factors may make it difficult to discern clear growth patterns.

Key words: growth rate, functional-group compositions, environmental gradients, logging regimes

Introduction

Various studies in the rainforests and other types of vegetation have suggested that floristic assemblages are associated with habitat characteristics, including topography and site history such as major disturbances (Clough, 1979; Golden, 1979; Queensland Department of Forestry, 1983; Floyd, 1990; Hawthorne, 1993; Myerscough et al., 1995; Grubb, 1996; Agyeman et al., 1999; Kyereh et al., 1999). In Australian subtropical rainforest vegetation, the percentage of species with microphyll leaves increases with increasing altitude and at 1200 m above sea level, these species constitute about 90% of the forest structural component (Webb 1968). Clark and Martin (1999) found species groups that reflect spatial floristic variation with a clear altitudinal trend in heath. While altitude is a large scale macroclimatic modifier, at the local stand scale disturbance, aspect and topography are microclimatic modifiers at least partly responsible for the floristic patterns. For example, patterns of floristic assemblages in habitats with easterly to southerly aspect in the subtropical rainforest of Australia have been associated with tree species with special attributes to regenerate and establish in less illuminated and moist conditions (Clough, 1979; Floyd, 1990). For similar reasons, these species are also frequently observed in lower topographic positions towards creeks and valley bottoms (see Clough, 1979; Golden, 1979).

Increases in shade intolerant species have been associated with increased logging intensity indicating these species preference to more open and intensively logged habitats (Hawthorne, 1993; Dickinson et al., 2000). However, increased numbers of juveniles of both shade tolerant and intolerant species following logging has been recorded. This has been attributed to the regeneration and establishment of shade tolerant species below the canopy of shade intolerant species coupled with initial floristic composition regeneration responses (Egler, 1954; Connell and Slatyer, 1977; Connell and Green, 2000; Dickinson et al., 2000). In contrast to these spatial floristic correlative studies, field experiments that directly test the influence of habitat characteristics on growth in a particular forest are less common. In a semi-deciduous forest in Ghana, shade intolerant pioneer species associated with high-rainfall forest with less fertile soil, had significantly lower growth rates than pioneers that are more abundant in low-rainfall forest with more fertile soils (Baker et al., 2003). While working on tree ring chronologies of seven tree species in a semi-deciduous forest in Venezuela, Worbes (1999) reported a positive correlation between

annual rainfall and growth rates. At three sites in a seasonal forest in Panama, Devall et al. (1995) found that annual rainfall correlated with variations in tree ring width for three species. These studies suggest that species associations with particular habitat characteristics are useful indicators of maximum growth rate (Baker et al., 2003).

In modelling stand dynamics (growth, recruitment and mortality), environmental effects can be estimated from habitat characteristics including canopy layer, vegetation type, elevation, soil type, depth of the humus horizon, slope and aspect (Bossel and Krieger, 1994; Vanclay, 1992, 1994a; Sterba and Monserud, 1997). However, information on some of these habitat characteristics are very expensive to collect while attempts to incorporate simple habitat characteristics in growth models has not always been successful (Gourlet-Fleury and Houllier, 2000). If growth models for uneven-aged mixed-species rainforests are to increase their global efficiency and provide greater insight regarding the biological and ecological factors that determine rainforest dynamics and their productivity, then simple habitat characteristics that influence these dynamics are needed. These needs are more urgent now that the forest managers are required not only to sustain production, but also to conserve biodiversity while accounting for site variations (Sayer and Wegge, 1992; Stork et al., 1997). This is also necessary to support and strengthen the emerging sustainable forestry systems based on ecological needs of both the stand and species in the rainforest (Seydack, 2000).

This paper focuses on the growth of rainforest trees in relation to habitat characteristics and species functional groups. The data span over 36-years from both logged and unlogged natural rainforest stands. Logging intensities included single-tree selection, repeated single-tree selection, moderate logging and intensive logging. Aside from these different logging regimes, a great heterogeneity occurs including plot sizes (750 through 2000 to 3648 m^2), elevations (low 210-300 through mid 600-700 to high 900-920 m above sea level) and complex patterns of correlation from repeated measurements and nested sources. This heterogeneity reflects different circumstances that existed during the plots establishment and it presented some difficulties. For example, the use of different plot size may distort the relationship between basal area and some environmental conditions, as small plots may indicate higher basal area per hectare than comparable estimates of basal area

derived from an extended larger plot that include the small plots (Baur, 1962). However, the heterogeneity makes the data series suitable to explore the association between tree species growth responses and environmental conditions (habitat characteristics). In this study we consider the following specific questions:

(i) How do growth rates differ between species functional-groups defined by level of shade tolerance and maximum size at maturity?

(ii) Are differences in growth rates between species functional groups related to habitat characteristics?

We discuss how each of the measured habitat characteristics may influence the major resources (soil water availability and solar irradiance) and hence limit tree growth over various environmental gradients.

Methods

Study area

The rainforests in the north-east NSW have been primarily used for selective timber harvesting (Baur, 1962). For example, as the supply of red cedar (*Toona ciliata* M.Roem) dwindled, species such as rosewood (*Dysoxylum fraserianum* (A.Juss) Benth.), native teak (*Flindersia australis* R.Br) and white beech (*Gmelina leichhardtii* F.Muell) were sought (Forestry Commission of NSW, 1984). After the rainforest were logged of their most valuable species, they were then alienated and cleared for farming (Baur, 1962). Management in rainforest of NSW as opposed to conversion to either farmland or plantation was instituted in late 1956, when a provisional research working plan was introduced (Baur, 1962; Forrest, 1963). According to Baur (1961) and Forrest (1963) this plan included the establishment of a network of experimental permanent sample plots (growth plots) most of which determined the study area.

The total study area covers approximately 5.4 hectares of subtropical rainforests in four former State Forests located in north-east of New South Wales, Australia including:

The former Wiangaree State Forest now part of the Border Ranges National Park where 11 Permanent Sample plots (PSP) each measuring 60.4 x 60.4 m were established in 1965 (see Horne and Gwalter, 1982).

Toonumbar and Edinburgh Castle State Forests, both in Toonumbar National Park where 3 PSP each measuring 50 x 40 m were established in 1965 in each of the State Forests following single-tree selection logging.

The Big Scrub Flora Reserve in the former Whian Whian State Forest now part of Nightcap National Park where the earliest 3 PSP each measuring approximately 30 x 25 m were established in 1957 following the withdrawal of repeated single-tree selection logging (Forrest, 1963).

The sites lie between 28° 30' and 28° 45' South, and 152° 45' and 153° 30' East, and range in altitude from about 210-300 (the Big Scrub Flora Reserve) through 600-700 (Toonumbar National Park) to 900-920 (Border Ranges National Park) meters above sea level (masl). The vegetation is Complex Notophyll Vine forest, the most floristically diverse and structurally complex form of subtropical rainforest in Australia (Webb et al., 1984). Detailed description of treatments and intensity of logging for the Border Ranges experiment are given in Pattemore and Kikkawa (1974), Burgess et al. (1975), and Horne and Gwalter (1982) who have analysed some of the data for other purposes. In this study treatments are reduced into four levels of disturbance based on the percentage overstorey basal area removed; control (0 % overstorey basal area removal), single-tree selection logging (1-35 %), moderate logging including repeated single-tree selection (36-65 %), and intensive logging (66-78 %).

Data description

Data used in this study are from 4064 trees ≥ 10 cm dbh, which have been identified to species, tagged and assessed at least once and at most 12 times resulting in 19303 individual measurements. The Research and Development Division of State Forests of NSW (and its predecessor) collected most of the data during 1957-1999 and in 2001 the first author reassessed the plots. Quality control using 5

plots revealed a random error of previously wrongly identified species ranging from 4 to 33 %. This necessitated a complete review of field identification and records of data to reconcile the previously collected data with that collected during the 2001 census. Most of the anomalies were reconciled, but due to mortality about 0.4% of trees remain unidentified and some 0.6 % of missing data remained in trees that were assumed dead, or were 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 measurement(s). However, some of the larger trees could have been trees that survived thinning (poisoning) treatments. In addition, estimated diameter of very large tree above buttresses (*dab*) during the first 3 assessments were either too small or too large compared to measurements obtained later using a ladder. For the purpose of accounting the basal area associated with the large trees and subjects missed on one or more occasions, their *dab* or *dbh* were extrapolated assuming a constant rate of growth where measurements were inaccurate or unavailable. When the subject's measurements were used, the estimates were incorporated in growth model parameter estimations. In case of inaccurate measurements and situations where the trees had no tag, growth rate of a similar trees species and size, preferably in the same plot was assumed. These estimates were combined with other data to calculate stand basal area and trees competition indices, but they were removed from growth parameter estimations.

Habitat characteristics

Habitat characteristics assessed during the 2001 census include environmental factors such as average slope (degrees), aspect (degrees) and topographic position in relation to the top (crest) and bottom of the ridge; upper slope, mid slope, lower slope, and creek/gully. These were assessed from the centre of the plot without any consideration to distance. Altitude was deduced from the topographic maps of the area. In addition, both slope and aspect were used simultaneously to determine the stand orientation in reference to north-south and east-west (northness and eastness respectively).

Northness = sine (slope) multiplied by the cosine (aspect) and

eastness = sine (slope) multiplied by sine (aspect).

This would theoretically assign 1 to north- and east-facing cliffs, and -1 to a south- and west-facing cliffs respectively, and a zero to flat ground.

Species groups

Within the scope of rainforest dynamics, woody species (mainly trees and shrubs) are categorised into groups that are based on life history and light requirement for germination, establishment and growth (Decocq and Hermy, 2003). In this study, the tree species maximum size, species regeneration strategy and level of shade tolerance were used to classify 117 species into 5 groups, each encompassing ecologically similar species (Hopkins, 1977; Floyd, 1990; Kooyman, 1996; Favrichon, 1998). This classification assumes that on average, species of similar adult size or with similar functional attributes exhibit similar growth characteristics during their development. The species groups are:

Group 1, the few emergent tree species that are tall and their crowns 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 2 consisted of shade tolerant medium sized trees whose crowns are mainly within the mid canopy such as *Acronychia pubescens* (F.M.Bailey), *Akania bidwillii* (Hogg) Mabb and *Zanthoxylum brachyacanthum* F.Muell.

Group 3 consisted of shade tolerant understoreys, mainly small trees and shrub such as *Actephila lindleyi* (Steud) Airy Shaw, *Denhamia celastroides* (F.Muell) Jessup and *Wilkiea huegeliana* (Tul) A.DC whose crowns are below those of other species mentioned above.

Group 4 consisted of moderate shade tolerant and persistent tree species such as *Toona ciliata* M.Roem, *Flindersia schottiana* F.Muell and *Cryptocarya triplinervis* R.Br.

Group 5 consisted of shade intolerant pioneer tree species such as *Acacia melanoxylon* R.Br, *Dendrocnide excelsa* (Wedd) Chew and *Polyscias elegans* (C.More & F.Muell) Harms.

Data analyses

The data used in this study are associated with complex patterns of variability, especially from repeated measurements and nested sources. Multiple observations on the same tree/plot are correlated because they contain a common contribution from the same tree/plot. This allows us to use a tree/plot as its own comparison, or control to some degree because many factors that might be related to the outcome of interest may be constants within individual trees/plots. However, measures on the same trees close in time tend to be more highly correlated than measures far apart in time and the variances of repeated measures often vary with time (see Littell et al., 1998). Statistically, therefore, the observations of the dependent variable are not independent and to get proper estimates of variability, we need to take this non-independence into account. To partly address this problem log-transformation of the dependent variable (see below) was used to make the non-uniform residuals (residuals that may get bigger for bigger values of the dependent variable) uniform (see Littell et al., 1998; Hopkins, 2000). In addition, Goldstein et al. (1994) proposed a multilevel time series model for repeated measurements data that could be extended to the data structure in this study with a basic 3-level hierarchical structure. This structure is defined by measurements (level one units) that are nested within trees (level two units), which in turn are nested within plots (level three units). The importance of this structure is based on the assumption that annual growth of each tree as well as of each species group in a given plot tend to be more similar than that of trees or plots chosen at random from the population at large (Goldstein, 1999). This approach has the strength to model the repeated measured growth response over time as a continuous curve rather than a series of abrupt changes. In addition, because the basic unit of comparison is plot rather than tree or periodic annual measurement, the approach is also more revealing on growth performance. One constraint is that all subject's curves

must have the same functional form. However, this constraint is not very restrictive because some parameters may be zero.

Negative diameter growth was observed in some trees during some intervals. While this may be partly due to measurements errors, senescing trees are usually associated with negative growth (Dickinson et al., 2000). In addition, during seasons of severe drought a tree may fail to register growth at all, and may even register a negative growth, but when conditions improve an unusual positive growth may occur (see Dawkins, 1956). Thus, periodic negative and nil tree diameter increments are common growth phenomenon in rainforests and hence should not be corrected else errors could be introduced where none existed. To cater for negative growth an offset of 0.5 cm was introduced (see Gourlet-Fleury and Houllier, 2000).

Annual growth during measurement periods was assumed to be constant. Due to some relatively longer growing periods (8 years or more), the calculated annual periodic growth was used to estimate the tree dbh 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.

The annualised periodic increment was used as the basic time unit for our growth model. This choice is certainly reasonable as it provides adequate temporal resolution to address the question of changes and facilitates estimation of parameters of the model equation in a view of temporal resolution not provided by the available data.

Habitat characteristics including stand conditions such as stand basal area and basal area of all trees greater than the subject tree, and tree attributes were used as explanatory variables. Habitat characteristics; altitude and topographic positions were categorised into 3 and 4 classes respectively through binary coding, 0 or 1 (dummy variables).

Annual growth model specification

To account for annual growth changes all the factors that could influence growth at any of the three hierarchical levels were used in the following equation.

$$\ln (g + 0.5) = \beta_0 \ln d + \beta_1 d^2 + \beta_2 C + \beta_3 E + \beta_4 C/E * (\ln d + d) \quad (1)$$

where g is annual growth in cm and 0.5 is the offset added ,

$\ln d$ is the natural logarithm of the tree dbh (cm),

d^2 is dbh-squared (both $\ln d$ and d^2 are also referred to as growth functions),

C is competition index estimated using changes in one or more factors including basal area, basal area removed, total basal area for all trees greater than the subject tree and time since logging,

E is an estimate for the habitat characteristics such as altitude, northness, eastness and the topography,

$C/E * (\ln d + d^2)$ is the interaction effects between growth functions and habitat characteristics, and

βs are parameters to be estimated.

The use of binary coding allowed the inclusion of both quantitative (numeric) and qualitative (categorical) variables in a single equation. Changes in tree annual growth was examined by fitting 3-level hierarchical multilevel model to each species group dataset using the MLwiN package (Rasbash et al., 1999; Snijders and Bosker, 1999). The multilevel model allowed each plot's summary line to vary (be raised or lowered) from the overall average plots' line, the ith tree in the jth plot varied from its plot's average line and the kth census in the n'th tree also varied from the tree's average line (Franklin et al., 2001). The -2 log likelihood statistic (*IGLS*), which provided the maximum likelihood test estimate and the Wald's test were used as tests of significance (Rasbash et al., 1999).

Using one species dataset at a time, a variance component model with a constant was fitted and the resulting maximum likelihood value noted. The growth functions; natural log of dbh (d) and dbh-squared (d^2) were then added and the change in the maximum likelihood value used to determine whether the growth functions have any significant effects on the annual growth of trees. The model with the growth functions formed the base model on which the main effects of various explanatory variables including habitat characteristics were tested for significance one at a time using both the log likelihood statistic and Wald's tests. Fitting the main effects involved adding one explanatory variable at a time to the base model in order of magnitude from the preliminary testing. When an added variable did not result in a significant decrease in maximum likelihood or a significant Wald test value, it was removed. The next variable was then added and the process repeated to assess whether any one of them in conjunction with those already fitted significantly improved the model. If improvement to the model occurred the variable was retained and the others including those rejected earlier tried individually and collectively. The best model with growth functions and main effects that showed significant improvement to the model formed the next base model on which the interaction (growth functions by other variables) effect terms were added, one at a time and tested for significance as described above. The fitted models were scrutinised to confirm that all the included variables were significant using the maximum likelihood statistics or the Wald's tests.

Significance test and model fit

An independent dataset can provide a convincing test of model accuracy, but in this case, it was not possible to set aside a comprehensive dataset for the purpose of model evaluation from 20 sampling stations. Parametric bootstrapping that uses the actual data set as an estimate of the population distribution through sampling with replacement was used to construct bootstrap datasets that were then used to summarise the parameters of interest (Rasbash et al., 2000). The Markov Chain Monte Carlo procedure was used to provide statistical summaries for the mean parameters, including quantiles used to construct intervals for the mean model estimates (Rasbash et al., 2000).

In addition, the estimated residuals resulting from fitting equation (1) to the entire dataset for each of the five species groups were calculated and scrutinized at each of the three levels; plot, tree and census. These residuals were used for making inferences about the unknown underlaying values of residuals given the estimates including diagnostic plotting to ascertain normality, examine independent distributions (unbiased), systematic deviations (biased) and outlier data. These were supplemented with residuals in ascending order with 95 % confidence interval to examine where the confidence interval for the plot residuals do overlap with zero providing inferences on apparent plot departure from the overall average line predicted by the fixed parameters. This provides inferences of significant difference from the average line at the 5 % level. The pseudo R^2 values (defined as the proportional reduction in mean squared prediction error at the three levels; census, tree and plot) were used as an indication of goodness of fit for the data (Snijders and Bosker, 1999), but the plot-level R^2 values were considered more important. According to Snijders and Bosker (1999), the explained variance R^2 at the three level could be estimated using the following equations.

$$R_1^2 = 1- (\delta_i^2 + \phi_i^2 + \tau_i^2)/ (\delta_0^2 + \phi_0^2 + \tau_0^2) \quad (2)$$

$$R_2^2 = 1- ((\delta_i^2/\mathrm{n}) + \phi_i^2 + \tau_i^2)/ ((\delta_0^2/n) + \phi_0^2 + \tau_0^2) \quad (3)$$

$$R_3^2 = 1- ((\delta_i^2/nm) + (\phi_i^2/m) + \tau_i^2)/ ((\delta_0^2/nm) + (\phi_0^2/m) + \tau_0^2) \quad (4)$$

Where the mean squared prediction is the sum of the variance components at the 3-levels; census (δ_i^2), tree (ϕ_i^2) and plot (τ_i^2) levels (that is $\delta_i^2 + \phi_i^2 + \tau_i^2$), and R_1^2, R_2^2 and R_3^2 refers to the proportional reduction in these three variance parameters respectively, the subscript *i* and 0 represent the final and initial variance component model, *n* and *m* represent the average number of annual periodic measurements per tree and the average number of trees per plot respectively.

Results

Mean annual diameter increment models for the five species groups

The results revealed that species group, size (dbh and dbh-squared also referred to as growth functions) and simple habitat characteristics such as levels of disturbance, altitude, topography, northness and eastness were important in describing the annual tree diameter growth in subtropical rainforests. Summary statistics including parameter estimates, standard errors, and Wald test results are presented in Table 1. Means for fixed parameter estimates from the bootstrapping results appeared normally distributed and compared favourably with the fixed parameter estimates from the models albeit with slightly wider confidence intervals. However, bootstrapping results depicted higher plot level variance in all species group because the underlying plot level variances were close to zero, and therefore poorly estimated in bootstrapping with large stand errors.

Some of the normal probability plots expressed gentle S-shape curves rather than straight lines indicating that they were outlier-prone. Because tree growth in rainforest can vary from negative (during droughts) to exceptionally high, such as that witnessed following logging and reduced competition, it was not justifiable excluding any data as outliers. Moreover, residual patterns at both tree and plot levels were plausible and did not exhibit any particular structure, and appeared to be of uniform distribution without major bias. This indicates the validity of the assumption that residual errors at higher levels were normally and independently distributed with mean zero and constant variance.

The random part of the model for the emergent and shade tolerance main canopy species (species group 1) suggested that the intercept is significant at the plot (stand), tree and census levels. This indicates that there are significant interactions between habitat characteristics and growth responses that remained at all levels. Thus, habitat characteristics have a set of relationships with the growth of these species as a group and these relationships vary between plots, trees and also between censuses. These may indicate the difficulty in accounting for these relationships at the plot, tree and census levels because tree growth in species group 1 may depend on habitat characteristics that were not

investigated in this study, the stage of tree development and prevailing climatic and competition conditions.

The random parts for shade tolerant mid canopy and understorey, and shade intolerant species models (group 2, 3 and 5 respectively) suggest that the intercept is not significant at the stand level, but it is significant at both tree and census levels. These results reinforce that interactions between habitat characteristics and growth response vary not only from one tree to next, but also from one census to another in these species groups. However, the relationships between habitat characteristics and the growth of these species groups had been adequately accounted for at the stand-level. For moderate shade tolerant species, the intercept is only significant at the census-level. This indicates that the species growth responses for this species group are adequately described at both stand and tree levels, but there remained some interactions between habitat characteristics and growth response that could not be accounted for at the census-level.

The overall mean tree diameter growth responses within the range of the available data have been adequately described with 49-88% stand level variations accounted for by the annual diameter growth model parameter estimates (Table 1). Comparison of the growth models with measurements over the 35-year history of regeneration using randomly selected stems of average diameter, average diameter minus one standard deviation and average diameter plus one standard deviation did not show any significance difference between the observed and predicted annual diameter growth. However, the models were found to be slightly overestimating the annual tree diameter growth in species groups 3, 4 and 5 while underestimating in species group 1 and 2. The underestimation of the annual tree diameter growth in species group 1 appeared to increase with time, especially in larger trees (Fig. 1). Because species group 1 comprised the majority of the stems in the stands, simulations done using the average estimates were found to be underestimating the annual growth performance beyond the range of the available data. Attempts to ameliorate this problem through the removal of trees with negative diameter growth and the use of longer growing periods failed to improve the simulation results. A method that considered more than one annual growth response for each species group was used to resolve this, but that is beyond the scope of the current study.

Species functional-group compositions and environmental gradients

To demonstrate the general relationship between the functional-group compositions and environmental gradients, we assessed the unique contribution of a single habitat characteristic to the annual tree growth responses (growth rate) in the model while holding all the other variables at their means. That is, the effects of changing an explanatory variable from 0 to 1 for dummies, and plus and minus one standard deviation from the mean for continuous variables, keeping all the other variables at their sample means.

For example, as would be expected increase in logging intensities (percentage of overstorey basal area removed) significantly increased the mean annual diameter growth in all species groups and the higher the logging intensity the higher was the growth rate (Fig. 2). The emergent and shade tolerant main canopy species (group 1) expressed a negative relationship indicating that smaller trees respond with high growth rates to gap creation compared to larger trees. Similar patterns were also observed in the shade tolerant mid canopy and understorey species (group 2, 3) where, although tree size was not significant, diameter terms were retained in the model because the resulting growth form was more appropriate than a constant growth response. The average diameter growth for species group 2 in unlogged control is depicted as negative showing that the hypothetical nature of holding all variables but one at their average including logging (average scenario) could be difficult from a practical viewpoint to interpret. However, this is useful here to demonstrate the extreme possibility that helps with the interpretation of the association between the functional-group compositions and environmental gradients. Species group 1 registered relatively high growth responses compared to groups 2 and 3. The annual diameter growth responses for both species groups 4 and 5 (moderate shade tolerant and shade intolerant tree species respectively) showed positive relationships with small stems reaching maxima at 30-40 cm dbh and then negative relationships in larger stems. Species groups 4 and 5 depicted relatively high growth responses compared to the other groups, but in general species group 5 registered the highest annual growth responses (Fig. 2). These results indicate a gradient in species functional-groups growth responses based on both level of shade tolerance and maximum size at maturity. Increasing growth responses were observed from shade tolerant

understoreys through shade tolerant mid canopy, emergent and shade tolerant main canopy, and moderately shade intolerant to shade intolerant trees.

Increase in altitude was associated with increase in annual tree diameter growth responses, except in the case of group 4, which exhibited mixed growth responses (Fig. 3). At low altitude, this species group showed a rapid increase in annual diameter growth that peaked at 40 cm dbh and an equally rapid decrease thereafter. The rapid increase in annual diameter growth in species group 4 indicates repeated single-tree selection opened the forest canopy to provide favourable growing conditions for the recruited moderate shade tolerant tree species. The abrupt decrease in annual diameter growth in species group 4 indicates lack of large trees at low altitude making it difficulty to examine growth response in large stems. At mid altitude, there were a lack of large trees due to culling and logging, in addition to unfavourable growing conditions associated with single-tree selection that failed to open the forest canopy for optimum growth. At high altitude, species group 4 exhibited moderate growth in stems below 60 cm, compared to relatively constant growth in stems between 60 and 100 cm dbh with a sign of decrease beyond 100 cm dbh. These may indicate that large gaps created at high altitude favoured more rapid growth responses in small stems compared to large trees (Fig. 3).

Northness and eastness appeared to affect different species groups differently. In species group 1, increase in northness (south through flat to northern facing sites) was associated with an increase in growth rates for trees < 67 cm dbh, where recruits (10-20 cm dbh) had the highest annual growth responses. Growth responses generally decreased as stem size increased. Annual growth responses for stems in sites with southern aspect were the mirror image of the responses observed in sites with northern aspect and growth responses for trees in sites of average aspect formed the mirror line (Fig. 4). Shade tolerant mid canopy tree species showed low, moderate and high growth responses in sites associated with northern, average and southern aspects respectively. Moderately shade tolerant species exhibited low growth responses in sites associated with both northern and eastern aspect, moderate response in flat sites, above average growth response with southern aspect and maximum growth responses were observed in trees associated with the western aspect. Shade intolerance species

exhibited slow growth responses in flat sites, closely followed by trees associated with the eastern aspect and high growth responses in western aspect (Fig. 4).

Topographic gradients also affected species groups differently. Excluding the lower slope topographic position, diameter growth in medium sized shade tolerant species (group 2) increased from the ridge towards the creek/gully. Excluding the creek/gully topographic position (which was associated with few trees that portrayed negative growth under unlogged stand conditions), growth responses in the moderate shade tolerant trees (group 4) increased from the ridge to the lower slope topographic position (Fig. 5). Shade intolerant species (group 5) exhibited significantly higher growth in the mid-slope topographic position compared to the upper and lower slope and creek/gully positions. The annual growth showed an increase for stems up to about 30 cm dbh followed by negative relationship where growth decreased with further increase in stem diameter (Fig. 5). In general, growth responses were significantly different between upper slope and creek/gully topographic positions.

Discussion

In this study species-specific regeneration strategy, maximum size and shade tolerance were used to classify 117 rainforest tree species into 5 functional groups, each consisting of ecologically similar species (see also Kohler and Huth, 1998; Finegan et al., 1999; Kohler et al., 2000; Baker et al., 2003). Using site characteristics and the heterogeneity in the data, multilevel models described the average annual tree growth indicating that the subtropical rainforest tree growth rates were functions of functional-group and environmental gradients (see Brokaw, 1985; Denslow, 1987; Brokaw and Busing, 2000). 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 their attempts to incorporate site information remained unsuccessful because the site characteristics did not improve their growth model.

The patterns of tree growth rates in the current study appear to decrease from the shade intolerant through moderate shade tolerant, emergent and shade tolerant main canopy, and shade tolerant mid canopy to shade tolerant understorey tree species. These findings support suggestions that interspecific

variation in maximum potential growth rate is one of the most important factors in the definition of robust functional groups (Baker et al., 2003). According to Baker et al. (2003), difference in species growth rates integrates numerous traits that underlie trade-offs among strategies for resource acquisition, defence against natural enemies and allocation to reproduction. For example, short-lived shade intolerant species grow faster due to higher intrinsic growth rates at a given irradiance and in high-light site characteristics in canopy gaps compared to the long-lived more shade tolerant species (Swaine, 1994; Baker et al., 2003). During the early stages of tree development an emergent and shade tolerant main canopy tree (group 1) may persist and endure dense shading effects without any growth for years, but when a canopy gap occurs the tree exhibits high growth rates. At the plot level, habitat characteristics that determine the amount of light at the stand are important to the diameter growth of these species as a group during ontogeny (Baker et al., 2003). At the census level, trees of this species group grow in response to the prevailing climatic and competition conditions, which changes from one year to the next, as does the growth response. As the results showed, these growth relationships and the scenario - where members of this group appear to switch from shade tolerant to intolerant during later stages of their development – can be partly explained, but it is difficult to account fully.

There was considerable spatial and temporal variation in the overall tree growth responses in relation to environmental gradients including logging intensity, altitude, site orientation (northness and eastness) and topography. For example, logging reduces competition and increases the availability of resources, and as would be expected the overall growth rates in all species groups increased from the unlogged control through single-tree selection, moderate tree selection to intensive logging (Fig. 2). Rainfall is an important factor setting limits to the spatial distribution of forests and at large scales it is closely associated with altitudinal variation (Walter, 1979; Woodward, 1987). In this study tree growth rates increased from low altitude (200-400) through mid (500-700) to high altitude (over 700 m above sea level), although this pattern does not match the trend in total amount of rainfall. In eastern Australia rainfall decreases with distance from the coast and mid altitude sites are farthest from the coast and therefore have the lowest rainfall. The increased growth at high altitude may therefore reflect other factors responsible for increased soil water availability such as the combined effects of

decrease in temperature and rates of evapotranspiration. There is also persistent low cloud at mid and high altitude and hence increased fog drip, which could compensate for the reduction in rainfall (Floyd, 1990).

Site orientation is a local microclimatic modifier that was associated with contrasting growth responses (Clough, 1979). The emergent and shade tolerant main canopy trees associated with the northern aspect recorded higher growth rates in trees < 67 cm dbh compared to trees on flat terrain and those in southern facing sites. The high growth rates for trees < 67 cm demonstrate that the saplings of this species group can respond to large increases in canopy illumination to reach the forest canopy (Clark and Clark, 1992; Milton et al., 1994; Hawthorne, 1995). However, once the trees reach the forest canopy, soil water availability rather than the amount of solar radiation may became limiting to growth. This is supported by the trees > 67 cm dbh in the relatively moist southern facing sites showing higher growth potential compared to those in flat sites, which in turn had higher growth responses compared to those in the relatively dry northern facing sites. This change parallels patterns in soil water availability due to change in aspect from north to south, which reduces the amount of solar radiation, increases shading effects, reduces both the temperature and rates of evapotranspiration, and improves moisture regimes (Clough, 1979; Floyd, 1990).

The growth rates in shade tolerant mid canopy trees increased from the northern facing sites through flat to southern facing sites (Fig. 4). This suggests that soil water availability was the main limiting factor to growth in the shade tolerant mid canopy trees, as they are in partial shade where they never reach the forest canopy, and hence they do not need large increase in canopy illumination. Growth rates for the moderate shade tolerant trees increased from the northern through eastern/flat and southern to western facing sites, while that of shade intolerant tree species increased from flat through east to western facing sites. This suggests that the afternoon solar radiation and increased temperature associated with western aspect are conducive for maximum growth potential in both moderate shade tolerant and shade intolerant tree species.

Topography also acts as a local microclimatic modifier where solar radiation decreases and shading effects increase down the slope. Corresponding decreases in both the temperature and rates of evapotranspiration result in improved moisture regimes (see Clough, 1979; Golden, 1979). In addition, experimental studies of seedling growth also demonstrate that topographic gradients in soil fertility can cause differences in growth of individual species (Gunatilleke et al., 1996; Veenendaal et al., 1996). Therefore, the role of topographic gradients in determining spatial variation in stand-level growth rates can be difficult to discern and interpret. For example, shade tolerant mid canopy species (group 2) registered low growth rates in upper and lower slope topographic positions, but high growth rates in mid slope and creek/gully topographic positions. While the low growth rates recorded in upper topographic position could be attributed to low soil water availability, low growth rates in the lower slope topographic position may be attributed to high competition, especially from the emergent and shade tolerant main canopy, and moderate shade tolerant trees (groups 1 and 4 respectively). The growth pattern of moderate shade tolerant tree species increased from the upper slope through mid to lower slope topographic positions (Fig. 5). While increasing trend of soil moisture may help to explain this pattern of tree growth, low irradiance and few trees may account for the lowest growth rates in the creek/gully topographic positions. Moreover, the few large mature trees and very small sized recruits in less illuminated creek/gully topographic position were showing very low growth responses despite relatively high moisture regimes (see Potter et al., 1998). The low growth rate observed in the shade intolerant species in both lower and upper topographic positions could be attributed to high competition in the former and low soil water availability in the latter.

Although our results considered growth responses of individual species groups along environmental gradients independently, the functional-group compositions and environmental gradients have complex interacting effects at both species and stand levels, and these effects may vary from one year to the next depending on the prevailing conditions. Variation in growth rates at the species level, may help to explain the species spatial distribution, while at the stand-level, understanding the site characteristics that control productivity may be critical in quantifying the general growth performance of the forest (see Baker et al., 2003). Indeed, large spatial variation in forest compositions and

dynamics at both species and stand levels suggest that there may be important difference between rainforest in the relative abundance of different species groups (Philips et al., 1994; Burslem and Whitmore, 1999; ter Steege et al., 2000).

The concern of the forest manager focuses particularly on quantifying changes at the stand level, particularly in modelling growth and yield. In general, the growth rates resemble that of other uneven-aged mixed-species forests with the majority of trees showing mean annual diameter increments between 0.1 and 0.5 cm per year (Horne and Gwalter, 1982; Vanclay, 1987, 1989; Alder and Synnott, 1992; Korning and Baslev, 1994; Vanclay, 1994b; Favrichon, 1998; Finegan and Camacho, 1999; Finegan et al., 1999). Comparison of the predicted versus observed annual tree diameter growth over the 35-year history of regeneration did not show any significance difference. The overall mean tree diameter growth responses within the range of the available data have been adequately described with 49-88% stand-level variations accounted for by the annual diameter growth model parameter estimates (Table 1). However, the models were underestimating the annual tree diameter growth, especially in the larger trees (Fig. 1). This could be attributable to majority of the trees registering very low growth rates tending more towards the lower value of 0.1 cm per year (e.g. Horne and Gwalter, 1982; Korning and Baslev, 1994; Favrichon, 1998; Finegan et al., 1999), while highly suppressed, diseased and senescent trees registered nil or negative growth. Therefore, to use both functional-group compositions and environmental gradients, and to improve the efficiency of simulation results beyond the range of available data we suggest the use of more growth rate categories in each species group. This is because in general, tree growth varies in space and time where a tree may exhibit growth ranging from negative through nil to large growth increments (Dawkins, 1956; Baur, 1964; Dickinson et al., 2000).

Conclusion

This study demonstrates that in subtropical rainforests spatial variations in tree growth responses are positively correlated with altitude and topography while temporal variations are positively correlated with disturbance gradients. Rainforest trees species-specific level of shade tolerance during recruitment, establishment and development, and maximum size are among the factors that can be

used to explain observed patterns of growth at the tree level. Habitat characteristics such as altitude, disturbance, site orientation and topography may influence the soil water availability, solar radiation and probably soil nutrient availability, and these affected stand-level growth responses. The combined effects of functional group compositions and environmental gradients will therefore determine the spatial variations in the stand-level growth.

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Table 1. Parameter estimates, standard errors (in parenthesis) and the proportional of explained variance (R^2) for annual diameter growth models (3-level hierarchical multilevel models) using growth datasets for various species groups in a subtropical rainforests north-east New South Wales, Australia. Wald's test; * at the 5 % confidence levels.

Variables	Species group				
	1	2	3	4	5
Fixed main effects					
Constant	-0.38739	-0.65456	-0.629	-2.79373	-1.09352
	(0.16323)*	(0.1105)*	(0.12070)*	(0.45031)*	(0.22417)*
Natural log of annual *dbh*	-0.03038	-0.01835	-0.01279	0.89804	0.28927
growth + 0.5)	(0.05554)	(0.029959)	(0.03912)	(0.16268)*	(0.06908)*
dbh-squared (dbh-sq)	-0.00002	-	-	-0.00031	-0.00015
	(0.00002)			(0.00009)*	(0.00005)*
Basal area (*bar*) removed	0.00229	0.00382	0.00199	0.00417	0.00215
	(0.00024)*	(0.00065)*	(0.00048)*	(0.00138)*	(0.00153)
Plot orientation					
Northerness	-0.15622	-0.05787	-	-0.08613	-
	(0.07207)*	(0.0297)		(0.0597)	
Easterness	-	-	-	-0.10164	-0.07526
				(0.04898)*	(0.03745)*
Altitude					
Mid altitude	-0.52592	0.11914	0.00068	1.14829	0.36603
	(0.17683)*	(0.06107)	(0.05175)	(0.60399)*	(0.12729)*
High altitude	-0.19415	0.2123	0.06508	1.91347	0.39393
	(0.16892)	(0.05617)*	(0.04316)	(0.54657)*	(0.061)*
Topographic positions					
Mid slope	-	0.08653	-	0.1363	0.14129
		(0.0371)*		(0.07032)	(0.04654)*
Lower slope	-	0.01431	-	0.20888	0.00000
		(0.04332)		(0.07865)*	(0.00000)
Creek/gully	-	0.09957	-	-0.01052	0.0593
		(0.05942)		(0.09977)	(0.04894)*
Time since logging	-	-0.00464	-	-0.00371	-
		(0.00084)*		(0.0014)*	
Stem density	-	-	-	-	-0.00083
					(0.00011)*
1/(Time since logging + 0.5)	-	-	0.46894	-	-0.27063
			(0.13109)*-		(0.80188)
Interaction effects					
Bar/(Time since	0.00341	-	-	-	0.0482
logging + 0.5)	(0.00070)*				(0.0154)*
Northerness by ln(dbh)	0.07695	-	-	-	-
	(0.02457)*				
Northerness by dbh-sq	-0.00003				
	(0.00001)*				
		-Table 1 continues-			
Mid altitude by	-0.16021	-	-	-0.52622	-
ln(dbh)	(0.06037)*			(0.23025)*	
Mid altitude by dbh-sq	0.00002		-	0.00011	
	(0.00002)			(0.00015)	
Higher altitude by	0.07213	-	-	-0.73344	-
ln(dbh)	(0.05749)			(0.2083)*	
Higher altitude by dbh-sq	0.00004		-	0.00030	
	(0.00002)			(0.00011)*	
Random effects					
σ^2_{u1} Level 1 censuses	0.00094	0.00097	0.00070	0.00000	0.00000
	(0.00043)*	(0.00108)	(0.00093)	(0.00000)	(0.00000)
σ^2_{u2} Level 2 trees	0.02403	0.01763	0.00911	0.00511	0.02979
	(0.00129) *	(0.00313)*	(0.00246)*	(0.00335)	(0.00763)*
σ^2_{u3} Level 3 plots	0.08754	0.05474	0.06078	0.062	0.1705
	(0.00127)*	(0.00279)*	(0.00333)*	(0.00555)*	(0.00917)*
R^2_1 explained variance	9.3684	14.0009	4.2068	31.6181	20.5766
censuses					
R^2_2 explained variance trees	19.7106	21.3674	6.5316	61.5230	28.0767
R^2_3 explained variance plots	84.7286	81.0525	49.0440	77.7623	88.24433
Deviance	326.96*	164.813*	23.49*	71.327*	98.202*
MAR mean absolute residuals	-0.000163	0.00245	0.00181	0.00178	0.000103

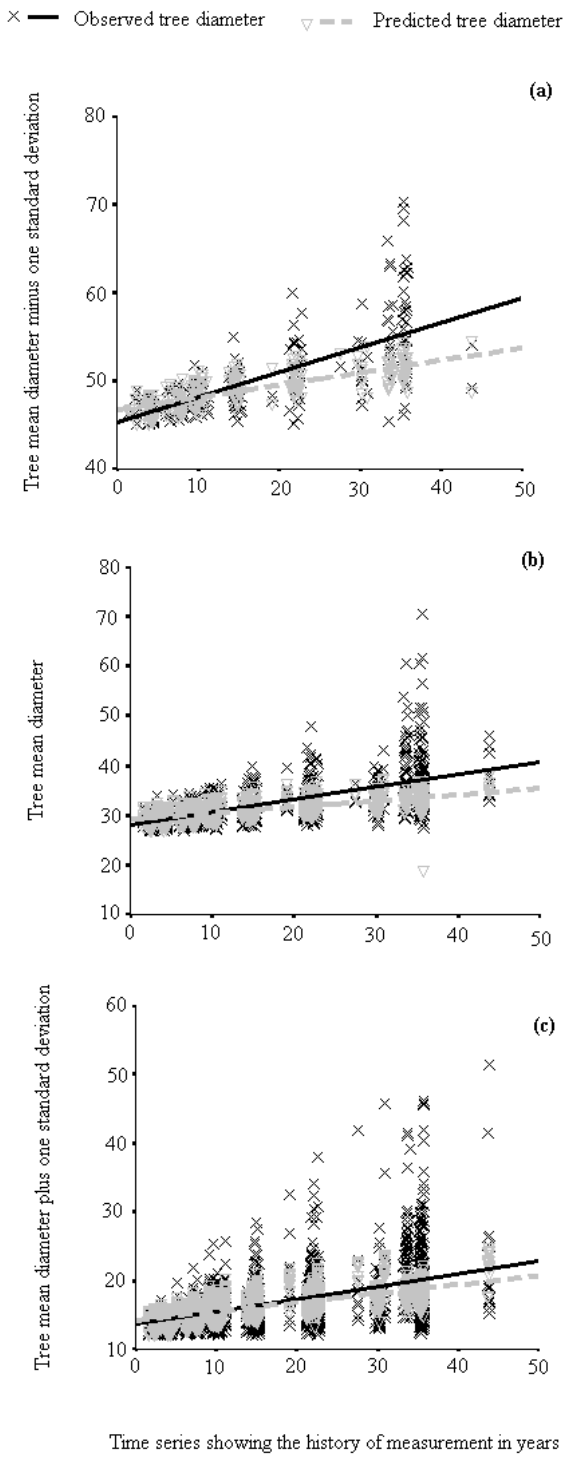

Fig. 1. Comparison between observed and predicted tree diameter growth for randomly selected stems in the emergent shade tolerant main canopy tree species in subtropical rainforest in north-east NSW, Australia. Tree sizes; mean diameter minus one standard deviation (a), mean diameter (b) and mean diameter plus one standard deviation (c).

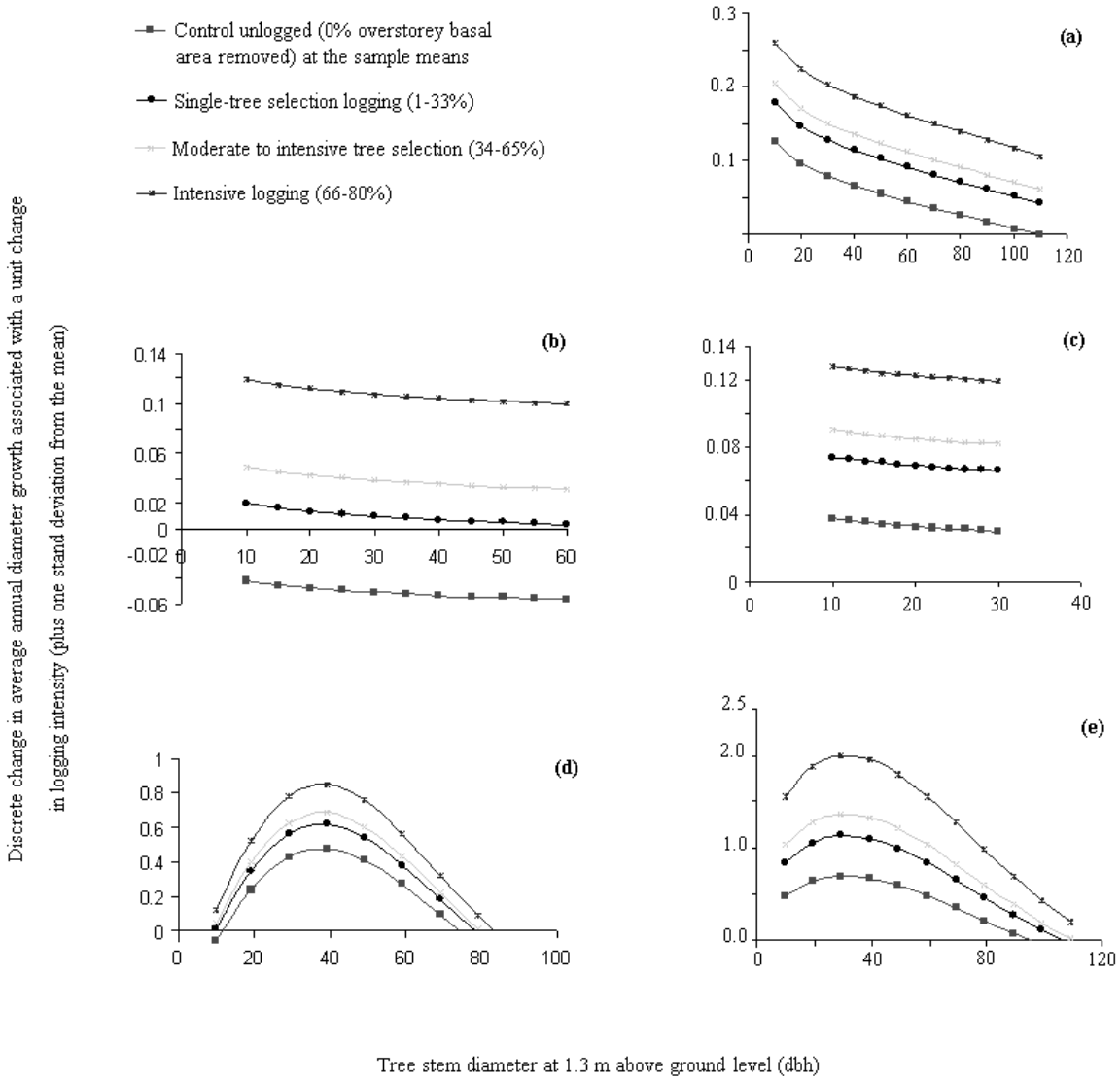

Fig. 2. Discrete change in average annual diameter growth associated with increase in logging intensity in relation to tree stem size for various species groups in subtropical rainforests north-east NSW, Australia. Species groups; emergent and shade-tolerant main canopy trees (a), shade-tolerant mid canopy trees (b), shade-tolerant understorey trees (c), moderate shade-tolerant trees (d) and shade-intolerant trees (e).

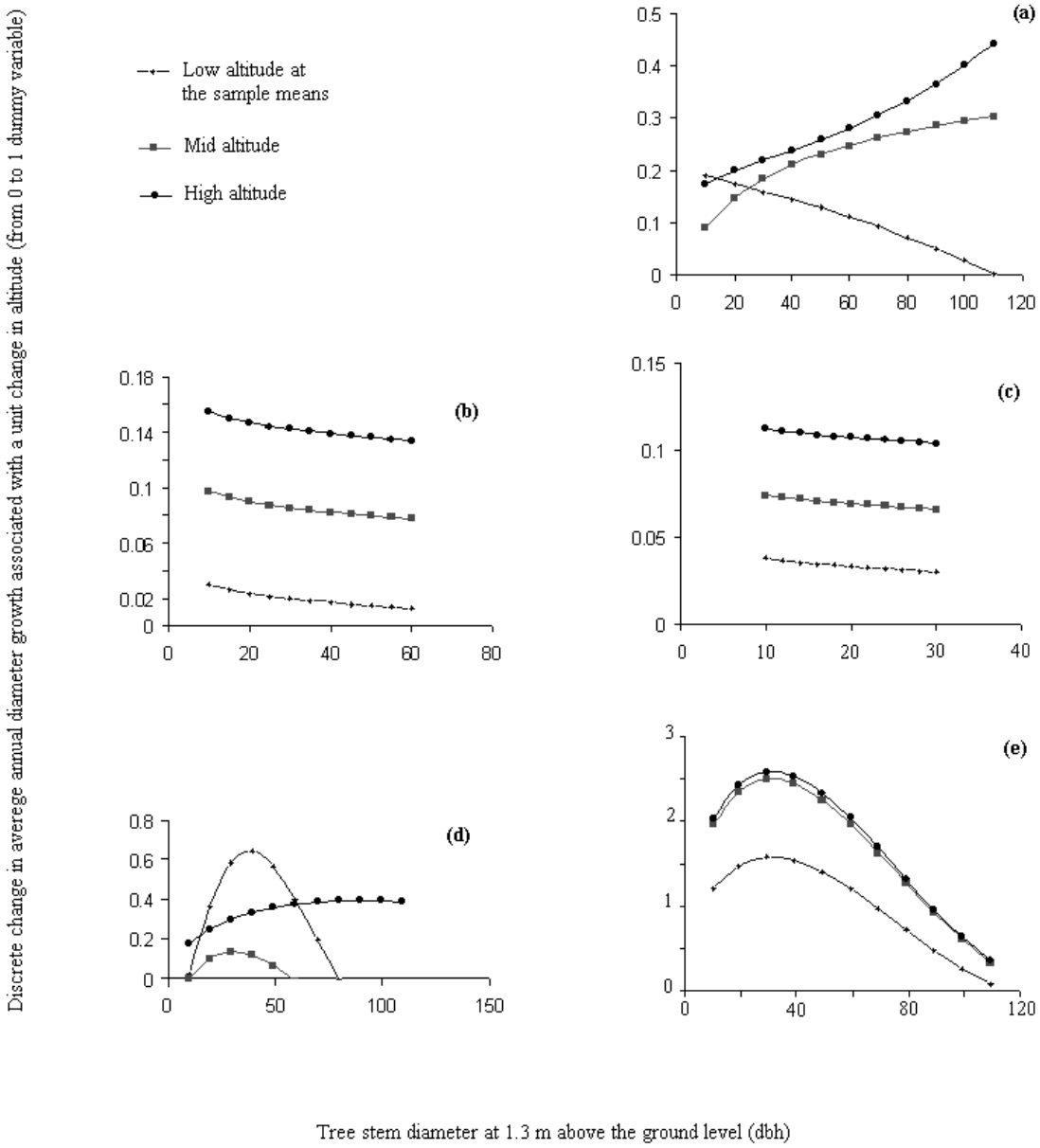

Fig. 3. Discrete change in average annual diameter growth associated with a change in altitude (from low through mid to high) in relation to tree stem size for various species groups in subtropical rainforests north-east NSW, Australia. Species groups; emergent and shade-tolerant main canopy trees (a), shade-tolerant mid canopy trees (b), shade-tolerant understorey trees (c), moderate shade-tolerant trees (d) and shade-intolerant trees (e).

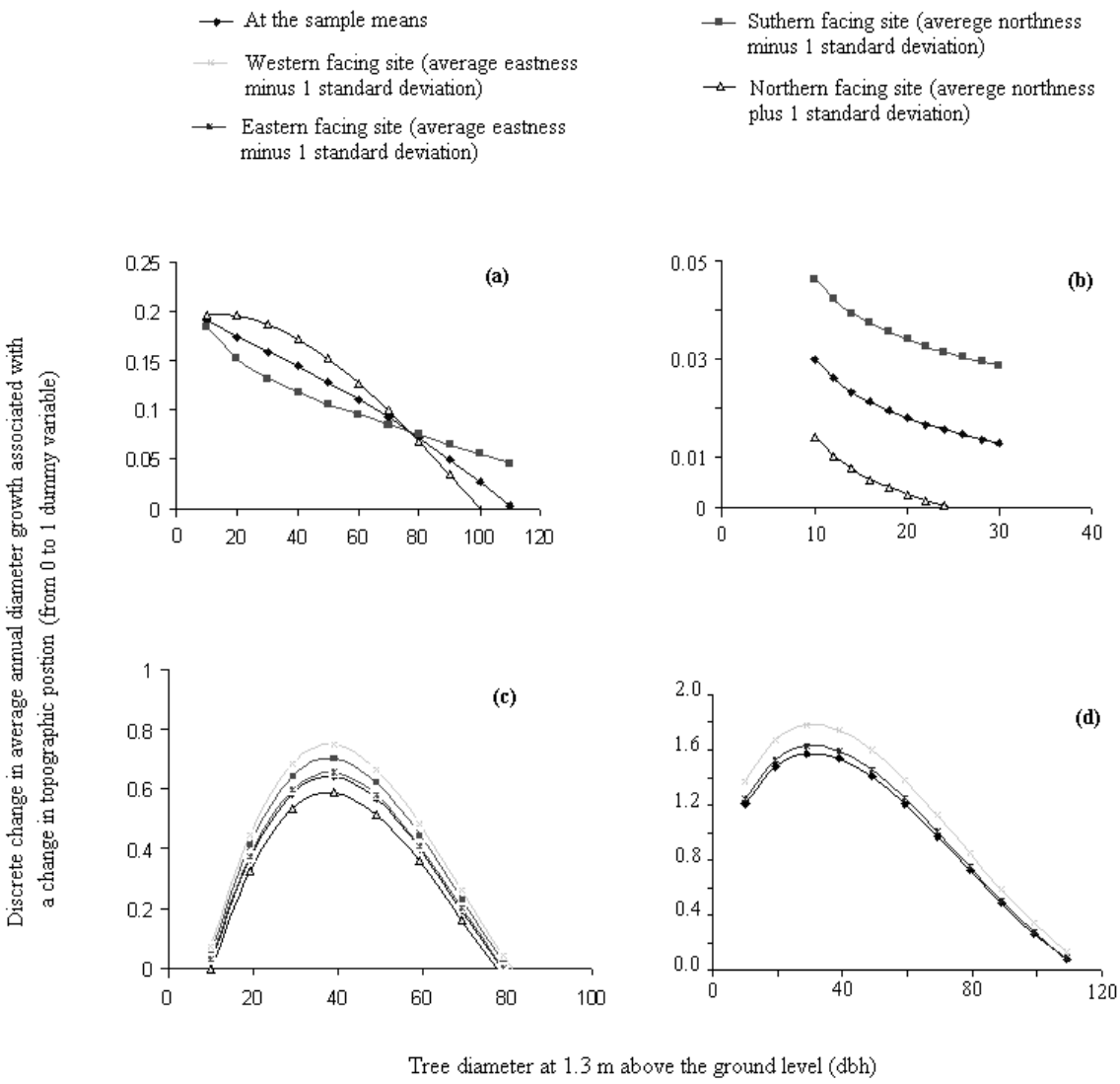

Fig. 4. Discrete changes in mean annual tree diameter growth associated with changes in site orientations in respect to north-south and east-west in various species groups in subtropical rainforest in north-east NSW, Australia. Species group; emegernt and shade tolerant main canopy trees (a), shade tolerant mid canopy trees (b), moderate shade tolerant trees (c) and shade intolerant tree species (d).

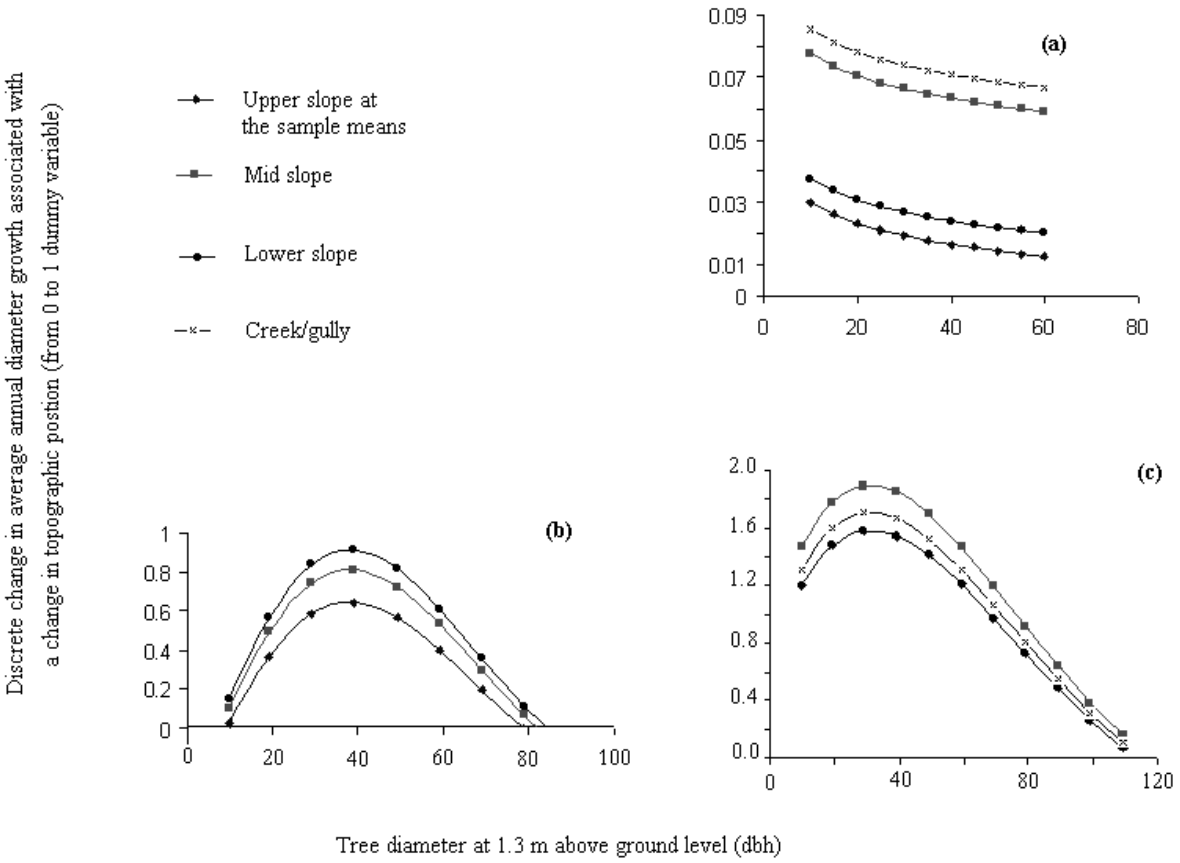

Fig. 5. Discrete change in average annual diameter growth associated with a change in topography (from upper, mid, through lower slope to creek/gully topographic position) in relation to tree stem size for various species groups in subtropical rainforests north-east NSW, Australia. Species groups; shade tolerant mid canopy trees (a), moderate shade tolerant trees (b) and shade intolerant trees (c).