# Native forest individual-tree modelling in Papua New Guinea

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*Abstract*

Quantitative study of the permanent sample plot (PSP) database can provide insights into growth, mortality and recruitment processes driving forest dynamics. Modelling the dynamics of forest growth and yield provides opportunities for optimising silvicultural systems and generating accurate growth and yield estimates, which are fundamental to sustainable forest management. This paper will outline model development based on analysis of a large native forest permanent sample plot database in Papua New Guinea. We quantify the competitive influences affecting individual tree growth and mortality, and build predictive models for growth and mortality based on a hierarchical Bayesian modelling methodology. This method allows the parameterisation of a global model with species-specific parameters; therefore, species-level growth and mortality traits are preserved in model predictions, even for rare species. We examine a range of spatial and non-spatial competition indexes for the data, and conclude that a simple non-spatial competition index (basal area of competing trees within 20 metres of the subject) adequately characterises competitive influences on growth and mortality. In future work, species-specific model parameters can be used as the basis of a forest simulation system (see http://twoe.org for developments) to improve the design and intensity of selective-harvesting regimes at the community and the concession level.

## Introduction

Tropical forests cover 10% of global land area but remain a scientific frontier due to structural and biological complexity and high temporal variability associated with complex successional processes (Chambers et al. 2001). A constraint is the limited number of long-term studies quantifying tropical forest dynamics, and the impacts of anthropogenic and natural disturbances such as harvesting and fire (Clark et al. 2001; Lewis et al. 2009). Long-term studies, while difficult to maintain, especially in developing countries, are essential to the development and testing of hypotheses regarding processes and rates of ecological recovery following disturbance, both anthropogenic and natural (Taylor et al. 2008). The forests of Papua New Guinea (PNG) are structurally diverse and complex, and have rarely been studied. The comprehensive permanent sample plot (PSP) database provides an opportunity to ameliorate this. Quantitative study of the database can provide insights into growth, mortality and recruitment processes driving forest dynamics in PNG.

The development of growth and yield models for PNG's native forests has never been a priority for the PNG Forest Authority (PNGFA), and this limited development has hindered the effective management of native forest resources. The only exception to this is the work on growth and yield undertaken by Alder (1998), who developed a stand-level growth model

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called PINFORM based on the first remeasurement of a PSP dataset. Unfortunately, PINFORM has not been routinely applied by PNGFA for forest planning or sustainable yield purposes. However, growth and yield models can be used for optimising silvicultural systems and generating accurate growth and yield estimates, which are fundamental to sustainable forest management. As part of Australian Centre for International Agricultural Research (ACIAR) project FST/2004/061, the limited extent of growth and yield modelling in PNG has been advanced with the development of individual-tree models for competition, growth and mortality. In future work, models will be developed for recruitment, and will be integrated into a forest simulation tool. This tool, under development at <http://twoe.org>:

- manages and modifies PSP datasets for analysis of growth, mortality and recruitment
- estimates model parameters using hierarchical Bayesian modelling
- can be used to simulate forest dynamics.

The individual-tree growth modelling approach is sufficiently flexible to accommodate forests with virtually any species mixture or size structure. Individual-tree models are also age independent, making them applicable to uneven-aged stands, as are commonly encountered in tropical forests. Many alternative growth and yield modelling methodologies exist and have been reviewed elsewhere (e.g. Vanclay 1994). It is the flexibility of the individual-tree growth model that has led to its application to the native forest resource of PNG, as much of the resource exists in mixed-aged, mixed-species stands, often of indeterminate age.

Forest utilisation in PNG is increasingly occurring at the community level using small-scale sawmills to extract individual trees. This small-scale use is the basis of Forest Stewardship Council (FSC; an international body that outlines social, environmental and economic certification requirements) certification efforts that aim to empower landowners, improve livelihoods, preserve the natural environment, and facilitate sustainable development (Bun and Scheyvens 2007). To examine whether these operations are sustainable, growth models are required for predicting tree growth at the scale of the individual tree. They can then be used in community forestry to inform small-scale (individual-tree) scenario analysis, species-specific carbon sequestration, and the impact of small-scale utilisation on carbon stocks.

Individual-tree models characterise the competitive, growth, mortality and recruitment dynamics of individual trees—this is challenging in the complex and diverse tropical forests of PNG. This paper will outline model development based on analysis of the PSP network in PNG. We quantify the competitive influences affecting individual-tree growth, and build predictive models for growth and mortality based on a hierarchical Bayesian modelling (HBM) methodology (Fox et al. 2011a). One of the challenges with statistical analysis of PSP data is autocorrelation between measurements. Autocorrelation eventuates when spatial, temporal or hierarchical variation cannot be captured by deterministic model structures (such as a simple mean), reducing estimation efficiency and biasing hypothesis tests on estimated parameters (Fox et al. 2001). PSP data have implicit hierarchical structure—trees are nested within plots that are repeatedly measured through time and/or space. HBMs are applied here because they can facilitate the explicit modelling of autocorrelation (Clark 2005; Clark and Gelfand 2006; Cressie et al. 2009). The hierarchical Bayesian approach also quantifies the response of growth and mortality to competition and tree size across the entire tree community. Using HBMs with species random effects, the variability of the growth/mortality response between all species can be estimated, including rare species with few observations (Dietze et al. 2008).

Competition indexes have been the subject of much attention in the forestry literature. Distance-dependent indexes (DDIs) use the spatial positions of individual trees in their formulations whereas distance-independent indexes do not. Because DDIs incorporate the spatial pattern of competitors, it should follow that they provide an improved quantitative expression of competition. The various competition indexes can be organised into several groups. DDIs comprise distance-weighted size ratio indexes (e.g. Hegyi 1974), area overlap indexes (e.g. Bella 1971) and area potentially available indexes (e.g. Nance et al. 1987). They consist of functions of subject tree attributes compared with the attributes of other trees on the plot (e.g. Stage 1973), and stand-level indexes such as basal area per hectare (BA/ha) and stems/ha. The various competition indexes described above have been quantified for trees from the PSP database in PNG, and will be compared in terms of their ability to predict individual tree dynamics.

# Methods

## PSP data

Over the past 20 years the Papua New Guinea Forest Research Institute (PNGFRI) has established and remeasured over 125 PSPs across PNG covering all major forest types. Each plot is 1 ha in size and is divided into 25 subplots of 20 × 20 m. The spatial location, diameter, height and crown characteristics are recorded for all trees over 10 cm in diameter. The PSP database represents a strong basis for the development of individual-tree models. Because individual trees in PSPs are spatially mapped, the spatial competitive processes governing tree growth can be extricated. The PSP data are described in detail elsewhere (Fox et al. 2010). The PSP data are a compilation of plot remeasurements undertaken by PNGFRI since 1994. They have been affected by persistent errors that have hindered their usefulness for modelling. A considered error correction methodology was required to correct persistent errors affecting the PSPs as described in Fox et al. (2010). Following this, the PSP dataset was clean and ready for analysis. Figure 1 shows the PSP team for the Danaru PSPs remeasured in August 2008.

Initially, competition indexes are evaluated against individual tree growth for the PSP data. The outcomes of this evaluation then inform individual-tree model development for growth and mortality. Prior to evaluation of competition indexes, allometric modelling was required to determine species-specific relationships between diameter and crown diameter.

## Allometric modelling

Diameter – crown diameter (DCD) allometry is required to quantify individual-tree competitive dynamics. To achieve species-specific DCD models, several nonlinear models were fitted that were found to perform well for tropical forests in the study of Fang and Bailey (1998): the log-linear model (Alexandros and Burkhart 1992; equation (1)); the hyperbolic model (Huang and Titus 1992; equation (2)); and the exponential model (Fang and Bailey 1998; equation (3)):

$$H = a + bLogD \tag{1}$$

$$H = aD/(b + D) \tag{2}$$

$$H = a + b\left(1 - e^{-c(D - D_{\min})}\right) \tag{3}$$

where: $a$, $b$ and $c$ are parameters estimated for each of the tree species; $D_{\min}$ is the minimum observed diameter for the species.

**Figure 1.** Measurement team for Danaru permanent sample plots, August 2008 (Photo: Julian Fox).

Analysis revealed that the hyperbolic model (equation (4); see Table 2) had a consistently lower mean squared error across species represented on PSPs. It was thus selected for crown diameter prediction on PSPs. This is the same model that was used to describe diameter–height (DH) allometry in Fox et al. (2010). To predict individual-tree merchantable volume, the same model was fitted to diameter-merchantable height (DMH) allometry. Table 1 provides species-specific allometric parameters for DCD, DH, and DMH models for the 30 most numerous species on the PSPs.

Allometric parameters described in Table 1 are the basis of lookup tables in the forest assessment tool described in Fox et al. (2011b).

## Competition indexes

### *Distance weighted size ratio competition indexes*

The distance-weighted size ratio (DWSR) competition indexes include those that use the distance between trees weighted by their respective sizes in their formulations. Two of the most successful DWSR variants were quantified in this study: those of Hegyi (1974) and Newnham (1966). The Newnham index (equation (5)) quantifies local density as the sum of angles subtended from the subject to either side of the stems of competitors. The two DWSR indexes are described in Table 2.

The choice of which competitors to include when calculating DWSR indexes is an unresolved problem

**Table 1.** Individual-tree allometric parameters for the hyperbolic model fitted to diameter–height, diameter – merchantable height, and diameter – crown diameter models for the 16 most numerous species on PSPs

| Species | Sp. code | Character | **DH-*a*** | **DH-*b*** | **DMH-*a*** | **DMH-*b*** | **DCD-*a*** | **DCD-*b*** |
|---|---|---|---|---|---|---|---|---|
| *Calophyllum* sp. | CAL SP | climax | 66.1 | 43.7 | 30.5 | 32.7 | 49.6 | 217.9 |
| *Canarium* sp. | CAN SP | climax | 56.1 | 34.4 | 30.0 | 31.6 | 24.4 | 77.2 |
| *Celtis* sp. | CEL | climax | 71.5 | 49.0 | 31.7 | 38.9 | 22.3 | 65.9 |
| *Cryptocarya* sp. | CRY SP | climax | 50.2 | 30.3 | 24.6 | 25.4 | 18.2 | 54.0 |
| *Dysoxylum* sp. | DYS SP | climax | 55.1 | 38.8 | 24.2 | 29.3 | 19.3 | 54.2 |
| *Ficus* sp. | FIC SP | climax | 61.5 | 49.6 | 32.3 | 53.6 | 27.5 | 86.8 |
| *Garcinia* sp. | GAR SP | climax | 57.6 | 39.3 | 32.4 | 40.6 | 15.5 | 38.7 |
| *Horsfieldia* sp. | HOR SP | climax | 65.9 | 47.1 | 33.6 | 37.1 | 15.9 | 43.8 |
| *Litsea* sp. | LIT SP | climax | 55.7 | 36.4 | 28.5 | 32.4 | 16.5 | 47.6 |
| *Macaranga* sp. | MAC SP | pioneer | 52.7 | 36.5 | 28.6 | 40.7 | 10.9 | 21.8 |
| *Myristica* sp. | MYR SP | climax | 51.0 | 33.0 | 23.5 | 24.5 | 9.1 | 16.8 |
| *Pimeleodendron amboinicum* | PIM AMB | climax | 53.3 | 35.6 | 26.5 | 34.4 | 14.4 | 38.9 |
| *Planchonella* sp. | PLA SP | climax | 56.8 | 33.7 | 30.0 | 30.3 | 21.9 | 74.9 |
| *Pometia pinnata* | POM SP | climax | 53.1 | 32.4 | 25.5 | 30.5 | 21.0 | 58.7 |
| *Syzygium* sp. | SYZ SP | climax | 55.7 | 37.1 | 27.9 | 32.3 | 18.3 | 56.3 |
| *Terminalia* sp. | TER SP | climax | 62.4 | 41.1 | 38.9 | 48.0 | 20.6 | 56.9 |

**Table 2.** Distance-weighted size ratio competition indexes

| Index | Formulation | Author |
|---|---|---|
| *HEG* | $HEG_i = \sum_{j=1}^{n_i} \left[ \frac{D_j}{D_i} \times \frac{1}{Dis_{ij}} \right]$ (4) | Hegyi (1974) |
| *NEW* | $NEW_i = \sum_{j=1}^{n_i} 2 \left[ \mathrm{atan} \frac{0.5 D_j}{Dis_{ij}} \right]$ (5) | Newnham (1966) |

Note:
$n_i$ = total number of competitors for the subject $i$; $D_i$ = diameter at breast height for the subject tree $i$; $Dj$ = diameter at breast height of the $j$th competitor; $Dis_{ij}$ = the distance in meters between the subject $i$ and competitor $j$.

(Burton 1993). To reduce subjectivity in estimates of competitor search radius, a methodology was used whereby an optimal search radius (OSR) was identified mathematically for each species. This could also provide insight into the range of the competitive dynamic affecting particular rainforest species. By examining the relationship between index performance and competitor search radius, it was confirmed that index performance generally approached a maximum value asymptotically. The point at which performance first began to level off was then estimated mathematically using a segmented, nonlinear equation similar to the spherical semi-variogram employed in geostatistics (e.g. Journel and Huijbregts 1978). This segmented, nonlinear model was fitted to characterise the correlation of the index with growth and competitor search radius, and can be described in equation (6):

$$\begin{aligned} Corr_i &= \alpha\left[1.5(sr_i/\beta) - 0.5(sr_i^3/\beta^3)\right], \; sr_i \le \beta \\ Corr_i &= \alpha, \qquad\qquad\qquad\qquad sr_i > \beta \end{aligned} \tag{6}$$

where: $sr_i$ is the search radius ($i$ = 2–20 m at 2 m increments), $Corr_i$ is the correlation between the competition index and annual diameter increment for search radius $i$, and $\alpha$ and $\beta$ are parameters estimated using the NLIN procedure in SAS (SAS Institute Inc. 1996). The parameter $\alpha$ can be interpreted as an estimate of the maximum correlation and $\beta$ as an estimate of the OSR.

*Area overlap competition indexes*

The area overlap (AO) indexes were formally introduced by Opie (1968), but the most successful formulation was presented by Bella (1971) (equation (7)):

$$AO_i = \sum_{j=1}^{n_i}\left[\left(ZO_{ij}/Z_i\right)\left(D_j/D_i\right)^{EX}\right] \tag{7}$$

where: $AO_i$ is the AO index of Bella (1971) for tree $i$; $Z_i$ is the area of the 'zone of influence' of the subject tree $i$; $ZO_{ij}$ is the area of 'zone of influence' overlap between the subject $i$ and competitor $j$. $EX$ is the exponent applied to ratios, and previous studies (e.g. Bella 1971) have identified the optimal exponent as being between 1 and 3.

The AO indexes use a function of the area of overlap between a subject's and a competitor's 'zone of influence' to quantify competition. Their success depends on a suitable estimate of 'zone of influence', which is defined as the total area over which a tree obtains or competes for resources (Opie 1968). A prediction of crown area is used to quantify the zone of influence of each tree. Studies on the zone of influence

A large *Alstonia scholaris* (diameter at breast height = 133 cm) overtops the canopy of Danaru permanent sample plot (Photo: Julian Fox).

(e.g. Bi and Jurskis 1996) have found that the area over which a tree obtains or competes for resources is approximately equivalent to the area enclosed by two crown radii. A crown radius prediction for each tree in the PSP dataset was generated using the DCD allometric model described above.

*Area potentially available competition indexes*

The area potentially available (APA) indexes, first introduced in the forestry literature by Brown (1965), are derived from the classical Voronoi diagram, which is a continuous tessellation of an area into non-overlapping polygons. Brown (1965) introduced APA indexes to forestry as a means of quantifying the area potentially available for growth, and they have since been widely adopted as competition indexes. Several variants exist, including the weighted (APAW) and the weighted and constrained (APAWC). The APAW (Moore et al. 1973) weights the position of the perpendicular bisector on the line joining a tree to its competitor by a ratio of tree sizes. Nance et al. (1987) proposed the APAWC to curtail the development of large irregular polygons when spatial arrangements become irregular. When constructing the tessellation, they selected the smaller of the distance to the polygon boundary or the output of a constraining function. Nance et al. (1987) proposed the constraining function based on the predicted crown radius for the subject tree.

Three variants of the APA index are described in Table 3.

The APA class of competition indexes is the most complex to compute. A SAS macro (SAS Institute Inc. 1990) was written for efficient computation of all APA variants along with DWSR, AO and distance-independent indexes. SAS macros for quantifying the various competition indexes detailed in this study are available upon request from the primary author. An example of the APAWC for the Krisa PSP plot is shown in Figure 2. The spatial irregularity of the PSP plot can be observed.

*Alleviating boundary effects*

A boundary effect is generated when boundary trees are subject to competition from outside the plot that is not incorporated in competition indexes. To minimise information loss from exclusion of trees subject to edge effects, we used a toroidal edge correction scheme commonly used in spatial statistical applications (Ripley 1981). Toroidal edge correction is implemented by considering a rectangular spatial array as a torus. This can be realised simply by translating the spatial arrangement to create eight new adjoining arrays. The validity of toroidal edge correction depends upon the assumption that boundary trees are subject to equivalent competition from both outside and inside the plot; this is tenuous for trees close to the boundary (i.e. less than 5 m) in an irregularly structured tropical forest, but it should be permissible for trees more than 5 m from the boundary. Therefore, trees within 5 m of the boundary were excluded from analysis and toroidal edge correction was applied to all other trees.

*Distance-independent competition indexes*

Distance-independent indexes consist of functions of subject tree attributes compared with the attributes of other trees on the plot (Stage 1973). They do not use spatial information. The summed BA of trees within 20 m of the subject tree was quantified (BAS). The index developed by Stage (1973) was also quantified (equation (8)):

$$DAL_i = \sum_{i=1}^{n_i} D_i \tag{8}$$

**Table 3.** Area potentially available competition indexes

| Index | Weighting function | Constraining function | Author |
|---|---|---|---|
| *APA* | - | - | Brown (1965) |
| *APAW* | $DB_{ij} = \left[\frac{D_i^2}{(D_i^2 + D_j^2)}\right] Dis_{ij}$ | - | Moore et al. (1973) |
| *APAWC* | $DB_{ij} = \left[\frac{D_i^2}{(D_i^2 + D_j^2)}\right] Dis_{ij}$ | $CF_i = \sqrt{\frac{(PA \times (D_i / \sum_{j=1}^{t} D_j)}{\pi}}$ | Nance et al. (1987) |

Note:
$DB_{ij}$ = the distance to the perpendicular bisector located on the straight line between the subject *i* and competitor *j*;
*APA* = area potentially available; *W* = weighted; *WC* = weighted and constrained.

*Evaluating competition indexes*

Competition indexes were evaluated for their ability to predict annual diameter increment in the next growing period using two criteria. The first criterion was the correlation between the index and the annual diameter increment in the next growing period. If the relationship between each variable and annual diameter increment was found to be nonlinear, a transformation was sought that rendered the relationship linear. In these instances the fit of the transformed variable was evaluated.

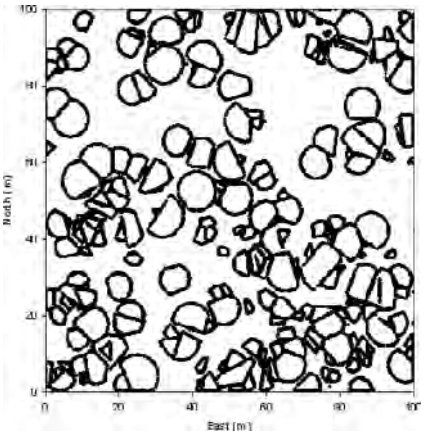

**Figure 2.** Graphic of the weighted and constrained area potentially available (APA) index for the Krisa permanent sample (PSP) plot

The second criterion was the significance of the competition index as a fixed effect in a mixed model with BA against annual diameter increment. BA was included as a fixed effect to extricate the influence of differing stand density on tree growth. A mixed model was used to account for the nested dependence (Fox et al. 2001) affecting PSPs; the growth of trees within each PSP will be more similar than that between the PSPs, as trees on the same plot will be subject to the same local environmental conditions, and will be of a similar forest type. To account for this, a random effect was used for each PSP measurement to ensure correct statistical inference on the growth and competition dynamics within and between PSP plots (Fox et al. 2001). After selecting an optimal competition index, individual tree growth (equation (9)) and mortality (equation (10)) models can be fitted.

A secondary species, *Dendrocnide longifolia*, grows quickly to gain access to light on the Danaru permanent sample plot (Photo: Julian Fox).

## Individual-tree models

*HBM model fitting*

A conditional posterior for each parameter was obtained using a Gibbs sampler (Gelfand and Smith 1990) written in C++, and a non-informative flat prior (with large variance) was used for each parameter. We ran one MCMC of 20,000 iterations for each parameter, with a 'burn-in' period set to 10,000 iterations and the 'thinning' to 1/10. We then obtained 1,000 estimations for each parameter.

*Growth model*

$$\begin{aligned}
&\log(G_{ik}+2) = (\beta_0 + b_{0,k}) + (\beta_1 + b_{1,k}) \\
&\quad \log(D_i) + (\beta_2 + b_{2,k}) \log(C_i + 1) + \varepsilon_i \\
&\varepsilon_i \sim \text{Normal}(0, V) \\
&[\beta_0, \beta_1, \beta_2] \sim \text{Normal}_3(0, V_\beta) \\
&[b_{0,k}, b_{1,k}, b_{2,k}] \sim \text{Normal}_3(0, V_b) \\
&V_b \sim \text{Inverse-Wishart}(r, rR) \\
&V \sim \text{Inverse-Gamma}(s_1, s_2)
\end{aligned} \tag{9}$$

where: $G_{ik}$ is the growth (mm/year) of tree $i$ of species $k$ between dates $t$ and $t + 1$; $D_i$ is the diameter (cm) of tree $i$ at date $t$; $C_i$ is the competition index ($m^2$/ha) in the neighbourhood of tree $i$ at date $t$; $\beta_0$, $\beta_1$, $\beta_2$ are global averages on the intercept, the slope of $D$ and the slope of $C$, respectively; $\beta_{0,k}$, $\beta_{1,k}$, $\beta_{2,k}$ are the species random effects on the intercept, the slope of $D$ and the slope of $C$, respectively.

*Mortality model*

$$\begin{aligned}
&S_{ik} \sim \text{Bernoulli}(\theta'_{ik}) \\
&\theta'_{ik} = 1 - (1 - \theta_{ik})^{Y_i} \\
&\text{logit}(\theta_{ik}) = (\beta_0 + b_{0,k}) + (\beta_1 + b_{1,k}) \\
&\quad (D_i - 20) + (\beta_2 + b_{2,k})(C_i - 20) + \varepsilon_i \\
&\varepsilon_i \sim \text{Normal}(0, V = 1) \\
&[\beta_0, \beta_1, \beta_2] \sim \text{Normal}_3(0, V_\beta) \\
&[b_{0,k}, b_{1,k}, b_{2,k}] \sim \text{Normal}_3(0, V_b) \\
&V_b \sim \text{Inverse-Wishart}(r, rR)
\end{aligned} \tag{10}$$

where: $S_{ik}$ is the status (0 = alive, 1 = dead) of tree $i$ of species $k$ between dates $t$ and $t + 1$; $Y_i$ is the time interval (years) between dates $t$ and $t + 1$; $\theta'_{ik}$ is the mortality rate for time interval $Y_i$; $\theta_k$ is the annual mortality rate.

For the mortality model, we included in the expression of logit ($\theta_{ik}$) a residual error term $\varepsilon_i \sim \text{Normal}(0, V)$ to account for overdispersion in the data (Hadfield 2010). We fixed V to 1. Using this parametrisation was convenient as it placed the estimation in the linear Gaussian regression framework and allowed us to use conjugated priors for parameters.

# Results

## Competition indexes

*Optimal competitor search radii*

Different trends in correlation across different search radii emerged for different species. An example of the fitted nonlinear model for Hegyi's (1974) index is shown in Figure 3. For *Pometia Pinnata*, $\alpha$ was estimated as 0.12 and $\beta$ as 13.7. These can be interpreted as an asymptotic correlation of 0.12 and an optimal search radius of 13.7 m.

Estimated OSRs for different species are detailed in Table 4. It can be observed that some species such as *Calophyllum* have small OSR values (3 m), while other species such as *Horsfieldia* have large OSR values (20 m). These results suggest that the range of the competitive effect is different among tropical species. For example, it could be hypothesised that *Calophyllum* is most affected by competition for light among immediate neighbours (competitors within 3 m) while, for *Horsfieldia*, competition for light and nutrients is more diffuse and occurs over a larger area (up to 20 m).

*Evaluating competition indexes*

Ten competition indexes were quantified for approximately 85,000 individual tree measurements across the 125 permanent sample plots. The 300 most numerous species on PSPs were selected for specific study of indexes. Preliminary analysis was used to identify a subset of indexes for further study. The best performing competition indexes were selected on the basis of strength of correlation with tree growth across the 300 species. The following subset was identified for further study:

- DBHOB (diameter at breast height over bark)
- BAS (sum of tree BA within 20 m of subject)
- SQAPAWC (square root of APAWC)
- LNNEW (natural logarithm of NEW)
- LNAO1 (natural logarithm of AO with exponent 1)

**Table 4.** Competition index performance and other statistics for the 16 most observed species on permanent sample plots

| Species | Sp code | Character | Obs | OSR | Optimal Corr | Corr | Optimal Mixed | Effect Sig | Wood Density | Diameter 90th quan | Mean Incr |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calophyllum* sp. | CAL SP | climax | 1,072 | 3.0 | BAS | –0.16 | BAS | 4.00E-03 | 0.50 | 47.0 | 0.53 |
| *Canarium* sp. | CAN SP | climax | 2,323 | 6.9 | BAS | –0.2 | BAS | 6.30E-08 | 0.48 | 36.5 | 0.42 |
| *Celtis* sp. | CEL | climax | 990 | 5.5 | LNNEW | –0.21 | BAS | 2.00E-04 | 0.55 | 50.0 | 0.52 |
| *Cryptocarya* sp. | CRY SP | climax | 1,993 | 7.4 | BAS | –0.09 | LNAO1 | 6.00E-02 | 0.46 | 34.7 | 0.44 |
| *Dysoxylum* sp. | DYS SP | climax | 1,846 | 14.2 | BAS | –0.2 | BAS | 3.00E-17 | 0.62 | 39.9 | 0.38 |
| *Ficus* sp. | FIC SP | climax | 1,536 | 5.9 | BAS | –0.2 | DBHOB | 2.90E-10 | 0.34 | 45.5 | 0.51 |
| *Garcinia* sp. | GAR SP | climax | 1,018 | 11.8 | LNNEW | –0.16 | LNNEW | 1.10E-04 | 0.64 | 31.5 | 0.37 |
| *Horsfieldia* sp. | HOR SP | climax | 1,682 | 20.0 | LNNEW | –0.14 | LNNEW | 1.30E-04 | 0.36 | 31.2 | 0.35 |
| *Litsea* sp. | LIT SP | climax | 1,022 | 5.7 | BAS | –0.25 | LNAO1 | 7.30E-11 | 0.40 | 38.4 | 0.51 |
| *Macaranga* sp. | MAC SP | pioneer | 1,426 | 14.3 | BAS | –0.27 | LNNEW | 9.50E-12 | 0.30 | 22.8 | 0.96 |
| *Myristica* sp. | MYR SP | climax | 3,113 | 9.6 | BAS | –0.16 | LNNEW | 1.40E-03 | 0.38 | 25.7 | 0.31 |
| *Pimeleodendron amboinicum* | PIM AMB | climax | 1,745 | 15.7 | LNNEW | –0.17 | DBHOB | 3.20E-07 | 0.48 | 39.8 | 0.42 |
| *Planchonella* sp. | PLA SP | climax | 1,683 | 9.0 | LNNEW | –0.21 | LNAO1 | 4.90E-09 | 0.45 | 37.6 | 0.44 |
| *Pometia pinnata* | POM SP | climax | 2,777 | 13.7 | LNAO1 | –0.16 | LNAO2 | 2.60E-10 | 0.58 | 54.4 | 0.67 |
| *Syzygium* sp. | SYZ SP | climax | 2,854 | 10.8 | BAS | –0.17 | BAS | 4.10E-12 | 0.61 | 41.1 | 0.37 |
| *Terminalia* sp. | TER SP | climax | 638 | 8.3 | BAS | –0.21 | LNAO1 | 3.40E-07 | 0.45 | 46.3 | 0.67 |

Note:
Obs is the number of observations; OSR is optimal search radius; Optimal Corr is the competition index with optimal correlation against annual diameter increment; Corr is the Spearman's correlation coefficient; Optimal Mixed is the competition index with optimal effect significance in a mixed model; Effect Sig is the t-test that the parameter is significantly different to zero; Wood density is basic density—the weight of wood (kg) at 0% moisture content occupying 1 $m^3$ from Eddowes (1977); Diameter 90th quan is the 90th quantile of the diameter distribution; and Mean Incr is the average annual diameter increment in the next growing period.

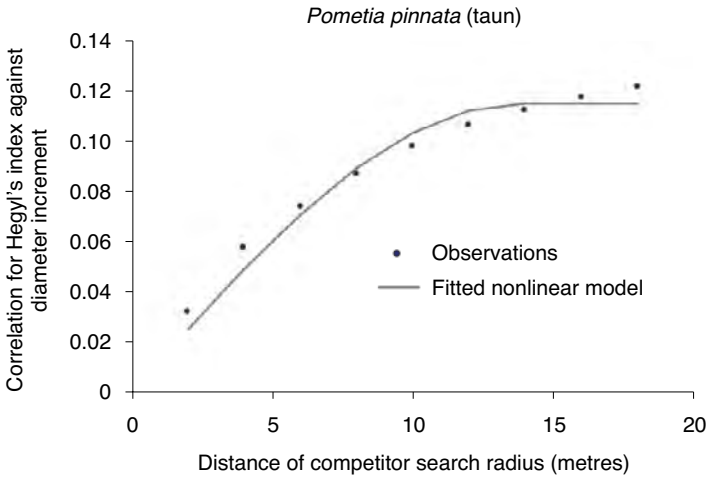


**Figure 3.** Fitted nonlinear model for estimating optimal competitor search radius for *Pometia pinnata*

The best performing competition index was then identified for each of the 300 species. Table 5 shows the indexes ranked for the percentage of the 300 species for which they were optimal (in terms of correlation with annual diameter increment). Table 5 also shows the indexes ranked for the number of times they were optimal in terms of fixed-effect significance in a mixed model with BA across the 300 species.

Table 5 demonstrates that no single competition index is optimal across the 300 species, and that distance-independent indexes such as DBHOB and BAS are equally as effective as distance-dependent indexes. BAS (28%, 21%) and LNNEW (29%, 29%) appear to be optimal most often across the 300 species. When BA was included as a fixed effect in a mixed model, distance-dependent indexes performed better (optimal for 61% of indexes). This may be due to total BA characterising stocking differences across PSPs and negating the influence of the distance-independent index, BAS (28% down to 21%).

Table 4 provides further detailed statistics of competition index performance for a subset of the 16 most observed species.

## Individual-tree models

Growth (equation (9)) and mortality (equation (10)) individual tree models were fitted to the PSP data with random species effects. Fitted models resulted in global average parameters ($\beta_0$, $\beta_1$, $\beta_2$) and species-specific parameters ($\beta_{0,k}$, $\beta_{1,k}$, $\beta_{2,k}$) describing growth and mortality processes for each species in equation (9) for growth and equation (10) for mortality for species $k$. The growth and mortality of individual trees was a function of tree size (diameter) and the local competitive environment (sum of BA within 20 m of subject). The global model with average parameters is shown in equation (11) for growth and equation (12) for mortality.

$$\log(G_{ik}+2) = (1.781+b_{0,k}) + (0.055+b_{1,k}) \log(D_i) + (-0.100+b_{2,k}) \log(C_i+1) \quad (11)$$

$$\log(G_{ik}+2) = (1.781+b_{0,k}) + (0.055+b_{1,k}) \log(D_i) + (-0.100+b_{2,k}) \log(C_i+1) \quad (12)$$

Global trends in growth and mortality against tree size ($D_i$) and competition ($C_i$) can be observed in equations (11) and (12). Growth increases with increasing tree size (positive parameter on $D_i$) but decreases with increasing competition (negative parameter on $C_i$). Both these observations are consistent with biological reality in tropical forests. The probability of mortality decreases with increasing tree size but increases with increasing competition (parameters in equation (12)). Again, these observations are consistent with biological reality.

Species-specific parameters such as $b_{1,k}$ in equations (11) and (12) allow each species to express its individual traits with respect to growth and mortality.

**Table 5.** Percentage of species for which each competition index was optimal

| Competition index | Correlation—percentage of species optimal | Mixed model—percentage of species optimal |
|---|---|---|
| DBHOB | 14 | 18 |
| BAS | 28 | 21 |
| SQAPAWC | 15 | 13 |
| LNNEW | 29 | 29 |
| LNAO1 | 14 | 19 |

Species-specific model parameters for the 16 most numerous species on PSPs, as well as predictions of growth and mortality for trees under conditions of low (10 $m^2$/ha) and high (50 $m^2$/ha) competition are shown in Table 6. All predictions are for medium-sized trees (40 cm dbh).

It can be observed that growth under low competition is always higher than under high competition, and this makes biological sense. Similarly, the probability of mortality under low competition is always lower than under high competition. For *Macaranga*, a pioneer species, the probability of mortality is twice as high under conditions of high competition relative to low competition.

## Discussion

Tropical forests are characterised by a high diversity of woody species, and no universally applicable species groupings exist that capture the continuum of growth, mortality and recruitment dynamics (Clark and Clark 1999). However, there is a need to group species for the development of forest growth models, as grouping similar species increases the sample size, thus reducing parameter variance, and may result in fewer and more frugal models that can be more easily applied in forest-management contexts. It is also important for the ecological insights it can offer on species growth habits. Ever since Whitmore (1975) first described tropical tree functional groups (fast-growing shade-intolerant pioneers, and slower growing shade-tolerant climax species), researchers have been attempting to group species using a variety of strategies, as reviewed by Gourlet-Fleury et al. (2005). Future work should explore if competition indexes can be used for species classification. For example, OSR values could be related to the shade-tolerance of different species. Species with small

Cultural immersion is likely to occur when undertaking forest assessment in remote areas of Papua New Guinea. Here, Heidi Zimmer is inducted as a 'Simbu girl' after spending time with the Kgwan community of Simbu province (Photo: Julian Fox).

**Table 6.** Growth and mortality parameters and example predictions for 16 most numerous species on permanent sample plots

| Species | Sp Code | Character | G-$b_0$ | G-$b_1$ | G-$b_2$ | M-$b_0$ | M-$b_1$ | M-$b_2$ | GLC | GHC | MLC | MHC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calophyllum* sp. | CAL SP | climax | 1.514 | 0.171 | –0.093 | –3.203 | –0.003 | –0.024 | 3.425 | 3.100 | 0.018 | 0.047 |
| *Canarium* sp. | CAN SP | climax | 1.501 | 0.106 | –0.074 | –3.539 | –0.005 | –0.016 | 2.919 | 2.683 | 0.016 | 0.030 |
| *Celtis* sp. | CEL SP | climax | 2.484 | –0.025 | –0.221 | –3.895 | –0.007 | –0.014 | 7.158 | 5.905 | 0.012 | 0.020 |
| *Cryptocarya* sp. | CRY SP | climax | 1.610 | 0.071 | –0.068 | –3.300 | 0.014 | –0.010 | 3.218 | 2.986 | 0.034 | 0.051 |
| *Dysoxylum* sp. | DYS SP | climax | 1.261 | 0.190 | –0.098 | –3.904 | 0.003 | –0.010 | 2.321 | 2.049 | 0.016 | 0.023 |
| *Ficus* sp. | FIC SP | climax | 1.786 | 0.094 | –0.134 | –3.362 | –0.006 | –0.017 | 4.029 | 3.513 | 0.018 | 0.035 |
| *Garcinia* sp. | GAR SP | climax | 1.771 | 0.074 | –0.149 | –3.392 | 0.003 | –0.019 | 3.664 | 3.129 | 0.020 | 0.041 |
| *Horsfieldia* sp. | HOR SP | climax | 1.543 | 0.025 | –0.042 | –3.990 | 0.018 | –0.004 | 2.664 | 2.537 | 0.023 | 0.027 |
| *Litsea* sp. | LIT SP | climax | 1.728 | 0.138 | –0.142 | –3.428 | 0.013 | –0.006 | 4.058 | 3.512 | 0.034 | 0.042 |
| *Macaranga* sp. | MAC SP | pioneer | 2.482 | 0.002 | –0.163 | –2.712 | 0.000 | 0.018 | 8.133 | 7.089 | 0.052 | 0.102 |
| *Myristica* sp. | MYR SP | climax | 1.591 | 0.045 | –0.086 | –3.873 | 0.017 | –0.005 | 2.827 | 2.559 | 0.024 | 0.030 |
| *Pimeleodendron amboinicum* | PIM AMB | climax | 2.631 | –0.230 | –0.091 | –4.139 | 0.027 | –0.027 | 6.736 | 6.223 | 0.012 | 0.035 |
| *Planchonella* sp. | PLA SP | climax | 1.565 | 0.132 | –0.107 | –3.544 | 0.013 | –0.008 | 3.289 | 2.925 | 0.029 | 0.039 |
| *Pometia pinnata* | POM SP | climax | 1.493 | 0.109 | –0.111 | –3.663 | 0.007 | –0.051 | 2.720 | 2.382 | 0.006 | 0.047 |
| *Syzygium* sp. | SYZ SP | climax | 1.636 | 0.057 | –0.102 | –3.564 | 0.006 | –0.021 | 3.060 | 2.728 | 0.017 | 0.038 |
| *Terminalia* sp. | TER SP | climax | 1.889 | 0.073 | –0.083 | –3.814 | 0.019 | –0.002 | 4.824 | 4.459 | 0.030 | 0.032 |

Note:
G-$b_0$, G-$b_1$, G-$b_2$ are parameters for the growth model (9), while M-$b_0$, M-$b_1$, M-$b_2$ are parameters for the mortality model (10). GLC, GHC, MLC, MHC are growth (cm/year) under low competition (10 $m^2$/ha), growth under high competition (50 $m^2$/ha), probability of mortality (between 0 and 1) under low competition, and probability of mortality under high competition, respectively.

OSR values that are most affected by competition for light would be expected to be shade intolerant, while species with large OSR with a more diffuse competitive affect would be shade tolerant.

Table 4 also provides insights into tree attributes that could be used as a basis for species grouping. Wood density, growth rate and potential size have been used in other studies to group species. *Macaranga* is a pioneer species with the largest growth rate (0.96 cm/year), smallest potential size (22.8 cm), lowest wood density (300 kg/m$^3$) and strongest correlation for competition indexes (0.27). This is congruent with previous findings that pioneer species tend to be fast growing, have small potential size and low wood density, and tend to be shade intolerant with a life cycle characterised by rapid growth to capitalise on canopy gaps. Intolerance to shade from nearby trees confirms the importance of competition indexes in explaining future growth. In contrast, *Pometia pinnata* (taun) is a climax species with a slower growth rate (0.67 cm/year), large potential size (54.5 cm), denser wood (580 kg/m$^3$) and weaker correlation for competition indexes (0.16). Again, this is congruent with climax species being slower growing, having larger potential size and denser wood, and being more tolerant of shade from nearby trees. More tolerance to competition explains the weaker correlation of competition indexes with future growth. The local spatial arrangement of soil fertility and topographic, geologic and climatic factors will be more important in explaining growth for shade-tolerant species. Other species in Table 4 fall on the continuum between pioneers such as *Macaranga* and climax species such as *Pometia pinnata*. This suggests that competition response, as characterised by competition indexes, could be used as an additional attribute for species groupings in tropical forests.

This analysis suggested that no single competition index is dominant, with indexes BAS and LNNEW performing well. The optimal index for each species explained only a modest amount (14–27%) of the variability in diameter increment. However, indexes were highly significant when evaluated in a mixed model with BA/ha. Failure to identify a single index as optimal in the mixed tropical forests of PNG could be associated with variability in competition response across the 300 species. Shade-intolerant species will compete strongly with first-order neighbours for light and nutrients. The SQAPAWC most accurately characterises these first-order interactions. The LNAO1 and LNNEW competition indexes may perform better for more shade-tolerant species, as competition for light and nutrients would be more diffuse, less intense, and would occur over a larger area. Following this hypothesis, distance-independent indexes such as BAS and DBHOB would perform well for very shade-tolerant species for which the location and size of nearby competitors is relatively unimportant. Future work should attempt to align the shade tolerance of different species with the performance of different competition indexes.

Diameter performed well as a predictor of growth—better than competition indexes for 14% and 18% of species. This is in agreement with previous studies (Lorimer 1983). Diameter can be considered a historical log of past competitive interactions, genotypic differences and localised environmental heterogeneity, and therefore tends to be strongly correlated with future growth.

Tree growth is a complex process. It is influenced by an intricate network of above- and below-ground competitive interactions as well as the local spatial arrangement of soil fertility and topographic, geologic and climatic factors. The vast majority of current competition indexes and growth models remain overly simplified (Fox et al. 2001). This results in large amounts of unexplained variability, and growth modellers have come to accept this as an 'occupational hazard' (Burkhart and Gregoire 1994). Competition indexes explained, at best, 25% of the variability in individual tree growth in mixed tropical forest in PNG. Future work requires insights into this unexplained variability that can improve growth model performance. Despite these shortcomings, the competition indexes examined here, and the insights into competitive dynamics they provided, can guide further growth model development for mixed tropical forest in PNG.

Work described in this paper represents an initial investigation of competition index selection in tropical forests, and application of individual-tree-based models with demographic hierarchical Bayesian models, including species random effects. Results suggest that the approach shows promise. Future work should fit a recruitment model and use species-specific competition indexes in growth/mortality models.

The forest assessment tool is described elsewhere and is based on a stratified random variable-radius plot inventory (Fox et al. 2011b). The assessment tool incorporates lookup tables that facilitate the

calculation of plot- and estate-level above-ground live biomass (t/ha) and merchantable volume ($m^3$/ha). In future work this forest assessment tool can used as a basis for the individual-tree growth and yield module, which can then be used to simulate forest development into the future. Data from the forest assessment tool can be read into the forest simulation tool, which is under development at <http://twoe.org>. Using individual-tree HBM model parameters estimated from the PSPs, assessment data can be used as the basis of a simulation. Lookup tables for species-specific HBM parameters for growth, mortality and recruitment models are available from the primary author. Each tree measured in the assessment therefore becomes a tree in the simulation that is subject to perturbations from growth and possible mortality into the future. New trees eventuate in the simulation from the recruitment model that uses tree density and species present on each plot to create a probability of recruitment.

A simple tree-level simulator housed in accessible software (http://twoe.org) can assist community-level decision-making with regards to the design and intensity of selective-harvesting regimes. For example, after the forest assessment is complete, a simulation of a harvesting event can be implemented with different size limits, cutting intensities and species. For community forest management, this will allow communities to maximise returns from harvesting while preserving other forest values. Small-scale, high-value utilisation scenarios can be effectively explored using such models. Utilisation below unsustainable levels, which has been set in the simulator according to species-specific growth rates, will ensure that high-end products can be harvested in community areas in perpetuity.

PNGFA is moving to a new preharvest inventory method based on a stratified random variable-radius plot inventory that will replace the 1% stripline inventory, which is both inefficient and biased. Therefore, PNGFA can populate the assessment tool with inventory information and run scenarios for large-scale harvesting using software available at <http://twoe.org>. The scenarios can help identify appropriate and sustainable harvesting in terms of size limits, species mixes and cutting cycles. Currently, a default size limit of 50 cm is used on a 35-year cutting cycle. It is intended that the assessment and modelling tools developed as part of ACIAR project FST/2004/061 can help refine this approach for more sustainable forest harvesting.

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