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## Using Plant Functional Attributes to Quantify Site Productivity and Growth Patterns in Mixed Forests

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**Abstract**

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Forest growth models are one of several important prerequisites for sustainable management. The complexity of tropical moist forest means that there is often little objective information to classify sites and species for growth modelling and yield prediction. Classification based on observable morphological characteristics may be a useful surrogate for, or supplement to other alternatives. This study investigated the utility of plant functional attributes (PFAs) for site and species classification.

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PFAs describe a plant in terms of its photosynthetic and vascular support system, and the sum of individual PFAs for all species on a plot provides an efficient summary of vegetation features at the site.

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Preliminary observations suggested that the PFA summary may also indicate site productivity, and that specific PFAs may be used to group species for modelling growth and yield. Data from 17 permanent

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plots in the tropical rainforests of North Queensland were used to test these preliminary observations.

Standard PFA proformas were completed for each plot in January 1995, and the relationships between

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the PFAs, site productivity and specific growth patterns were examined using discriminant analysis, linear regression and standard statistical tests. Results indicate that mean leaf size, and the incidence of

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species with vertical leaf inclination ( $>30^\circ$  above horizontal) are significantly correlated with site productivity. Of the PFAs assessed, five elements appear to offer a useful basis for grouping species for

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modelling: leaf size and inclination, a furcation index (i.e., relative height to first fork or break in the main stem), and the presence of lenticels and chlorophyllous tissue on the main stem. The restricted

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nature of our database limits comment on the general utility of the method, but results suggest that further work on PFAs is warranted.

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*Key words:* Plant functional attributes; site productivity; growth rate; species groups; growth modelling;

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Queensland, Australia; rain forest.

## Introduction

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Growth models may assist forest management and planning in many ways, but their use may be restricted by the need for permanent plot data to calibrate the model. Application of an existing model based on such long-term data to a new region may be problematic, even if species composition and growing conditions in the new situation are similar, because local growth data are needed for each recalibration of the model. Estimates of forest growth rates and sustainable harvests of timber and other forest products are needed in many parts of the tropics but there are few data available for development of new models, or for re-calibration of existing models. The problem is compounded by the species richness and variability in tropical regions. Forest managers in the tropics cannot afford the luxury of waiting for long-term data from newly-established plots; they need reliable resource information now to provide a factual basis for management planning and harvest controls. A number of models based on long-term growth measurements have been developed for tropical forests (Vanclay, 1995) and these might be successfully applied to new situations if new ways can be found to allow existing models to be extrapolated to other sites and to other species.

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There are two specific difficulties in attempting to apply an existing growth model to a new location: quantifying the overall productivity of the new site, and modelling the growth of species not present at the original site (Vanclay, 1994). Quantitative estimates of site productivity remain a formidable obstacle to efficient growth and yield forecasting in mixed tropical forests (Vanclay, 1992), and any objective approximation warrants further research. Similarly, unbiased growth modelling of these forests requires that growth relationships are specified for all species, including those not represented in the database used to calibrate the model (Vanclay, 1994). Thus objective ways to assign species to groups with established growth relationships are required. Many experienced foresters and modellers are able to make reasonable subjective appraisals of site productivity and species groups based on visual characteristics of the site and the trees (e.g., Vanclay, 1989*a*, 1992), but these are unavoidably

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subjective, and may not be reproduced by other observers. This paper examines a procedure to make such appraisals more objective, explicit and repeatable.

Gillison (1981, 1988; Gillison and Carpenter, 1994) suggested a formal approach to describe and document selected characteristics of plants, focusing on morphological attributes indicative of plant function and site characteristics. The system describes individual plants in terms of their photosynthetic envelope and vascular support system or life form. The photosynthetic envelope is described according to the most frequent functional leaf-unit using four attributes (size, inclination, chlorotype and form). Together these define the spatial and temporal distribution of photosynthetic tissue within the plant. The vascular support system is described according to life form (modified from Raunkiaer, 1934) and above-ground rooting habits. These plant functional attributes or PFAs (Gillison, 1981; Gillison and Carpenter, 1994) are essentially morphological adaptations that make no assumptions about guilds or life histories, but instead, provide a functional "snapshot" of an individual via attributes that reflect the essentials of growth, physiology and survival. This PFA description of the plants and the site may formalise some of the factors implied in subjective appraisals of site productivity and growth patterns (or species affiliations). Here, we test this assumption with linear regression (in the case of site productivity) and discriminant analysis (for growth patterns).

There is some evidence that within a given region, site productivity can be inferred from the presence or absence of selected indicator species (e.g., Webb *et al.*, 1967; Vanclay, 1992, 1994), but these inferences may be valid only locally. Although indicator species may perform well in temperate environments (e.g., Corns and Pluth 1984), their utility in the tropics is reduced by the large number of species with localised distributions. Thus, the chosen indicator species may be replaced by other functionally-similar species within relatively short distances. For tropical forests, the use of PFAs, rather than indicator species, to record the natural expression of site characteristics may improve our ability to extrapolate site productivity estimates.

2 Attempts to use an existing growth model in a new region may encounter new species not present in the  
calibration database, and for which no growth data or equations are available. If suitable data exist,  
4 established relationships may be recalibrated or new ones formulated. Unfortunately, such data are  
rarely available, and it is usual for new species to be assigned to one of the established relationships in  
6 an existing calibration of the model (Vanclay, 1994). Taxonomic relationships (i.e., botanical  
nomenclature) and broad successional guilds (cf. van Steenis, 1958; Swaine and Whitmore, 1988) do  
8 not always provide a good guide (Vanclay, 1991*a*). Empirically, the best strategy may be to assign such  
species to the most common group (Vanclay, 1991*b*). However, PFAs may offer a more rational basis  
10 for grouping species for modelling purposes.

12 We examine whether PFAs can be used in an explicit and objective way to quantify site productivity for  
growth and yield modelling, and to classify tree species so that new species can be assigned to existing  
14 growth equations. Specifically, we wish to test the following hypotheses:

1. That a quantifiable relationship exists between site productivity and the PFAs recorded at the  
16 site, and that this relationship enables the productivity of new sites to be inferred more  
accurately than with alternatives such as indicator species alone.
- 18 2. That the PFAs exhibited by a species can be used to reliably allocate species to groups with  
statistically similar diameter increment and mortality functions and thus provide an objective  
20 way to assign new species to existing growth equations.

## 22 **Background**

### *Study Location and QFRI Database*

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The study was conducted in the rainforests of north Queensland, Australia. These rainforests occupy an  
26 area of about 1 million ha along the eastern coast between the latitudes of 16 to 19°S, extending from

the lowlands to 1200 m above sea level, and from the coast to some 60 km inland. They consist of forests with a range of stand structures and species compositions that differ markedly to adjacent sclerophyll forest types (Tracey, 1983). The Queensland Forest Research Institute (QFRI) has an extensive computerized database derived from over 200 permanent plots across the range of these forests, some of which have been measured at regular intervals for up to 40 years (Vanclay *et al.*, 1991). These data, and many of the plots, are easily accessible, have been carefully checked for errors, have been used in many studies (see e.g., Vanclay, 1993, for a review of some studies), and are well known to many researchers, including the authors. Of particular significance for this study was the availability of site productivity estimates for most of the plots (Vanclay, 1989*b*), and established species groups for both diameter increment and mortality relationships (Vanclay, 1991*b*). These factors collectively made the QFRI plots ideal for the present study.

The plots range in size up to 0.5 ha (Vanclay *et al.*, 1991). Many have been logged at some time during their history (a few as many as 3 times), and some have been silviculturally treated (e.g., poisoning of unwanted trees and/or enrichment planting with commercial species; Vanclay *et al.*, 1991). At the time of last measurement, plots were clearly marked, and all trees were numbered and painted or tagged, simplifying plot relocation. However, commercial harvesting (and road maintenance, plot remeasurement, etc.) ceased in these forests following their inclusion on the World Heritage List in 1988 (Trott, 1996), and, as a result, access and plot relocation are becoming increasingly difficult.

#### *Estimating site productivity*

We use an index of site productivity developed from the permanent plot measurements and based on individual tree growth of 18 reference species (Vanclay, 1989*b*). The reference species are *Acronychia acidula*, *Alphitonia whitei*, *Argyrodendron trifoliolatum*, *Cardwellia sublimis*, *Castanospora alphanthii*, *Cryptocarya angulata*, *C. mackinnoniana*, *Darlingia darlingiana*, *Elaeocarpus largiflorens*, *Endiandra* sp. aff. *E. hypotephra*, *Flindersia bourjotiana*, *F. brayleyana*, *F. pimenteliana*, *Litsea leefeana*,

*Sterculia laurifolia*, *Syzygium kuranda*, *Toechima erythrocarpum* and *Xanthophyllum octandrum*. An increment function was fitted simultaneously for all these species, to all non-overlapping measurement pairs on 80 permanent plots (for some plots measured more frequently, selected remeasurements with approx. 5 year intervals were used). The plot identifier was included as a qualitative variable (cf., a vector of  $n$  binary variables, Vanclay, 1994 p. 104) to gauge the effect of site:

$$\ln(\Delta d_{ijk} + \alpha) = \sum_i \beta_{0i} Z_i + \sum_i \beta_{1i} Z_i d_{ijk} + \sum_i \beta_{2i} Z_i \ln d_{ijk} + \sum_i \beta_{3i} Z_i G_k + \sum_i \beta_{4i} Z_i G_{>dijk} + \sum_k \gamma_k Z_k \ln d_{ijk} \quad (1)$$

where  $\Delta d_{ijk}$ ,  $d_{ijk}$  and  $G_{>dijk}$  are the diameter increment ( $\text{cm y}^{-1}$ ), initial diameter ( $\text{cm dbh}$ ) and basal area in larger trees ( $\text{m}^2 \text{ha}^{-1}$ ) respectively for tree  $j$  of species  $i$  on plot  $k$ ,  $G_k$  is the stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ) on plot  $k$ ,  $Z_i$  is a binary variable which takes the value 1 for trees of species  $i$  and zero otherwise,  $Z_k$  is a binary variable which takes the value 1 for trees on plot  $k$  and zero otherwise, and  $\alpha$ ,  $\beta_i$  and  $\gamma_k$  are parameters to be estimated. This equation can be re-arranged to estimate the growth index for a given permanent plot:

$$S_{\Delta d} = 11.35 \{ \sum_{ij} \ln(\Delta d_{ij} + 0.02) - \sum_{ij} (\beta_{0i} + \beta_{1i} d_{ij} + \beta_{2i} \ln d_{ij} + \beta_{3i} G + \beta_{4i} G_{>dij}) \} / \sum_{ij} \ln d_{ij}$$

where  $S_{\Delta d}$  is the growth index of the plot (notice that this is the parameter  $\gamma_k$  from Equation 1, rescaled to more convenient units),  $d_{ij}$  is the diameter ( $\text{cm}$ ) of tree  $j$  of species  $i$ ,  $\Delta d_{ij}$  is its diameter increment ( $\text{cm y}^{-1}$ ),  $G_{>dij}$  is the basal area of trees within the plot that are bigger than tree  $ij$  ( $\text{m}^2 \text{ha}^{-1}$ ),  $G$  is the plot basal area ( $\text{m}^2 \text{ha}^{-1}$ ), and the  $\beta$ s are those obtained by fitting Equation 1. The value 11.35 was subjectively determined to scale the growth indices into the range 0–10. This equation provides an estimate of site productivity based on the diameter increment adjusted for tree size and competition, of all trees of the 18 reference species using all available remeasures for the plot. This is analogous to taking the average of growth indices read from growth curves for each of the 18 reference species that occur on a plot.



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*Species Groups and Growth Equations*

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Data limitations and the need for parsimonious models mean that species must be grouped to reduce the number of mathematical relationships and parameters within a model. Such grouping should combine species that are in some sense similar so as to minimize within-group variability and maximize variation between groups. While there is no way to group species that is satisfactory in every sense, useful results may be obtained with simple pairwise comparisons based on F-tests (e.g., for linear regressions with diameter increment data) or  $\chi^2$  tests (e.g., for logistic regressions with mortality data). The procedure used to group north Queensland species (Vanclay, 1991a, 1994) involved:

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1. Ranking species in order of increasing number of observations.
2. Assigning the species of highest rank the founding species of group 1.
3. For each species in decreasing order of rank, conducting pairwise tests with all the founding species of higher rank. If the incoming species is significantly different from all existing founding species, it becomes the founding species of a new group. Species not significantly different from all founding species remain ungrouped during this initial pass.
4. After the founding species have been identified, the remaining species are compared, in order of rank, with all existing groups, and combined with the most similar group. Similarity is determined as the grouping which leads to the smallest increase in residual sum of squares (based on the whole group, not just the founding species) when the incoming species is amalgamated with the group.

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This approach provided 41 species groups with statistically similar diameter increment relationships (Vanclay, 1991a), and 10 groups with similar mortality patterns (Vanclay, 1991b), from a database comprising some 237 species. These groups exhibited a diverse range of growth patterns with two desirable characteristics:

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1. all species within a group exhibited a growth pattern indistinguishable (in a statistical sense,  $P < 0.05$ ) from those of other members of the same group; and
  2. each group exhibited a growth pattern significantly different ( $P < 0.05$ ) from all other groups.
- Although these represent the best empirical classifications presently available, there is no guarantee that the outcome is optimal, and the grouping is specific to the particular data set and growth function used.
- The species and groupings involved in the present study are indicated in Table 1.

### 8 *Plant Functional Attributes*

PFAs have been proposed as a generic method to describe compare in a quantitative way, any assemblage of vascular plants, by recording attributes from selected individuals of each species present at the site (Gillison and Carpenter, 1994). PFAs are recorded for each individual as a *modus*, a prescribed series of 2-character codes (typically 4–6, but in theory as many as 18 are possible; Table 2). The mapping of species to modi is many-to-many. More than one species may occupy the same modus, and different individuals of the same species may exhibit different modi. Although the number of possible modi exceeds 7 million, field data can be readily checked by noting the simple grammar specified in the PFA system (Gillison and Carpenter, 1994), evident when expressed in Backus-Naur form in which spaces imply *and*, the vertical bar ("|") implies *or*, brackets ("[ ]") indicate an optional element, and parentheses ("()" and "{ }") indicate precedence (see Table 2 for an explanation of codes):

20        PFA     = LS LI CL LH LF RH  
           LS     = PI | LE | NA | MI | NO | ME | PL | MA | MG | NR  
 22        LI     = VE | LA | PE | CO  
           CL     = { ( DO | IS ) [DE] [CT] } | AC  
 24        LH     = [RO] [SO] [SU] [PV] [FI] [CA]  
           LF     = ( PH | CH | HC | CR | TH ) [LI]  
 26        RH     = [AD] [AE] [EP] [HY] [PA]

These data can be converted to binary strings, indicating the presence (1) or absence (0) of each of these 36 elements. The plot PFA modus represents the sum of these strings for each species recorded on the 40×5 m strip sample. Thus the PFA modus for any individual comprises a string of 36 binary elements (0 or 1), while the modus for a plot comprises a vector of 36 integers ( $\geq 0$ ). Our contention, explored in this paper, is that the modus for an individual reflects the characteristics of both the species and the site, while the modus for a plot primarily reflects site characteristics.

## Data

We chose the QFRI plots for the preliminary test of our hypotheses because of the quality of the database, the comparative ease of plot access, and our knowledge of these forests. To efficiently test PFAs under a wide range of representative environments, we selected a subset of north Queensland rainforest plots that included extremes of site productivity over a wide range of altitude, soil type (Fig. 1), rainfall and management history. Although we selected plots that could be accessed within a day, available resources limited our PFA assessments to 17 plots, all of which were sampled during January 1995. PFA assessments typically took 90 minutes per plot, half of which was committed to gathering data additional to the standard PFA procedure (Gillison, 1988) to allow an appraisal of the utility of PFAs for grouping species. We sampled four of the six most important soil parent material types: acid volcanic, basic volcanic, coarse granite, and sedimentary-metamorphic (fine-grained granite and alluvial-colluvial were not sampled); and a wide range of physical and biotic site characteristics (Fig. 1, Table 3).

PFAs were recorded on a 40×5 m strip transect in each plot. This transect was located to sample a representative and homogeneous part of the plot, and was generally placed along the contour. We recorded PFAs for each species represented in the transect (both canopy or understorey species). Formal species identification is not required *a priori* for the PFA system (where “morphospecies” are accepted)

although for practical purposes voucher specimens may be taken for subsequent identification. In our case, species identification was simplified by access to field sheets from previous measures. We also recorded PFAs of 20 additional mature canopy trees in the vicinity of each plot to investigate species groupings. In this way, we obtained PFA data on 17 plots and on 340 mature trees of 94 species (the 20 additional trees; Table 3).

A number of other items were also recorded, e.g., crown cover (%), mean canopy height (m), basal area ( $\text{m}^2 \text{ha}^{-1}$ ), litter depth (cm), approximate soil depth (3 classes), and an estimate of the relative abundance of woody plants and bryophytes based on the Domin-Krajina cover-abundance scale (0–10; Mueller-Dombois and Ellenberg, 1974). A furcation index was recorded for the 20 canopy trees nearest to the transect centre. The index is based on the linear axis of the main stem rather than on lateral branches, and represents the relative height, as a percentage of total height, from the crown to the first fork or break in the main axis. Thus trees with a monopodial (e.g., coniferous or excurrent) habit may score 0% whereas multistemmed trees branching at or near ground level may score 100%. The presence or absence of lenticels on the bark of the main stem of each tree was also recorded, even though not part of the standard PFA proforma. Their prevalence in seasonally flooded forests suggests they may be potentially useful indicators of seasonally-limited soil aeration and thus growth performance.

## Analyses

### *Regression Analysis with Productivity Data*

The PFA data, for both sites and species, pose special problems for analysis since much is sparse binary data (i.e., vectors comprising mainly zeroes with a few ones, e.g., parasitic species, PA in Table 3). The inclusion of these variables in a statistical model may greatly reduce the residuals associated with the non-zero entries, so that the variables appear to be statistically significant, even though the result is most

probably due to chance. The danger of this is greater than it appears, since this effect may also arise with bimodal data (e.g., vectors comprising many values  $p+\delta_i$  and a few values  $q+\delta_j$  where  $p\neq q$  and the  $\delta$ s are small), and with linear combinations (i.e.,  $\beta_1 X_1 + \beta_2 X_2 + \dots$ ) of variables apparently not sparse. Thus any variables which appeared sparse (e.g., parasitic species, PA), which exhibited a disjoint bimodal distribution with few points contributing to the second mode (e.g., species with pendulous leaves, PE in Table 3), or which exhibited an exceptionally strong leverage in the fitted model (e.g., chamaephytes, which when regressed against site productivity, exhibited a leverage three times the accepted limit of  $2p/n$ ) were omitted from the final analyses.

There are few statistical guidelines for dealing with such data (other than techniques for assessing the magnitude of the problem, e.g., Verbyla, 1986), so the following "rules of thumb" were used (where  $n$  is the number of data sets):

1. If a strongly bimodal distribution(  $[0, 1]$  or  $[p, q]$  ) contains fewer than  $\sqrt{n}$  data in one mode, consider it sparse and be wary of including it in the model.
2. Do not screen endless alternative variables and transformations for possible inclusion in a model, but consider at most  $n/2$  variables chosen for biological relevance.
3. Allow a maximum of  $\sqrt{n}$  variables in the model.

Regression techniques were used to explore the ability of PFA modi to indicate site productivity, using data from the standard PFA assessments on the 40x5 m transects (i.e., excluding the 20 supplementary trees). Although stepwise regression was used in initial screening of possible variables, suitable relationships were not self-evident (cf. Equation 2 below), and the relationships finally selected were "hand-crafted" after careful inspection of partial correlations, residuals and leverage values in many prototypes. Despite this subjective element in our analyses, the relationships reported make both biological and statistical sense, and faithfully reflect the potential of PFAs to reveal site properties.

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*Discriminant Analysis of Group Membership*

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The individual tree data (including the supplementary 20 trees) obtained in this study included species in 33 of the 41 established diameter increment groups (Vanclay, 1991a), and in 9 of the 10 mortality groups (Vanclay, 1991b). Our sample included some species with insufficient data to be empirically grouped (i.e., in the original studies by Vanclay, 1991a,b), and these were omitted from the present study. Some species groups contained very few data, so we omitted 9 records with single observations in each of 4 diameter increment groups (Groups 24, 26, 34 & 35), and  $\leq 3$  observations in 3 mortality groups (Groups 2, 7 & 9). This left 246 observations on 44 species, representing 29 diameter increment and 6 mortality groups, for the final analyses (Table 4).

Since 44 species are insufficient for a meaningful explanation of possible assignments into 29 diameter groups, diameter increment groups were amalgamated into six "hypergroups" (Table 4) using hierarchical cluster analysis (Ward's method). Other algorithms were also evaluated and offered comparable results (hypergroup membership differed slightly, but the same PFAs were chosen as discriminants of hypergroup membership). While our decision to use six hypergroups was arbitrarily based on the presence of six mortality groups, the results were comparable with other clustering algorithms and maintained 90% of the variability observed in the original parameter estimates (i.e., the 7 parameters defining the 29 increment equations given by Vanclay, 1991a).

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Because "true" group membership has been established for both increment and mortality patterns, discriminant analyses may be used to indicate variables which discriminate between groups. The algorithm which was used minimized Wilk's lambda and assigned equal prior probabilities to each group. Such analyses can be carried out three ways:

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1. with individual trees (i.e.,  $n = 246$ , unweighted),

2. with single tree data but mean PFAs for the species (effectively  $n = 44$ , weighted by the number of observations), or
3. with aggregated species data (i.e.,  $n = 44$ , unweighted).

These alternatives yield slightly different results. Discriminating variables were generally similar, but the apparent accuracy of the classification varied greatly (e.g., 20 – 80%). Results from the second strategy are reported because for modelling purposes it is necessary to assign all individuals of any given species to the same species group, and because model users generally will be able to observe the PFAs of several individuals of any species and could use the central tendency as a basis for grouping species. The mean, rather than the mode, was used because it makes greater use of the available information (e.g., reflects variability as non-integer numbers), and avoids subjective decisions for equal modes.

## Results

### *Site Productivity*

Stand-level variables alone did not account for any significant variation in growth index (e.g., dominant height,  $r^2 = 0.17$ ,  $P > 0.10$ ). Even when many other site variables (e.g., altitude, slope, aspect, litter depth, species richness, rainfall, soil type, etc.) were also considered as potential predictors, the "best" relationship explained only 32 percent of the variation ( $P < 0.10$ ):

$$S_{\Delta d} = 9.8 - 3.2S_{as} - 0.0032E \quad (2)$$

where  $S_{\Delta d}$  is growth index, an index of site productivity,  $E$  is elevation (m asl), and  $S_{as}$  is a binary variable that takes the value 1 if the soil parent material is acid volcanic or sedimentary-metamorphic

(standard errors associated with these parameters are 1.6, 1.2 and 0.0017 respectively). When up to three PFA variables were included in the analysis in conjunction with predominant height, a substantial amount of the variation could be explained (e.g.,  $r^2 = 0.6 - 0.8$ ). Because of the nature of these data, many alternatives provide similar goodness-of-fit statistics, and Equation 3 given below is just one possibility that appears to be relatively robust. However, the purpose of this analysis is not to provide an equation to predict growth index, but to illustrate the potential of PFAs to indicate, or supplement other indicators of site productivity. One equation of some interest was the following ( $r^2 = 0.60$ ,  $P < 0.01$ ):

$$S_{\Delta d} = 0.21 H_d + 3.92 L + 0.74 VE - 13.26 \quad (3)$$

where  $S_{\Delta d}$  is growth index,  $H_d$  is dominant height,  $L$  indicates mean leaf size observed (NA=1, MI=2, NO=3, ME=4, PL=5), and  $VE$  is the number of species with vertical leaf inclination recorded on the 200 m<sup>2</sup> plot (standard errors for these parameter estimates are 0.10, 2.00, 0.20 and 6.08 respectively). This is a substantial improvement over the previous equation (2) based on site and stand-level variables ( $F_{1,13} = 9.19$ ,  $P < 0.01$ ). Although the contribution attributable to dominant height in this equation is small, it is significant both statistically ( $t = 2.1$ ,  $P = 0.05$ ) and ecologically (height has long been recognised as a useful indicator of site productivity; see e.g., Vanclay, 1992). The PFA elements,  $L$  and  $VE$ , contribute substantially to the relationship ( $F_{2,13} = 7.08$ ,  $P < 0.01$ ). Soil parent material, which has served as a useful indicator of site productivity in other studies (e.g., Vanclay, 1989*a,b*), made no further contribution to this relationship ( $F_{3,10} = 0.32$ ,  $P > 0.10$ ). Comparable equations based on eight established indicator species provide an inferior fit (e.g., without soils,  $r^2 = 0.38$ ; with soils,  $F_{8,5} = 0.04$ ,  $P > 0.10$ ).

The equilibrium stand basal area attained in undisturbed stands has been found useful as an indicator of site productivity (e.g., Vanclay, 1992), and despite logging and treatment in some of these plots, the inclusion of stand basal area ( $G$ , m<sup>2</sup>/ha) significantly reduced unexplained variance ( $r^2 = 0.73$ ; For inclusion of  $G$ ,  $F_{1,12} = 5.71$ ,  $P < 0.05$ ; for overall model,  $F_{4,12} = 8.09$ ,  $P < 0.01$ ):



$$S_{\Delta d} = 0.24 H_d + 3.85 L + 0.90 VE + 0.083 G - 17.4 \quad (4)$$

(standard errors are 0.09, 1.71, 0.18, 0.035 and 5.49 respectively). No other site or stand variables offered a significant reduction in unexplained variance. Note the small change in parameter estimates with the inclusion of basal area (cf. Equations 3 and 4), indicating that the selected variables are approximately orthogonal and supporting our contention that the model is relatively robust (also see correlation matrix, Table 5).

There may be some limitations with the use of the variable *VE*, the number of species with vertically inclined leaves, since it may depend on sample size (i.e., area of the strip transect), but it provided a better model than alternatives such as the proportion of species characterised as *VE*. Evidently, it is not only the proportion of such species, but also the total species richness that correlates with site productivity.

### *Species Groups and Growth patterns*

The variables with greatest power to discriminate species group membership (for both increment and mortality) were leaf inclination and size, cortic chlorophyll (i.e., photosynthetic stem), lenticels and furcation index. A relationship using these variables was able to classify 77% of individuals and 43% of species into their correct diameter growth group (Table 6) and 75% of individuals and 48% of species into the correct mortality group (Table 7). Whilst a success rate of 40–50% (for species, 75–80% for individuals) leaves considerable scope for improvement, it is considerably better than many alternatives (e.g., Vanclay, 1991*b*). For comparison, a random assignment of group membership would result, on average, in 17% being correctly classified.

For diameter growth groups, leaf size and inclination (coded as  $VE = 1$ ,  $PE = 1$ ,  $CO = 0.5$  and  $LA = 0$ ) were the most important variables (i.e., the first two canonical discriminant functions, essentially leaf inclination and size, accounted for 77% of the total variation explained by the model), while the furcation index contributed very little (0.5%). However, the furcation index was critical for explaining the mortality pattern, with the canonical discriminant functions relating to furcation and leaf inclination accounting for 91% of the variation. Note that all these variables have a limited range. The mean leaf inclination for a species had a bimodal distribution in the range 0.5–1.0 (a lateral leaf habit was not observed amongst these 44 species). Mean leaf size ranged from 2 (microphyll) to 4 (mesophyll) with a conspicuous mode (50%) at 3 (notophyll), and furcation ranged from 0–60%, with a mode (50%) at 10%. Because of the coarse resolution of these variables, it is unlikely that the classification of species into groups could be improved without additional variables.

These rather promising results led us to explore the possibility of predicting the seven coefficients of the diameter increment equation (Vanclay, 1991a) directly from specific PFAs, but preliminary attempts suggested that good predictions could not be made ( $r^2 = 0.15 - 0.30$ ).

## Discussion

These results indicate that a quantifiable relationship exists between plant morphological characteristics, objectively described using PFAs, and site quality and productivity. They also indicate that PFAs descriptions of individuals can be used, with a relatively high degree of success given the limited data set, to allocate species into groups with similar diameter increment and mortality patterns. Mean leaf size, and the incidence of species with vertical leaf inclination ( $>30^\circ$  above horizontal) were significantly correlated with site productivity, while five PFAs appear to offer a useful basis for forming species groups for modelling: leaf size and inclination, a furcation index (i.e., relative height to first fork or break in the main axis), and the presence of lenticels and chlorophyllous tissue on the main stem. The

discriminating attributes seem consistent with the ecology of species groups. Leaf size is generally correlated with altitude in the study area (Tracey, 1983) and it may be that it serves as a surrogate for the effect of decreasing growing season with altitude on forest productivity. In the case of mortality, leaf inclination is associated with successional guild (e.g., many short-lived pioneers have lateral leaves), and furcation reflects seral stage, site disturbance and the ability of the species to recover after damage. Attributes discriminating diameter increment groups may reflect specific strategies for intercepting sunlight (e.g., large, lateral leaves), conserving water (e.g., pendulous leaves) and exploiting other resources.

The utility of selected PFAs such as leaf size and inclination, in this preliminary case study does not imply that other PFAs are not equally useful in this regard. Despite our attempts to sample the full range of accessible plots, our results are unavoidably influenced by the limitations of our data: namely, that they derive from a small number of plots located exclusively in forest stands (previously) of commercial interest in north Queensland. Other PFAs may have been better predictors of growth index if we had been able to sample a larger number of plots across a wider range of site conditions (e.g., including waterlogged sites). If more data had been available, we would not have had to omit so many sparse binary variables from our analysis, and may have found other useful indicators of site condition and specific growth habits. Thus our study is indicative rather than definitive. Notwithstanding these limitations, we anticipate that these preliminary findings will stimulate greater interest and further research in this area.

PFAs appear to offer some potential to help characterize site productivity. When used in isolation, their ability to predict site productivity seems limited, but they offer considerable potential when used in conjunction with other stand-level variables such as dominant height (e.g., Equation 3). Although Equation (3) looks promising (i.e.,  $r^2 = 0.60$ ;  $P < 0.01$ ), we advocate caution and further research, since this relationship may not be independent of stand condition (cf. equation 4). The species grouping

arising from the discriminant analysis was better than alternatives, even though it used only five elements from the PFA system. Nonetheless, it left considerable room for improvement.

We have demonstrated that PFAs offer some potential to help characterize site productivity and define broad groups based on growth patterns. However, before this potential can be realized, the PFA system should be shown to be *logical, useful, objective, repeatable* and *efficient*. Two of these qualities (logic and efficiency) have been demonstrated (e.g., Gillison, 1981, 1988; Gillison and Carpenter, 1994), and the present study is one of a series intended to test the utility and efficiency of the PFA concept. Further work is in hand to demonstrate that the system is objective and repeatable. It is important that these criteria are satisfied before the system is recommended for assessing site productivity and species groupings, even though few methods of vegetation classification have been subjected to such scrutiny and testing. Few alternative classification systems appear to offer the predictive potential of the PFA system.

## Conclusion

Plant functional attributes (PFAs), particularly those relating to leaf inclination and size, were able to improve predictions of site productivity in moist tropical forest over estimates based on environmental factors or stand characteristics alone. PFAs also showed some utility for classifying species into growth and mortality groups. Data from the 17 plots used in this study are too limited to provide definitive insights into these relationships, but the correlations between PFAs and site/species characteristics appear to be more useful than traditional vegetation structure and species-based indicators for research and management. Specifically, we find no evidence to reject our hypotheses that PFAs are indicative of site productivity, and that PFAs may help to group species for growth models. Our results suggest that further work on PFAs is warranted.

If further investigations can establish the utility of PFAs in identifying forest growth characteristics, it will facilitate wider application of the relatively limited set of long-term measurement data available for tropical forests and the growth models based upon these data. Lack of such long-term growth information and appropriate growth models are major constraints on the development of realistic estimates of sustained yield and levels of allowable harvest for most natural forests in the tropics.

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2 **Table 1.** Nomenclature, codes and groups of species encountered in the present study.

QFRI Code	Botanical Name	Increment Equation (Vanclay, 1991a)	Mortality Equation (Vanclay, 1991b)
BBN	<i>Castanospermum australe</i>	28	10
BLA	<i>Sloanea australis</i>	41	1
BLO	<i>Opisthiolepis heterophylla</i>	30	5
BRO	<i>Darlingia darlingiana</i>	10	1
BRT	<i>Argyrodendron trifoliolatum</i>	32	1
BSL	<i>Acacia aulacocarpa</i>	18	1
BSW	<i>Cryptocarya oblata</i>	37	6
BWD	<i>Litsea leefeana</i>	7	1
CHS	<i>Syzygium luehmannii</i>	25	10
CLO	<i>Carnarvonia araliifolia</i>	5	5
CNN	<i>Aleurites moluccana</i>	21	4
EVD	<i>Euodia elleryana</i>	5	4
FIG	<i>Ficus</i> spp.	28	10
GCB	<i>Sloanea macbrydei</i>	8	1
HMW	<i>Alstonia muellerana</i>	22	1
ILL	<i>Cryptocarya angulata</i>	27	1
KRQ	<i>Elaeocarpus bancroftii</i>	16	3
KRS	<i>Syzygium kuranda</i>	9	10
MSW	<i>Flindersia pimenteliana</i>	1	1
MWN	<i>Endiandra</i> sp. aff. <i>E. muelleri</i>	28	5
NEV	<i>Euodia bonwickii</i>	7	1
NRA	<i>Alphitonia whitei</i>	15	5
NRW	<i>Endiandra cowleyana</i>	9	1
NSO	<i>Cardwellia sublimis</i>	5	10
NSS	<i>Doryphora aromatica</i>	6	1
NTQ	<i>Elaeocarpus foveolatus</i>	37	5
PAL	<i>Gillbeea adenopetala</i>	16	5
PKA	<i>Alphitonia petriei</i>	20	6
PMH	<i>Dysoxylum oppositifolium</i>	9	1
QMP	<i>Flindersia brayleyana</i>	2	1
QSA	<i>Flindersia bourjotiana</i>	4	10
RBN	<i>Blepharocarya involucrigera</i>	3	3
RCD	<i>Toona australis</i>	36	4
RDT	<i>Argyrodendron peralatum</i>	11	10
RPS	<i>Syzygium endophloium</i>	8	1
RSS	<i>Syzygium johnsonii</i>	25	1
SBS	<i>Polyscias elegans</i>	19	5
SLQ	<i>Elaeocarpus grandis</i>	36	6
SST	<i>Dendrocnide photinophylla</i>	33	4
SSW	<i>Flindersia acuminata</i>	27	10
STS	<i>Ceratopetalum succirubrum</i>	8	10
TST	<i>Franciscodendron laurifolium</i>	14	5
WCB	<i>Sloanea langii</i>	32	1
YWN	<i>Beilschmiedia bancroftii</i>	25	1



2 **Table 2.** Elements of the Plant Functional Attribute system.

<b>Photosynthetic elements</b>	
<i>Leaf size (LS)</i>	
PI	picophyll (<2 mm <sup>2</sup> )
LE	leptophyll (2–25)
NA	nanophyll (25–225)
MI	microphyll (225–2025)
NO	notophyll (2025–4500)
ME	mesophyll (4500–18200)
PL	platyphyll (18200–36400)
MA	macrophyll (36400–180000)
MG	megaphyll (>180000)
NR	no repeating unit
<i>Leaf inclination (LI)</i>	
VE	vertical (>30° above horizontal)
LA	lateral (horizontal ±30°)
PE	pendulous (>30° below horiz.)
CO	composite
<i>Chlorotype (CT)</i>	
DO	dorsiventral
IS	isolateral or isocentric
DE	deciduous
CT	cortic
AC	achlorophyllous
<i>Leaf habit (LH)</i>	
RO	rosulate or rosette
SO	solid (3-dimensional)
SU	succulent
PV	parallel-veined
FI	filicoid (fern-like)
CA	carnivorous (e.g., <i>Nepenthes</i> )
<b>Vascular support elements</b>	
<i>Life form (LF)</i>	
PH	phanerophyte
CH	chamaephyte
HC	hemicryptophyte
CR	cryptophyte
TH	therophyte
LI	liane
<i>Rooting habit (RH)</i>	
AD	adventitious
AE	aerating
EP	epiphytic
HY	hydrophytic
PA	parasitic

2 **Table 3.** PFA data from the 17 transects used in this study, in chronological order (left to right).

<b>Site details</b>																	
Experiment <sup>1</sup>	616	616	617	617	617	625	625	622	594	609	618	614	610	78	78	311	434
Plot	1	2	3	4	6	5	4	2	2	2	2	3	3	2	1	1	7
Elevation (m)	1100	1100	1130	1130	1130	730	790	640	720	770	760	30	440	680	680	140	670
Slope (°)	12	14	17	28	20	20	34	10	5	25	6	22	20	18	19	22	24
Aspect (°)	15	335	345	350	52	330	90	150	100	190	115	230	75	345	345	197	130
Posn on slope <sup>2</sup>	Up	Up	Top	Up	Up	Low	Up	Up	Top	Up	Up	Mid	Up	Mid	Mid	Mid	Up
Rainfall (cm)	165	165	165	165	165	165	165	203	203	170	180	400	203	132	132	165	200
Soil type <sup>3</sup>	CG	CG	CG	CG	CG	CG	CG	BV	BV	AV	BV	SM	SM	SM	BV	AV	BV
<b>Stand details</b>																	
Growth Index <sup>4</sup>	9.2	7.1	5.7	8.3	3.9	7.2	6.9	6.6	8.3	3.8	6.2	5.6	6.0	2.0	7.8	9.2	6.5
Dom. height (m)	25	28	18	25	20	28	20	25	28	19	26	19	25	22	28	19	28
Crown cover (%)	80	85	70	85	85	75	80	80	85	85	90	90	90	85	80	90	90
Litter depth (cm)	6	4	3	3	3	4	5	4	6	2	4	2	4	7	6	4	5
Basal area (m <sup>2</sup> /ha)	34	23	29	41	45	25	45	37	52	39	41	27	50	33	31	46	49
Bryophytes (0–10)	5	4	5	4	6	2	2	2	2	4	5	2	1	1	1	5	4
Species richness <sup>5</sup>	37	21	29	28	33	45	35	33	29	36	35	28	26	29	32	40	27
<b>Plant functional attributes<sup>6</sup></b>																	
<i>Leaf size</i> - NA	0	1	0	0	1	1	0	1	0	2	1	1	1	2	1	4	0
MI	3	2	9	7	8	8	8	4	4	17	4	7	2	5	11	8	3
NO	20	8	9	13	11	22	14	13	12	9	16	11	19	12	14	15	9
ME	12	9	10	7	11	13	13	12	11	7	12	9	4	8	5	11	14
PL	2	1	1	1	2	1	0	3	2	1	2	0	0	2	1	2	1
<i>Leaf incl.</i> - VE	6	2	5	4	0	5	3	3	1	5	2	4	2	2	5	7	1
LA	22	12	21	17	25	27	23	21	25	24	22	14	18	16	14	29	21
CO	5	6	2	6	6	9	9	5	3	6	10	10	6	1	1	3	5
PE	4	1	1	1	2	4	0	4	0	1	1	0	0	10	12	1	0
<i>Chlorotype</i> - DO	36	20	28	27	33	43	35	33	29	36	35	27	25	29	32	40	27
IS	1	1	1	1	0	2	0	0	0	0	0	1	1	0	0	0	0
CT	14	5	11	8	16	17	16	10	16	15	14	5	10	14	6	14	13
DE	1	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0
<i>Leaf habit</i> - RO	3	4	1	4	3	2	2	4	1	4	5	9	4	2	1	7	3
SO	0	1	1	1	0	1	1	1	0	3	0	0	0	0	1	3	0
SU	0	2	1	2	0	3	1	4	0	3	2	1	0	0	5	4	0
PV	3	4	3	6	5	5	8	11	4	3	6	10	4	3	4	6	3
FI	3	2	4	3	2	2	3	6	2	4	4	3	2	3	3	8	2
<i>Life form</i> - PH	32	16	23	19	27	37	30	20	25	26	25	20	22	24	22	24	23
CH	1	2	1	2	2	1	2	2	2	1	2	1	1	1	1	3	1
HC	4	3	5	7	4	7	3	11	2	8	8	6	3	4	9	13	3
CR	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
LI	6	6	6	4	8	8	7	8	8	3	4	5	5	5	5	8	4
<i>Root habit</i> - AD	1	2	0	1	2	1	1	2	0	2	2	4	2	2	1	4	2
EP	2	3	5	7	2	5	2	9	1	7	5	4	2	4	5	11	2
PA	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
<b>Other observations</b>																	
Lenticels	4	4	2	1	4	6	5	1	0	2	6	5	2	4	1	2	0
Furcation (%)	15	20	12	14	3	20	26	24	18	17	17	19	28	29	25	9	12

4 **Notes:** 1. See Vanclay *et al.* (1991) for more details. 2. Position on slope: Low = lower, Mid = mid-slope, Up =  
6 Upper slope, Top = ridge-top. 3. Soil parent material: AV = acid volcanic, BV = basic volcanic, CG = coarse  
8 granite, SM = sedimentary-metamorphic. 4. Open-ended index calibrated so most plots occur in the range 0–  
10 (see Vanclay, 1989b). 5. Based only on species within the 40 × 5 m transect. 6. Null rows have been  
omitted from this Table.

2 **Table 4.** Species in data by increment clusters and mortality equations (Vanclay, 1991*b*).  
 4 Entries show increment equation (Vanclay, 1991*a*), QFRI species code (see Table 1) and number of trees.

Mort Eqn	Cluster formed on Diameter Increment Equation						Total (spp, <i>n</i> )
	1	2	3	4	5	6	
1	1 MSW 33	6 NSS 6	7 BWD 6	8 GCB 1	10 BRO 7	18 BSL 3	18
	2 QMP 28	9 NRW 1	7 NEV 1	8 RPS 4			107
	27 ILL 1	9 PMH 1	41 BLA 2	32 BRT 4			
		22 HMW 4		32 WCB 2			
		25 RSS 1					
	25 YWN 2						
3		16 KRQ 1			3 RBN 19		2
							20
4	21 CNN 3	5 EUD 1				33 SST 5	4
		36 RCD 2					11
5		5 CLO 1	30 BLO 3	15 NRA 4			8
		14 TST 3		19 SBS 4			19
		16 PAL 1		28 MWN 1			
		37 NTQ 2					
6		36 SLQ 2				20 PKA 6	3
		37 BSW 1					9
10	27 SSW 4	5 NSO 7		4 QSA 22			9
		9 KRS 10		8 STS 15			80
		25 CHS 1		11 RDT 14			
				28 BBN 5			
				28 FIG 2			
Total (spp, obs)	5 69	18 47	4 12	12 78	2 26	3 14	44 246

2 **Table 5.** Correlation matrix for variables included in Equation (4).

<b>Variable</b>	$S_{\Delta d}$	$H_d$	$L$	$VE$	$G$
$S_{\Delta d}$	1	0.41	0.26	0.42	0.10
$H_d$	0.41	1	0.48	-0.28	-0.01
$L$	0.26	0.48	1	-0.49	0.15
$VE$	0.42	-0.28	-0.49	1	-0.38
$G$	0.10	-0.01	0.15	-0.38	1

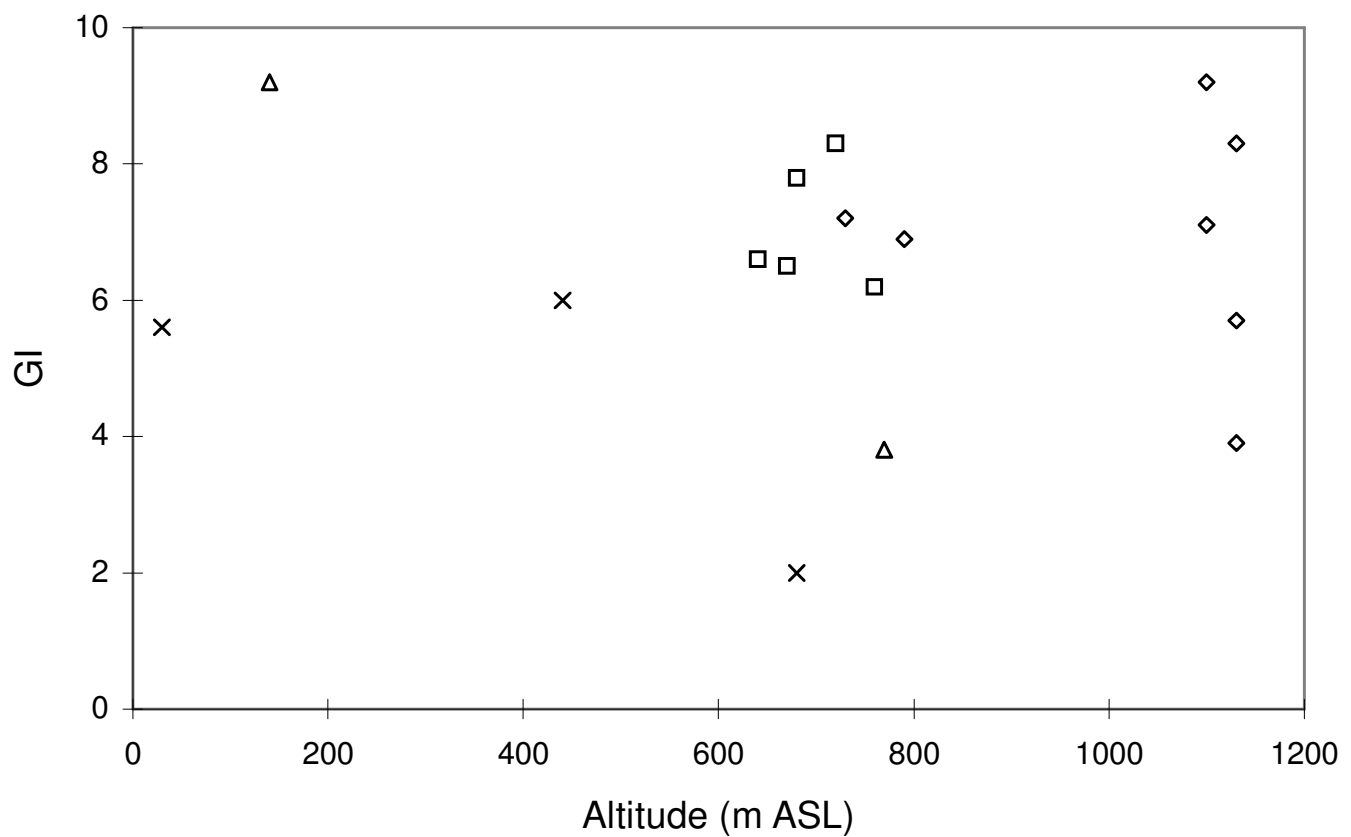
4

**Table 6.** Predicted membership of groups based on diameter increment.

Actual Group	Predicted Membership						Total (spp, <i>n</i> )
	1	2	3	4	5	6	
1	3 65			1 3		1 1	5 69
2	3 4	4 20	2 5	6 8	2 9	1 1	18 47
3			2 9		2 3		4 12
4		2 5	1 2	7 65	1 4	1 2	12 78
5			1 7		1 19		2 26
6		1 3				2 11	3 14
Total	6 69	7 28	6 23	14 76	6 35	5 15	44 246

**Table 7.** Predicted membership of groups based on mortality.

Actual Group	Predicted Membership						Total (spp, <i>n</i> )
	1	2	3	4	5	6	
1	8 86	1 1	2 8	3 5	1 1	3 6	18 107
2		1 19				1 1	2 20
3	1 1		1 5			2 5	4 11
4	1 2	1 1		5 15	1 1		8 19
5	1 1		1 2		1 6		3 9
6	1 4	1 7	1 2		1 14	5 53	9 80
Total	12 94	4 28	5 17	8 20	4 22	11 65	44 246



2 **Figure 1.** The range of site productivity and altitude sampled on each soil parent material (× denotes soils derived  
4 from sedimentary-metamorphic parent materials, ◇ from coarse granites, □ from basic volcanics and △ from acid volcanics).