



Height – Diameter allometry in South Africa’s indigenous high forests: Assessing generic models performance and function forms

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ABSTRACT

Height-diameter equations are essential to understand forest dynamics and estimate forest biomass and carbon stocks. Most existing large scale height-diameter equations in Africa are based on data from rain forests, and their application to species from southern and eastern parts of Africa can result in large estimation error. Using a dataset of 1130 trees measured for their diameter and height from four forest sites with varying environmental characteristics across South Africa, we (1) evaluated the deviations in height estimated from existing generalized height-diameter equations; (2) compared the predictive ability of eight function forms applied to develop height-diameter models; (3) tested for sites and species effects on tree height-diameter allometries; and (4) developed country scale and site-specific height-diameter models in South Africa natural forests. The existing continental height-diameter equations significantly overestimated tree height in South Africa. The deviations associated with these equations, though varied with sites, remained substantially large and increased with increasing tree diameter. The power function outperformed the other theoretical functions forms and proved to be the most suitable for height-diameter allometry at country scale. As expected, forest sites and species respectively had significant effects on height-diameter allometry, suggesting further need for site and functional groups-specific height-diameter relationships. The effect of site was shown by higher scaling allometric exponents at warmer and wetter sites. On the other hand, species potentially occupying same canopy niche seem to have similar allometric relationships. Our results reveal that tree height in South Africa is more accurately predicted using locally developed models. Site-specific and country scale allometric models were thus documented for future use.

1. Introduction

Due to the complex nature of tropical evergreen or closed-canopy forest ecosystems, height measurements are often influenced by visual obstructions and observer error (Larjavaara and Muller-landau, 2013). This often limits the accuracy of height measurements in those forests even if modern laser hypsometers or LiDAR are used. As a result, forest ecologists measure tree diameter in most forest inventories in tropical forests at national or regional scale, which they rely on as a main input variable. This requires that tree height be estimated from tree diameter, and be accounted for in growth and yield models, and analyses of stand dynamics and ecosystem functioning, including biomass and carbon estimation.

Estimating tree height from trunk diameter (Curtis, 1967; Winsor, 1932) has important implications for forest management, through understanding of tree architecture and forest stand dynamic (Aiba and Kohyama, 1996; King, 1986; Pretzsch, 2010, 2009; Sokpon and Biaoou, 2002), calibration of remote sensing techniques (Colgan et al., 2013; Kunneke et al., 2014) and estimation of timber volume, forest biomass and carbon (Brown, 1997; Chave et al., 2014; Colgan et al., 2013; Garber et al., 2009; Kunneke et al., 2014; Mensah et al., 2016b). Forest growth simulators use tree height-diameter models to understand competition dynamics and predict stand growth in both commercial and natural forests (Gobakken et al., 2008; Pretzsch et al., 2002; Seifert et al. 2014, Vanclay, 1994). In addition, there is mounting evidence

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that accounting for tree height in allometric biomass models leads to significantly reduced biomass estimation error (Chave et al., 2014; Mensah et al., 2017, 2016c; Rutishauser et al., 2013). Similarly, the impact of height on volume estimation (Garber et al., 2009) showed the need to develop accurate height-diameter models. While this is critical for yield modelling and management decision-making, it also has implications for tree volume and carbon stock accounting. For instance, biased estimation of tree height may result in large uncertainties of carbon stock estimates, and may also jeopardize outputs from ecological and physiological processes based forest growth models. Furthermore, height – diameter equations are also relevant for mechanical stability and wood quality. Consideration of both diameter and height offer flexible perspectives for understanding species- or functional groups-specific differences in resources allocations and growth.

The study of height – diameter relationships has attracted many research questions exploring different modelling approaches for height prediction and testing sites or environmental conditions, resource availability, taxonomic and phylogenetic effects (Banin et al., 2012; Pretzsch, 2010; Pya and Schmidt, 2016; Schmidt et al., 2011; Sumida et al., 1997; Temesgen and Gadow, 2004; Temesgen et al., 2014; Tewari and Gadow, 1999; Zucchini et al., 2001). The specific function form in the height diameter model has also been of interest for the last fifty decades (Curtis, 1967; Pretzsch et al., 2013). Substantially, the relationship between height and diameter can be expressed using linear and non-linear models, which are based on mean regression, and can be regarded as the most commonly used. Simple linear models suggest that relative tree height should scale with a constant proportion of relative tree diameter, which is not realistic, because trees reach maximum/asymptotic heights. On the other hand, non-linear functions assume that growth in tree height is a multiplicative process through exponential scaling with diameter growth. Accordingly, several theoretical distributions were proposed to improve height–diameter models. For instance, bivariate height - diameter distributions, including the S_{BB} distribution, and mixture of two bivariate normal distributions (Zucchini et al., 2001) were used to model height - diameter relationship (Tewari and Gadow, 1999). Similarly, the two and three-parameter exponential and Weibull distributions, as well as many others such as the power law, Gompertz and logistic distributions, and the Chapman–Richards function were tested (Curtis, 1967; Fang and Bailey, 1998; Huang et al., 1992; Sánchez et al., 2003; van Laar and Akça, 2007; Zeide, 1993). While some authors found the power law model (or its linearized form, log-log model) useful to normalize the data and suitable to use (Mensah et al., 2017; Motallebi and Kangur, 2016), fitting the three-parameter exponential and Weibull functions also reduced errors in height estimations (Kearsley et al., 2017; Ledo et al., 2016). Furthermore, spatially explicit mixed modelling approaches were also proposed, based on stand quadratic mean diameter and spatial information (plot geographical coordinates), allowing for high accuracy prediction from a minimum set of predictor variables (Schmidt et al., 2011).

Both generalized and generic models were developed to estimate height-diameter equations (Banin et al., 2012; Chave et al., 2014; Feldpausch et al., 2011; Temesgen and Gadow, 2004). Generic models are simple general equations that lack species-specific coefficients and describe the relationship between height and diameter from global data sets across continents. Some account for environmental effects, but a few also take into account stand structure effects (Feldpausch et al., 2011). These are regional, continental and pan-tropical height – diameter models applied for tree height estimation in regions where height are difficult to measure (Chave et al., 2014; Lewis et al., 2013). Generalized models, on the other hand, are extended forms that incorporate in addition to tree diameter, stand-level variables such as stem density, basal area, quadratic mean diameter (Li et al., 2015; Temesgen et al., 2014), and relative position of trees (Temesgen and Gadow, 2004), thus accounting for species competition, spatial and temporal ecological environments (Forrester et al., 2017). They may also incorporate the

between-habitat type variability of height – diameter relationship. The reason for developing generalized models is to avoid having to establish individual height–diameter relationships for each stand (Temesgen and Gadow, 2004).

The generality in these generic regional, continental and pan-tropical height – diameter models is ensured by the use of data spanning a variety of species and a wide range of environmental conditions; and hence they offer flexible perspectives for distinguishing between effects of environments, sites and different groups of species at large scale (Banin et al., 2012; Feldpausch et al., 2012, 2011). In addition these generic models offer a cost effective (less ground-based measurements and inventory efforts) and relatively accurate (for large scale application) approach of estimating tree heights. However these models can be very unsatisfactory for local or fine scale application (Kearsley et al., 2017, 2013), especially for species in environments other than those where these equations have been developed. This is likely because height – diameter relationships are inherently species-specific, and determined by plant growth through effects of environment, site quality and site productivity (Skovsgaard and Vanclay, 2013). Thus, the application of these models without consideration of site conditions and/or species information might result in large systematic errors (Kearsley et al., 2017, 2013).

Pantropical model parameters were originally developed without data from Africa (Chave et al., 2005), and the recent expansions of the spatial coverage in Africa to improve height estimates (Feldpausch et al., 2011, 2012; Banin et al., 2012; Chave et al., 2014) were mostly limited to the tropical central (Gabon and Congo Basin), eastern and western regions. Data from southern Africa is still largely under-represented in continental and regional scale analyses of these studies. Such a gap has been somewhat filled with a recent study that developed generic tree height-diameter using additional environmental stress variables (Chave et al., 2014). However, the validity of these continental height-diameter allometric equations has rarely been tested in southern Africa, while comparatively, more research effort has gone into that same aspect in central Africa and other parts of the world (Kearsley et al., 2013; Rutishauser et al., 2013).

Although indigenous high forests cover only about 0.1% of land area of South Africa, they have a high ecological and conservational value. The structure and functioning in these forests have been extensively studied to understand their stand dynamics (Gadow et al., 2016; Mensah et al., 2016b; Seifert et al., 2014; Seydack et al., 2012, 2011), yet there is still a research gap on height – diameter allometries in South African high forests. In particular, there is a need for validation of height – diameter models, using locally available data in southern Africa.

Therefore, the aim of this paper is to develop models for estimation of tree height in natural forest systems in South Africa. Because generic models developed for Africa in Feldpausch et al. (2012) and Banin et al. (2012) did not consider data from South Africa, we suspect that the application of these models to local situations will result in significant errors. Our study was therefore built on that hypothesis and addressed the following specific objectives: (1) evaluate the potential deviations in tree height estimation when using existing continental height – diameter models; (2) compare commonly used height-diameter function forms to determine the best model fit for South Africa based on local data; (3) use the best selected function to test for site and species effects on height-diameter relationship; and (4) use the best selected model to develop a country scale and site-specific height-diameter equations for natural forests.

2. Materials and methods

2.1. Study sites and height – diameter data

We used tree diameter and corresponding height data from four natural forest sites spanning a considerable range of environmental and

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