• 研究报告 •

基于枝条木材密度分级的鼎湖山南亚热带常绿阔叶林树高曲线模型

张剑坛^{1,2,3}, 李艳朋⁴, 张入匀⁵, 倪云龙^{1,2,3}, 周文莹^{1,2,3}, 练琚愉^{1,2,6*}, 叶万辉^{1,2,6}

1. 中国科学院华南植物园退化生态系统植被恢复与管理重点实验室, 广州 510650; 2. 中国科学院华南植物园广东省应用植物学重点实验室, 广州 510650; 3. 中国科学院大学, 北京 100049; 4. 中国林业科学研究院热带林业研究所森林生态研究中心, 广州 510520; 5. 华东师范大学生态与环境科学学院, 上海 200241; 6. 南方海洋科学与工程广东省实验室(广州), 广州 511458

摘要: 如何便捷准确地测量树高一直是林学及群落生态学所关心的问题。由于木材密度与树木生长密切相关, 因此基于木材密度建立树高曲线模型能够为测量树高提供新的方法。本文以鼎湖山南亚热带常绿阔叶林1.44 ha塔吊样地内119个物种的4,032个个体为研究对象, 利用树高、胸径和木材密度数据来探究基于枝条木材密度分级的树高曲线模型。首先, 对个体进行随机抽样, 将其划分为建模样本(占总样本量的70%)和检验样本(占总样本量的30%), 并通过聚类分析将所有个体的木材密度划分为4级。其次, 基于建模样本利用常见的5种理论生长方程(Richards、Korf、Logistic、Gompertz和Weibull方程)对不同分级建立树高-胸径模型; 基于检验样本检验模型精度, 并确定各分级的最适模型。最后, 构建基于物种分类的树高曲线模型, 并比较其与木材密度分级模型的差异。结果表明: 基于木材密度分级的模型, 各分级小组检验样本的平均绝对误差(MAE)和均方根误差(RMSE)最小值所对应的模型类型与建模样本结果一致, 确定Gompertz模型和Weibull模型为鼎湖山南亚热带常绿阔叶林最适树高模型类型。比较基于木材密度分级的模型与基于物种分类的模型, 发现二者的MAE、RMSE指数差异小。综上, 基于木材密度分级的树高曲线模型对树高估测精度高, 使用方便, 为树高预测提供了新方法, 可以更好服务森林调查等生产实践。

关键词: 植物功能性状; 木材密度分级; 理论生长方程; 非线性回归; 树高-胸径模型

张剑坛, 李艳朋, 张入匀, 倪云龙, 周文莹, 练琚愉, 叶万辉 (2021) 基于枝条木材密度分级的鼎湖山南亚热带常绿阔叶林树高曲线模型. 生物多样性, 29, 456–466. doi: 10.17520/biods.2020369.

Zhang JT, Li YP, Zhang RY, Ni YL, Zhou WY, Lian JY, Ye WH (2021) Height-diameter models based on branch wood density classification for the south subtropical evergreen broad-leaved forest of Dinghushan. Biodiversity Science, 29, 456–466. doi: 10.17520/biods.2020369.

Height-diameter models based on branch wood density classification for the south subtropical evergreen broad-leaved forest of Dinghushan

Jiantan Zhang^{1,2,3}, Yanpeng Li⁴, Ruyun Zhang⁵, Yunlong Ni^{1,2,3}, Wenying Zhou^{1,2,3}, Juyu Lian^{1,2,6*}, Wanhui Ye^{1,2,6}

1 Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650

2 Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650

3 University of Chinese Academy of Sciences, Beijing 100049

4 Forest Ecology Research Center, Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou 510520

5 School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241

6 Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 511458

ABSTRACT

Aims: Knowing how to measure tree height conveniently and accurately has always been a concern for the fields of

收稿日期: 2020-09-19; 接受日期: 2020-11-05

基金项目: 中国科学院战略性先导科技专项(XDB31030000)、国家重点研发计划(2017YFC0505802)、南方海洋科学与工程广东省实验室(广州)人才团队引进重大专项(GML2019ZD0408)和中国森林生物多样性监测网络建设项目

* 通讯作者 Author for correspondence. E-mail: lianjy@scbg.ac.cn

forestry and community ecology. Since wood density is closely related with tree growth, building a tree height curve model based on wood density could provide a new method for measuring tree height. This method would provide data support for vegetation investigation of forest dynamics plots and exploration of spatial differences in the radial and vertical distribution of community species resources.

Methods: Here, we explored tree height using a curve model based on branch wood density classification using tree height data, diameter at breast height (DBH), and wood density of 4,032 individuals belonging to 119 species in a 1.44 ha plot in a south subtropical evergreen broad-leaved forest in Dinghushan (DHS). First, we randomly sampled individuals, and divided them into model development (70% of the total sample size) and model validation (30% of the total sample size). We then classified wood density of all individuals into one of several categories using a cluster analysis. Second, we built a tree height-DBH model for different classifications based on modeling samples using five common theoretical growth equations (Richards, Korf, Logistic, Gompertz and Weibull equations). We estimated the fitting accuracy using the root mean squared error (RMSE) and Akaike information criterion (AIC). A smaller RMSE index and AIC index indicated the best fitting effect. Third, we determined the most optimal models based on the one model with the smallest mean average absolute error (MAE) and RMSE index. Finally, we established tree height curve models using species classification and compared the differences between models based on wood density and species classifications using the MAE index and RMSE index.

Result: Results suggest that when the classification order of cluster analysis was 4, the SSI (simple structure index) value was the largest, so the individual wood density of the plot was unevenly divided into four categories: [0.06, 0.31), [0.31, 0.45), [0.45, 0.57), and [0.57, 0.82]. There was little difference when fitting the five equations and all the parameter values were extremely significant. Models based on wood density classification corresponding to the MAE index and RMSE index were consistent with the results of the modeling samples. The Gompertz equation and Weibull equation were selected as the optimal tree height models and the Weibull equation had the highest frequency equation for the DHS plot. Moreover, when comparing models based on wood density classification with species classification, the MAE and RMSE indices of the two models in 17 species were less different. In addition, since the estimation accuracy of models based on wood density classification and species classification was low, the tree height of *Caryota maxima*, *Schima superba* and *Castanea henryi* was hardly to be estimated.

Conclusions: The tree height curve model based on wood density classification has a well-fitting effect and high estimation accuracy. It is also more convenient and generally used than the species classification model, which can realize the establishment of tree height curve models for many species easily. What's more, models based on wood density classification directly reflect plant response to the environment from a mechanistic perspective, and represents the ecological trade-off among individuals with different wood densities in the vertical growth of trees. In summary, this model based on wood density classification provides a new method for tree height prediction and can better serve production practices such as forest surveys and help with understanding scientific issues.

Key words: plant functional traits; wood density classification; theoretical growth equations; nonlinear regression analysis; height-diameter model

树木生长量表征着个体水平在一定时间内的增长量, 其中树高和胸径是衡量树木生长的两个重要指标(Bowman et al, 2013)。树高反映了树木在垂直梯度上对光照竞争能力的大小, 而胸径与树木的机械支撑和吸水能力相关, 并且树高和胸径之间存在密切的异速生长关系(Aiba & Kohyama, 1996; King, 1996)。森林生物量的反演是当今生态学和全球变化研究的热点问题之一(Houghton, 2005; 汤萃文等, 2010)。研究表明, 地上生物量与树高因子紧密相关(贺鹏等, 2020), 因此, 可通过建立胸径、树高与树木生物量之间的异速生长关系来估算生物量(石玉立等, 2014)。在野外调查过程中, 利用胸径尺或生长环可以对树木的胸径进行测量或长期监

测, 并获得相对精确的数据。相较胸径而言, 树高的测量既费时耗力又不精确。目前森林调查中树高的获取方法主要包括目测法、测高器法、遥感法以及模型预估法等(van Leeuwen & Nieuwenhuis, 2010; 刘发林等, 2011; Adamec & Drápela, 2016)。目测法主要根据测量人员的经验进行估测, 该方法的缺点是主观性强且误差大; 测高器法尽管理论上能较准确地获得树高, 但在实际操作中往往受到林分过密或地形等因素的限制而不便于操作。因此, 如何获取精度较高的树高数据一直都是林学和生态学领域亟待解决的问题之一。

近几十年来, 科研人员已经建立了多种树高曲线模型, 并通过实测的胸径数据对树高进行间接估

算。对于树高曲线模型的研究,最常见的方法是基于物种进行分类,然后对二次函数、幂函数等经验方程或Richards、Korf、Logistic等理论生长方程进行回归拟合,最后选择最适方程(Liu et al, 2008; 徐悦等, 2008; 陈飞鹏等, 2012)。然而基于物种分类的模型通常都较为复杂,适用范围有限,不仅难以参数化,并且需要大量数据支持(Garrard et al, 2013; Weiss et al, 2014)。除了基于物种进行分类外,基于亲缘关系分类(Aiba & Kohyama, 1996; 张瑜和贾黎明, 2013; 李明华和肖舜祯, 2019)以及林分类型分类(朱永红和翁国庆, 2000; Feldpausch et al, 2011; Vibrans et al, 2015)的树高曲线模型也得到了较好的应用。因此,选择合适的对象构建树高曲线模型,可为森林中树高的精准获取提供一条便捷且有效的途径(Mehtätalo, 2004)。

为提高树高模型的预测精度,研究人员将立地条件、林分密度和林分结构等因素纳入模型当中,并通过建立混合模型来提高拟合精度(Sharma & Parton, 2007; Meng et al, 2008; 赵俊卉等, 2009)。曹美等(2019)利用主成分分析法确定影响隆林县油茶(*Camellia oleifera*)林分布的主要立地因子为土壤类型、坡度、地貌和坡向,从而构建了不同立地类型的油茶树高生长模型。但在实际的野外调查过程中通常难以获取物种在不同地区的立地条件,因此李海奎和法蕾(2011)采用树高分级方法建立了比较适用的全国主要树种树高模型。此外,研究人员发现植物功能性状(plant functional traits)可以有效表征植物的存活、生长、繁殖以及死亡等生态策略(刘晓娟和马克平, 2015),例如树高、比叶面积和冠层结构与植物邻体之间的竞争能力有关(Westoby et al, 2002; 贺鹏程和叶清, 2019); 植物生长速率与木材密度(wood density, WD)呈负相关(Poorter et al, 2010); 木材密度与存活率和个体寿命呈正相关,而与最大树高呈负相关(Martínez-Cabrera et al, 2011),同时,研究还发现基于植物功能性状建立的模型通常可以简化模型参数化工作,且具有更好的普适性,因此将其纳入分析可能有助于构建更为精确、普适的树高曲线模型(Zakharova et al, 2019)。

本研究以鼎湖山亚热带常绿阔叶林1.44 ha塔吊样地(以下简称塔吊样地)内的4,032个个体为研究对象,通过测量个体水平的木材密度性状,探究了基于木材密度分级建立树高曲线模型的可行性,

并比较了其基于物种分类构建的树高曲线模型的差异性,试图为森林动态监测样地的植被调查以及群落物种资源径向与垂直分配的空间差异研究提供数据支撑。

1 材料与方法

1.1 研究区域概况

鼎湖山塔吊样地位于广东省肇庆市鼎湖山国家级自然保护区内(23°09'–23°11'N, 112°30'–112°33'E),面积为1.44 ha (120 m × 120 m)。该区属亚热带湿润型季风气候,年平均温度20.9℃,年平均降水量1,927 mm,年均蒸发量1,115 mm,年均相对湿度80.3%,样地植被类型为亚热带常绿阔叶林(黄忠良等, 1998; 叶万辉等, 2008)。

鼎湖山森林塔吊的独立起升高度为54.4 m,吊臂最大工作半径为60.0 m,旋转一周可覆盖的样地面积超过1.0 ha (张入匀等, 2019)。参照美国史密森热带森林研究中心(Center for Tropical Forest Science, CTFS)的调查技术规范(Condit, 1998), 2014年10月完成了对塔吊样地内所有胸径 ≥ 1.0 cm的木本植物的调查,测量并记录了每个植株的树号、胸径、树高、生长状态以及相对于样地起始点的坐标等。该样地于2018年11月完成第一次复查工作,在复查过程中,胸径数据由胸径尺实测获得,树高则利用林冠塔吊和测高杆对样地内每个个体的高度进行了准确测量。具体方法为:对于高度较低的树木利用测高杆直接测量;对于难以用测高杆直接测量的高树,则利用塔吊吊篮在森林林冠层之上用皮尺向下进行垂直测量,并记录该树树冠顶部到根部的高度,作为该树的树高(桂旭君等, 2019)。第一次复查结果显示,塔吊样地在本次调查期间的新增及死亡个体分别为1,890个和393个,目前共有存活植株4,484个,隶属于48科91属122种。本研究采用的是第一次复查数据。

1.2 木材密度测量

Swenson和Enquist (2008)研究表明,枝条木材密度与茎木材密度呈高度相关。因此,为了避免取样对样地内树木个体造成大的破坏,本研究选择以枝条木材密度作为测量对象。2018年12月,对样地内的所有个体进行枝条取样以获得枝条木材密度。由于个别高树位于塔吊作业范围外,不能保证树高的精准获取,加之部分个体处于濒死或叶片稀少等

状态,因而无法对它们的枝条进行采集,所以最终仅采集了119种树木4,032个个体的枝条样品。每个个体剪取成熟的枝条,然后将其剪成6 cm长的小段,并选取大小相近的5个小段作为木材密度的测量样本。先采用排水法(Cornelissen et al, 2003)测定木材体积,然后将枝条样本放入70℃烘箱中烘干至少96 h,直至恒重,测量枝条样本干重;枝条干重与枝条体积之比即为枝条木材密度(g/cm³)。

1.3 数据分析

1.3.1 模型选择

本文选择了常见的Richards、Korf、Logistic、Gompertz和Weibull 5种理论生长模型作为树高曲线候选模型(表1)。对于林木生长模型来说, Richards模型的应用最广,不仅形式灵活多样,而且也具有广泛的适应性(Richards, 1959)。Gompertz模型和Logistic模型被提出的时间最早,且最早用于描述种群的增长及分布问题; Gompertz模型是Richards模型的特殊形式,而Logistic模型的S型曲线由于能够体现自然界大量事物的变化规律且具有良好的预测精度,因而应用较为广泛(段爱国和张建国, 2013)。此外, Korf模型和Weibull模型在构建树高生长模型方面也取得了较好的效果(Mehtatalo, 2004; Ng'Andwe等, 2019)。

1.3.2 木材密度分级

以往的研究表明植物生长速率与木材密度呈负相关关系(Poorter et al, 2010), 因此, 首先对木材密度进行分级处理, 进而获得不同木材密度等级下的树高关系。对塔吊样地内4,032个个体的木材密度进行K均值聚类分析, 以获得木材密度分级数和各分级的密度范围。本文采用ssi指数(simple structure index)判断确定最佳分类数。通常情况下, ssi值最大时对应的分类数为最佳分类组数(Dolnicar et al,

1999)。将最佳分类组数代入K均值聚类法中, 进而得出每一级的木材密度范围; 最后再根据每个个体木材密度的大小, 将样地内4,032个个体划分到相应的层级之中。

1.3.3 建立树高曲线模型

对所有个体通过随机无放回抽样划分为拟合样本(70%)和检验样本(30%), 通过非线性回归模型将拟合样本应用于5种候选模型, 进而得到不同分级区间对应的树高曲线模型。模型拟合精度通过均方根误差(root mean squared error, RMSE)和赤池信息准则(Akaike information criterion, AIC)判断; 其中, RMSE和AIC越小, 模型拟合效果越好。具体计算公式如下:

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2}$$
 (1)

$$AIC = 2k - 2\ln(L)$$
 (2)

式中, *n*为拟合样本量, *y_i*和 $\hat{y}_i$ 分别为第*i*个真实值和预测值, *k*为参数数量, *L*为似然函数。

1.3.4 树高曲线模型检验

将检验样本的胸径数据应用于各分级区间模型中, 得到树高预测值。通过比较真实值与预测值的差异判断模型模拟的精确度。模型检验通过平均绝对误差(mean absolute error, MAE)和RMSE判断, MAE和RMSE值越小, 说明模型预估精度越好, 最终确定各分级区间的最适树高模型。具体公式如下:

$$MAE = \frac{1}{m} \sum_{j=1}^m |y_j - \hat{y}_j|$$
 (3)

式中, *m*为检验样本量, *y_j*和 $\hat{y}_j$ 分别为第*j*个真实值和预测值。

1.3.5 基于物种分类的树高曲线模型

为了保证基于物种分类的树高曲线模型的分析功效, 首先筛选出塔吊样地建模样本中个体数大于50的17个物种, 然后利用上述5种候选模型对每个物种进行树高-胸径关系建模, 最后根据RMSE和AIC值确定每个物种的最适模型。此外, 为了比较其与基于木材密度分级构建的树高曲线模型的差异, 在前文已确定的各分级区间最适树高模型基础上, 本文还对筛选出的物种构建了基于木材密度分级的树高曲线模型, 并通过计算MAE和RMSE指数探究两种方法的差异。

本研究所有数据分析与绘图均在R 3.6.2中完

表1 5种候选树高-胸径曲线模型。H为树高; D为胸径; a, b, c为参数。

Table 1 Five kinds of height-diameter models. H, Tree height; D, Diameter at breast height; a, b and c are parameters.

序号 No.	模型类型 Model types	模型表达式 Model forms
1	Richards	$H = a \times (1 - e^{-b \times D^c})$
2	Korf	$H = a \times (e^{-b \times D^c})$
3	Logistic	$H = a / (1 + b \times e^{-c \times D})$
4	Gompertz	$H = a \times (e^{-b \times e^{-(c \times D)}})$
5	Weibull	$H = a \times (1 - e^{-b \times D^c})$

成。主要使用了R软件的vegan包(Oksanen et al, 2019)、stats包和ggplot2包(Wickham, 2016)。

2 结果

2.1 木材密度分级划分

由图1可知, 划分级数为4时, ssi指数值最大。因此, 确定木材密度最优划分级数为4级, 即可将塔吊样地个体木材密度划分为4级, 木材密度(g/cm³)范围由低到高依次为[0.06, 0.31)、[0.31, 0.45)、[0.45, 0.57)和[0.57, 0.82] (表2)。

2.2 各分级区间最适树高曲线模型

在4个分级小组中, 5种方程类型拟合结果差异较小, 所有的参数值均极显著。在各分级小组中, 依据RMSE和AIC值均最小的评价标准, 选定I、II、III、IV组的最适模型类型分别为Weibull模型、Weibull模型、Gompertz模型和Weibull模型(表3)。

利用检验样本验证模型的精度发现, I、II和IV组Weibull模型的MAE和RMSE值在5种模型中最小

(表3), 表明Weibull模型在这3个等级区间内预估精度最好, Weibull模型为I、II、IV组的最适模型类型; III组Gompertz模型的MAE和RMSE值在5种模型中最小(表3), 表明Gompertz模型在第III组中预估精度最好, Gompertz模型为III组最适模型类型。综上, 本文最适树高模型有两种: 第III组的最适模型类型为Gompertz模型, I、II和IV组的最适模型均为Weibull模型(表3)。

各分级区间中, 真实值在模型拟合曲线上均匀分布, 较好地拟合了数据的分布和变化趋势(图2)。综上, 建立了鼎湖山南亚热带常绿阔叶林基于木材密度分级的树高曲线模型(表2)。

2.3 与基于物种分类的树高曲线模型的比较

在17个物种中, 两种方法的MAE和RMSE值差异总体小, 而鱼尾葵(*Caryota maxima*)、木荷(*Schima superba*)和锥栗(*Castanea henryi*) 3个物种基于两种方法构建的模型MAE值均大于1.6, 且RMSE值均大于2.2, 表明对于这3个物种, 两种模型的预估值

图1 木材密度分级最优分级组数判断指标。(a)表示每个对象在不同分级情况下的归属, 一种颜色代表一个分级组; (b)展示了不同分级组数对应的ssi值大小。

Fig. 1 The judgment index partitioning optimal groups of wood density classification. (a) The groups that each object is categorized with different conditions and different groups were distinguished by different colors; (b) The value of simple structure index (ssi) for different number of groups.

表2 基于木材密度分级的树高曲线模型。H为树高, D为胸径。

Table 2 Height-diameter models based on wood density classification. H, Tree height; D, Diameter at breast height.

组别 Groups	木材密度范围 Wood density ranges (g/cm ³)	个体数 No. of individuals	胸径范围 D ranges (cm)	树高范围 Tree height ranges (m)	模型表达式 Model expressions
I	[0.06, 0.31)	747	[1.0, 32.8]	[1.5, 21.5]	$H = 20.100 \times (1 - e^{-0.111 \times D^{0.680}})$
II	[0.31, 0.45)	908	[1.0, 47.8]	[1.4, 25.7]	$H = 54.000 \times (1 - e^{-0.040 \times D^{0.656}})$
III	[0.45, 0.57)	1,577	[1.0, 66.0]	[1.4, 27.1]	$H = 20.890 \times e^{-2.257 \times e^{(-0.098 \times D)}}$
IV	[0.57, 0.82]	800	[1.0, 62.6]	[1.6, 27.1]	$H = 51.700 \times (1 - e^{-0.040 \times D^{0.704}})$

表3 不同木材密度分级区间树高曲线模型的拟合与检验。AIC: 赤池信息准则; MAE: 平均绝对误差; RMSE: 均方根误差。***, $P < 0.001$.

Table 3 The fitting and validation results of tree height curve model in different wood density grading ranges. AIC, Akaike information criterion; MAE, Mean absolute error; RMSE, Root mean squared error. ***, $P < 0.001$.

组别 Group	样本数 Sample site		模型 Model	参数 Parameter			拟合精度 Fitting accuracy		预估精度 Prediction accuracy		最适模型 Optimal model
	拟合 Fitting	检验 Validation		a	b	c	RMSE	AIC	MAE	RMSE	
I	504	204	Richards	13.300***	0.068***	0.680***	1.070	1,503.427	0.796	1.313	Weibull
			Korf	27.100***	2.689***	0.349***	1.098	1,529.476	0.821	1.338	
			Logistic	12.168***	4.165***	0.232***	1.069	1,502.340	0.844	1.334	
			Gompertz	13.370***	1.841***	0.141***	1.056	1,489.855	0.814	1.281	
			Weibull	20.100***	0.111***	0.680***	1.055	1,489.608	0.783	1.250	
II	637	283	Richards	34.200***	0.013***	0.648***	1.537	2,357.280	0.966	1.532	Weibull
			Korf	99.700***	4.112***	0.241***	1.621	2,430.865	1.052	1.598	
			Logistic	20.517***	6.009***	0.132***	1.575	2,394.034	1.075	1.571	
			Gompertz	21.977***	2.140***	0.078***	1.532	2,359.453	1.013	1.529	
			Weibull	54.000***	0.040***	0.656***	1.531	2,358.118	0.960	1.520	
III	1,095	476	Richards	26.816***	0.030***	0.759***	1.753	4,344.796	1.071	1.689	Gompertz
			Korf	163.700***	4.627***	0.216***	1.788	4,388.426	1.132	1.735	
			Logistic	19.723***	6.575***	0.160***	1.796	4,398.290	1.126	1.702	
			Gompertz	20.890***	2.257***	0.098***	1.746	4,335.966	1.043	1.655	
			Weibull	28.980***	0.065***	0.796***	1.758	4,350.653	1.077	1.693	
IV	587	243	Richards	33.700***	0.018***	0.697***	1.401	2,069.142	1.030	1.639	Weibull
			Korf	83.600***	3.979***	0.271***	1.504	2,152.666	1.133	1.729	
			Logistic	21.793***	6.432***	0.139***	1.488	2,140.307	1.107	1.727	
			Gompertz	23.945***	2.236***	0.080***	1.422	2,087.314	1.059	1.663	
			Weibull	51.700***	0.040***	0.704***	1.394	2,063.593	1.025	1.624

图2 四组木材密度分级区间模型拟合曲线。图A、B、C、D木材密度分别为[0.06, 0.31)、[0.31, 0.45)、[0.45, 0.57)和[0.57, 0.82]。阴影部分为95%置信区间范围。

Fig. 2 Four groups of wood density grading interval model fitting curve and original data distribution diagram. Figure A, B, C and D represent the interval of wood density [0.06, 0.31), [0.31, 0.45), [0.45, 0.57), [0.57, 0.82], respectively. The shaded part represent the 95% confidence interval.

均与真实值相差较大, 预估精度较低(表4)。因此, 基于木材密度分级模型的预估精度与基于物种分类的模型相当。

3 讨论

3.1 木材密度分级模型为树高预测提供了新方法

本研究发现, 基于木材密度分级的树高曲线模型能为树高预测提供新方法。通过聚类分析将木材密度划分为4级, 基于木材密度分级方法构建模型, 将个体在不同分级范围中匹配相应的树高模型, 反映物种在个体水平的生长状态; 而模型的RMSE和AIC值均较小(表3), 说明基于分级方法能够较好地提高模型的拟合精度(李海奎和法蕾, 2011; 李杰, 2019)。本研究中最适树高模型的类型为Gompertz模型和Weibull模型, 这两种类型的数学函数特性有所不同, Gompertz模型以生长年龄的指数形式表示树木的相对生长率, Weibull模型以生长年龄指数与幂函数的混合形式表示树木的相对生长率(段爱国和张建国, 2013)。Yang等(1978)曾发现Weibull模型

的精度高于Gompertz模型, Ng'Andwe等(2019)利用Weibull模型发展建立了适用于赞比亚思茅松(*Pinus kesiya*)的树高-胸径生长模型, 得到各模型中的最佳效果, 而本文中Weibull模型作为最佳树高模型出现频次最高, 也表明该方程具有更好的拟合效果。

3.2 木材密度分级模型比物种分类模型更具普适性

目前, 研究人员对树高-胸径关系的研究多基于物种分类构建模型, 尽管这种方法的精度较高, 但在复杂的混合林分中, 林木的生长情况呈现多样化现象, 导致树高曲线拟合难度增大, 其适用性和精确性也有待完善(雷相东和李希菲, 2003; 庄崇洋等, 2017)。本研究对鼎湖山亚热带常绿阔叶林塔吊样地内17个物种分别建立树高曲线模型, 发现建模过程复杂, 而且因受到样本个体数的限制, 导致其余102个物种难以构建合适的树高模型。而基于木材密度分级的模型预估精度与物种分类模型相当, 且能够快速实现多个物种树高曲线模型的建立。因此, 木材密度分级模型比物种分类模型具有更好的普适性。

表4 个体数大于50的17个物种基于物种分类模型和木材密度分级模型的差异。H为树高, D为胸径; MAE: 平均绝对误差; RMSE: 均方根误差。

Table 4 Differences between species classification model and wood density classification model of 17 species with more than 50 individuals. H, Tree height, D, Diameter at breast height; MAE, Mean absolute error; RMSE, Root mean squared error.

物种 Species	基于物种分类模型 Model based on species classification				基于木材密度分级模型 Model based on wood density classification			
	模型表达式 Model expressions	MAE	RMSE		模型表达式 Model expressions	MAE	RMSE	
白楸 <i>Mallotus paniculatus</i>	$H = 18.621 \times e^{-1.727 \times e^{(-0.088 \times D)}}$	0.805	1.198		$H = 54.000 \times (1 - e^{-0.040 \times D^{0.656}})$	0.961	1.323	
橄榄 <i>Canarium album</i>	$H = 20.194 \times e^{-2.230 \times e^{(-0.115 \times D)}}$	0.677	0.979		$H = 20.100 \times (1 - e^{-0.111 \times D^{0.680}})$	0.950	1.705	
黄杞 <i>Engelhardia roxburghiana</i>	$H = 22.881 \times (1 - e^{-0.118 \times D^{0.774}})$	0.678	0.992		$H = 54.000 \times (1 - e^{-0.040 \times D^{0.656}})$	1.418	1.795	
假苹婆 <i>Sterculia lanceolata</i>	$H = 12.486 \times e^{-1.837 \times e^{(-0.144 \times D)}}$	0.565	0.839		$H = 54.000 \times (1 - e^{-0.040 \times D^{0.656}})$	0.611	0.960	
九节 <i>Psychotria asiatica</i>	$H = 4.063 / (1 + 1.628 \times e^{-0.471 \times D})$	0.312	0.482		$H = 20.890 \times e^{-2.257 \times e^{(-0.098 \times D)}}$	0.848	0.927	
鰲蒴锥 <i>Castanopsis fissa</i>	$H = 9.203 \times (1 - e^{-0.177 \times D})^{0.742}$	0.585	0.823		$H = 20.890 \times e^{-2.257 \times e^{(-0.098 \times D)}}$	0.934	1.567	
罗伞树 <i>Ardisia quinquegona</i>	$H = 7.523 / (1 + 4.178 \times e^{-0.637 \times D})$	0.454	0.593		$H = 51.700 \times (1 - e^{-0.040 \times D^{0.704}})$	0.497	0.648	
蒲桃 <i>Syzygium jambos</i>	$H = 11.534 / (1 + 4.412 \times e^{-0.242 \times D})$	0.718	1.030		$H = 51.700 \times (1 - e^{-0.040 \times D^{0.704}})$	1.050	1.616	
肉实树 <i>Sarcosperma laurinum</i>	$H = 12.527 \times e^{-1.966 \times e^{(-0.159 \times D)}}$	0.386	0.532		$H = 54.000 \times (1 - e^{-0.040 \times D^{0.656}})$	0.460	0.678	
水同木 <i>Ficus fistulosa</i>	$H = 9.300 \times (1 - e^{-0.204 \times D^{0.881}})$	0.560	0.749		$H = 20.100 \times (1 - e^{-0.111 \times D^{0.680}})$	0.674	0.873	
鱼骨木 <i>Canthium dicoccum</i>	$H = 15.121 \times e^{-2.057 \times e^{(-0.215 \times D)}}$	1.109	1.516		$H = 51.700 \times (1 - e^{-0.040 \times D^{0.704}})$	1.527	1.951	
鱼尾葵 <i>Caryota maxima</i>	$H = 32.827 / (1 + 8.650 \times e^{-0.090 \times D})$	1.881	2.563		$H = 54.000 \times (1 - e^{-0.040 \times D^{0.656}})$	2.572	3.412	
木荷 <i>Schima superba</i>	$H = 20.978 / (1 + 5.011 \times e^{-0.131 \times D})$	2.020	2.694		$H = 20.890 \times e^{-2.257 \times e^{(-0.098 \times D)}}$	2.055	2.724	
黄果厚壳桂 <i>Cryptocarya concinna</i>	$H = 8.149 / (1 + 4.416 \times e^{-0.604 \times D})$	0.481	0.710		$H = 20.890 \times e^{-2.257 \times e^{(-0.098 \times D)}}$	0.691	1.066	
鹅掌柴 <i>Schefflera heptaphylla</i>	$H = 12.604 \times e^{-1.740 \times e^{(-0.137 \times D)}}$	0.777	1.097		$H = 20.100 \times (1 - e^{-0.111 \times D^{0.680}})$	0.791	1.106	
银柴 <i>Aporosa dioica</i>	$H = 18.300 \times (1 - e^{-0.107 \times D^{0.725}})$	0.634	0.931		$H = 20.890 \times e^{-2.257 \times e^{(-0.098 \times D)}}$	0.764	1.105	
锥栗 <i>Castanea henryi</i>	$H = 19.793 \times e^{-2.253 \times e^{(-0.101 \times D)}}$	1.662	2.247		$H = 20.890 \times e^{-2.257 \times e^{(-0.098 \times D)}}$	1.752	2.346	

3.3 木材密度分级模型方法的机理解释及其潜在优势

实际上, 基于木材密度分级的树高曲线模型不仅具有较好的拟合效果或预测能力, 也较好地反映了树木个体在生长过程中的生态权衡策略(Zakharova et al, 2019)。木材密度不仅可以有效表征物种对光照、水分和土壤养分等因子的耐受能力或偏好程度, 其大小也是植物物种沿降水梯度分布的最佳指示性状之一(Maharjan et al, 2011; 何东, 2016)。对于本研究而言, 不同分级水平下的树高曲线模型表征了不同木材密度个体在树木垂直生长上的生态权衡。通常情况下, 木材密度低则含有更高的水分, 结构投资较少, 生长速率较快(Chave et al, 2009), 所以树木的垂直生长速率会随着木材密度的增大而降低(Poorter et al, 2010)。因此, 木材密度从机理上直接反映了植物在垂直方向上对环境的响应。此外, 前人的研究也表明, 树木的径向生长与导管直径大小密切相关, 且随着海拔的增高, 树干导管直径和木材密度降低, 径向生长缓慢(Chave et al, 2006; Fisher et al, 2007)。木材密度不仅直接影响着树木的生长, 也间接影响着树木的存活与死亡(Wright et al, 2010)。如先锋树种通常具有较低的木材密度以确保能够在林窗内快速生长, 而耐阴物种通常具有较高的木材密度, 以增加自身在林下层的存活率(van Gelder et al, 2006; Poorter et al, 2008)。

与物种分类模型相比, 性状分级模型具有诸多优势, 比如可在不同生物类群、区系和生境之间通用, 可在不同观察尺度上通用, 可独立于分类学上的不确定性, 以及可提供相对明确的机理线索等(Weiher & Keddy, 1995)。McGill等(2006)认为基于性状的研究方法有望改善以往群落生态学过于纠缠物种问题而难以发现普适法则的局面。本文基于木材密度分级的树高曲线模型在鼎湖山南亚热带常绿阔叶林中总体稳定, 参数可靠, 表现出良好的树高预估精度, 具有较好的普适性。若已知木材密度和胸径, 就能够方便、准确地得到树高值, 为林分树高测量提供了新方法, 从而为森林动态监测样地的植被调查及探究物种垂直-径向生长权衡机制提供数据支撑。此外, 利用该模型获得较为准确的树高, 结合生物量模型能够更好地推算出森林地上生物量, 对亚热带混合林的地上生物量估算具有实

践意义。但是, 该方法目前也存在一些局限性, 例如对木材密度取样及测定有严格的要求和方法, 操作复杂, 一定程度上增加了工作量; 再者, 利用木材密度分级构建树高模型增加了模型复杂程度, 且对于分级方法尚不具有普遍性和推广意义。因此本研究结果目前较适宜用于探讨树高科学问题, 为树高测量提供参考方法, 要想真正实现实际应用, 还需对模型作进一步改进与完善。研究表明, 生境类型和群落演替阶段与木材密度及物种多样性密切相关(刘文平等, 2011; Poorter et al, 2019), 未来可以在基于木材密度分级基础上, 探讨将生境及群落演替特征等因子纳入模型, 构建混合效应模型, 使模型具有更好的普适性和预估精度。

ORCID

张剑坛 <https://orcid.org/0000-0001-7933-1870>
李艳朋 <https://orcid.org/0000-0002-2977-6289>
张入匀 <https://orcid.org/0000-0002-4173-2668>
倪云龙 <https://orcid.org/0000-0002-1857-661X>
练琚愉 <https://orcid.org/0000-0001-6777-7170>
叶万辉 <https://orcid.org/0000-0003-2900-5828>

参考文献

- Adamec Z, Drápela K (2016) Generalized additive models as an alternative approach to the modelling of the tree height-diameter relationship. *Journal of Forest Science*, 61, 235–243.
- Aiba SI, Kohyama T (1996) Tree species stratification in relation to allometry and demography in a warm-temperate rain forest. *Journal of Ecology*, 84, 207–218.
- Bowman DMJS, Brien RJW, Gloor E, Phillips OL, Prior LD (2013) Detecting trends in tree growth: Not so simple. *Trends in Plant Science*, 18, 11–17.
- Cao M, Mo H, Ye JQ (2019) The height growth model of *Camellia oleifera* based on site type. *Forestry and Environmental Science*, 35(3), 56–62. (in Chinese with English abstract) [曹美, 莫辉, 叶嘉齐 (2019) 基于立地类型的油茶树高生长模型. *林业与环境科学*, 35(3), 56–62.]
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366.
- Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, 16, 2356–2367.
- Chen FP, Xu WQ, Yang X, Lu HF (2012) A review of *Eucalyptus* plantation growth model. *World Forestry Research*, 25(4), 34–38. (in Chinese with English abstract)

[陈飞鹏, 许文强, 杨雪, 陆宏芳 (2012) 桉树人工林生长模型研究进展. 世界林业研究, 25(4), 34–38.]

- Condit R (1998) Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and A Comparison with Other Plots. Springer, Berlin.
- Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany, 51, 335–380.
- Dolnicar S, Grabler K, Mazanec JA (1999) A tale of three cities: Perceptual charting for analyzing destination images. In: Consumer Psychology of Tourism, Hospitality and Leisure (eds Sakai MY, Woodside AG, Crouch GI, Mazanec JA, Oppermann M), pp. 39–62. CAB International, New York.
- Duan AG, Zhang JG (2013) Research progress of theoretical growth equations. East China Forest Management, 27(1), 1–7. (in Chinese with English abstract) [段爱国, 张建国 (2013) 理论生长方程研究概述. 华东森林经理, 27(1), 1–7.]
- Feldpausch TR, Banin L, Phillips OL, Baker TR, Lewis SL, Quesada CA, Affum-Baffoe K, Arets EJMM, Berry NJ, Bird M, Brondizio ES, de Camargo P, Chave J, Djabbletey G, Domingues TF, Drescher M, Fearnside PM, França MB, Fyllas NM, Lopez-Gonzalez G, Hladik A, Higuchi N, Hunter MO, Iida Y, Salim KA, Kassim AR, Keller M, Kemp J, King DA, Lovett JC, Marimon BS, Marimon-Junior BH, Lenza E, Marshall AR, Metcalfe DJ, Mitchard ETA, Moran EF, Nelson BW, Nilus R, Nogueira EM, Palace M, Patiño S, Peh KSH, Raventos MT, Reitsma JM, Saiz G, Schrodte F, Sonké B, Taedoumg HE, Tan S, White L, Wöll H, Lloyd J (2011) Height-diameter allometry of tropical forest trees. Biogeosciences, 8, 1081–1106.
- Fisher JB, Goldstein G, Jones TJ, Cordell S (2007) Wood vessel diameter is related to elevation and genotype in the Hawaiian tree *Metrosideros polymorpha* (Myrtaceae). American Journal of Botany, 94, 709–715.
- Garrard GE, McCarthy MA, Williams NSG, Bekessy SA, Wintle BA (2013) A general model of detectability using species traits. Methods in Ecology and Evolution, 4, 45–52.
- Gui XJ, Lian JY, Zhang RY, Li YP, Shen H, Ni YL, Ye WH (2019) Vertical structure and its biodiversity in a subtropical evergreen broad-leaved forest at Dinghushan in Guangdong Province, China. Biodiversity Science, 27, 619–629. (in Chinese with English abstract) [桂旭君, 练琚愉, 张入匀, 李艳朋, 沈浩, 倪云龙, 叶万辉 (2019) 鼎湖山南亚热带常绿阔叶林群落垂直结构及其物种多样性特征. 生物多样性, 27, 619–629.]
- He D (2016) Plant Functional Trait Variation and Community Assembly: A Case Study in a Subtropical Evergreen Forest. PhD dissertation, Sun Yat-Sen University, Guangzhou. (in Chinese with English abstract) [何东 (2016) 植物功能性状变异与群落构建: 以黑石顶常绿阔叶林为例. 博士学位论文, 中山大学, 广州.]
- He P, He DB, Chen ZX, Xiao QH (2020) Compatibility model of stand volume and above-ground biomass based on tree height and crown characteristics. Journal of Central South University of Forestry & Technology, 40(4), 28–33. (in Chinese with English abstract) [贺鹏, 贺东北, 陈振雄, 肖前辉 (2020) 基于树高和树冠因子的立木材积与地上生物量相容模型研究. 中南林业科技大学学报, 40(4), 28–33.]
- He PC, Ye Q (2019) Plant functional traits: From individual plant to global scale. Journal of Tropical and Subtropical Botany, 27, 523–533. (in Chinese with English abstract) [贺鹏程, 叶清 (2019) 基于植物功能性状的生态学研究进展: 从个体水平到全球尺度. 热带亚热带植物学报, 27, 523–533.]
- Houghton RA (2005) Aboveground forest biomass and the global carbon balance. Global Change Biology, 11, 945–958.
- Huang ZL, Kong GH, Wei P (1998) Plant species diversity dynamics in Dinghu Mountain forests. Chinese Biodiversity, 6, 116–121. (in Chinese with English abstract) [黄忠良, 孔国辉, 魏平 (1998) 鼎湖山植物物种多样性动态. 生物多样性, 6, 116–121.]
- King DA (1996) Allometry and life history of tropical trees. Journal of Tropical Ecology, 12, 25–44.
- Lei XD, Li XF (2003) A review on growth models of mixed forests. Journal of Beijing Forestry University, 25(3), 105–110. (in Chinese with English abstract) [雷相东, 李希菲 (2003) 混交林生长模型研究进展. 北京林业大学学报, 25(3), 105–110.]
- Li HK, Fa L (2011) Height-diameter model for major tree species in China using the classified height method. Scientia Silvae Sinicae, 47(10), 83–90. (in Chinese with English abstract) [李海奎, 法蕾 (2011) 基于分级的全国主要树种树高-胸径曲线模型. 林业科学, 47(10), 83–90.]
- Li J (2019) Classification based height-diameter model for *Castanopsis fargesii* in Jiangle, Fujian. Journal of Northwest A & F University (Natural Science Edition), 47(11), 34–42. (in Chinese with English abstract) [李杰 (2019) 基于分级的福建将乐地区栲树树高曲线模型研究. 西北农林科技大学学报(自然科学版), 47(11), 34–42.]
- Li MH, Xiao SZ (2019) Diameter-height models of main tree species in Shanghai. Acta Agriculturae Universitatis Jiangxiensis, 41, 501–511. (in Chinese with English abstract) [李明华, 肖舜祯 (2019) 上海市主要造林树种的胸径-树高模型研究. 江西农业大学学报, 41, 501–511.]
- Liu FL, Lü Y, Zeng SQ (2011) Status and prospects of forest measurement instruments. Forest Resources Management, (1), 96–99. (in Chinese with English abstract) [刘发林, 吕勇, 曾思齐 (2011) 森林测树仪器使用现状与研究展望. 林业资源管理, (1), 96–99.]

- Liu RT, Bi RC, Zhao HL (2008) Mathematical simulations of the relationship between height and DBH of *Juglans mandshurica* population in Taiyue forest region. *Journal of Biomathematics*, 23, 416–422.
- Liu WP, Cao HL, Liu W, Lian JY, Wu LF (2011) Study on diversity of monsoon evergreen broad-leaved forest in different kinds of habitat in Dinghushan. *Journal of Anhui Agricultural Sciences*, 39, 16159–16163. (in Chinese with English abstract) [刘文平, 曹洪麟, 刘卫, 练琚愉, 吴林芳 (2011) 鼎湖山季风常绿阔叶林不同生境物种多样性研究. *安徽农业科学*, 39, 16159–16163.]
- Liu XJ, Ma KP (2015) Plant functional traits—Concepts, applications and future directions. *Scientia Sinica Vitae*, 45, 325–339. (in Chinese with English abstract) [刘晓娟, 马克平 (2015) 植物功能性状研究进展. *中国科学: 生命科学*, 45, 325–339.]
- Maharjan SK, Poorter L, Holmgren M, Bongers F, Wieringa JJ, Hawthorne WD (2011) Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica*, 43, 552–561.
- Martínez-Cabrera HI, Schenk HJ, Cevallos-Ferriz SRS, Jones CS (2011) Integration of vessel traits, wood density, and height in angiosperm shrubs and trees. *American Journal of Botany*, 98, 915–922.
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.
- Mehtätalo L (2004) A longitudinal height-diameter model for Norway spruce in Finland. *Canadian Journal of Forest Research*, 34, 131–140.
- Meng SX, Huang S, Lieffers VJ, Nunifu T, Yang YQ (2008) Wind speed and crown class influence the height–diameter relationship of lodgepole pine: Nonlinear mixed effects modeling. *Forest Ecology and Management*, 256, 570–577.
- Ng'Andwe P, Chungu D, Yambayamba AM, Chilambwe A (2019) Modeling the height-diameter relationship of planted *Pinus kesiya* in Zambia. *Forest Ecology and Management*, 447, 1–11.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) *vegan: Community Ecology Package*. <https://CRAN.R-project.org/package=vegan> (accessed on 2020-10-27)
- Poorter L, McDonald I, Alarcón A, Fichtler E, Licona JC, Peña-Claros M, Sterck F, Villegas Z, Sass-Klaassen U (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, 185, 481–492.
- Poorter L, Rozendaal DMA, Bongers F, de Almeida-Cortez JS, Zambrano AMA, Álvarez FS, Luís Andrade JL, Arreola Villa LF, Balvanera P, Becknell JM, Bentos TV, Bhaskar R, Boukili V, Brancalion PHS, Broadbent EN, César RG, Chave J, Chazdon RL, Dalla Colletta G, Craven D, de Jong BHJ, Denslow JS, Dent DH, DeWalt SJ, Díaz García ED, Manuel Dupuy J, Durán SM, Espírito Santo MM, Fandiño MC, Fernandes GW, Finegan B, Moser VG, Hall JS, Hernández-Stefanoni JL, Jakovac CC, Junqueira AB, Kennard D, Lebrija-Trejos E, Letcher SG, Lohbeck M, Lopez OR, Marín-Spiotta E, Martínez-Ramos M, Martins SV, Massoca PES, Meave JA, Mesquite R, Mora F, Moreno VDS, Müller SC, Muñoz R, Muscarella R, de Oliveira Neto SN, Nunes YRF, Ochoa-Gaona S, Paz H, Peña-Claros M, Piotto D, Ruíz J, Sanaphre-Villanueva L, Sanchez-Azofeifa A, Schwartz NB, Steininger MK, Thomas WW, Toledo M, Uriarte M, Utrera LP, van Breugel M, van der Sande MT, van der Wal H, Veloso MDM, Vester HFM, Vieira ICG, Villa PM, Williamson GB, Wright SJ, Zanini KJ, Zimmerman JK, Westoby M (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution*, 3, 928–934.
- Poorter L, Wright SJ, Paz H, Ackerly DD, Condit R, Ibarra-Manríques G, Harms KE, Licona JC, Martínez-Ramos M, Mazer SJ, Muller-Landau HC, Peña-Claros M, Webb CO, Wright IJ (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, 89, 1908–1920.
- Richards FJ (1959) A flexible growth function for empirical use. *Journal of Experimental Botany*, 10, 290–301.
- Sharma M, Parton J (2007) Height-diameter equations for boreal tree species in Ontario using a mixed-effects modeling approach. *Forest Ecology and Management*, 249, 187–198.
- Shi YL, Wang L, Xia Z (2014) Current progress in the research of allometric scaling and resource limitations models. *Science Technology and Engineering*, 14(19), 159–166. (in Chinese with English abstract) [石玉立, 王林, 夏振 (2014) 异速生长和资源限制生物量模型研究的最新进展. *科学技术与工程*, 14(19), 159–166.]
- Swenson NG, Enquist BJ (2008) The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. *American Journal of Botany*, 95, 516–519.
- Tang CW, Chen YP, Tao L, Xiao DN (2010) Overview of forest biomass and models of estimating NPP. *Arid Zone Research*, 27, 939–946. (in Chinese with English abstract) [汤萃文, 陈银萍, 陶玲, 肖笃宁 (2010) 森林生物量和净生长量测算方法综述. *干旱区研究*, 27, 939–946.]
- van Gelder HA, Poorter L, Sterck FJ (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist*, 171, 367–378.
- van Leeuwen M, Nieuwenhuis M (2010) Retrieval of forest structural parameters using LiDAR remote sensing. *European Journal of Forest Research*, 129, 749–770.
- Vibrans AC, Moser P, Oliveira LZ, de Maçaneiro JP (2015)

- Height-diameter models for three subtropical forest types in southern Brazil. *Ciência e Agrotecnologia*, 39, 205–215.
- Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion: New questions from old patterns. *Oikos*, 74, 159–164.
- Weiss L, Pfestorf H, May F, Körner K, Boch S, Fischer M, Müller J, Prati D, Socher SA, Jeltsch F (2014) Grazing response patterns indicate isolation of semi-natural European grasslands. *Oikos*, 123, 599–612.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33, 125–159.
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Díaz S, Engelbrecht BMJ, Harms KE, Hubbell SP, Marks CO, Ruiz-Jaen MC, Salvador CM, Zanne AE (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, 91, 3664–3674.
- Xu Y, Chen CH, Jiang ZF, Pan HB, Long ML, Cui TQ (2008) Study on correlated models between the diameter at breast height and the tree height of natural red pine. *Forest Inventory and Planning*, 33(3), 56–58. (in Chinese with English abstract) [徐悦, 陈昌华, 蒋之富, 潘海波, 龙妙玲, 崔同琦 (2008) 天然赤松胸径与树高相关模型的研究. 林业调查规划, 33(3), 56–58.]
- Yang RC, Kozak A, Smith JHG (1978) The potential of Weibull-type functions as flexible growth curves. *Canadian Journal of Forest Research*, 8, 424–431.
- Ye WH, Cao HL, Huang ZL, Lian JY, Wang ZG, Li L, Wei SG, Wang ZM (2008) Community structure of a 20 hm² lower subtropical evergreen broadleaved forest plot in Dinghushan, China. *Journal of Plant Ecology* (Chinese Version), 32, 274–286. (in Chinese with English abstract) [叶万辉, 曹洪麟, 黄忠良, 练璐愉, 王志高, 李林, 魏识广, 王章明 (2008) 鼎湖山南亚热带常绿阔叶林20公顷样地群落特征研究. 植物生态学报, 32, 274–286.]
- Zakharova L, Meyer KM, Seifan M (2019) Trait-based modelling in ecology: A review of two decades of research. *Ecological Modelling*, 407, 108703.
- Zhang RY, Li YP, Ni YL, Gui XJ, Lian JY, Ye WH (2019) Intraspecific variation of leaf functional traits along the vertical layer in a subtropical evergreen broad-leaved forest of Dinghushan. *Biodiversity Science*, 27, 1279–1290. (in Chinese with English abstract) [张入匀, 李艳朋, 倪云龙, 桂旭君, 练璐愉, 叶万辉 (2019) 鼎湖山南亚热带常绿阔叶林叶功能性状沿群落垂直层次的种内变异. 生物多样性, 27, 1279–1290.]
- Zhang Y, Jia LM (2013) Study advances in growth models of *Quercus* spp. *World Forestry Research*, 26(2), 48–53. (in Chinese with English abstract) [张瑜, 贾黎明 (2013) 栎属树种生长模型研究进展. 世界林业研究, 26(2), 48–53.]
- Zhao JH, Kang XG, Zhang HD, Liu Y (2009) Relationships between coefficient of variation of diameter and height and competition index of main coniferous trees in Changbai Mountains. *Chinese Journal of Applied Ecology*, 20, 1832–1837. (in Chinese with English abstract) [赵俊卉, 亢新刚, 张慧东, 刘燕 (2009) 长白山主要针叶树种胸径和树高变异系数与竞争因子的关系. 应用生态学报, 20, 1832–1837.]
- Zhu YH, Weng GQ (2000) Introduction to tropical rainforest growth and harvest estimation. *Forest Resources Management*, (6), 14–17. (in Chinese) [朱永红, 翁国庆 (2000) 热带雨林生长与收获预估简介. 林业资源管理, (6), 14–17.]
- Zhuang CY, Huang QL, Ma ZB, Zheng QR, Wang H (2017) Study on height-diameter relationship in each stratum of typical natural broadleaved forests in mid-subtropics. *Forest Research*, 30, 479–485. (in Chinese with English abstract) [庄崇洋, 黄清麟, 马志波, 郑群瑞, 王宏 (2017) 典型中亚热带天然阔叶林各林层树高胸径关系研究. 林业科学研究, 30, 479–485.]

(责任编辑: 臧润国 责任编辑: 黄祥忠)