

# Patterns in height–diameter relationships for selected tree species and sites in eastern Texas

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**Abstract:** Relationships between tree height and diameter at breast height were described for 15 species across a range of sites in eastern Texas using a two-parameter equation. Maximum height varied significantly from site to site within a species, but the ratio of initial slope to maximum height was generally constant. Sites favoring tall trees of one species tended to favor tall trees of all species, especially among species found in the overstory. The greatest rates of height growth for a given diameter at breast height increment were found among some midstory and understory species.

**Résumé :** Les relations entre la hauteur et le diamètre à hauteur de poitrine ont été décrites chez 15 espèces d'arbres sur une variété de sites de l'est du Texas à l'aide d'une équation à deux paramètres. Pour une même espèce, la hauteur maximale varie significativement d'un site à l'autre. Par contre, le rapport de la pente initiale sur la hauteur maximale est généralement constant. Les sites qui supportent des arbres de grande taille chez une espèce ont tendance à supporter des arbres de grande taille chez toutes les espèces, particulièrement chez les espèces qui font partie de l'étage dominant. Les plus forts taux de croissance en hauteur pour un accroissement donné en diamètre à hauteur de poitrine ont été observés chez les espèces de l'étage intermédiaire et du sous-étage.

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## Introduction

Knowledge of the relationship between tree height and diameter is useful in a number of contexts, including stand biomass estimation (Huang et al. 1992), simulation of forest dynamics (Leemans and Prentice 1987; Canham et al. 1994), and theoretical considerations of tree growth (King 1990). The relationship is asymptotic; height is constrained to a maximum, and diameter is not (Prentice and Helmsaari 1991; Niklas 1995). Height may be constrained by limitations of mechanical support (McMahon 1973; Niklas 1989), increasing respirational load of stem tissues, or water stress in the upper shoots of tall trees (Friend 1993; Ryan and Yoder 1997). Because the relationship between height and diameter depends on site conditions, it would be useful to identify features of the relationship that are constant within a taxon across a range of sites.

The objectives of this study were (i) to find a parsimonious model of height–diameter relationships and (ii) to compare variation in model parameters among common tree species across three contrasting sites in eastern Texas. The data were analyzed using likelihood (Edwards 1992), allowing estimation, model comparison, and statistical testing to be carried out within a single framework.

## Methods

Three permanent 4-ha study sites have been established by P.A. Harcombe and colleagues in or near the Big Thicket National Preserve in southeastern Texas. Forest vegetation types mentioned be-

low follow the classification of Marks and Harcombe (1981). Each site has relatively uniform soil conditions, and together the sites span the range of moisture conditions in the area. Neches Bottom, a seasonally inundated river floodplain forest (Hall and Harcombe 1998), is dominated by widely spaced individuals of sweetgum (*Liquidambar styraciflua* L.), water oak (*Quercus nigra* L.), and red maple (*Acer rubrum* L.) with a midcanopy layer of American hornbeam (*Carpinus caroliniana* Walt.). Wier Woods is a lower slope hardwood–pine stand (Glizenstein et al. 1986) with mesic soil conditions located on a Nature Conservancy holding. It is dominated by loblolly pine (*Pinus taeda* L.), water oak, American beech (*Fagus grandifolia* Ehrh.), and white oak (*Quercus alba* L.) in closed canopy, with American holly (*Ilex opaca* Ait.) and flowering dogwood (*Cornus florida* L.) important in the midstory. Turkey Creek is an excessively well-drained upper slope pine–oak stand (Harcombe et al. 1993), with an open canopy of post oak (*Quercus stellata* Wangenh.), southern red oak (*Quercus falcata* Michx.), and black hickory (*Carya texana* Buckl.) below emergent longleaf pine (*Pinus palustris* Mill.), loblolly pine, and shortleaf pine (*Pinus echinata* Mill.). Trees were chosen from the three study sites randomly, with stratification on species and 4-cm diameter at breast height (DBH) size classes. Species were chosen on the basis of importance at the sites and sufficient numbers over a range of sizes to assure an accurate regression (Table 1).

Relationships between height and diameter were analyzed using likelihood (Edwards 1992) and the Akaike information criterion (AIC) (Akaike 1992). The definitions of likelihood and AIC, as well as a discussion of their use in statistical inference, are given in Hillborn and Mangel (1997). A few key points are mentioned here. The general approach of likelihood is the comparison of alternative models of a data set, rather than the determination of the probability that a particular model is “true” (Edwards 1992). In the absence of other selection criteria, the statistical model with the highest likelihood for a given data set is preferred. Models with different numbers of parameters may be compared by the AIC, which is a function of the likelihood and the number of free parameters; the model with the lowest AIC may be taken to be the most parsimonious model supported by the data.

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**Table 1.** Number of sample trees by species and site.

Species	Location		
	Neches Bottom	Wier Woods	Turkey Creek
<i>Acer rubrum</i> L.	51	49	—
<i>Carpinus caroliniana</i> Walt.	54	—	—
<i>Carya texana</i> Buckl.	—	—	57
<i>Cornus florida</i> L.	—	38	38
<i>Fagus grandifolia</i> Ehrh.	—	49	—
<i>Ilex opaca</i> Ait.	49	59	—
<i>Liquidambar styraciflua</i> L.	57	55	52
<i>Magnolia grandiflora</i> L.	—	59	—
<i>Nyssa sylvatica</i> Marsh.	50	58	—
<i>Pinus palustris</i> Mill.	—	—	55
<i>Pinus taeda</i> L.	—	54	60
<i>Quercus alba</i> L.	—	56	—
<i>Quercus falcata</i> Michx.	—	—	51
<i>Quercus nigra</i> L.	39	57	—
<i>Quercus stellata</i> Wangenh.	—	—	43
Total	300	534	356

Several equations relating height and diameter were compared in a preliminary analysis. Among the species and range of sizes considered, there was no evidence of an inflection point in the height–diameter relationship, so only two parameter equations (cf. Huang et al. 1992) were considered. The best equation (written to have a y intercept of 1.4 m) was

$$[1] \quad H = \hat{H} + \varepsilon = 1.4 + (H_{\max} - 1.4)[1 - \exp(-sD)] + \varepsilon$$

where  $H$  is height in metres,  $\hat{H}$  is the predicted height,  $D$  is the diameter (cm) at 1.4 m breast height,  $H_{\max}$  and  $s$  are parameters, and  $\varepsilon$  is a normally distributed error term of mean equal to zero.  $H_{\max}$  is the asymptotic maximum height (m), and  $s$  is the ratio of the initial slope ( $dH/dD$ ) at  $D = 0.0$ ) to  $H_{\max}$ . This was the best two-parameter equation in the study of Huang et al. (1992) and has also been used by several other authors (Farr et al. 1989; Leemans and Prentice 1989; Pacala et al. 1993). Scatterplots (cf. Fig. 1) showed that the error variance was correlated with diameter, so the standard deviation of the error ( $\varepsilon$ ) was made to be a function of diameter. The highest likelihoods for simple expressions of the error term were attained when the standard deviation was equal to  $b\hat{H}$ ;  $b$  may then be interpreted as the coefficient of variation of height when predicted from diameter. This situation is handled in likelihood estimation by basing the likelihood function directly on the equation for the error term. The equivalent conventional approach is weighted least-squares regression (cf. Huang et al. 1992).

Several alternative models were considered for species found in more than one of the study sites. All the models were based on eq. 1, but varied in which parameters were held constant from site to site. In the “species” model, all parameters ( $H_{\max}$ ,  $s$ , and  $b$ ) were a function of species only, and the likelihood estimate was based on all the data for that species regardless of site. In the “species  $\times$  site” model, all parameters ( $H_{\max}$ ,  $s$ , and  $b$ ) were a function of both species and site. In the “constant  $s$ ” model, only  $H_{\max}$  was a function of both species and site;  $s$  and  $b$  were a function of species only. In this model,  $s$  is held constant for a species; sites with a higher  $H_{\max}$  have a proportionately steeper initial slope. In the constant  $s_0$  model,  $H_{\max}$  was also a function of both species and site, but an alternative formulation of eq. 1 was used

$$[2] \quad \hat{H} = 1.4 + (H_{\max} - 1.4)[1 - \exp[-s_0 D / (H_{\max} - 1.4)]]$$

where  $s_0$  is  $dH/dD$  at  $D = 0$ . This model differs from the constant  $s$  model in that  $s_0$ , the initial slope of the equation ( $dH/dD$  at  $D = 0$ ) is held constant as  $H_{\max}$  varies by site instead of being proportional to  $H_{\max}$ . For the five overstory species found at two or more sites (*Acer rubrum*, *Liquidambar styraciflua*, *Pinus taeda*, *Nyssa sylvatica*, *Quercus nigra*), a “site factor” model was evaluated. The rationale behind this model is that maximum heights may vary proportionally from site to site as species are compared. The parameters  $s$  and  $b$  were held constant within a species as in the constant  $s$  model, and  $H_{\max}$  was given by

$$[3] \quad H_{\max}(\text{site}) = f(\text{site}) \times H_{\max}(\text{standard})$$

where  $f(\text{site})$  is the site factor (the same value for all species at a given site), and  $H_{\max}(\text{standard})$  is  $H_{\max}$  evaluated for the species at the standard site. For this analysis, Wier Woods (the one site containing all five species) was taken to be the standard site, so  $f(\text{Wier Woods}) = 1.0$  by definition. The site factor,  $f(\text{site})$ , then becomes one of the parameters to be estimated, along with  $s$ ,  $b$ , and  $H_{\max}(\text{standard})$  evaluated for each species.

Parameters were estimated either by direct search (Hillborn and Mangel 1997) or, where this was impractical, by the downhill simplex method (Press et al. 1989) using multiple starting points.

## Results

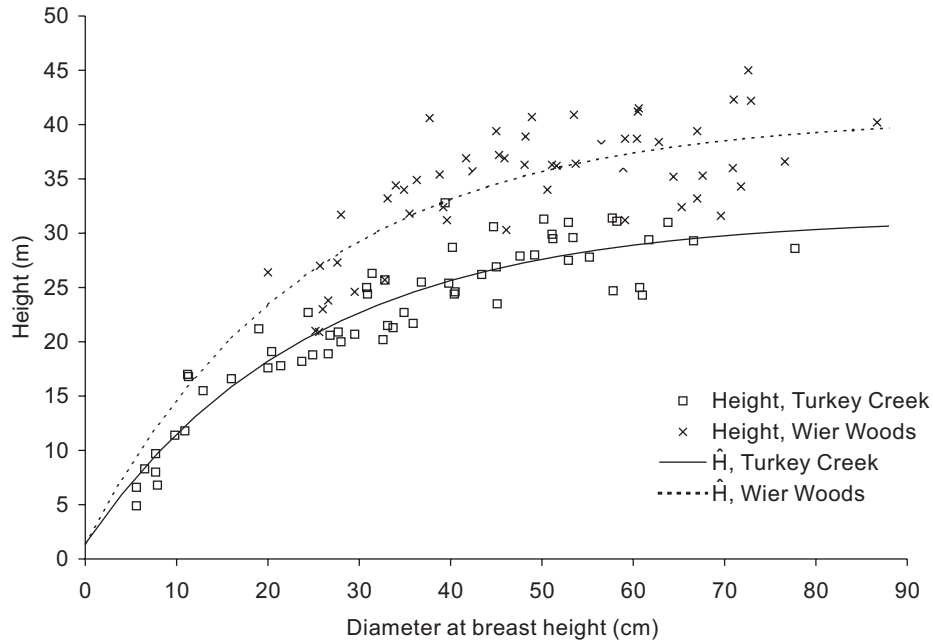
For species found on multiple sites, the highest likelihoods were attained for the species  $\times$  site model; this is expected because this model has the largest number of free parameters. For most species, the best multiple site model by the AIC was the constant  $s$  model; the exceptions were *Cornus florida*, for which the constant  $s_0$  model was the best, and *Nyssa sylvatica*, for which any model except the species  $\times$  site model performed well. When the five overstory species found at multiple sites were considered as a group, calculating an overall AIC for each model, the best model was constant  $s$ .

Parameters for the constant  $s$  model are summarized in Table 2. The highest values for  $H_{\max}$  were found at Wier Woods. Values of  $H_{\max}$  at Neches Bottom were slightly less than those at Wier Woods and values of  $H_{\max}$  at Turkey Creek, a dry upland site, were much lower. Values of  $s$ , the ratio of initial slope to  $H_{\max}$ , ranged from 0.024 to 0.114, corresponding to initial height growth increments ( $s_0$ ) of 0.8–1.3 m per centimetre of diameter increment for small trees. The largest values of  $s$  were for the midstory tree *Carpinus caroliniana* and the understory tree *Cornus florida*. Values of  $b$ , the coefficient of variation of height as predicted from diameter, ranged from 0.119 to 0.181 (12–18%), with the lowest value for *Pinus taeda*. Scatterplots of the data and the best equations give reasonable fits, with no obvious distortion of the relationship (Fig. 1).

## Discussion

Wier Woods and Neches Bottom, both well-watered sites with comparatively rich soil, support the tallest trees and the highest values for  $H_{\max}$  in this study; the Turkey Creek site, with excessively drained soils, has the shortest trees and the lowest values for  $H_{\max}$ . This pattern is consistent with either the water-stress or maintenance-respiration hypotheses of tree height limitation (Friend 1993; Ryan and Yoder 1997). The pattern of  $H_{\max}$  values among the study sites is difficult to reconcile with the hypothesis of mechanical support

**Fig. 1.** Height vs. diameter for *Pinus taeda* at Wier Woods and Turkey Creek. Fitted lines are for the constant  $s$  model; parameters are given in Table 2.



**Table 2.** Parameters for the constant  $s$  model for all species and sites.

Species	$H_{max}$			$s$	$b$
	Neches Bottom	Wier Woods	Turkey Creek		
<i>Acer rubrum</i>	27.6	33.8	—	0.043	0.165
<i>Carpinus caroliniana</i>	18.5	—	—	0.075	0.156
<i>Carya texana</i>	—	—	36.5	0.024	0.161
<i>Cornus florida</i>	—	14.6	12.9	0.114	0.150
<i>Fagus grandifolia</i>	—	39.0	—	0.029	0.175
<i>Ilex opaca</i>	21.9	25.1	—	0.043	0.181
<i>Liquidambar styraciflua</i>	37.0	39.0	32.9	0.035	0.136
<i>Magnolia grandiflora</i>	—	30.0	—	0.035	0.142
<i>Nyssa sylvatica</i>	35.1	37.2	—	0.031	0.152
<i>Pinus palustris</i>	—	—	31.9	0.039	0.132
<i>Pinus taeda</i>	—	40.8	31.5	0.041	0.119
<i>Quercus alba</i>	—	34.0	—	0.041	0.120
<i>Quercus falcata</i>	—	—	27.3	0.042	0.151
<i>Quercus nigra</i>	34.2	36.8	—	0.035	0.147
<i>Quercus stellata</i>	—	—	24.4	0.038	0.173

limitations. In the first instance, the site with the most obvious mechanical constraints on height (Neches Bottom, with shallow rooting due to seasonal soil anoxia) does not have the shortest trees. In the second instance, the tallest trees measured in the whole study were canopy emergent *Pinus taeda* at Wier Woods; these trees are not sheltered by the surrounding canopy, and almost all of them survived a hurricane passing directly over the site in 1986.

Increasing height can lead to increased water stress both through the increased water potential required to raise water against gravity and the increased resistance of long transport through the xylem (Friend 1993; Ryan and Yoder 1997). Low water potentials in turn can either directly limit leader

elongation during growth or inhibit photosynthesis through stomatal closure. Water stress is probably common in the area, which is close to the southwestern range limits of most of the trees considered in this study. The correlation of  $H_{max}$  with site water availability is consistent with the operation of the water stress constraint.

Maintenance respiration increases with height because of the increased length of stem needed for support of a given leaf area (Friend 1993; Ryan and Yoder 1997). Lower availability of soil resources, by forcing higher allocation to construction and maintenance of root tissue, could also limit height by increasing the overall respiration load; this could account for the site-to-site differences in  $H_{max}$ . Maintenance

respiration is possibly the preferred explanation for constraints on  $H_{\max}$  in midstory and understory species (*Ilex opaca*, *Cornus florida*, and *Carpinus caroliniana*);  $H_{\max}$  is unlikely to be limited by water stress in these species unless xylem conductivity to water is much lower than in overstory species.

While  $H_{\max}$  is related to ultimate constraints on height, the  $s_o$  parameter ( $dH/dD$  at  $D = 0$ ) is related to relative allocation between stem-diameter growth and leader elongation. A high value of  $s_o$  is associated with a slender growth form until the tree approaches  $H_{\max}$ . The large  $s_o$  values for *Cornus florida* and *Carpinus caroliniana* are consistent with the fact that these species can generally rely on the shelter of other trees and so do not risk the mechanical instability associated with a slender growth form in a canopy tree. A constant value of  $s$  as  $H_{\max}$  varies from site to site implies that the initial slope of the height-diameter function ( $s_o$ ) is approximately proportional to  $H_{\max}$ ; trees growing on sites supporting taller trees have a more slender growth form as saplings. This may reflect a correlation between rapidity of leader growth (or frequency of leader die-back) and constraints on maximum height. Leader die-back is common during droughts in this area (M.R. Fulton and P.A. Harcombe, personal observations), and the driest sites are also those that support the lowest values of  $H_{\max}$ . Alternatively, the pattern may be associated with optimal foraging for resources. Trees growing on better soils are expected to allocate more resources to height growth (Tilman 1988), resulting in a slender growth form, because they are more likely to be limited by light competition under those conditions.

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