

Height-diameter Relationships in Longleaf Pine and Four Swamp Tree Species

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Abstract

The scaling relationship between height and diameter is important for understanding the dynamic patterns of tree growth and estimating the accrual of tree biomass. Metabolic ecology predicts that tree growth follows a universal scaling invariant relative to the height-diameter relationship (i.e., no variation based on taxonomy or resource availability). Comparing field data for different tree species across a range of site conditions should be an informative test of that prediction. Our results indicate that the scaling exponents of height and diameter for longleaf pine (*Pinus palustris* Mill.) vary at the four locations across its natural range. As for swamp trees, the scaling exponents for red maple (*Acer rubrum* L.) and river birch (*Betula nigra* L.) were consistent with that predicted by metabolic ecology; however, those for water tupelo (*Nyssa aquatica* L.) and bald cypress (*Taxodium distichum* (L.) Rich) were not. Our study confirms that high plasticity and variation in allometric scaling of the tree height and diameter relationship may very well be the rule, rather than the exception.

Keywords: allometric scaling, precipitation, scaling invariant, wetland

1. Introduction

The tree height and diameter relationship has been a subject of theoretical and empirical research (Henry & Aarssen, 1999; Ducey, 2012; Forrester, Benneter, Bouriaud, & Bauhus, 2017). Tree scaling of the height-diameter relationship is very important in forestry and ecological science, because it is used to describe tree or stand growth, productivity and yield (Parresol, 1992). If the scaling algorithm is erroneous, it will result in inaccurate estimates (Kearsley et al., 2013). In forestry research, much effort has been invested in developing algorithms for scaling this relationship for various tree species and under different conditions (e.g., Zhang, Ma, & Guo, 2009). Recent developments in metabolic ecology propose that all tree species share an optimal design for the vascular system, which is related to plant physiology, biomass partitioning and population and community dynamics (Enquist, West, Charnov, & Brown, 1999; West, Brown, & Enquist, 1999). One of the important predictions and hypotheses from metabolic ecology concerning tree growth is the claimed universal scaling invariant in the tree height-diameter relationship $H \propto D^{2/3}$ (i.e., no variation based on taxonomy or resource availability).

Yet, other researchers found no evidence in their empirical studies for the universal scaling invariant (e.g., Chen & Li, 2003; Li, Han, & Wu, 2005; Ducey, 2012; Forrester et al., 2017). Tree allometry significantly differs across the United States largely because of climate (Hulshof, Swenson, & Weiser, 2015). It is possible that tree species living under frequently stressed conditions may have different scaling exponents, resulting from environmental stress or resource limitation. Trees growing in heath and peat-swamp forests exhibit differentiation in allometric relationships among their seedlings (Nishimura & Suzuki, 2001). Thus, trees having different scaling exponents are expected to exist in environments with frequent stress. This type of environment may exist for trees near the edge of their natural range or for some swamp trees with small habitat areas and frequent change in water level.

Although historically quite extensive (37 million ha) and then greatly reduced by exploitive logging (to 1.3 million ha), longleaf pine (*Pinus palustris* Mill.) forests are today making a steady recovery primarily on public lands, with somewhat slower gains on private lands. While the restoration goal is to eventually achieve an occupancy of 3.2 million ha, longleaf pine is still narrowly distributed across its native range in the southeastern United States (Fig. 1). Comparing the height-diameter relationships for trees growing in the central portion and

near the northern and southern edges of this large natural range should prove insightful, as will a similar analysis for water tupelo (*Nyssa aquatic* L.), bald cypress (*Taxodium distichum* (L.) Rich), red maple (*Acer rubrum* L.) and river birch (*Betula nigra* L.) naturally growing in the small swamps and wetlands of northern Alabama. Using tree height and diameter data from numerous sites, the objective of this study is to determine whether there are deviations in the scaling exponent (2/3) for forest trees growing in this environment, specifically (i) whether longleaf pine have a consistent scaling exponent for trees across their native range or vary between the central and boundary areas and (ii) whether the four swamp tree species have a consistent scaling exponent. Comparing these scaling relationships should be helpful in better understanding the complexity of tree growth and also provide specific information for continuing research in tree allometric scaling.

2. Materials and Methods

Tree species and study sites

Longleaf pine were measured at four sites representing the northernmost (Bankhead National Forest in northern Alabama), central (Tuskegee National Forest in central Alabama) and southernmost (Goethe State Forest and Blackwater River State Forest in northern Florida) portions of its native range (Table 1, Fig. 1). The Bankhead NF (34°15'N, 87°15'W), Tuskegee NF (32°50'N, 85°50'W) and Blackwater River SF (30°47'N, 86°44'W) are typical of mesic uplands with broad, moderately-inclined ridges and deep, well-drained sandy soils, low in organic matter and nutrients and low to moderate in water holding capacity (Weeks, Hyde, Roberts, Lewis, & Peters, 1980; USDA Forest Service, 1995). Longleaf pine at the Bankhead NF was a young forest plantation, about 15 -20 years in age. There were also some loblolly pine (*Pinus taeda* L.), vines (*Smilax* spp. L.) and shrubs in the stand, but limited broadleaved trees. At the Tuskegee NF and Blackwater River SF, overstories were dominated by longleaf pine, with lesser components of loblolly pine, shortleaf pine (*Pinus echinata* Mill.), slash pine (*Pinus elliotti* Englem.), southern red oak (*Quercus falcata* Michx.), bluejack oak (*Quercus incana* W. Bartram), post oak (*Quercus stellata* Wangenh.) and persimmon (*Diospyros virginiana* L.). The understory at the Blackwater River SF was rich in herbaceous plants, resulting from a history of frequent prescribed burning, while that at the Tuskegee NF contained somewhat greater shrub cover along with the grasses and forbs. These uplands were occupied by second-growth forest that naturally regenerated following cutover of the original forest in the early 1900s. Although most of the overstory pines ranged from 60 to 80 years in age, multiple waves of natural regeneration resulted in uneven-aged stand structures. The Goethe SF (29°13'N, 82°33'W) is characterized by a nearly-level flatwoods environment with deep, poorly-drained sands, low in organic matter and nutrients and low in water holding capacity (Slabaugh, Jones, Puckett, & Schuster, 1996). Overstory vegetation was dominated by longleaf pine, with lesser amounts of slash pine, oaks and sweetgum (*Liquidambar styraciflua* L.). The understory was dominated by saw-palmetto (*Serenoa repens* (W. Bartram) Small) and other shrubs, with little herbaceous cover. These flatwoods were also cutover in the early 20th century and naturally regenerated thereafter. Overstory pines here ranged from 48 to 74 years in age. Site index at these study sites is fairly consistent, ranging from 21 to 24 m at 50 years (Brockway & Outcalt, 2017).

Table 1. Mean height and diameter of surveyed tree species

Tree species	Location	Number of trees sampled	Mean diameter (cm) (\pm standard deviation)	Mean height (m) (\pm standard deviation)
Longleaf pine	Goethe State Forest, FL	359	30.78 (\pm 7.05)	22.13 (\pm 2.99)
	Blackwater River State Forest, FL	332	31.90 (\pm 9.93)	22.18 (\pm 5.45)
	Tuskegee National Forest, AL	40	29.22 (\pm 15.72)	22.10 (\pm 8.90)
	Bankhead National Forest, AL	200	10.36 (\pm 4.78)	6.92 (\pm 2.51)
Red maple	Wheeler Wildlife Refuge, AL	110	10.04 (\pm 4.66)	10.77 (\pm 4.13)
River birch	AAMU Agricultural Experimental Station Bradford Creek, AL	105	16.60 (\pm 7.38)	14.04 (\pm 4.99)
Water tupelo	Wheeler Wildlife Refuge, AL	107	34.90 (\pm 17.90)	26.68 (\pm 7.69)
Bald cypress	Wheeler Wildlife Refuge, AL	109	47.82 (\pm 17.00)	30.95 (\pm 6.96)

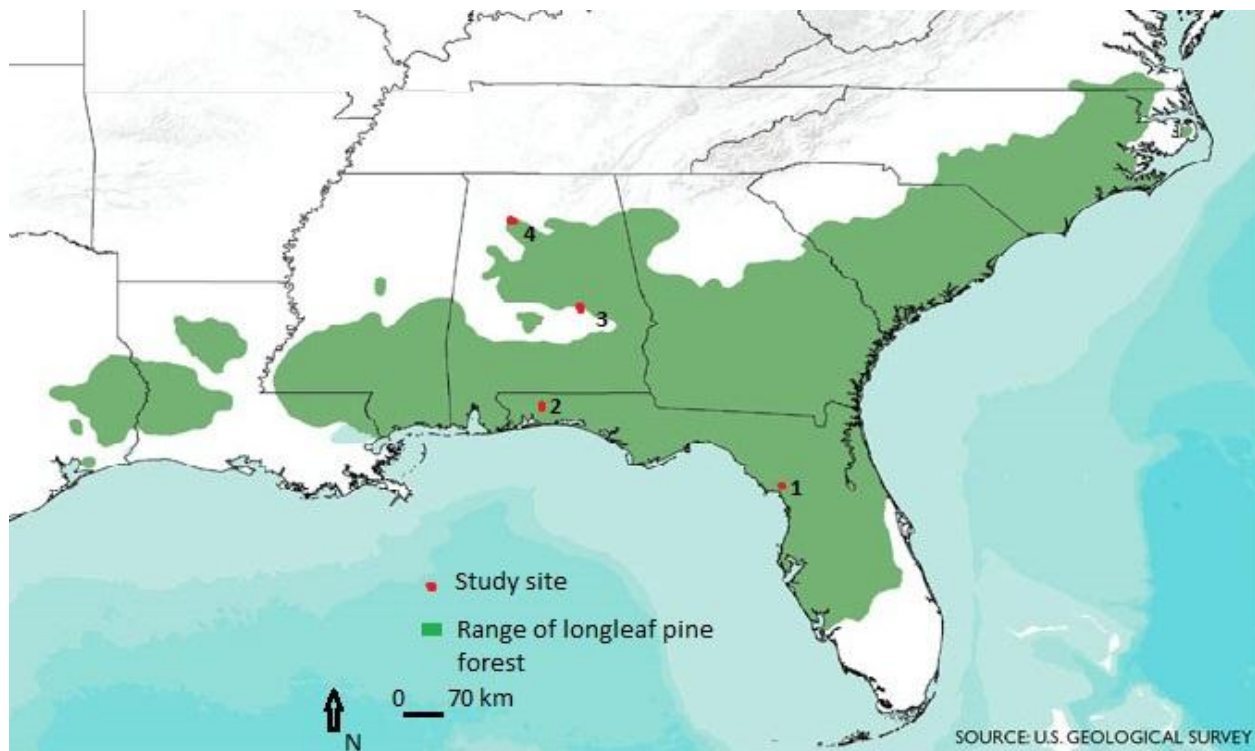


Figure 1. Natural range of longleaf pine and our study sites (1: Goethe State Forest; 2: Blackwater River State Forest; 3: Tuskegee National Forest; 4: Bankhead National Forest)

Water tupelo and red maple were measured along Beaver Dam Creek at the Wheeler Wildlife Refuge, near Madison, Alabama. Water tupelo dominated the forest and red maple co-occurred with it in a swamp environment. Bald cypress was measured near the visitor center at the Wheeler Wildlife Refuge, near Decatur, Alabama. Small seedlings of red maple were present on the floor of this bald cypress forest. River birch was measured along Bradford Creek and at the Alabama A & M University Agriculture Experimental Station in Madison, Alabama. These river birch were accompanied by southern red oak, tulip poplar (*Liriodendron tulipifera* L.), sycamore (*Platanus occidentalis* L.) and others. All these forest locations are in close proximity to one another (34°40'N, 87°00'W).

Measurements and analysis

Diameter at breast height (DBH 1.37 m above the ground) and total tree height were measured for randomly selected individuals in forests at the study sites. However, for water tupelo and bald cypress, DBH was measured at 46 cm above the flared buttress. Tree diameter was measured by using a d-tape, with accuracy to 1 mm. Tree height was measured by a Pulse Rangerfinder Hypsometer (Laser Technology Inc., Centennial, Colorado), with accuracy to 1 cm.

The exponent of $H \propto D^x$ is estimated through \log_{10} - \log_{10} transformation. Figures illustrating \log_{10} of H and \log_{10} of D relationships were produced from our study data. To be consistent with early literature concerning the estimation of allometric relationships, a reduced major axis (RMA) of regression analysis Model Type II was used to determine scaling exponents (α RMA). The difference between estimated scaling exponents at each site and the theoretical value (2/3) was then statistically tested (Sokal & Rohlf, 1995). Significant differences were discerned at the $p = 0.05$ level.

3. Results and Discussion

Deviations in the scaling relationship between tree height and diameter existed for longleaf pine trees at the Goethe State Forest (0.4229) and Blackwater River State Forest (0.713) (Fig. 2), but scaling exponents at the Tuskegee National Forest (0.6866) and Bankhead National Forest (0.6442) were not different from 2/3. Overall, the scaling exponent for longleaf pine at the four sites across its native range was 0.8146, which was significantly different from 2/3.

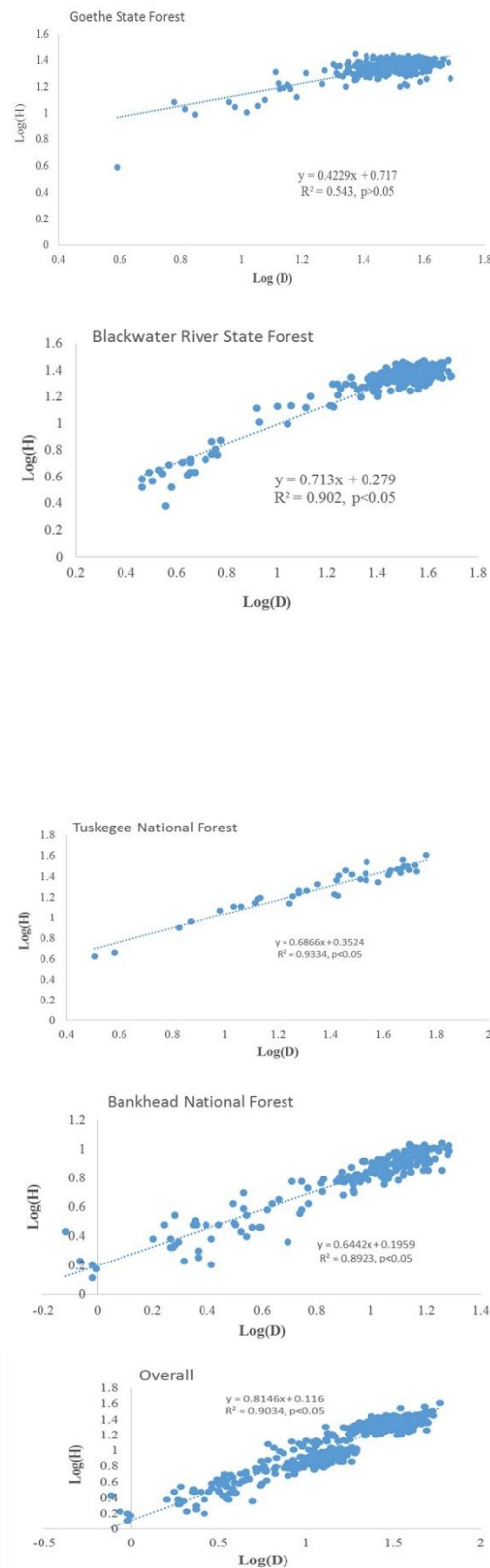


Figure 2. Allometric scaling of height and diameter for longleaf pine at different locations across its native range. Scaling exponents of height and diameter for red maple (0.6556) and river birch (0.6489) were not different from 2/3 (Fig. 3). But, the scaling exponents for water tupelo (0.3117) and bald cypress (0.5252) were significantly different from 2/3. The overall scaling exponent of height and diameter for all trees of these four species was 0.4396, this value was significantly low than 2/3.

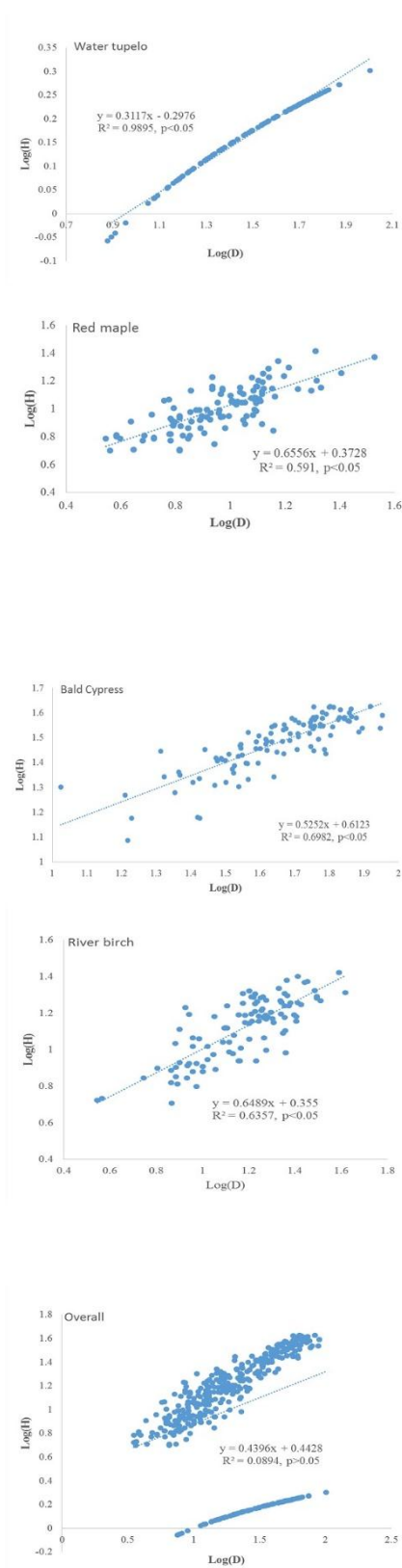


Figure 3. Allometric scaling of height and diameter for water tupelo, red maple, bald cypress and river birch in northern Alabama

We found spatial variations in the scaling exponents for longleaf pine trees at the four study sites across its natural range. The overall scaling exponent also deviated from the theoretical prediction of 2/3. Based on the

assumption that larger geographic distances might result in the greatest disparity, scaling exponents for longleaf pine trees at the Goethe State Forest (southern portion of range) and Bankhead National Forest (northern edge of range) might be expected to deviate most from $2/3$. However, scaling exponent deviations were observed instead at the Blackwater River State Forest and Goethe State Forest, both in the southern portion of the native range. Since annual precipitation is lowest at the Goethe State Forest (~ 127 cm) and highest at the Blackwater River State Forest (~ 158 cm), the scaling exponent may be related to annual precipitation. Among these four longleaf pine sites, there was a positive correlation between annual precipitation and scaling exponents (Fig. 4). Hulshof et al. (2015) suggested that tree height is negatively influenced by decreasing mean precipitation. Thus, height-diameter scaling for longleaf pine may vary across its natural range because of differing amounts of precipitation (and evapotranspiration) across this extensive geographic area.

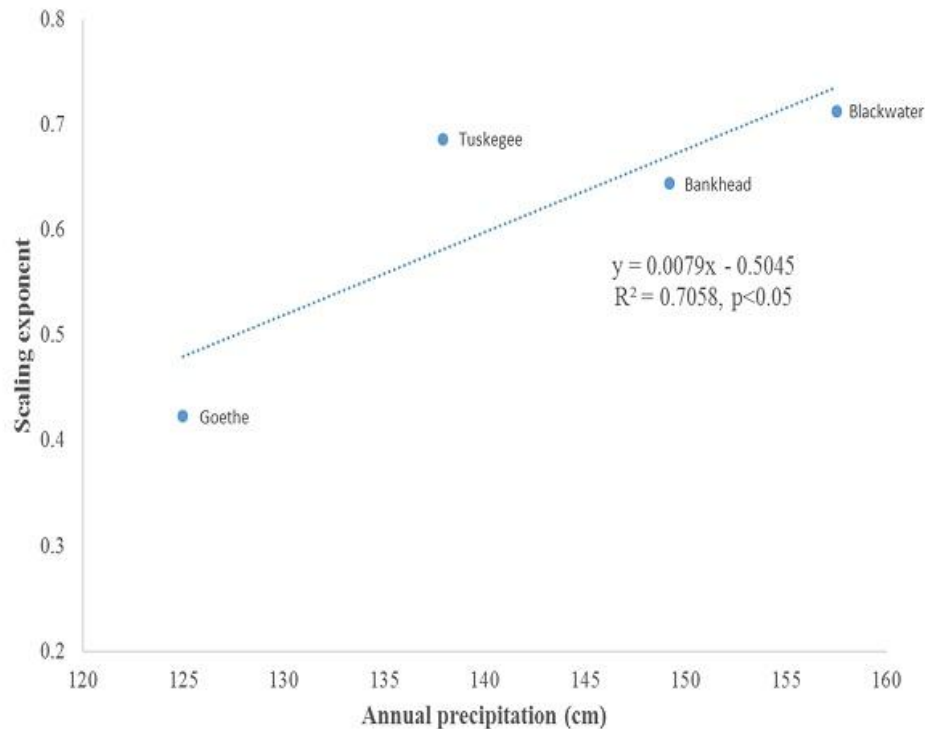


Figure 4. Correlation between mean annual precipitation and the scaling exponent of height and diameter

Our findings for red maple and river birch supported the exponent predicted by metabolic ecology; however, the results for water tupelo and bald cypress did not. Both scaling exponents of water tupelo and bald cypress were significantly less than the predicted $2/3$. These two tree species can live in flooded conditions for prolonged periods and are characterized by swollen trunks called “buttresses” or “knees”. One function of a swollen lower trunk is to provide enhanced stability by physically supporting a tree on a larger-diameter base and keeping it standing upright in wet soil. Another function attributed to a swollen trunk is that of providing oxygen to roots which grow in an environment of low dissolved oxygen. Otherwise, the tree would be expected to die from suffocation, since water-saturated soils contain less oxygen than well-aerated, better-drained soils. But, there is little actual evidence for this assertion (Angelov et al., 1996). Metabolic ecology postulates a power law with an invariant exponent, because all tree species share an optimal design for their vascular system, which is related to plant physiology (Enquist et al., 1999; West et al., 1999). However, trees may not exhibit the most efficient hydraulic architecture, because of limitations related to mechanical safety (Sperry, Meinzer, & McCulloh, 2008) and/or environmental stress. Despite no consensus on the role of the swollen trunks, their construction must consume energy and photosynthate, which could otherwise be used for increasing tree height. Thus, the scaling exponent for height and diameter was lower for water tupelo and bald cypress.

We conclude that the height-diameter scaling relationship for longleaf pine was not consistent across its natural range, most likely because of varied patterns of precipitation and the locally adaptive response of this species to water availability across the varied environments, which comprise the vast geographic area in which it can occur.

Although two of the swamp tree species, red maple and river birch, conformed to the scaling invariant of $2/3$ predicted by metabolic ecology, bald cypress (another conifer) and water tupelo, both species observed to form buttresses at their lower trunks, did not support that prediction. Other studies have indicated that this scaling relationship can also be affected by light, tree health condition and others (Ducev. 2012; Ishihara, Konno, Umeki, Ohno, & Kikuzawa, 2016; Swetnam, O'Connor, & Lynch, 2016; Forrester et al., 2017). This study puts forth additional data supporting the concept of a universal height-diameter scaling invariant of $2/3$ for some tree species, while providing a strong argument for deviation by other tree species directly related to possible environmental stresses that cause them to adapt to unique localized conditions throughout their range. Our findings confirm that high plasticity and variation across environments in the allometric scaling of tree height and diameter may very well be the rule, rather than the exception.

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