Using Plant Functional Attributes to Quantify Site Productivity

6

and Growth Patterns in Mixed Forests

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Abstract

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. 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. 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 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 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 species with vertical leaf inclination (>30° above horizontal) are significantly correlated with site productivity. Of the PFAs assessed, five elements appear to offer a useful basis for grouping species for 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 nature of our database limits comment on the general utility of the method, but results suggest that further work on PFAs is warranted.

Key words: Plant functional attributes; site productivity; growth rate; species groups; growth modelling; Queensland, Australia; rain forest.

Introduction

2

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.

16

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

subjective, and may not be reproduced by other observers. This paper examines a procedure to make

2   such appraisals more objective, explicit and repeatable.

4   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

6   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

8   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

10   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,

12   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

14   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

16   affiliations). Here, we test this assumption with linear regression (in the case of site productivity) and

discriminant analysis (for growth patterns).

18

There is some evidence that within a given region, site productivity can be inferred from the presence or

20   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.,

22   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

24   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

26   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 an

6   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 not always

8   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 for grouping

10   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.

       ## Background

22   *Study Location and QFRI Database*

24   The study was conducted in the rainforests of north Queensland, Australia. These rainforests occupy an

       area of about 1 million ha along the eastern coast between the latitudes of 16 to 19°S, extending from the

26   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

2   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

4   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

6   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

8   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

10   ideal for the present study.

12   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

14   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,

16   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

18   (Trott, 1996), and, as a result, access and plot relocation are becoming increasingly difficult.

Estimating site productivity

20

We use an index of site productivity developed from the permanent plot measurements and based on

22   individual tree growth of 18 reference species (Vanclay, 1989*b*). The reference species are *Acronychia*

acidula, Alphitonia whitei, Argyrodendron trifoliolatum, Cardwellia sublimis, Castanospora alphandii,

24   *Cryptocarya angulata, C. mackinnoniana, Darlingia darlingiana, Elaeocarpus largiflorens, Endiandra*

sp. aff. *E. hypotephra, Flindersia bourjotiana, F. brayleyana, F. pimenteliana, Litsea leefeana, Sterculia*

26   *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

2 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

4 variables, Vanclay, 1994 p. 104) to gauge the effect of site:

6
$$\ln(\Delta d_{ijk}+\alpha) = \Sigma_i\beta_{0i}Z_i +\Sigma_i\beta_{1i}Z_id_{ijk} +\Sigma_i\beta_{2i}Z_i\ln d_{ijk} +\Sigma_i\beta_{3i}Z_iG_k +\Sigma_i\beta_{4i}Z_iG_{>dijk} +\Sigma_k\gamma_kZ_k\ln d_{ijk} \tag{1}$$

8 where Δd_{ijk}, d_{ijk} and $G_{>dijk}$ are the diameter increment (cm y^{-1}), initial diameter (cm dbh) and basal area in

larger trees (m^2 ha^{-1}) respectively for tree j of species i on plot k, G_k is the stand basal area (m^2 ha^{-1}) on

10 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 α, β_i and γ_k are

12 parameters to be estimated. This equation can be re-arranged to estimate the growth index for a given

permanent plot:

14

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

16

where $S_{\Delta d}$ is the growth index of the plot (notice that this is the parameter γ_k from Equation 1, rescaled to

18 more convenient units), d_{ij} is the diameter (cm) of tree j of species i, Δd_{ij} is its diameter increment (cm y$^-$

^{1}), $G_{>dij}$ is the basal area of trees within the plot that are bigger than tree ij (m^2 ha^{-1}), G is the plot basal

20 area (m^2 ha^{-1}), and the βs 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

22 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

24 growth indices read from growth curves for each of the 18 reference species that occur on a plot.

26 *Species Groups and Growth Equations*

2   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

4   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

6   may be obtained with simple pairwise comparisons based on F-tests (e.g., for linear regressions with

diameter increment data) or χ^2 tests (e.g., for logistic regressions with mortality data). The procedure

8   used to group north Queensland species (Vanclay, 1991*a*, 1994) involved:

10   1. Ranking species in order of increasing number of observations.

2. Assigning the species of highest rank the founding species of group 1.

12   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

14   becomes the founding species of a new group. Species not significantly different from all founding

species remain ungrouped during this initial pass.

16   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

18   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.

20

This approach provided 41 species groups with statistically similar diameter increment relationships

22   (Vanclay, 1991*a*), and 10 groups with similar mortality patterns (Vanclay, 1991*b*), from a database

comprising some 237 species. These groups exhibited a diverse range of growth patterns with two

24   desirable characteristics:

1. all species within a group exhibited a growth pattern indistinguishable (in a statistical sense, $P<0.05$)

26   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.

2   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.

4   The species and groupings involved in the present study are indicated in Table 1.

6   *Plant Functional Attributes*

8   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

10   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

12   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 diferent modi. Although the number of possible

14   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

16   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):

18   PFA   = LS LI CL LH LF RH

            LS   = PI | LE | NA | MI | NO | ME | PL | MA | MG | NR

20   LI   = VE | LA | PE | CO

            CL   = {(DO | IS) [DE] [CT] } | AC

22   LH   = [RO] [SO] [SU] [PV] [FI] [CA]

            LF   = (PH | CH | HC | CR | TH) [LI]

24   RH   = [AD] [AE] [EP] [HY] [PA]

26   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

28   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 (≥0). Our contention, explored in this

2   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.

4

Data

6

We chose the QFRI plots for the preliminary test of our hypotheses because of the quality of the

8   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

10   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,

12   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

14   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

16   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).

18

PFAs were recorded on a 40×5 m strip transect in each plot. This transect was located to sample a

20   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

22   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

24   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

2   additional trees; Table 3).

4   A number of other items were also recorded, e.g., crown cover (%), mean canopy height (m), basal area

$(m^2 ha^{-1})$, litter depth (cm), approximate soil depth (3 classes), and an estimate of the relative abundance

6   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

8   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

10   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

12   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

14   useful indicators of seasonally-limited soil aeration and thus growth performance.

16   **Analyses**

18   *Regression Analysis with Productivity Data*

20   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

22   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

24   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 δs are

26   small), and with linear combinations (i.e., $\beta_1 X_1 + \beta_2 X_2 + ...$) of variables apparently not sparse. Thus any

variables which appeared sparse (e.g., parasitic species, PA), which exhibited a disjoint bimodal

2 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,

4 which when regressed against site productivity, exhibited a leverage three times the accepted limit of

$2p/n$) were omitted from the final analyses.

6

There are few statistical guidelines for dealing with such data (other than techniques for assessing the

8 magnitude of the problem, e.g., Verbyla, 1986), so the following "rules of thumb" were used (where n is

the number of data sets):

10 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.

12 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.

14 3. Allow a maximum of $\sqrt{n}$ variables in the model.

16 Regression techniques were used to explore the ability of PFA modi to indicate site productivity, using

data from the standard PFA assessments on the 40×5 m transects (i.e., excluding the 20 supplementary

18 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

20 "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

22 biological and statistical sense, and faithfully reflect the potential of PFAs to reveal site properties.

24 *Discriminant Analysis of Group Membership*

2   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, 1991*a*), and in 9 of the 10 mortality groups

4   (Vanclay, 1991*b*). Our sample included some species with insufficient data to be empirically grouped

     (i.e., in the original studies by Vanclay, 1991*a,b*), and these were omitted from the present study. Some

6   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 ≤3 observations in 3 mortality groups (Groups

8   2, 7 & 9). This left 246 observations on 44 species, representing 29 diameter increment and 6 mortality

     groups, for the final analyses (Table 4).

10

     Since 44 species are insufficient for a meaningful explanation of possible assignments into 29 diameter

12   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

14   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

16   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

18   parameters defining the 29 increment equations given by Vanclay, 1991*a).*

20   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

22   algorithm which was used minimized Wilk's lambda and assigned equal prior probabilities to each

     group. Such analyses can be carried out three ways:

24   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

26   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 ($P < 0.10$):

$$S_{\Delta d} = 9.8 - 3.2S_{as} - 0.0032E \tag{2}$$

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 ($r^2 = 0.60$, $P < 0.01$):

$$S_{\Delta d} = 0.21\,H_d + 3.92\,L + 0.74\,VE - 13.26 \tag{3}$$

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^2

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, m²/ha) significantly reduced unexplained variance ($r^2 = 0.73$; For

inclusion of G, $F_{1,12} = 5.71$, $P < 0.05$; for overall model, $F_{4,12} = 8.09$, $P < 0.01$):

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

(standard errors are 0.09, 1.71, 0.18, 0.035 and 5.49 respectively). No other site or stand variables

2   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

4   approximately orthogonal and supporting our contention that the model is relatively robust (also see

correlation matrix, Table 5).

6

There may be some limitations with the use of the variable *VE*, the number of species with vertically

8   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

10   only the proportion of such species, but also the total species richness that correlates with site

productivity.

12

Species Groups and Growth patterns

14

The variables with greatest power to discriminate species group membership (for both increment and

16   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

18   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

20   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

22   average, in 17% being correctly classified.

24   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

26   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

2   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

4   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

6   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

8   into groups could be improved without additional variables.

10 These rather promising results led us to explore the possibility of predicting the seven coefficients of the

diameter increment equation (Vanclay, 1991*a*) directly from specific PFAs, but preliminary attempts

12 suggested that good predictions could not be made ($r^2 = 0.15 – 0.30$).

Discussion

16 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

18 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

20 size, and the incidence of species with vertical leaf inclination (>30° above horizontal) were significantly

correlated with site productivity, while five PFAs appear to offer a useful basis for forming species

22 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

24 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

26 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.

2   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

4   resources.

6   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

8   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

10 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

12 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

14 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

16 research in this area.

18 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

20 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

22 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

24 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

2   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

4   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

6   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

8   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

10   system.

12   **Conclusion**

14   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

16   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

18   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

20   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

22   further work on PFAs is warranted.

24   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

26   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

2 estimates of sustained yield and levels of allowable harvest for most natural forests in the tropics.

4 *Acknowledgements*

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

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

Photosynthetic elements	
Leaf size (LS)	
PI	picophyll (<2 mm²)
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
Leaf inclination (LI)	
VE	vertical (>30° above horizontal)
LA	lateral (horizontal ±30°)
PE	pendulous (>30° below horiz.)
CO	composite
Chlorotype (CT)	
DO	dorsiventral
IS	isolateral or isocentric
DE	deciduous
CT	cortic
AC	achlorophyllous
Leaf habit (LH)	
RO	rosulate or rosette
SO	solid (3-dimensional)
SU	succulent
PV	parallel-veined
FI	filicoid (fern-like)
CA	carnivorous (e.g., *Nepenthes*)
Vascular support elements	
Life form (LF)	
PH	phanerophyte
CH	chamaephyte
HC	hemicryptophyte
CR	cryptophyte
TH	therophyte
LI	liane
Rooting habit (RH)	
AD	adventitious
AE	aerating
EP	epiphytic
HY	hydrophytic
PA	parasitic

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

Site details

Experiment[1]	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[2]	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[3]	CG	CG	CG	CG	CG	CG	CG	BV	BV	AV	BV	SM	SM	SM	BV	AV	BV

Stand details

Growth Index[4]	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 (m²/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[5]	37	21	29	28	33	45	35	33	29	36	35	28	26	29	32	40	27

Plant functional attributes[6]

Leaf size - 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
Leaf incl. - 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
Chlorotype - 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	0	1	1	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
Leaf habit - 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
Life form - 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
Root habit - 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

Other observations

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

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

Table 4. Species in data by increment clusters and mortality equations (Vanclay, 1991*b*). 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, n)
	1	2	3	4	5	6	
1	1 MSW 33 2 QMP 28 27 ILL 1	6 NSS 6 9 NRW 1 9 PMH 1 22 HMW 4 25 RSS 1 25 YWN 2	7 BWD 6 7 NEV 1 41 BLA 2	8 GCB 1 8 RPS 4 32 BRT 4 32 WCB 2	10 BRO 7	18 BSL 3	18 107
3		16 KRQ 1			3 RBN 19		2 20
4	21 CNN 3	5 EUD 1 36 RCD 2				33 SST 5	4 11
5		5 CLO 1 14 TST 3 16 PAL 1 37 NTQ 2	30 BLO 3	15 NRA 4 19 SBS 4 28 MWN 1			8 19
6		36 SLQ 2 37 BSW 1				20 PKA 6	3 9
10	27 SSW 4	5 NSO 7 9 KRS 10 25 CHS 1		4 QSA 22 8 STS 15 11 RDT 14 28 BBN 5 28 FIG 2			9 80
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).

Variable	$S_{\Delta d}$	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,*n*)
	1	2	3	4	5	6	
1	3			1		1	5
	65			3		1	69
2	3	4	2	6	2	1	18
	4	20	5	8	9	1	47
3			2		2		4
			9		3		12
4		2	1	7	1	1	12
		5	2	65	4	2	78
5			1		1		2
			7		19		26
6		1				2	3
		3				11	14
Total	6	7	6	14	6	5	44
	69	28	23	76	35	15	246

Table 7. Predicted membership of groups based on mortality.

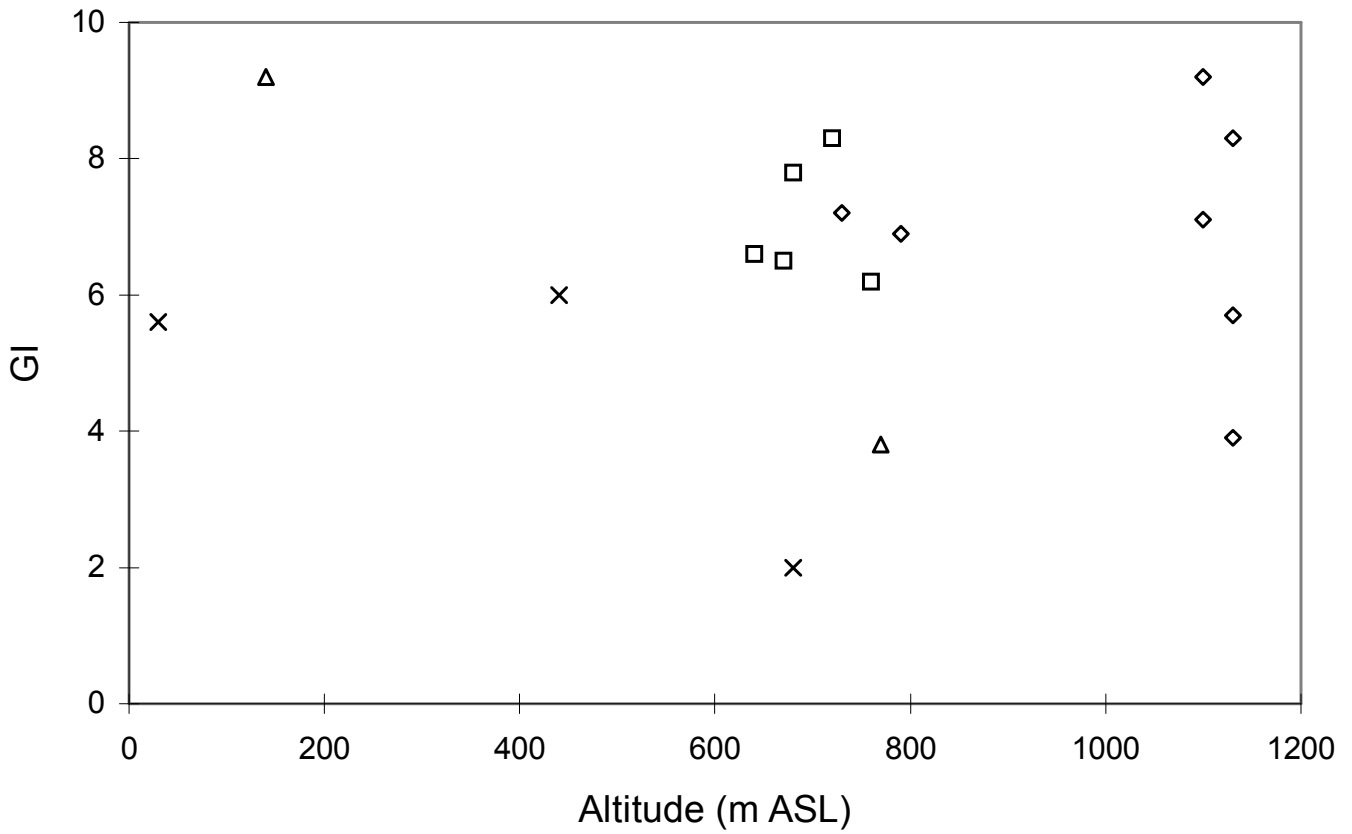| Actual Group	Predicted Membership						Total (spp,*n*)
	1	2	3	4	5	6	
1	8	1	2	3	1	3	18
	86	1	8	5	1	6	107
2		1				1	2
		19				1	20
3	1		1			2	4
	1		5			5	11
4	1	1		5	1		8
	2	1		15	1		19
5	1		1		1		3
	1		2		6		9
6	1	1	1		1	5	9
	4	7	2		14	53	80
Total	12	4	5	8	4	11	44
	94	28	17	20	22	65	246

FIGURE CAPTIONS

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 Δ from acid
volcanics).

6

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