Functional evaluation of height–diameter relationships and tree development in an Australian subtropical rainforest

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Handling Editor:
James Camac

ABSTRACT

Context. Allometric equations describing the relationships between tree height (H) and breast height diameter (D) should be both statistically efficient and biologically relevant. **Aims.** To determine whether selected allometric equations can meet established criteria for both efficiency and relevance. **Methods.** Nine equations were compared to define the H–D relationships of 1122 individuals and 18 species from an Australian subtropical rainforest. **Key results.** Three-parameter asymptotic equations described initial slope (a), curvature (b), and asymptotic height (H_a). Each equation was evaluated for precision (root mean square error, RMSE) and bias in H estimates, and ease of interpretation of function parameters. For both individual species and all stems, a non-rectangular hyperbola (NRH) provided almost equally high precision and low bias as did the statistically most parsimonious generalised Michaelis–Menten function, plus linear parameter values easily relatable to tree structural and functional attributes. The value of NRH a increased linearly with wood density for canopy species, but not for understorey and subdominant species, whereas the value of NRH b decreased as H_a increased from understorey to canopy species. **Conclusions.** Species within understorey, subdominant, and canopy structural groups shared similar ranges of parameter values within groups that reflect both intrinsic architectural and developmental patterns, and environmental limitations to H_a. **Implications.** The NRH can be used to visualise both early and later tree development stages and differences among the growth patterns of species occupying different positions within a forest.

Keywords: allometric relationships, asymptotic tree height, canopy layers, convexity factor, non-rectangular hyperbola, proportionality factor, saplings, stem taper, understorey, tree architecture.

Introduction

Allometric relationships between total tree height (H) and stem diameter at breast height (1.3 m; D) have been applied to intersecting and potentially conflicting practical and explanatory objectives. First, the more accurate prediction of forest biomass (B) from inventories of D (Chave *et al.* 2005; Cook *et al.* 2005) has been sought by the incorporation of H (Williams *et al.* 2005; Feldpausch *et al.* 2012; Chave *et al.* 2014; Ledo *et al.* 2016; Martínez Cano *et al.* 2019*b*). Second, greater understanding has been sought of fundamental biological attributes of tree species that influence their ecological and evolutionary outcomes, particularly in structurally and floristically diverse rainforests (Kohyama *et al.* 2003; Banin *et al.* 2012; Forrester *et al.* 2017; Falster *et al.* 2018).

An effective allometric relationship should provide logical, biologically realistic, accurate, precise, parsimonious, and unbiased descriptions of the processes underlying tree and forest growth in different environments (Vanclay and Skovsgaard 1997; Cifuentes Jara *et al.* 2015). Model selection has been resolved most often in favour of statistical efficiency (Burnham and Anderson 2004; Ledo *et al.* 2016; Loubota Panzou *et al.* 2021*b*) over mechanistic interpretations of biological relevance (Hunt 1979).

Advanced statistical techniques (Aertsen *et al.* 2010; Cysneiros *et al.* 2021; Loubota Panzou *et al.* 2021*a*; Lu *et al.* 2021) have been used, especially on large, aggregated datasets, to describe multiple functional relationships across different environments and

their effects on structure and growth of trees (Falster *et al.* 2018; Martínez Cano *et al.* 2019*a*). Following Hunt (1979), the present study seeks to complement this computational sophistication with an analysis of biological bases and ease of interpretation of allometric relationships that underpin tree growth models applied to different species in a single environment.

Categories of height–diameter relationships

Other than empirical solutions (Zeide 1993), three categories of biologically realistic allometric relationship have been applied to trees, including unbounded functions based on biophysical principles, and asymptotic functions based on growth rate and on process rate functions. Representative basic equations from each category are presented in Table 1.

Biophysical equations assume unrestricted proportionality in organ or organism construction, which can be related to the distribution of resources (Huxley 1924; Higham *et al.* 2021) and in trees to mechanical properties such as bending, shear and rupture strengths of wood (McMahon and Kronauer 1976; Niklas 2007). These proportions arise because wood strength is closely related to wood density (Kollmann 1968; Walton and Armstrong 1986; van Gelder *et al.* 2006), so trees with high wood strength have characteristically slender stem taper.

The most widely applied biophysical allometric relationship is the power equation, commonly expressed as a log–log relationship (Huxley 1924; Niklas 1995; Kooyman and Westoby 2009; Loubota Panzou *et al.* 2021*a*). The structural characteristics of tree saplings are reflected in the initial value of the allometric proportionality factor, *a*, which varies among species in a particular environment with wood density (van Gelder *et al.* 2006; Kooyman and Westoby 2009; Fournier *et al.* 2013; Francis *et al.* 2017), and among environments with different tree spacing (Hummel 2000; Vanclay 2009; del Río *et al.* 2019) or site

resource availability (Vanclay and Henry 1988; Lines *et al.* 2012; Cysneiros *et al.* 2021), and by external stresses such as wind (Jacobs 1954; King 1986; Thomas *et al.* 2015). Changes in the *H*–*D* relationship with increasing organism size are described by the convexity factor, *b*, which appears as an exponent (Table 1, Eqn 2) and is related to species maximum dimensions, especially with the transition from early stage to late-stage successional species (Kohyama *et al.* 2003; Poorter *et al.* 2006; Martínez Cano *et al.* 2019*a*). Although it may describe accurately the early *H*–*D* relationships of tree stems (King 1990; Niklas 1995), the power equation does not incorporate the maximum or asymptotic height, H_a, and overestimates *H* at larger values of *D* (Ledo *et al.* 2016; Chenge 2021; Loubota Panzou *et al.* 2021*b*).

Growth rate functions are long-established and thoroughly reviewed (e.g. Evans 1972; Vrána *et al.* 2019). Most widely used equations (Table 1, Eqns 3–8) assume a sigmoidal pattern of plant growth (e.g. total height, *H*) as a negative exponential function of time, including a rate parameter, *a*, which describes the initial slope, an asymptote (e.g. maximum height, H_a) and usually a convexity factor, *b*, which describes the shape of the growth curve, both in its early acceleration and later deceleration as it approaches the asymptote (Tjørve and Tjørve 2010). These exponential parameters are not easy to interpret visually. For application to *H*–*D* allometry, *D* replaces time as the independent variable.

Process rate functions describe the rate of a reaction or process in relation to the availability of a resource, typically a substrate, that initially is entirely limiting but eventually becomes non-limiting, as described by the Michaelis–Menten equation (Table 1, Eqn 9). For application of this function to *H*–*D* allometry, *D* replaces resource availability as the independent variable, and H_a replaces maximum reaction rate; the proportionality factor is represented by *k*, the value of *D* at half-H_a (Canham *et al.* 1994).

Table 1. Height–diameter allometric functions selected for application to subtropical rainforest trees.

Equation	Function type	Identity	Function	Reference
(1)	–	Linear (*H* < 8 m)	$H = 1.3 + aD$	
(2)	Biophysical	Power	$H = 1.3 + aD^b$	Huxley (1924)
(3)	Growth rate	Mitscherlich	$H = 1.3 + H_a[1 - \exp(-aD)]$	Meyer (1940)
(4)	Growth rate	Pacala	$H = 1.3 + H_a\{1 - \exp[-(a/H_a)D]\}$	Pacala *et al.* (1993)
(5)	Growth rate	Weibull	$H = 1.3 + H_a[1 - \exp(-aD^b)]$	Yang *et al.* (1978)
(6)	Growth rate	Richards	$H = 1.3 + H_a[1 - \exp(-aD)]^b$	Richards (1959)
(7)	Growth rate	Gompertz	$H = 1.3 + H_a \exp[-b\exp(-aD)]$	Winsor (1932)
(8)	Growth rate	Logistic	$H = 1.3 + H_a/[1 + b\exp(-aD)]$	Winsor (1932)
(9)	Process rate	Michaelis–Menten (GMM)	$H = 1.3 + H_aD^b/(k + D^b)$	Martínez Cano *et al.* (2019*b*)
(10)	Process rate	Non-rectangular hyperbola (NRH)	$H = 1.3 + \{aD + H_a - [(aD + H_a)^2 - 4baDH_a]^{0.5}\}/2b$	Johnson and Thornley (1984)

D, stem diameter at 1.3 m (DBH) (cm); *a*, *b*, *k*, parameters to be estimated; exp, base of the natural logarithm; *H*, estimated total tree height (m); H_a, estimated or assigned asymptotic (maximum) tree height (m). Parameters, symbols and abbreviations are described in Appendix 1.

The convexity factor, *b*, introduced by Martínez Cano *et al.* (2019*b*) as an exponent of *D*, has the same meaning as for biophysical functions. This expression has been recognised as the generalised Michaelis–Menten (GMM) equation (Ledo *et al.* 2016; Martínez Cano *et al.* 2019*a*, 2019*b*; Loubota Panzou *et al.* 2021*b*).

The reaction kinetics of photosynthesis were described by Johnson and Thornley (1984) as a non-rectangular hyperbola (Table 1, Eqn 10), comprising the initial change in reaction rate with respect to light availability, *a*, the maximum reaction rate, and the convexity of the reaction rate curve, *b*, which varies from 0 to 1 as the maximum rate is approached and is interpreted as reflecting the transition from progressive to abrupt imposition of limiting conditions on the process (Prioul and Chartier 1977; Johnson and Thornley 1984; Thomas and Bazzaz 1999). This equation can also be applied to *H–D* allometry, adopting the terminology described above.

In principle, the initial course of *H–D* change in a tree may be assumed to be determined by resource distribution (Huxley 1924; Niklas 1995, 2007) and the mainstem, branching and foliation characteristics widely recognised as tree architecture (Hallé *et al.* 1978; Sterck *et al.* 2001; Poorter *et al.* 2006; Osunkoya *et al.* 2007; Iida *et al.* 2011; Loubota Panzou *et al.* 2018). This phase of tree development should be described accurately by all biophysical or process rate functions but not by growth rate functions that incorporate increasing stem slenderness in seedling and sapling tree growth stages (Tjørve and Tjørve 2010). Later changes in tree *H–D* relationships result in the attainment of a maximal *H* and *D*, characteristic for a species and its environment (Francis 1970; Thomas 1996; Floyd 2008) and should be described realistically and accurately by growth rate or process rate functions.

Most allometric equations in wide use, judged on their statistical attributes, have been based on biophysical or growth rate functions, although some recent analyses have favoured the GMM process rate function (Ledo *et al.* 2016; Martínez Cano *et al.* 2019*b*). Hunt (1979) argued that, when the objective is to understand patterns of plant growth, selective weight should also be given to biological relevance when it provides a clearer depiction of the factors influencing each allometric parameter, even if one or more statistical test is denied pre-eminence in model selection.

The following work explores the extent to which different categories of allometric equation satisfy the stated criteria for selection, taking account of both modelling objectives and the desire to incorporate relevant biological characteristics, such as stem strength and the elements of tree architecture. It also examines whether the non-rectangular hyperbola (NRH) might be applicable to the *H–D* allometry of species occupying different strata of an Australian subtropical rainforest.

Materials and methods

Study site

The study site was in the Main Range National Park, Queensland, Australia (28.23S, 152.42E, 1120 m asl), within the Gondwana Rainforests remnant basalt volcanic landscape of eastern Australia, covered by ferrosols up to 2 m deep (Debski *et al.* 2000). The average annual rainfall in the vicinity is approximately 1125 mm and cloud interception may contribute an additional 40% rainfall equivalent (Hutley *et al.* 1997). Mean annual temperature at the site is 14.5°C; summer daily mean maxima vary from 30°C to 35°C, and winter minima are close to 0°C within the forest (Hutley *et al.* 1997). The vegetation is designated as complex notophyll vine forest on Cainozoic igneous rocks, Regional Ecosystem 12.8.5 (Queensland Herbarium 2019).

Two plots, each 0.2075 ha, were established in 1962 in a portion of the then Gambubal State Forest. One plot, with an initial stand basal area of 67 m^2 ha^{-1}, was left unlogged, and one was subjected to typical Queensland Forestry Department timber harvesting practices that removed approximately 25 m^2 ha^{-1} (Dale 1983). All trees with *D* greater than 10 cm were identified and *D* was measured periodically to monitor the regeneration of, first, commercial timber species, and later, all species (Dale 1983). Neither plot was subjected to any silvicultural treatment after 1962.

In 2003, each woody stem greater than 1.8 m tall was identified to species and its *D* was measured by callipers or girth tape, above buttresses if necessary. The accuracy of *D* measurement was established by checking current and recent values. Total height, to the uppermost location in the crown, was measured by height stick (up to 5 m) or by clinometer (over 5 m), verified through assessment of a sample of trees by two observers. Trees were excluded from analysis if the bole was broken, leaning by >10 degrees, or multi-stemmed.

The spacing and shading conditions for trees in the two plots were described respectively, by the number of stems surrounding and overtopping trees of a given size and indicated by frequency distributions for *D* and *H* in Supplementary Information and Supplementary Fig. S1. Because of the indistinguishable stand structures (Fig. S1) and *H–D* distributions for representative species (Fig. S2) at 40 years after disturbance, and their conformity to undisturbed forest structures (Coomes *et al.* 2003), the data for logged and unlogged plots were combined for further analysis.

Of the 1586 arborescent stems recorded, 401 were excluded because they belonged to understorey shrub species with a maximum height at the site (H_{maxL}) shorter than 10 m, and 57 because they were damaged or leaning. Six trees were excluded because their estimated heights appeared as extreme outliers (Zea-Camaño *et al.* 2020)

from the H–D distributions for all tested equations. Analyses of the whole-sample data were based on 1122 tree stems.

Detailed species analyses were performed on 946 stems representing 18 species, with at least 18 stems being distributed among at least eight D classes (specified in Fig. S1) for each species, which was allocated to one of four published maximum height (H_{maxP}) classes (Supplementary Table S1). Of the stems included in the whole-sample estimates, 187 were excluded from species analyses, but were included in pooled data for H_{maxP} classes.

Evaluation of allometric relationships

The Microsoft Excel Solver (Excel) generalised reduced gradient (GRG) non-linear routine (Frontline Systems, Inc., Incline Village, Nevada, USA) was used to describe H–D relationships for the whole sample of 1122 tree stems, 18 selected species (Table S1) and all individuals in four height-class groups.

This routine maximised the regression coefficient of determination (R^2) and minimised the root mean square error (RMSE) and mean bias by adjustment of the parameters a, b and H_a. Of the many allometric equations that have been developed, those listed in Table 1 were selected to provide the simplest basis for comparing categories of equations, using two or three fitted parameters, with no adjustments for local conditions. Linear and power regressions were applied to all trees <8 m tall as a basis for comparison with the initial proportionality parameter, a, in other equations. Three-parameter versions of the Weibull and generalised Michaelis–Menten (GMM) equations are presented as preliminary studies showed them to be more precise than are the two-parameter versions (cf. also Ledo *et al.* 2016). The GMM equation (Eqn 9) expresses the initial proportionality (slope) factor as a half-saturation constant, k. The reliability of these estimates was assessed by corresponding calculations on the whole sample conducted in R (R Core Team 2021), by using the *modelr* maximum-likelihood procedure (Wickham 2020) to optimise parameter values and their variance, and to minimise R^2, RMSE, Akaike's information criterion (AIC) and mean bias (Table S2).

Selected equations were applied to all trees ≥2 m tall from the whole sample, from all trees in four published species maximum height (H_{maxP}) classes (10–19 m, 20–29 m, 30–39 m, and 40+ m; Francis 1970; Floyd 2008), and from 18 selected species (Table S1). Data for six trees that were clearly outliers from sample distributions (Zea-Camaño *et al.* 2020) were excluded from analysis. Where a fitted relationship for an individual species ($H_{a\text{-fitted}}$) yielded unrealistic predictions of H_a, the mean H of the largest D class for the species at the site (H_{maxL}; Thomas 1996; Davies *et al.* 1998) was inserted as a fixed value ($H_{a\text{-forced}}$), and fitting was achieved by optimising a and b.

The explanatory value of a quantitative model is enhanced if it provides a reasonable depiction of responses of the system to changing conditions. For this purpose, attention is focused on the central statistics (chiefly parameter means) of an allometric relationship (Hunt 1979). The following three criteria from Vanclay and Skovsgaard (1997) are most applicable to single equations that describe H–D trajectories for both assemblages of trees within a single environment and for individual species with few measured individuals:

1. biological representation (adequate representation of the biological processes involved),
2. description of errors (attainment of specified accuracy requirements),
3. description of data (absence of bias in predictions throughout the likely range of application).

Quantitative values obtained in some tests could not be compared directly with qualitative assessments of utility in others. Biological representation was deemed to have been achieved if the parameters a, b and H_a could be described independently in a logical and easily interpreted way, if the assumptions underlying parameter determination were consistent with biophysical principles, and if predicted values (H, H_a) were consistently and reasonably close to observed data.

Results

Evaluation of allometric equations

Application of the $H_{a\text{-fitted}}$ form of each allometric equation (Table 1) to the whole sample yielded estimates of parameters a, b, H_a, and the attributes R^2, RMSE and mean bias (Table 2). Model precision was indicated by RMSE values, which for six of the equations were within 0.03 m of the lowest value (1.399 m for the GMM), including 1.409 m for the NRH (Table 2). The very close similarities between parameter and precision estimates using the R *modelr* package (Wickham 2020) and Excel procedures (Table S2) established the reliability of the latter for use in further analyses. Standard error estimates of parameter values determined by R (Table S2) were generally between 2% and 3% of respective means, but the differences were not consistent among equations. AIC values indicated that the GMM was clearly the most parsimonious model (Table S2).

Table 2 also shows the estimated maximum tree height, H_{maxC} (H_a + 1.3 m), and the estimated height (H_{D150}) of the largest-diameter tree in the study (D = 149.6 cm, H = 36 m). Of the six best-fitting equations, the predicted H_{D150} from four functions (Mitscherlich, Pacala, Weibull and Richards) ranged between 33.2 and 34.0 m, being close to the H_{maxC} (Table 2). The $H_{a\text{-fitted}}$ and $H_{a\text{-forced}}$ versions of

Table 2. Parameters of tree height–diameter relationships determined by non-linear regression routines.

Equation	n	H_a (m)	H_{D150} (m)	H_{maxC} (m)	a (m cm^{-1})	b	R^2	RMSE (m)	Bias (m)
(1) Linear ($H < 8$ m)	869	–	–	–	0.760	–	0.733	0.946	−0.048
(2) Power	1122	–	51.5	–	1.563	0.692	0.903	1.756	0.279
(3) Mitscherlich	1122	32.61	33.4	33.9	0.029	–	0.937	1.426	0.081
(4) Pacala	1122	32.59	33.4	33.9	0.936	–	0.937	1.424	0.057
(5) Weibull	1122	33.37	34.0	34.2	0.029	0.989	0.937	1.422	0.082
(6) Richards	1122	32.90	33.7	34.2	0.028	0.989	0.937	1.422	0.067
(7) Gompertz	1122	25.27	26.6	26.6	0.088	2.902	0.908	1.719	0.113
(8) Logistic	1122	22.98	24.1	24.1	0.167	11.43	0.882	1.949	0.172
(9) GMM	1122	41.42	35.4	42.7	48.43$^{(k)}$	1.083	0.939	1.399	0.044
(10) NRH	1122	43.36	36.2	44.6	0.968	0.236	0.938	1.409	0.100

n, sample size; H_a, a, b and k values all obtained by fitting equations; H_{D150}, estimated H for the largest tree ($D = 149.6$ cm, $H = 36$ m); H_{maxC}, calculated maximum tree height for the dataset ($H_a + 1.3$ m); R^2, regression coefficient of determination; RMSE, root mean square error; Bias, mean bias of equation; '–' indicates that a parameter not estimated by the relevant procedure.

the GMM equation predicted H_{D150} of 35.2 and 35.4 m respectively, compared with 35.9 and 36.2 m for the equivalent NRH equations; predictions by these last two equations were close to the recorded tree height, but were 7–8 m less than respective H_{maxC} values.

The mean H–D trajectories for the whole sample, as described by nine allometric equations (Fig. 1*a*), indicated a close similarity among six equations for smaller trees, but divergence at values of $D > 100$ cm. The proximity of the GMM and NRH curves throughout their data ranges, their relatively low and similar RMSE values and their similar and limited biases throughout the data range (Fig. S3) suggested that either equation could provide an acceptably precise description of the whole-sample H–D relationship at the study site. Fig. 1*b* shows the distribution of data around the NRH mean H–D curve. Its accuracy and ease of application justified the use of the fitting routine, and the potential to visualise H–D trajectories for different species justified application of the

NRH in the subsequent analyses of individual species and groups of species.

H–D relationships of individual species

Statistical analyses of selected $H_{a\text{-fitted}}$ and, where applicable, $H_{a\text{-forced}}$ versions of the nine non-linear H–D equations (cf. Table 1) for 18 species listed in Table S1 are presented in Table S3. The relative precision of $H_{a\text{-fitted}}$ and $H_{a\text{-forced}}$ solutions for the 18 species as determined by six equations was compared by differences between their RMSE values (Fig. S4*a*). For most species and most equations, $H_{a\text{-forced}}$ equations were less precise than the $H_{a\text{-fitted}}$ forms, but for GMM and NRH equations, the differences in RMSE were mostly less than 0.1 m.

There was considerable variation in the range of RMSE values determined by the nine $H_{a\text{-forced}}$ equations for different species (Fig. S4*b*). No equation was consistently more precise than the others, although GMM and NRH
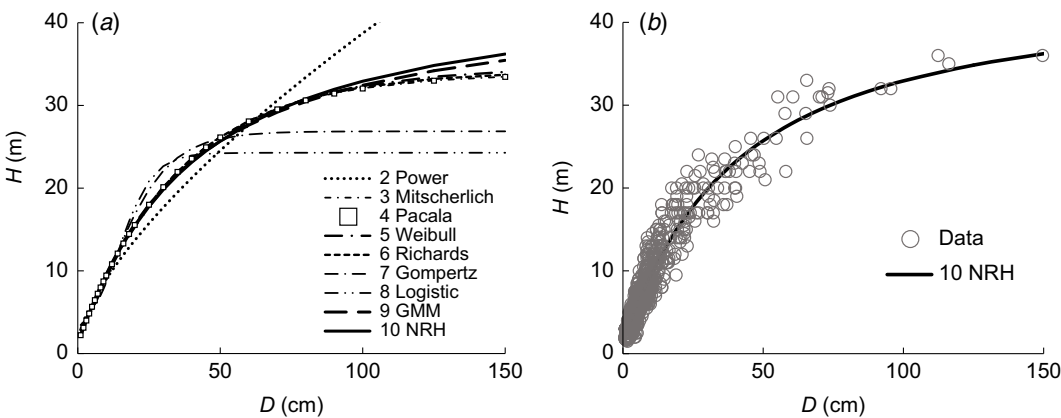
Fig. 1. Relationships between H and D for all trees: (*a*) comparisons of nine fitted equations, (*b*) data and fitted non-rectangular hyperbola (NRH).

were among the most precise for most species. Greater variation in RMSE values was associated with limited size ranges (*Acronychia pubescens* and *Denhamia apetala*) or, for *Diploglottis australis*, with RMSE values for both $H_{\text{a-fitted}}$ and $H_{\text{a-forced}}$ NRH that were much smaller than those for all other equations (Table S3).

The generally consistent RMSE values for each species suggest that valid interpretations may be made using either the $H_{\text{a-fitted}}$ or $H_{\text{a-forced}}$ forms of the selected equations. All subsequent analyses of the whole sample and the four height-class groups used $H_{\text{a-fitted}}$ equations, but $H_{\text{a-forced}}$ equations were adopted for individual species because they avoided many unrealistic estimates of H_{a}.

Initial *H–D* proportionality factor for species

The forms of most *H–D* regression equations involve exponential functions of the initial slope, *a*, (Table 1), so direct visual comparison of *H–D* slope values was restricted to the linear (<8 m tall), power, Pacala, GMM and NRH functions. Assuming that sapling stem allometry was determined by biophysical factors, the power equation applied to trees <8 m tall was used as the basis for comparison (Fig. 2). There was no correspondence between values of *a* (or for the GMM, *k*) determined by the power <8 m and other equations for trees with H_{maxP} of <30 m,

and only weak associations in trees with H_{maxP} of 30+ m for all equations tested except the $H_{\text{a-forced}}$ NRH (Fig. 2e). This suggests that comparisons of *a* among species at a given site, or within a species but among different conditions, may be attempted by using the NRH. The outlying species, *Diploglottis australis* (Fig. 2a, e), has a distinctive growth habit that was also expressed in other allometric parameters.

Variation in *a* was compared with a proxy for timber strength, namely published species wood density (Cause *et al.* 1989; Fig. 3). No equation indicated a close association for the two shorter H_{maxP} < 30 m classes. In contrast, linear relationships between *a* and wood density were found for the two taller H_{maxP} classes combined, positive for linear, power <8 m and NRH, and negative for GMM equations. Two outlying species in some analyses, *Polyscias elegans* and *Diploglottis australis*, with proportionally higher values of *a* (less rapid taper) than other species from their height-class groups, were also distinguished by their architectural characteristics.

Convexity factor and asymptotic height

For three-parameter growth-rate equations, *b* is an exponential value describing the abruptness of a sigmoid curve, which is difficult to interpret visually, but linear values are presented in the GMM and NRH equations. For understorey species (H_{maxP} 10–19 m), *b* estimated in
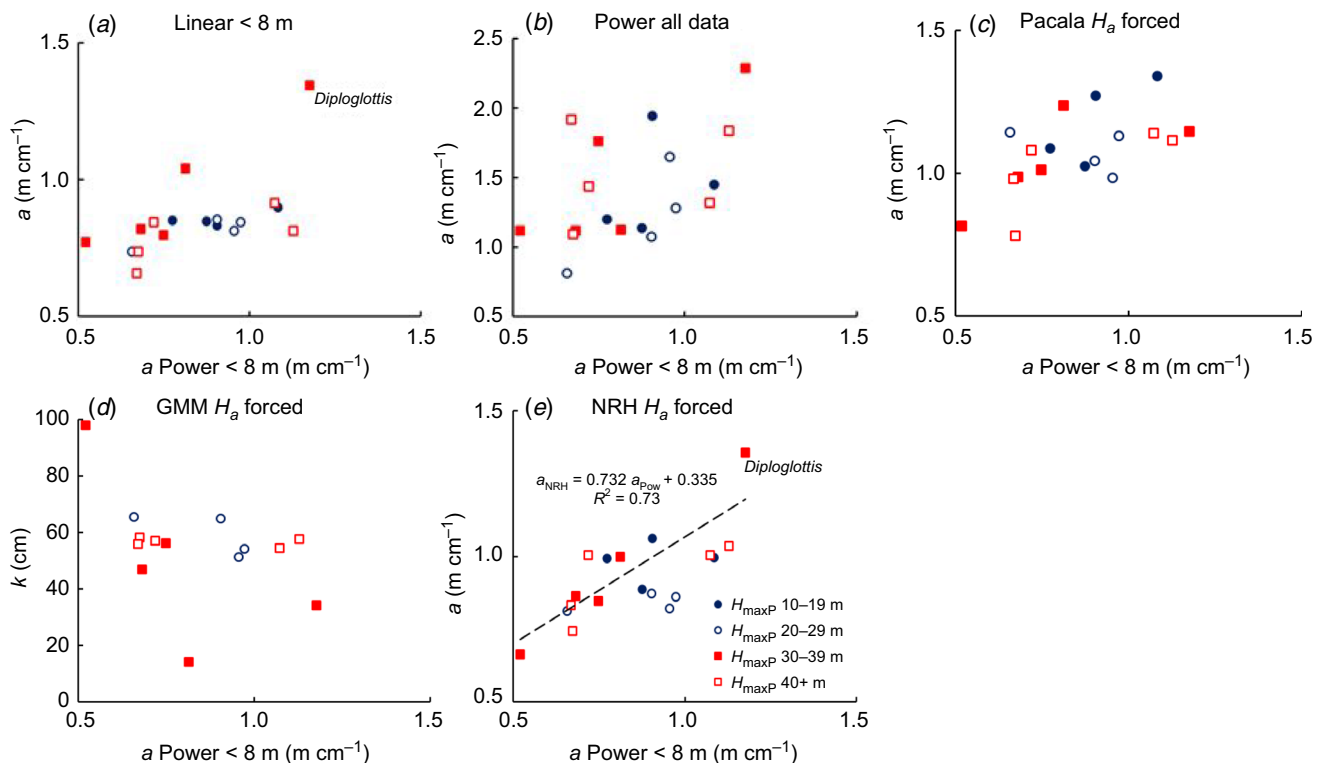
Fig. 2. Relationships between initial slope, *a*, of *H–D* relationships determined by the power function for 18 species of trees <8 m tall and by (*a*) linear regressions for trees <8 m tall, and for all species data from four H_{maxP} classes derived by (*b*) power, (*c*) $H_{\text{a-forced}}$ Pacala, and (*d*) $H_{\text{a-forced}}$ generalised Michaelis–Menten (GMM) (parameter *k*), and (*e*) $H_{\text{a-forced}}$ non-rectangular hyperbola (NRH; parameter *a*) equations.
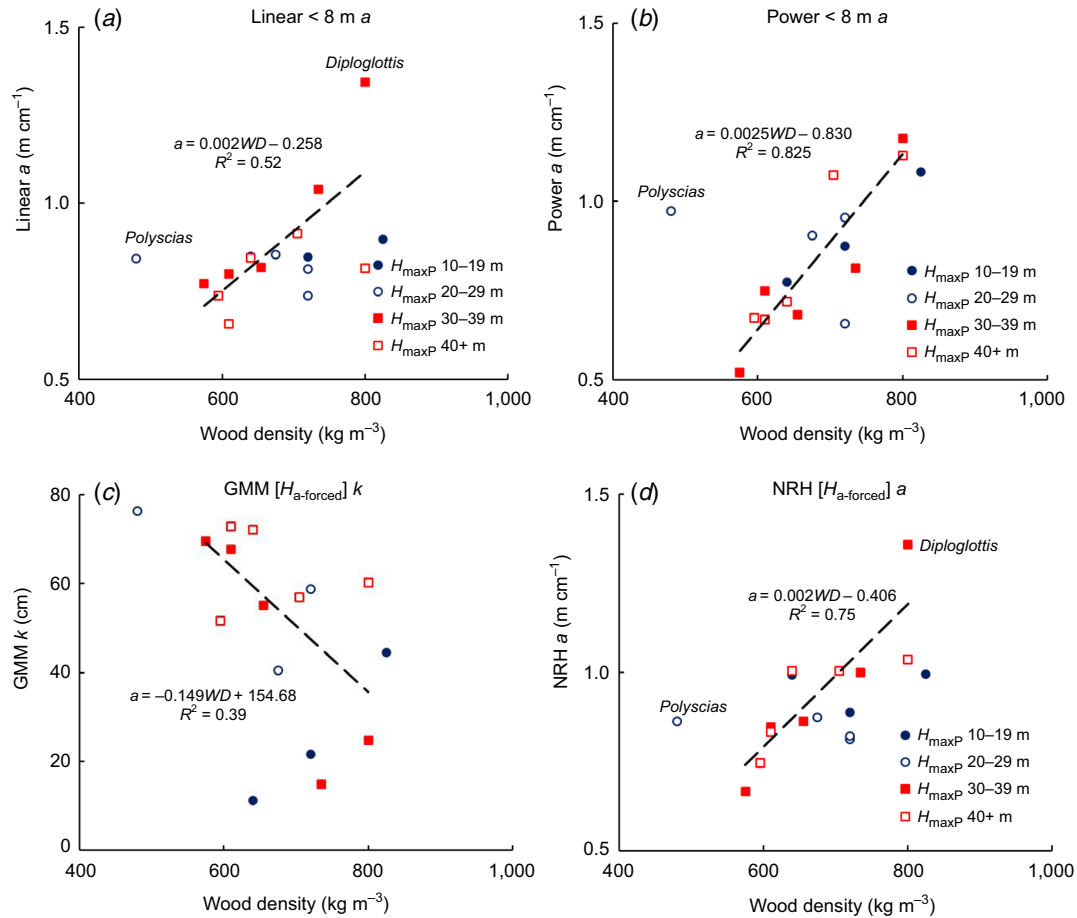
Fig. 3. Relationships between wood density and the initial allometric regression slope, *a*, for species allocated to published maximum height (H_{maxP}) classes in trees <8 m tall for (*a*) linear, and (*b*) power equations, and in all trees for $H_{a\text{-forced}}$ functions for (*c*) GMM and (*d*) NRH; dashed lines indicate regressions for species with H_{maxP} 30+ m. Wood-density data are from Cause *et al.* (1989).
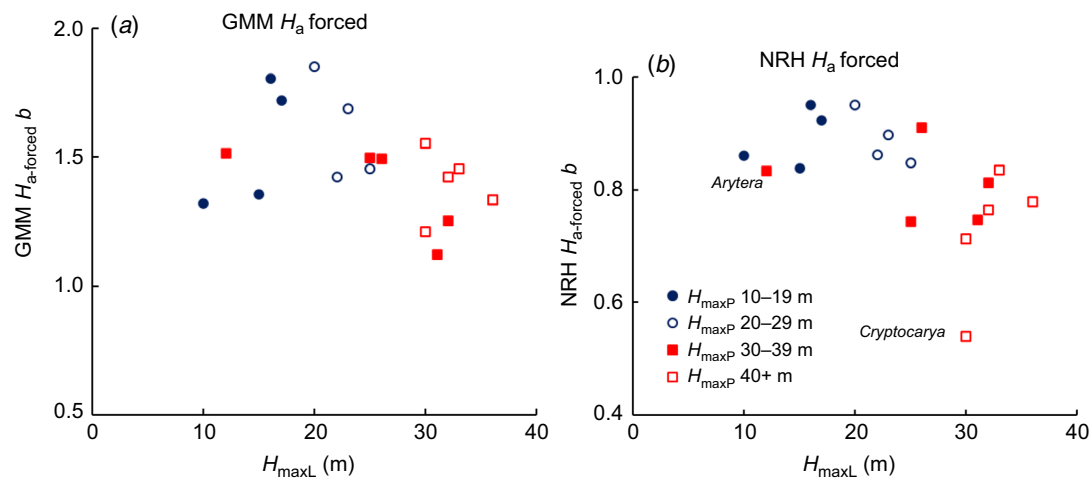
Fig. 4. Relationships between convexity factor, *b*, of *H–D* functions local maximum tree height (H_{maxL}) for species in four published H_{maxP} classes: (*a*) generalised Michaelis–Menten (GMM) *b* forced to H_{maxL} vs H_{maxL}, (*b*) non-rectangular hyperbola (NRH) *b* forced to H_{maxL} vs H_{maxL}. Note the different scales.

$H_{\text{a-forced}}$ regressions approached 2.0 in the GMM and 0.95 in the NRH (Fig. 4). The value of b decreased progressively and consistently in both the GMM and NRH for species in subdominant (H_{maxP} 20–29 m), co-dominant (H_{maxP} 30–39 m), and emergent (H_{maxP} 40+ m) classes (Fig. 4). These trends are taken to indicate that understorey trees mature in a uniform, low-stress environment, whereas canopy species experience progressive changes in their environment associated with light, spacing and wind. Two outlier species (*Arytera divaricata* and *Cryptocarya obovata*) lacked stems in the upper half of their published size ranges (Table S1).

One objective of fitting *H–D* regressions is to estimate H_{a} for local datasets. Two species for which most equations greatly overestimated H_{a} (*Neolitsea australis* and *Orites excelsus*) were notable for being the only ones for which a solution of the $H_{\text{a-fitted}}$ NRH equation required a constraint of $b > 0$. Neither of these species showed evidence of having approached an asymptotic height. Realistic $H_{\text{a-fitted}}$ estimates were not attained for *Acronychia pubescens*, and a solution of the $H_{\text{a-fitted}}$ NRH equation required a constrain of $b < 1$ for four species (*Arytera divaricata, Cryptocarya obovata, Daphnandra apetala* and *Zanthoxylum brachyacanthum*), for which measured (D_{maxL} and H_{maxL}) values were much smaller than corresponding published (D_{maxP} and H_{maxP}) values (Table S1). Estimation of H_{a} for individual species clearly requires model-generating data from the full range of sizes, and larger samples than were available for some species in this study.

Aggregation into H_{maxP} classes

The *H–D* relationships described by Eqns 2–10 from Table 1 were applied to all individuals of all species belonging to four H_{maxP} classes (10–19 m, 20–29 m, 30–39 m, and 40+ m; extracted from Francis 1970; Boland *et al.* 2006; Floyd 2008), using the $H_{\text{a-fitted}}$ form of each asymptotic equation (Table S4). The variation in accuracy, as assessed by its RMSE for each equation and each H_{maxP} class, is presented in Fig. S5.

The relative precision of allometric equations varied between H_{maxP} classes, but power, Gompertz and logistic equations resulted in consistently higher RMSEs than did the others. In contrast, RMSEs derived using the NRH differed by less than 3% from those obtained using the Mitscherlich, Pacala, Weibull, Richards or GMM equations for the three shorter H_{maxP} classes. This result was taken to indicate that the NRH could be used to describe *H–D* relationships of all H_{maxP} classes with acceptable precision.

Comparisons of NRH *H–D* trajectories for individual species and their H_{maxP} class means (Fig. 5) showed several features that assist in the interpretation of tree growth in these four structural classes (Table S4). For the understorey trees (H_{maxP} 10–19 m; Fig. 5*a*), the initial slopes of the *H–D* curve vary only slightly. Some D_{maxL} and H_{maxL} values (Table S1) indicate that some *H–D* trajectories (Fig. 5*a*) are incomplete (*Acronychia pubescens*), whereas in others

(*Denhamia celastroides*), there is evidence of some increase in D after H_{a} is attained.

The H_{maxP} 20–29 m class (Fig. 5*b*) may be described as subdominant and is notable for the almost identical *H–D* trajectories for the four species, in both their initial slopes and convexities, despite showing a range of maximum sizes. The codominant H_{maxP} 30–39 m class (Fig. 5*c*) showed more variation in both the initial *H–D* slope and convexity as trees approach maturity. *Diploglottis australis* is notable for the higher slope (more gradual stem taper) than other species, although the convexity was not so distinctive. Extension of the class *H–D* curve well beyond the bounds of the four species shown was due to the inclusion in the H_{maxP} class data set of two individuals of *Brachychiton acerifolium*, one being the largest tree in the whole sample The emergent H_{maxP} 40+ m class showed more variation than others among initial slope, convexity, D_{max} and H_{a} of the five species (Fig. 5*d*).

Because the H_{maxP} class mean curves for co-dominant (H_{maxP} 30–39 m) and emergent classes (H_{maxP} 40+ m) were very similar, these were combined into a canopy species group (H_{maxP} 30+ m) for a simpler structural comparison of the H_{maxP} class groups (Fig. 5*e*). The *H–D* curves for understorey (H_{maxP} 10–19 m) and subdominant (H_{maxP} 20–29 m) classes were sufficiently distinct, so as to warrant their separate classifications.

Discussion

Application of allometric models

Precision of H estimates for datasets, such as the RMSE (Huang *et al.* 1992; Zhang 1997; Williams *et al.* 2005; Qiu *et al.* 2021) has been used widely in the evaluation of allometric functions. Although the NRH was less precise than the GMM, it was much closer than all other tested equations (Table 2). Trends of bias in *H–D* predictions for D class means (Fig. S3) indicated a pattern of bias in the NRH that is very similar to that previously described for the GMM (Ledo *et al.* 2016; Martínez Cano *et al.* 2019*a*). Both equations have similar assessed utility for relating allometric parameters of datasets, except that the GMM initial proportionality factor cannot be visualised directly. For describing and comparing tree development for individual species (Fig. 5), the NRH was judged to be the better equation.

Where the developmental patterns of individual species are an important objective for investigation, explanations for plant attributes (e.g. tree height or crown width) may be sought in multivariate associations with functional attributes (Wright *et al.* 2007; Apgaua *et al.* 2015; Loubota Panzou *et al.* 2018). For individual species, more emphasis can be placed on the biological relevance of function parameters (Hunt 1979) and their utility in understanding the intrinsic factors underlying these developmental patterns.
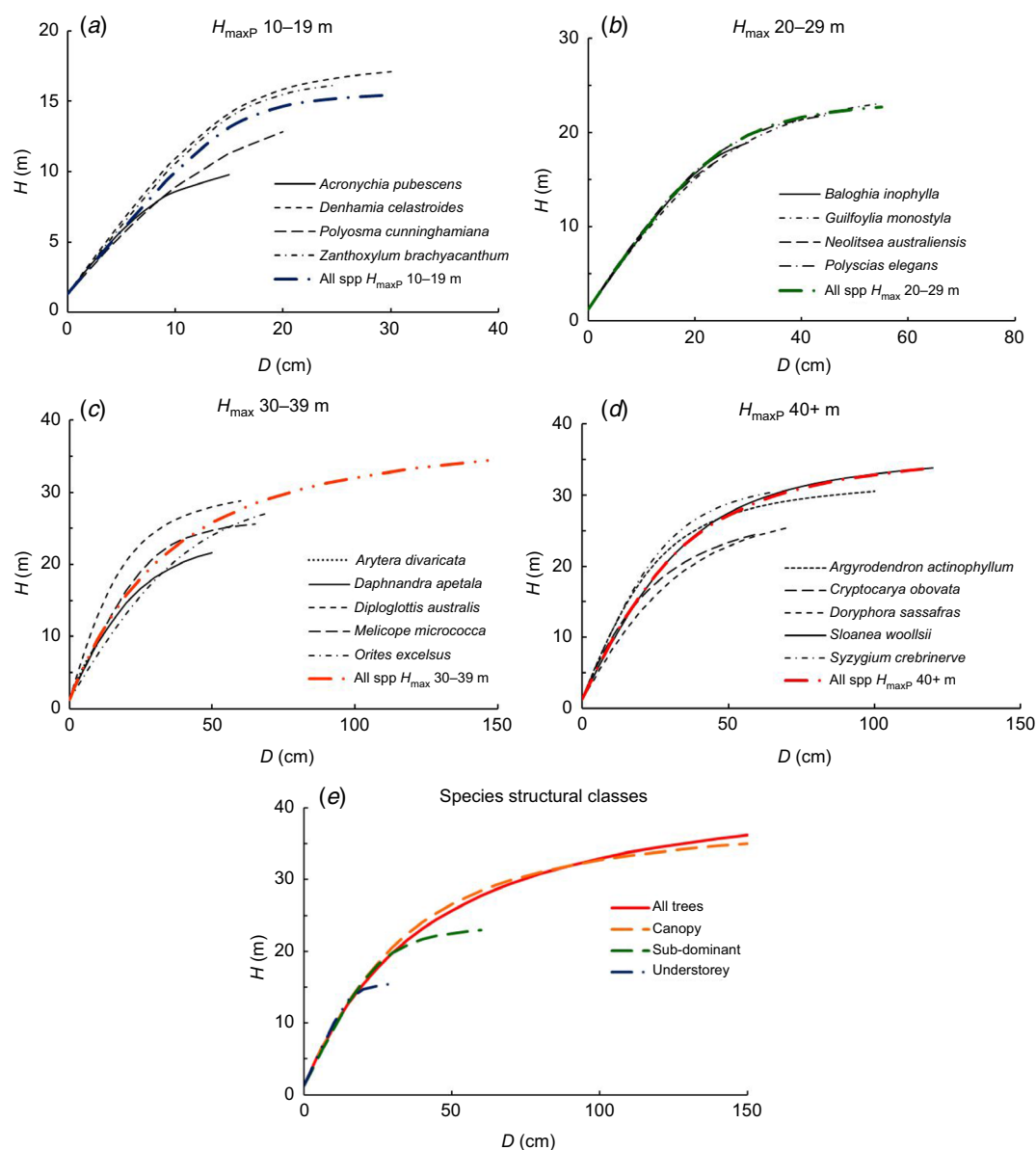
Fig. 5. Non-rectangular hyperbola *H*–*D* regressions forced to H_{maxL} for 18 selected subtropical rainforest tree species within maximum height (H_{maxP}) classes: (*a*) 10–19 m; (*b*) 20–29 m; (*c*) 30–39 m; (*d*) 40+ m, and (*e*) for all species within three canopy classes and for all trees in the study area.

Initial *H*–*D* proportionality factor

The average stand densities of trees overtopping regeneration <5 m tall (Fig. S1*d*) indicated that the environments in which small stems developed were at least equivalent to those in natural multi-species stands (Coomes *et al.* 2003; Ledo *et al.* 2016). It is suggested that the growing conditions within the Gambubal rainforest understorey did not prevent or exaggerate tree sway, but allowed direct interspecific comparison of the allometric parameter, *a*, as a basis for identifying critical functional attributes.

Under such conditions, the *H*–*D* ratio in sapling stems of different species is limited by the species' intrinsic structural properties of the stem (King 1990; Morgan and Cannell 1994; Niklas *et al.* 2006) and related functional attributes (Poorter *et al.* 2006; Hérault *et al.* 2011; Martínez Cano *et al.* 2019*a*). If the power function for trees <8 m tall is a valid biophysical basis for comparison (Banin *et al.* 2012), the only function with a closely correlated and readily visualised form of *a* was the $H_{a\text{-forced}}$ NRH for species with H_{maxP} of 30+ m (Fig. 2*e*). This association indicates the utility of the NRH for describing early development of canopy trees in this forest. Unlike the forest described by Martínez Cano *et al.* (2019*a*), both understorey and canopy species exhibited similar ranges of *a* (Fig. 2*e*). This may

Table 3. Qualitative evaluation of allometric equations against model criteria and tests.

Criterion	Test	Parameter	Allometric equation (cf. Table 1)								
			2	3	4	5	6	7	8	9	10
Biological representation	Biologically realistic and easily interpreted – species	a	A		A						A
		b								A	A
		H_a			A			A	A		
	Biologically realistic and easily interpreted – whole sample	a	A		A						A
		b								A	A
		H_a		A	A	A	A			A	A
	Theoretically consistent			A		A	A	A	A	A	A
	Predicts sensible responses			A	A	A	A			A	A
Description of errors	Accuracy (model: RMSE)			A	A	A	A			A	A
	Statistical parsimony (AIC)									A	
Description of data	Lack of bias across size range									A	A
	Goodness of fit of size distributions									A	A
Score			2	4	6	4	4	2	2	9	10

A, equation judged to yield an acceptable result.
Test: AIC, Akaike's information criterion. Parameters: a, initial slope; b, convexity coefficient; H_a, fitted asymptotic tree height. Allometric equations: 2, power; 3, Mitscherlich; 4 Pacala; 5, Weibull; 6, Richards; 7, Gompertz; 8, logistic; 9, generalised Michaelis–Menten (GMM); 10, non-rectangular hyperbola (NRH).

reflect less vertical environmental segregation within a subtropical as compared with an equatorial rainforest.

Wood density is closely associated with timber strength, stem allometry and tree stability (Falster and Westoby 2003; van Gelder *et al.* 2006; Fournier *et al.* 2013). Variations in a within the understorey (H_{maxP} 10–19 m) and subdominant (H_{maxP} 20–29 m) classes were not closely associated with wood density for the respective species, as was observed by Kooyman and Westoby (2009) for some species common to this study. In contrast, the closest positive linear relationships between these parameters occurred in canopy species (H_{maxP} 30+ m) when described by the linear (Fig. 3*a*) and power (Fig. 3*b*) equations for trees <8 m tall and by the NRH equation for all trees in this H_{maxP} class (Fig. 3*d*). This finding conforms to the observations of van Gelder *et al.* (2006) and Osunkoya *et al.* (2007) and gives credibility to the biophysical limitation of stem taper in these rainforest saplings (Niklas *et al.* 2006; Fournier *et al.* 2013). It also indicates the biological relevance of a determined by fitting the NRH to total data for a species.

Interspecific differences in initial stem taper can also be related to the architecture of each species (Claussen and Maycock 1995; Poorter *et al.* 2005, 2006; Duursma *et al.* 2010; Falster *et al.* 2018). The present analysis differs from some of these studies in that it relates to the initial stages of growth, and not to mature tree dimensions (Wang *et al.* 1998). Most species in the present study had simple or small compound leaves, carried on stems with slender primary growth, short internodes and, except in very low light conditions, a tendency to retain lateral branches (Floyd 2008). These species typically conform to Rauh's

architectural model, with monopodial rhythmic growth and tiers of branches that have indefinite growth potential (Hallé *et al.* 1978). As a result, height growth would be expected to accompany thickening of the stem, consistent with the number and physiological activity of lateral branches (Niklas 1995; Osunkoya *et al.* 2007: Falster *et al.* 2018; Loubota Panzou *et al.* 2018, 2021*a*).

In contrast, *Polyscias elegans* had an unusually high NRH $H_{a\text{-forced}}$ a value for its wood density (Fig. 3*d*), but an overall *H–D* trajectory that was indistinguishable from other members of the H_{maxP} 20–29 m group (Fig. 5*b*). *Polyscias elegans* was notable for its large compound leaves carried on plagiotropic branches, and a very shallow crown, consistent with the Aubreville architectural model (Hallé *et al.* 1978), shade intolerance, and its occurrence in relatively high light environments and appearance soon after forest disturbance (Kariuki *et al.* 2006; Floyd 2008). A similar initial growth pattern was described for *Polyscias australiana* by Claussen and Maycock (1995), an early successional species from north Queensland rainforests.

Diploglottis australis, with the highest value of NRH $H_{a\text{-forced}}$ a, 1.36 m cm^{-1} (Table S3, Panel 10B, Fig. 3*d*) possessed large compound pinnate leaves, commonly arranged oppositely or in pseudowhorls, separated by unusually long and robust internodes, consistent with the Aubreville architectural model (Hallé *et al.* 1978). These characteristics, with a high wood density (800 kg m^{-3}), are suggested to impart stiffness that would increase height growth per unit of secondary xylem dry matter as compared with species having short and thin primary internodes. This pattern of height growth was maintained until trees were

more than 20 m tall, making the H–D trajectory of *D. australis* distinctive among the H_{maxP} 30–39 m class (Fig. 5*c*).

Convexity factor and asymptotic height

For the species studied here, values of $H_{a\text{-forced}}$ *b* for both GMM and NRH showed consistent and proportional patterns of decrease with an increasing H_{maxL} (Fig. 4). There was no clear difference between these two equations in the precision of these trends, and both were judged to reflect tree growth patterns.

The observed range of *b* for the NRH was about 0.7–0.95, and for the GMM it was about 0.8–1.9 (Fig. 4). Trees with low H_a usually have a small range of maximum stem diameter (D_{max}), whereas trees that reach the upper canopy may continue to increase D for many years after they effectively reach H_a (Francis 1970; Thomas 1996, 2003; Floyd 2008; Banin *et al.* 2012).

The change in H–D trajectory for different H_{maxP} classes is very similar to that for photosynthesis in rainforest species from different strata (Thomas and Bazzaz 1999). It is suggested that species showing NRH *b* values close to 1.0 will reach H_a while growing in a constantly light-limited environment, with sufficient water, favourable temperatures, and limited wind, where the H–D relationship is determined principally by the intrinsic biophysical properties of the species, the static forces on the tree stem (King *et al.* 2009; Fournier *et al.* 2013) and stem hydraulic conductivity (Becker *et al.* 2000; Apgaua *et al.* 2015). Trees in these conditions would be expected to grow to their potential height, but lateral crown extension would be limited because of the high effective stand density (Vanclay 2009; Matos *et al.* 2015; Loubota Panzou *et al.* 2021*a*), so D would increase only very slowly with age after maturity. This pattern of growth is consistent with the application of the power equation to understorey species (Banin *et al.* 2012).

Once trees emerge from the forest understorey, a situation occurs that is analogous to the light response of photosynthetic rate, where multiple factors influence the rates of processes (Givnish 1988; Falster *et al.* 2018). The effective stand density decreases, intercepted radiation and atmospheric exposure increase, and the distance between neighbours may influence tree stem allometry (Wang *et al.* 1998; Poorter *et al.* 2005; Blanchard *et al.* 2016). These changes occur through a capacity for branch extension to continue, while crown depth increases through height growth (Poorter *et al.* 2006; Osunkoya *et al.* 2007; Loubota Panzou *et al.* 2021*a*), so that crown diameter and stem diameter increase in proportion (Henry and Aarssen 1999; Jucker *et al.* 2017), but varying with species' architecture (Sterck *et al.* 2001; Bohlman and O'Brien 2006; Loubota Panzou *et al.* 2018; Xu *et al.* 2019) and strength properties of their wood (van Gelder *et al.* 2006; Fournier *et al.* 2013).

In addition, exposure to increased wind speeds would result in greater swaying of the stems, which tends to increase stem taper (Jacobs 1954; Mayer 1987; Meng *et al.* 2008) and may limit height growth through damage to the uppermost twigs and branches (McEwan *et al.* 2011; Fournier *et al.* 2013; Thomas *et al.* 2015) and result in mainstem breakage and overturning (Cremer *et al.* 1982; Niklas 2007).

Aggregation into structural groups

Amalgamations of data used to provide generalised descriptions of forest structure (Thomas 2003; Osunkoya *et al.* 2007; Iida *et al.* 2011; Banin *et al.* 2012; Martínez Cano *et al.* 2019*a*) or regional estimates of forest biomass (Djomo *et al.* 2010; Feldpausch *et al.* 2012; Chave *et al.* 2014; Jucker *et al.* 2017) are reflected in the analyses for species and H_{maxP} classes shown here.

Aggregation of species H–D curves into structural groups can help identify the similarities and differences between functional attributes of the constituent species and structural groups of species (Aiba and Kohyama 1997; Poorter *et al.* 2006; Falster *et al.* 2018; Martínez Cano *et al.* 2019*a*). The overall H–D patterns are more consistent in the two smaller H_{maxP} classes (<30 m) than in the two taller classes (>30 m; Fig. 5). This differentiation would be consistent with the increasing variability in environmental conditions surrounding the crowns of trees as they became taller (O'Brien *et al.* 1995; Poorter *et al.* 2003; Iida *et al.* 2011; Banin *et al.* 2012). Consistent with this proposition, there may be limited segregation of H_{maxL} values in many species from Malaysian lowland rainforests (King *et al.* 2009; Iida *et al.* 2011), but continental-scale differences in H_{maxL} (Banin *et al.* 2012) and crown dimensions (Loubota Panzou *et al.* 2021*a*) of tropical forests, possibly reflecting the lower frequency of storm events in Malaysia and Asia generally than in many other rainforest environments (de Gouvenain and Silander 2003).

The total sample NRH *b* value of about 0.24 (Table 2) is attributed to the fact that mature trees in the lower H_{maxP} classes are not distinguished from younger trees in the taller H_{maxP} classes (Falster and Westoby 2005; Thomas 2003).

Utility of the non-rectangular hyperbola

Vanclay and Skovsgaard (1997) identified six criteria for the assessment of forest growth models. Tests for the description of errors and description of data have been comprehensively reviewed elsewhere (Vanclay and Skovsgaard 1997; Ledo *et al.* 2016). Assessable criteria, as applied to nine allometric equations in this study, are shown in Table 3.

Parameter variance and statistical parsimony are the critical attributes for predictive modelling (Cifuentes Jara *et al.* 2015; Ledo *et al.* 2016, Loubota Panzou *et al.* 2021*b*), making the AIC value the determinant of model fitness. In

this study, the GMM was the most efficient *H–D* allometric model for the whole sample (Tables 3, S2).

However, if the purpose of investigation is to visualise the components of species *H–D* trajectories, the NRH offers some advantages. The parameters of the NRH provide easily comprehended linear descriptions of three elements of tree growth in a specific environment, namely *a*, H_a and *b*. Application of the NRH across different environments would require modifications, as have been made to power (Lines *et al.* 2012; Zhao *et al.* 2021), logarithmic (Feldpausch *et al.* 2012; Chave *et al.* 2014; Cysneiros *et al.* 2021), Weibull and exponential (Banin *et al.* 2012; Mensah *et al.* 2018) models. An advantage of the NRH is that variations in environmental resource availability as reflected in forest type (Cysneiros *et al.* 2020), site quality (Vanclay 2009) and tree density (Vanclay 1992; Deng *et al.* 2019) may be identified and described quantitatively as factors independently altering *a*, *b* and H_a, and other dependent parameters, including crown dimensions and biomass.

Combination of the explanatory advantages of the NRH with statistical attributes that are equal or almost equal to those of several other widely used allometric equations, and especially the GMM (Table 3), suggests that the NRH can be used with confidence for both large datasets and for individual species, provided precautions are taken if the range of tree sizes is limited.

Conclusions

Although many allometric equations have been applied to describe *H–D* relationships for trees, and even though it is possible to estimate several tree dimensions and forest attributes remotely, value may be gained from understanding the development of individual species in complex vegetation associations such as rainforests. This analysis of individual species development depends on reliable identification and measurement of trees in the subcanopy zone of the forest as well as in the emergent canopy.

The non-rectangular hyperbola (NRH), although not as efficient as the generalised Michaelis–Menten (GMM) equation, is considered to provide a useful explanatory model for the development of tree height, *H*, in relation to stem diameter at breast height, *D*, over the complete range from saplings to mature trees. Application of the NRH to small samples of individual species may require the insertion of local maximum height, H_{maxL}, as asymptotic height, H_a, into the equation fitting routine; this value can best be obtained from measurement of a designated sample of trees. For more general application, the calculated maximum height, H_{maxC}, of a forest overstorey species may be related to climate and soil conditions. Advantages of this function are the accuracy and easy visualisation of realistic allometric relationships. The conceptual simplicity of the NRH allows testing of differences among forest environments through the comparison of numerical values for allometric parameters of individual species, especially where these differences are associated with climatic regime, site quality, tree spacing, and exposure to wind or to water deficits.

Supplementary material

Supplementary material is available online.

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Appendix 1. Symbols and abbreviations

Symbol	Definition
a	Proportionality factor (initial slope) of allometric function (m cm^{-1})
b	Convexity factor of allometric function
D	Diameter of individual tree at breast height (DBH, 1.3 m from ground) (cm)
D_{maxL}	Maximum value of D for a species at the study site (cm)
D_{maxP}	Maximum value of D for a species from published records (cm)
GMM	Generalised Michaelis–Menten equation
H	Height of individual tree (measured or calculated) (m)
H_a	Asymptotic value of tree height calculated by equation (m)
$H_{a\text{-fitted}}$	Allometric equation parameters all derived by fitted regression
$H_{a\text{-forced}}$	Allometric equation parameters derived by fitted regression after setting H_a as H_{maxL}
H_{D150}	Calculated value of H for $D = 150$ cm (m)
H_{maxC}	Calculated maximum tree height for species or larger datasets ($H_a + 1.3$ m) (m)
H_{maxL}	Maximum measured tree height for a species from study site (m)
H_{maxP}	Maximum value of H for a species from published records (m)
k	Proportionality factor of Michaelis–Menten equation (D at half-H_a, cm)
NRHs	Non-rectangular hyperbola equation