Practical Extension of a Lake States Tree Height Model

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ABSTRACT

By adapting data from national and state champion lists and the predictions of an existing height model, an exponential function was developed to improve tree height estimation. As a case study, comparisons between the original and redesigned model were made with eastern white pine (*Pinus strobus* L.). For example, the heights predicted by the new design varied by centimeters from the original until the pines were more than 25 cm dbh, after which the differences increased notably. On a very good site (50-year base age site index [SI_{50}] = 27.4 m) at the upper end of the range of basal area (BA; 68.9 m²/ha) for the region, the redesigned model predicted a champion-sized eastern white pine (actual measurements: 97.0 cm dbh, 50.9 m tall) to be 51.3 m tall, compared with 38.8 m using the original formulation under the same conditions. The NORTHWDS Individual Response Model (NIRM) individual tree model further highlighted the influence of these differences with long-term simulations of eastern white pine height. On a moderate site (SI_{50} = 18.7 m) with intermediate (BA = 15 m²/ha) stand density, NIRM results show that the original model consistently predicts heights to be 20–30% lower for mature white pine.

Keywords: champion trees, eastern white pine, NIRM, nonlinear model

T he desire to predict some future state or to more readily anticipate certain biophysical attributes has long driven modelers in many fields, including forestry. As a result, allometric relationships between easily measured tree attributes and those not as readily acquired have been developed for decades. For example, dbh is one of the most commonly used characteristics of trees because it is easy to accurately measure and generally serves as a good predictor of other attributes such as height, bole volume, and crown width (Colbert et al. 2002). Accurate portrayal of allometry is increasingly important because of a growing trend to model rather than measure certain tree characteristics in large-scale inventories to save time and money (e.g., Bechtold et al. 2002, Barrett 2006).

Models of tree height based on diameter have been generated with considerable success, and most published height–diameter equations explain a large proportion of the variation in the data from which they were derived. However, a truly successful height model depends on more than just a high coefficient of determination (Hasenauer and Monserud 1997). It should also conform to the biology of the species across the range of possible sizes (Lei and Parresol 2001). Genetics, competitive dynamics, hydraulics, and bole loading all help constrain trees from maintaining a strictly linear rise in height with increasing diameter (King 1990, Ryan and Yoder 1997, Becker et al. 2000, Koch et al. 2004). Experimentation suggests that there is an absolute upper tree height (e.g., Koch et al. 2004, Woodruff et al. 2004, Burgess and Dawson 2007, Domec et al. 2008), but for most species, this is considerably greater than what is seen in nature. Because height increment gradually tapers off compared with diameter, models of height–diameter relationships should reflect this property. However, it is possible to fix the maximum height asymptote too low, thereby unnecessarily constraining predictions, resulting in a gradually increasing bias that propagates as error. There is evidence that many height–diameter models systematically underestimate height for larger trees. For instance, Peng

et al. (2001) reported that all the functions they tested underestimated height for six of the nine species considered.

Height prediction errors can be further accentuated when regression models are extended outside the range of data from which they were derived (e.g., Payandeh and Wang 1994). This statistically questionable practice, although undesirable, is often driven by the needs of the user and the lack of a more appropriate model (Shifley and Brand 1984). Given that many users apply tree height models regardless of their statistical limits, it behooves model developers to ensure reasonable behavior of these models beyond their original source data. This can be shown with a commonly applied height–diameter model. Using data from forest survey plots in Michigan, Minnesota, and Wisconsin, Ek et al. (1984) fit the function,

$$\hat{H}_R = 4.5 + b_1(1 - e^{-b_2 \text{DBH}})^{b_3} SI^{b_4} T^{b_5} BA^{b_6}, \qquad (1)$$

where $\hat{H}_R$ is the predicted height (in feet), b_i are fitted regression coefficients, SI is site index (SI; in feet at 50 years), BA is stand basal area (in square feet per acre), and T is a simple upper stem taper expression for total tree height. Because most of their inventory data were less than 60 cm in dbh and the vast majority of trees in Lake States forests are less than this diameter, predictions from Equation 1 are probably as reliable as any other model for small- to moderate-sized trees.

Some species, however, grow considerably larger than this on a regular basis. In the northern Lake States, eastern white pine (*Pinus strobus* L.) often grows to 75–100 cm dbh and between 40 and 50 m tall (e.g., American Forests 2000, Eastern Native Tree Society [ENTS] 2004; D.C. Bragg, unpublished data, 2008) and historically may have exceeded 180 cm dbh and 60 m tall (Leech 1939, Rucker 2004). The original data of Ek et al. (1984) included a maximum eastern white pine dbh of 91.2 cm. With this as an upper diameter threshold, Equation 1 produces a distinctive height–diameter curve. Given a high stand density (68.9 m²/ha) and a very good site quality (50-year base age, SI_{50} = 27.4 m), Equation 1 predicts a

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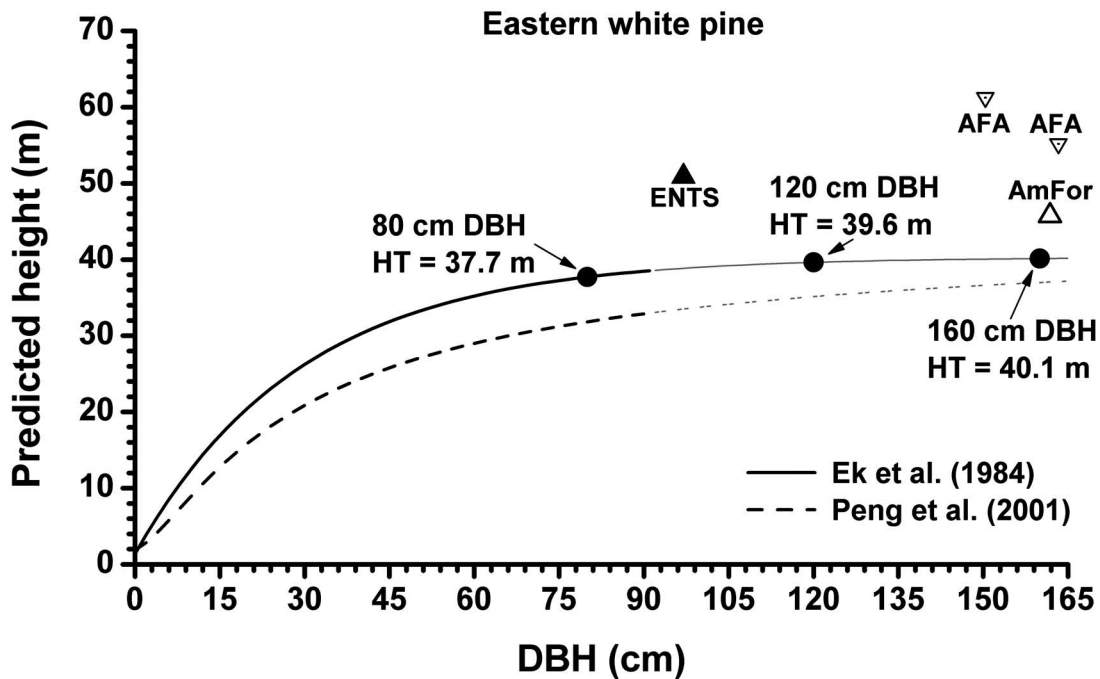
Figure 1. Plot of Ek et al.'s (1984) and Peng et al.'s (2001) height–diameter equations for eastern white pine, assuming an SI of 27.4 m and a stand density of 68.9 m²/ha. The diminished segments of their curves are extrapolations beyond the range of data used to derive them. The triangles in the upper right represent the height–diameter relationship of several current and former national champion eastern white pines. AFA = American Forestry Association (1990); AmFor = American Forests (2000); ENTS = Eastern Native Tree Society (2004).

37.7-m tall eastern white pine at a dbh of 80 cm (Figure 1). Afterward, total height increases to 39.6 m when the pine grows to 120 cm in dbh and 40.1 m at 160 cm dbh. Thus, it appears that for densely grown eastern white pine on a high-quality site, the original model asymptotes at a maximum height of just over 40 m—not a good reflection of the potential of this species.

Low asymptotic height curves are not exclusive to the model of Ek et al. (1984). Eastern white pine SI models for this region (e.g., Hahn and Carmean 1982) also reflect a greatly diminished rate of increase over large portions of their age structure, especially past 150 years. If these relationships were developed for the maximum height physiologically possible, this flattening would probably not be an issue. However, this is not the case, and dramatic underestimates of total tree height are likely for very large individuals. Hence, we need to extend existing height models to project across more of the range of possible tree size— other researchers have noted curves fit solely to shorter individuals do not adequately predict height in very tall trees (e.g., Smith 1984). This article offers a possible solution to this problem without involving new field-based height measurements by merging existing height–diameter model predictions with readily available champion tree information.

Methods

Conceptual Limits to Tree Height Models

Height–diameter models should have intuitive beginning and ending points. Most tree models use dbh as one starting point—by definition, trees shorter than 1.37 m tall have no dbh. Therefore, a logical height–diameter model would ideally yield a height of 1.37 m when dbh approaches zero, i.e., $\mathrm{Lim}_{\mathrm{dbh} \to 0} f(\mathrm{dbh}) = 1.37$, where $f(\mathrm{dbh})$ is the diameter-based height equation. However, the intercept at dbh = 0.0 may vary if the diameter is measured at a different location. For example, Parresol (1992) measured baldcy-

press (*Taxodium distichum* [L.]) Rich.) at 3.0 m aboveground to avoid the massive buttress typical of this species. Also, some height–diameter functions are optimized for other portions of the diameter range and thus may not pass through the nominal lower intercept of [0, 1.37].

The end point of this function occurs at the maximum diameter possible for a species growing on its best possible site at a local density conducive to the greatest vertical elongation (assuming no crown breakage or dieback). Unfortunately, this optimal suite of conditions is unknown for every species. However, "big trees" can be used to approximate this state (e.g., Shifley and Brand 1984, Parresol 1995). Champion tree information is readily available for virtually every species in the United States (e.g., American Forests 2000). Many states and organizations (e.g., the ENTS) maintain their own lists, allowing for more regional calibration. Furthermore, most big trees reported in these lists benefit from having both their total height and their circumference validated by trained observers.

Champion tree information is easily available and readily adaptable. However, a couple of issues related to data quality and type should be recognized. First, a considerable degree of measurement error has been noted in some big tree reports (e.g., Rucker 2004, Blozan 2006, Bragg 2007)—grossly erroneous champions must be identified and avoided. Second, trees listed as champions are usually scored from the sum of height, diameter, and some fraction of crown width, so the combination of these factors may not actually reflect the most appropriate allometry for developing a maximized height–diameter model. It is possible for a large open-grown tree with a spreading crown and thick stem to have a "bigness index" score significantly higher than a taller but thinner tree in a closed canopy forest. Thus, a champion tree may not reflect the maximum proportion of height to diameter. For instance, while noticeably larger in
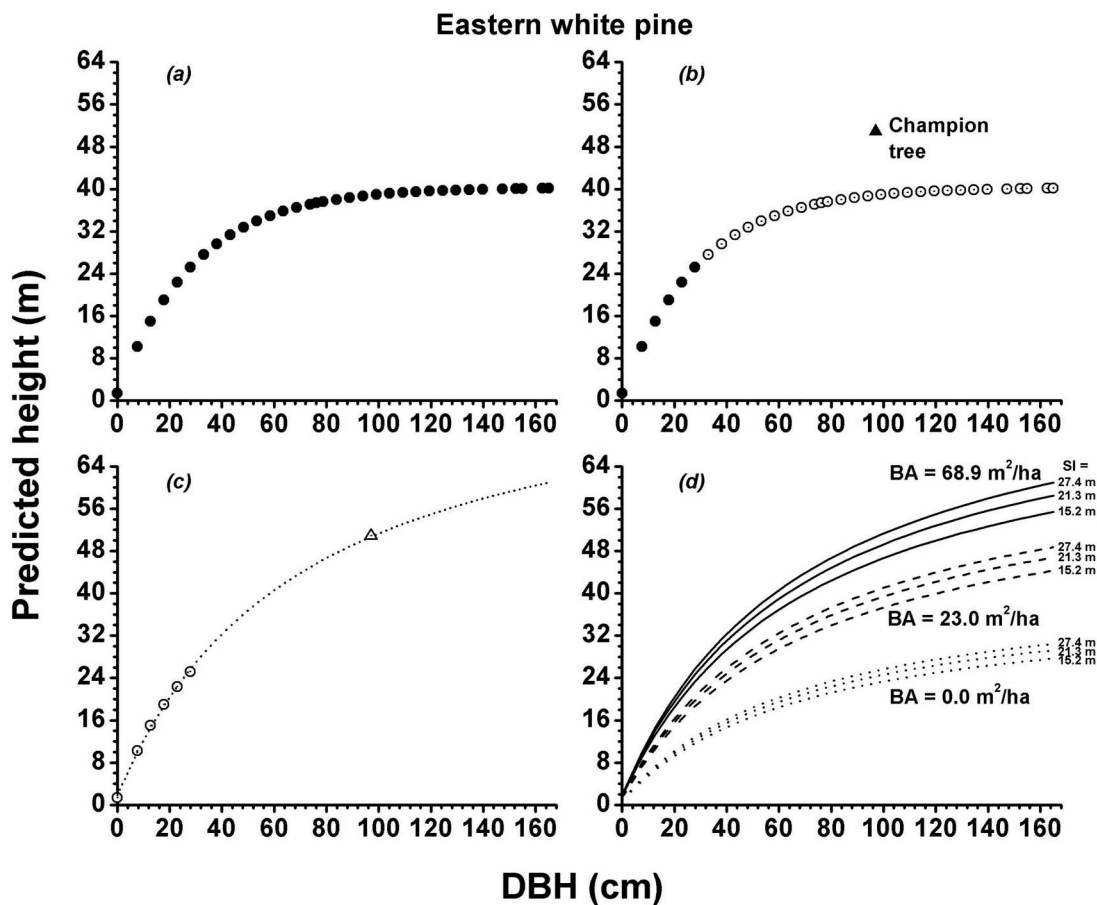
Eastern white pine

Figure 2. Graphical representation of the procedures used to extend the Ek et al. (1984) tree height model for eastern white pine. (a) First, the original height–diameter equation was plotted for all possible diameters. (b) Next, the two end points (when dbh = 0 and dbh = dbh$_{max}$) are added, and the majority of the original predicted points are removed with the exception of those used to define the shape of the curve. (c) Using ordinary least squares nonlinear regression, a curve was then fitted to the remaining points, and (d) when adjusted for site quality and local BA, a range of height–diameter curves became available.

diameter, the 2000 national champion eastern white pine (American Forests 2000) is shorter than the tallest eastern white pine from Wisconsin reported on the ENTS website (ENTS 2004, Figure 1). Fortunately, so long as the geographic extent of the sampled big tree is appropriate and the dimensions used are reliable, any accurately measured tree (living or dead, past or present) is a valid end point. Some state lists (e.g., Wisconsin's) are also more useful than the national register because they list multiple examples from which to select the maximum height–diameter relationship.

Point Selection and Modeling Approach

For this article, the height model extension procedure is straightforward. Using Equation 1 (hereafter called the "original model"), a series of points along this curve are generated extending out to the largest dbh in the original data, assuming maximum site quality and stand density conditions (Figure 2a). Two additional points are included in this data set—one for height when dbh becomes just more than 0 (at 1.37 m, in this case), and one representing the assumed maximum height–diameter value (Figure 2b). In the end, only a few of the Ek et al. (1984) predicted height–diameter points are retained to help define the shape of the curve (Figure 2b). This subset of points was chosen to best fit the curve through the champion tree point, and the rest were deleted as underestimates of height potential. Although this may not seem to provide adequate data to

express height over such a range of diameters, it is possible to fit reasonable allometric curves using very limited information (e.g., Zeide 1978).

It is likely that any of a number of height formulations could fit different species equally well, and that no single model will always yield the best fit in every species. However, modelers prefer to use one general model form to economize their code development. Because the ultimate destination of these height–diameter models is an ecological simulator, a single response function will be used in this article. The following exponential function was fit to the remaining points (Figure 2c):

$$\hat{H}_{\max} = b_0 + b_1 e^{b_2/(\mathrm{DBH}+b_3)}, \qquad (2)$$

where $\hat{H}_{\max}$ equals the maximum possible tree height and b_0 to b_3 are nonlinear ordinary least squares coefficients. Equation 2 was chosen for its relatively simple form, few coefficients, and sigmoidal relationship between the independent and dependent variables. Another advantage is that the exponential function is also less prone to yield a flattened height–diameter relationship commonly observed with the Chapman-Richards equation.

The $\hat{H}_{\max}$ is probably rarely achieved and almost never measured. This suggests that a more useful formulation of Equation 2 would include a set of n modifying functions (m) to act as multipliers

and rescale height as a function of suboptimal site and stand conditions:

$$\hat{H}_R = [b_0 + b_1 e^{b_2/(DBH+b_3)}] \prod_{i=1}^{n} m_i. \qquad (2a)$$

The rescaling of an optimized function has been used in a number of ecological models (e.g., Botkin et al. 1972, Chertov 1990, Bragg 2001, Papaik and Canham 2006). This technique allows the user to separate the general response curve from the factors influencing its behavior, as long as the estimate of the function is a valid expression of the response to a known, easily measured parameter (in this case, diameter). If this condition is met, the modifier functions yield a value of [0, 1], with a value of 1 indicating an "optimal" state, and any outcome less than this reduces potential. For height prediction, critical response functions include the relationship between the tree and site quality, and the tree and stand density (e.g., Ek et al. 1984, Parresol 1992), but factors such as crown position, hydraulic conductivity, genotypic differences, and/or geographic location could be incorporated as appropriate. As an example, one of the most relevant environmental factors influencing tree height is site quality. Hence, a relation between tree height and relative SI could be expressed as,

$$m_1 = \left(\frac{SI}{SI_{max}}\right)^{b_4}, \qquad (3a)$$

where SI_{max} is the maximum reported SI (or the mean height of dominants and codominants at 50 years) for a species, and b_4 is a fitted regression coefficient (in this case, the same b_4 value reported in Ek et al. [1984]). All other conditions being equal, trees of the same diameter will be shorter on poorer sites than good sites (Ryan and Yoder 1997, Fulton 1999).

Stand density also helps to control tree height response—the denser the stand and greater the competition for light, the taller the trees grow in relation to diameter. Conversely, open-grown trees have no competitive driver to grow taller, even though tree biology ensures some vertical elongation. In more physiological terms (e.g., Lanner 1985), open-grown trees have many more apical meristems competing for carbohydrates during the early season periods of vertical elongation. For dominant and codominant trees in closed canopy stands, height growth after bud elongation is more likely to be focused on a single (or small number of) leader(s), thus ensuring a fairly consistent level of height production regardless of crown position in all but the most suppressed individuals.

Note the empirical derivation of predominantly forest-grown trees in the original formulation of Equation 1 does not allow for vertical height for purely open-grown individuals, as the multiplier under this case equals 0 (making total height 1.37 m regardless of tree size or site quality). To avoid this problem, an adjustment to this modifier was used:

$$m_2 = \left(0.5 + \frac{(BA/BA_{max})^{b_5}}{2}\right), \qquad (3b)$$

where the stand basal area (BA) for the individual tree is rescaled as a proportion of the maximum possible (BA_{max}) for the region (assumed, in this case, to be 68.9 m²/ha) and $b_5 = 2 \times$ the b_6 coefficient from Ek et al. (1984, Table 2). This design yields open-grown (BA = 0) trees 50% as tall as those in maximally dense stands (when BA = BA_{max}), thereby avoiding the logical discontinuity of the original design, while still closely tracking height patterns of Equation 1 at more common forest densities. Currently, this adjustment is one-sided (linear) as opposed to being two-sided (modal) because this model focuses on dominant or codominant individuals. Highly suppressed trees have very little height growth under high stand densities—a modifier to reflect this tendency would require some measure of crown position to differentiate tree canopy level.

By incorporating these site and stand modifiers, the following instantaneous height function is produced:

$$\hat{H}_R = [b_0 + b_1 e^{b_2/(DBH+b_3)}]\left(\frac{SI}{SI_{max}}\right)^{b_4}\left(0.5 + \frac{[BA/BA_{max}]^{b_5}}{2}\right), \qquad (3)$$

where all coefficients and variables are as previously described. Because SI and BA are always less than or equal to SI_{max} and BA_{max}, respectively, and b_4 and b_5 are between 0 and 1, these modifiers reduce growth from the potential implied in the first term of Equation 3 and, hence, can produce a surface reflecting the influence of both site quality and stand density (Figure 2d). This approach also allows for additional modifiers to be included as needed, or for different response functions between site quality and stand density to be used, if desired.

A very good site for most species in the northern Lake States is usually about 27.4 m (base age of 50 years) and stand basal area rarely exceeds 68.9 m²/ha. Hence, an equation fit assuming the champion tree found on the highest site quality possible (SI/SI$_{max}$ = 1) actually produces a conservative estimate of maximum height potential because (probably without exception) champion trees are not found in a maximally dense stand on site of best quality for that species. In other words, a tree living on such a hypothetical site reaching the diameter of a champion tree would almost certainly be taller than those reported in the literature.

Results and Discussion

Table 1 lists maximal dimensions for 31 species common to the northern Lakes States (Michigan, Minnesota, and Wisconsin). Note that these values are not assumed to represent the absolute maxima possible for each species—one of the advantages to this height model extension technique is that new information can be used to continually improve on the process. This list of species is also larger than those originally reported in Ek et al. (1984), reflecting the needs of a new model system capable of projecting tree height for more taxa. However, for the purposes of this article, eastern white pine will provide most of the examples, given that the other taxa responded similarly.

Table 2 provides the parameter estimates of the tree species in Table 1. Where possible, the species equations were fit to generate a height of 1.37 m at dbh = 0, the height of a tree of champion size and the lower tail of the predictions of Ek et al.'s equation (including the inflection point, if possible). Figure 3 illustrates the original and new height–diameter equations for three basal areas (0.0, 23.0, and 68.9 m²/ha) for eastern white pine at an SI$_{50}$ = 21.3 m. Given its original formulation, Equation 1 returns a value of 1.37 m for all diameters under open-grown conditions. This particular outcome is a result of the original equation's structure and data-based derivation (which did not include open-grown individuals). As basal area increased, Equation 1 produced trees with height, although the model's form helped constrain the range. For instance, even under the most favorable conditions for tall, dominant, or codominant

Table 1. Champion tree dimensions and sources used in this study.

Common name	Species	Champion dbh (cm)	Champion height (m)	State	Source[a]	Maxmum SI (m)
Balsam fir	*Abies balsamea* (L.) Mill.	67.8	35.36	MI	1	22.0
Red maple	*Acer rubrum* L.	179.6	42.37	MI	1	23.0
Silver maple	*Acer saccharinum* L.	223.3	38.10	MI	1	27.4
Sugar maple	*Acer saccharum* Marsh.	111.8	38.40	WI	4	23.0
Yellow birch	*Betula alleghaniensis* Britton	99.1	30.48	WI	4	24.0
Paper birch	*Betula papyrifera* Marsh.	177.8	32.61	MI	3	25.0
American hornbeam	*Carpinus caroliniana* Walt.	25.1	20.90	SC	5	12.0
American beech	*Fagus grandifolia* Ehrh.	86.9	30.48	WI	4	20.0
White ash	*Fraxinus americana* L.	88.9	34.44	WI	4	26.0
Black ash	*Fraxinus nigra* Marsh.	80.0	47.24	MI	1	24.0
Green ash	*Fraxinus pennsylvanica* Marsh.	82.6	25.91	WI	4	27.4
Tamarack	*Larix laricina* (Du Roi) K. Koch	79.2	25.91	WI	4	22.0
Eastern hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	42.0	21.60	MI	3	12.0
White spruce	*Picea glauca* (Moench) Voss	101.6	39.62	MN	3	22.0
Black spruce	*Picea mariana* (Mill.) B.S.P.	48.5	25.30	MN	1	22.0
Jack pine	*Pinus banksiana* Lamb.	56.1	29.57	WI	4	22.0
Red pine	*Pinus resinosa* Ait.	99.6	46.94	MI	1	27.4
Eastern white pine	*Pinus strobus* L.	97.0	50.90	WI	5	27.4
Balsam poplar	*Populus balsamifera* L.	131.8	42.06	MI	1	14.0
Eastern cottonwood	*Populus deltoides* Bartr.	236.0	39.62	WI	4	27.4
Bigtooth aspen	*Populus grandidentata* Michx.	83.8	40.23	MI	3	26.0
Quaking aspen	*Popolus tremuloides* Michx.	98.6	33.22	MI	3	26.0
Pin cherry	*Prunus pennsylvanica* L.	21.1	19.20	MN	2	17.0
Black cherry	*Prunus serotina* Ehrh.	146.3	42.06	MI	1	24.0
White oak	*Quercus alba* L.	138.2	32.92	WI	4	24.0
Bur oak	*Quercus macrocarpa* Michx.	200.4	24.99	MN	2	21.0
Northern red oak	*Quercus rubra* L.	111.8	34.44	WI	4	23.0
Northern white-cedar	*Thuja occidentalis* L.	120.4	28.04	WI	4	20.0
American basswood	*Tilia americana* L.	139.7	35.05	WI	4	24.0
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	100.3	30.78	WI	4	15.0
American elm	*Ulmus americana* L.	175.3	36.58	WI	4	24.0

Maximum SI values for species are inferred from existing Lake States equations (e.g., Hahn and Carmean 1982).
[a]Champion tree source: 1 = American Forestry Association (1990); 2 = Minnesota State Champions List (www.dnr.state.mn.us/trees_shrubs/bigtree/list.html); 3 = American Forests (2000); 4 = Wisconsin State Champions List (www.dnr.wi.gov/forestry/UF/champion/); 5 = ENTS List (www.nativetreesociety.org/bigtree/webpage_tall_tree_list.htm).

Table 2. Regression coefficients for the new height equation, including number of samples used to derive the coefficients (n), SI, and stand BA components.

Species	n	b_0	b_1	b_2	b_3	b_4[a]	b_5	Notes[b]
Balsam fir	12	−3.5690	55.6720	−28.5025	11.5348	0.23349	0.24798	
Red maple	8	−61.2065	109.3265	−10.9460	19.5471	0.40115	0.24806	
Silver maple	7	−107.2704	148.7370	−5.8860	19.0611	0.48660	0.03236	
Sugar maple	8	−80.2615	126.6577	−8.8148	20.1736	0.54194	0.12744	
Yellow birch	8	1.0393	32.8188	−11.3292	2.4467	0.38884	0.22822	
Paper birch	10	−2.2639	36.5706	−9.4084	4.0686	0.41179	0.22092	
American hornbeam	8	−9.6322	71.5267	−39.0985	20.7910	0.20000	0.16456	1
American beech	8	1.3213	33.6118	−13.0625	0.8975	0.55634	0.19186	1
White ash	8	1.2955	38.3576	−13.4365	2.1370	0.38694	0.21694	
Black ash	7	−74.5467	155.2930	−29.4781	41.1166	0.35711	0.13718	
Green ash	6	1.3797	27.5871	−8.4203	0.6061	0.35711	0.13718	
Tamarack	8	1.4037	27.5595	−8.3440	0.8704	0.25831	0.21542	
Eastern hophornbeam	10	0.3520	29.8218	−15.8764	4.6614	0.20000	0.16456	1
White spruce	10	−4.6559	61.2225	−38.5219	16.1819	0.05000	0.32400	2
Black spruce	9	0.9019	32.5804	−15.0132	3.5622	0.17836	0.20318	
Jack pine	8	−44.1874	89.7923	−15.6964	23.1881	0.20854	0.25804	
Red pine	9	−110.2130	205.1634	−47.6949	78.9359	0.05000	0.36462	2
Eastern white pine	17	−101.2377	187.0880	−31.0606	52.1397	0.16220	0.46632	
Balsam poplar	7	−76.5267	134.0617	−20.9845	38.7892	0.47370	0.16456	
Eastern cottonwood	8	0.3186	41.7305	−15.1331	4.0280	0.30651	0.14920	
Bigtooth aspen	7	−110.7650	161.1770	−6.8805	19.1626	0.46918	0.23564	
Quaking aspen	8	0.8275	36.7523	−12.9056	3.0611	0.47370	0.16456	
Pin cherry	10	−5.1546	51.3821	−23.2703	11.1475	0.30000	0.16576	1
Black cherry	7	−8.7875	57.1306	−18.4043	10.5846	0.40000	0.24806	1
White oak	8	−30.4205	66.6220	−7.6467	10.3271	0.31723	0.26930	
Bur oak	6	1.3773	24.4655	−6.1258	0.7108	0.31723	0.26930	1
Northern red oak	7	−30.6767	70.6273	−10.1616	12.8602	0.55634	0.21612	
Northern white-cedar	7	0.3832	31.7892	−17.4951	5.0296	0.33978	0.23332	
American basswood	8	1.2327	37.5967	−15.4059	2.6184	0.49589	0.11682	
Eastern hemlock	7	0.8326	36.3368	−20.4602	4.7204	0.68454	0.00002	2
American elm	8	1.3063	38.4440	−15.5705	2.3001	0.34894	0.25188	

[a]With a few exceptions, this is b_4 from Table 2 of Ek et al. (1984, p. 4).
[b]Notes: 1 = since this species was absent from Ek et al. (1984), an estimate was included; 2 = adjusted from the original Ek et al. (1984) values.
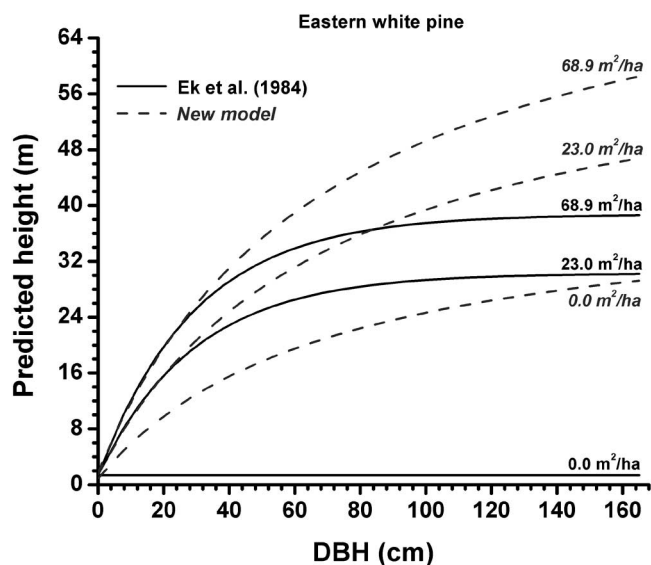
Figure 3. Comparison of eastern white pine curves from the new height–diameter equation and the original Ek et al. (1984) function. Note the close approximation of the original predictions by the new model until approximately 25 cm dbh, when the two models began to deviate sharply from each other. The exception to this pattern is found at the lowest basal area (for an open-grown tree, or 0 m²/ha), for which the original formulation can not predict anything taller than 1.37 m.

Figure 4. SI curves for eastern white pine adapted from Hahn and Carmean (1982). Note that heights in excess of 45 m are possible on better quality sites.

stems (i.e., high local density), Equation 1 fails to produce a 40-m tall pine, even at dbh = 165 cm.

The asymptotic nature of the Ek et al. (1984) height–diameter equation at a relatively modest size is very apparent in all species. In practical terms, this flattening means that a tree will increase only a fraction of a meter over a range of diameters that could triple or quadruple. Hence, a tree of national champion size would never be attained using the original formulation's predictions. However, Equation 3 is fully capable of predicting a tree of champion size while still reasonably forecasting heights of trees of smaller diameters. As an example (Figure 3), even at a moderate SI and high BA, Equation 3 predicts eastern white pine heights over 50 m tall for trees greater than 120 cm dbh. This range of heights is comparable with champion trees reported regionally and found in Lake States SI curves (e.g., Hahn and Carmean 1982) that suggest 300-year-old eastern white pine can exceed 40 m and may reach 50+ m under certain circumstances (Figure 4).

Finally, the progressive height increase with larger diameters (especially for very big trees) displayed by the new model is consistent with the limited published information on height growth in champion-sized individuals. Fowells (1965, p. 332) reported that 100-year-old eastern white pine added height at approximately 12 cm annually, and reached a minimum rate of about 6 cm annually at 165 years old, which the species "… apparently sustained for the life of the tree." If maintained over the long-term, this increment under favorable conditions would eventually yield 60+ m eastern white pines.

Differences between New and Original Height–diameter Equations

Just as important as being able to predict large-sized trees, Equation 3 is also capable of emulating heights for small- to moderate-sized trees. With the notable exception of an open-grown tree, Fig-
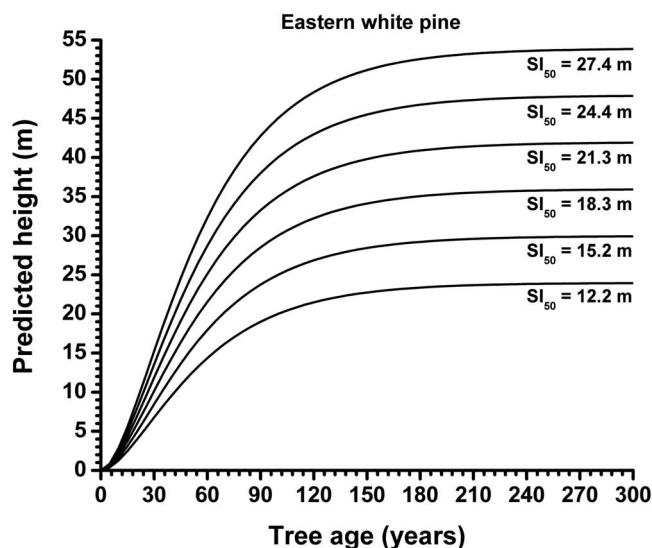
ure 3 shows that the differences between the new and original height models are very small. For eastern white pine, heights predicted with Equation 3 differed by only 20–30 cm from those predicted with Equation 1 until the species reach 25 cm dbh (Table 3). Above this diameter, fundamental differences in curve shape lead to increasingly large departures.

The minor differences between the models in small- to moderate-sized trees is not unique to eastern white pine—using a subset of other taxa (Table 3) predicted height variation between the models was also measured in centimeters. Projections of sugar maple (*Acer saccharum* Marsh.), quaking aspen (*Populus tremuloides* Michx.), northern red oak (*Quercus rubra* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.) all fell within 1.25 m of the original function up to about 25 cm dbh. However, discrepancies grow rapidly with increasing diameter—quaking aspen, eastern white pine, and northern red oak differed by 2.86–4.05 m in height by 50 cm dbh, and sugar maple and eastern hemlock varied by almost 6 m at 50 cm dbh (Table 3).

The inability to accurately predict the heights of moderate- to large-sized trees is largely a consequence of inadequacies in the original data. Eastern white pines, e.g., frequently reach diameters of 60–90 cm dbh. The original model (on an intermediate SI_{50} = 18.3 m and with BA = 34.4 m²/ha) would only yield a height of between 28 and 31 m for this diameter range, although eastern white pines of this size commonly reach 35–40 m (e.g., Fowells 1965, Wendel and Smith 1990). This disparity gets progressively more apparent as the trees get larger. In every case presented in Table 4, the original model underestimates tree height for an individual of champion size between 6 and 13 m. Because the new model has been optimized for a tree of champion dimensions, the differences in predicted height differed by 4 cm or less for quaking aspen, northern red oak, and eastern hemlock to as much as 22 cm for eastern white pine (Table 4).

It is not unusual for data-limited height–diameter models to underpredict maximum tree height. The two examples presented in this work (Ek et al. 1984, Peng et al. 2001) fit equations with regression techniques that optimize model fit to the totality of the data, not the extremes. Although statistically sound, this places

Table 3. Absolute and relative departure comparison between Equations 1 and 3 by size class for select species, including the standard error from Ek et al. (1984), assuming SI_{50} equivalent to the species maximum (Table 1) and a local basal area of 68.9 m²/ha.

Species and Prediction	0.0	2.5	5.0	10.0	25.0	50.0	100.0	Reported standard error (m)[a]
				Tree dbh (in cm)				
Sugar maple								
Ek et al. height (m)	1.37	5.25	9.00	14.81	22.88	25.46	25.76	2.35
New equation height (m)	1.56	5.60	8.98	14.31	23.94	31.44	37.44	
Difference[b] (m)	0.19	0.35	−0.02	−0.50	1.07	5.98	11.68	
Relative difference[c] (%)	13.7	6.6	−0.2	−3.4	4.7	23.5	45.3	
Eastern white pine								
Ek et al. height (m)	1.37	4.54	7.45	12.57	23.64	33.17	38.99	3.26
New equation height (m)	1.88	4.73	7.40	12.25	23.84	36.79	51.30	
Difference (m)	0.51	0.19	−0.05	−0.32	0.20	3.63	12.31	
Relative difference (%)	37.0	4.2	−0.7	−2.6	0.9	10.9	31.6	
Quaking aspen								
Ek et al. height (m)	1.37	4.50	8.20	14.49	23.78	26.79	27.12	2.04
New equation height (m)	1.37	4.44	8.24	14.51	24.03	29.64	33.25	
Difference (m)	0.00	−0.06	0.04	0.02	0.25	2.86	6.14	
Relative diff. (%)	−0.1	−1.4	0.5	0.1	1.0	10.7	22.6	
Northern red oak								
Ek et al. height (m)	1.37	4.32	7.82	13.76	22.52	25.36	25.67	2.50
New equation height (m)	1.37	5.77	9.31	14.61	23.33	29.41	33.87	
Difference (m)	0.00	1.45	1.49	0.85	0.80	4.05	8.20	
Relative difference (%)	0.0	33.5	19.0	6.2	3.6	16.0	31.9	
Eastern hemlock								
Ek et al. height (m)	1.37	2.67	5.10	10.12	17.87	19.91	20.05	2.19
New equation height (m)	1.31	2.97	5.26	9.88	19.09	25.83	30.72	
Difference (m)	−0.06	0.30	0.16	−0.23	1.22	5.93	10.67	
Relative difference (%)	−4.6	11.2	3.1	−2.3	6.8	29.8	53.2	

[a] Standard error reported in Table 2 of Ek et al. (1984, p. 4).
[b] Difference = new model − predicted Ek et al. height.
[c] Relative difference = [(new model − predicted Ek et al. height)/predicted Ek et al. height] × 100.

Table 4. Absolute and relative height differences for select species between the Ek et al. (1984) and new model predictions with trees of champion-caliber dimensions.

Species	Champ.[a] dbh (cm)	Champ. height (m)	Ek et al. prediction — Height at champ. dbh (m)	Diff. w/ champ.[b] (m)	Rel. diff. w/champ.[c] (%)	New model prediction — Height at champ. dbh (m)	Diff. w/ champ. (m)	Rel. diff. w/champ. (%)
Sugar maple	111.8	38.40	25.76	−12.64	−32.91	38.21	−0.19	−0.49
Eastern white pine	97.0	50.90	38.85	−12.05	−23.67	50.68	−0.22	−0.44
Quaking aspen	98.6	33.22	27.12	−6.10	−18.37	33.20	−0.02	−0.07
Northern red oak	111.8	34.44	25.67	−8.77	−25.46	34.42	−0.02	−0.05
Eastern hemlock	100.3	30.78	20.05	−10.73	−34.86	30.74	−0.04	−0.14

[a] Champ. = champion from American Forests (2000), the Wisconsin state champion list, and the ENTS website.
[b] Diff(erence) w/champ(ion tree) = model predicted height − champion height.
[c] Rel(ative) diff(erence) w/champ(ion) = [(model predicted height − champion height)/champion height] − 100.

certain constraints on the predictive capacity of the equation. These models predict height well for their observed range of data, but extrapolation beyond this point proves increasingly tenuous as tree size increases. Ecological models often forecast trees to their known longevities (potentially hundreds of years) and to the maximum limits of known stem size. Without a means to extend existing height–diameter models toward these logical end points, extrapolated models will systematically bias height outcomes (typically negatively) and any other prediction (e.g., volume) based on them.

Sensitivity Analysis

Although using champion trees allows for the extension of height modeling, there is considerable uncertainty in the actual maximum height values to apply. Some of this is systemic—there are likely taller (or more proportionally appropriate) individuals still unmeasured across the range of most species that could significantly influence the outcome of this approach. Similarly, regional differences in maximum tree height may prove important. Other issues are proce-

dural, because there can be significant errors in maximum height measurements based on the technique used (e.g., Blozan 2006, Bragg 2008).

To evaluate the influence of champion tree height uncertainty on model extension outcomes, the height trend forecast by Equation 3 was compared for eastern white pine (Figure 5) with trajectories based on the same champion dbh with ±10% variation in the height (50.9 m) of this tree (thus, 45.81 and 55.99 m, respectively, for the lower and upper bounds). Graphically, the sensitivity analysis shows that up to about 30 cm dbh there is virtually no difference between the predictions from Equation 3 and those fit to the other champion tree heights (Figure 5). Not surprisingly, the models diverged rapidly after this point.

Another lesson from this exercise is that overestimates of maximum tree height are more likely to produce larger absolute responses in tree heights than underestimates. By the time these trees reach 200 cm dbh (certainly on the upper end of eastern white pine dimensions), a 10% overestimate of height (roughly 5 m) translates
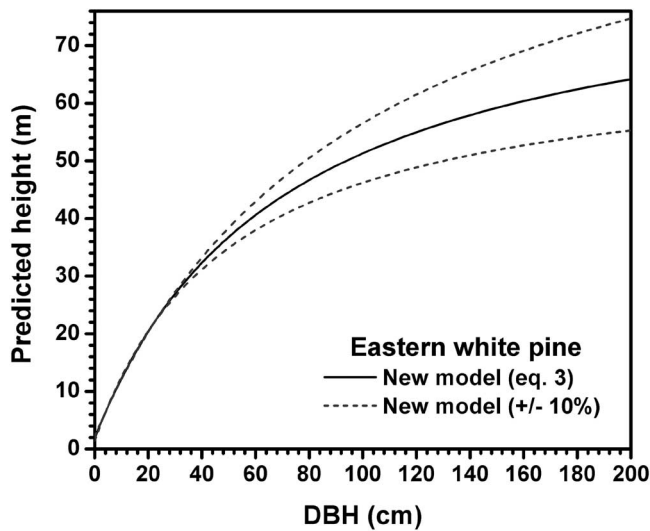
Figure 5. Sensitivity analysis based on ±10% height added to the champion eastern white pine (same dbh used), the refit to Equation 3.

into over 10 m in height, while a 10% underestimate was just under 9 m less at 200 cm dbh. Either condition suggests that model extension utility depends on the accuracy of maximum tree height measurements.

An Example Modeling Application

The original Ek et al. (1984) height–diameter equations have been incorporated into the Lake States variant of the Forest Vegetation Simulator (LS-FVS; FVS Staff 1993), as well as ecological models such as NORTHWDS and NORTHWDS Individual Response Model (NIRM; Bragg et al. 2004). Hence, these simulators are theoretically subject to the same constraints imposed by the statistical limitations of Equation 1. Because their predictions reflect the behavior of their internalized algorithms, departures from true tree height impact other simulated outcomes. For instance, NIRM uses height to calculate total live crown surface area, which in turn drives tree growth and vigor and thus influences attributes such as biomass accumulation and propagule production. Likewise, LS-FVS depends on tree height to predict outcomes such as total and merchantable tree volumes.

The choice of height–diameter model significantly influenced predictions of tree height in NIRM, because both Equations 1 and 3 were used to compare eastern white pine height growth under the exact same environment. For an intermediate site (SI_{50} = 18.7 m) in a moderately dense stand (BA = 15 m^2/ha), simulations produced increasingly disparate heights during the model run, with a 10% discrepancy after 40 years, 20% difference at 90 years, and over 30% less height after 300 simulated years—a realized height departure of 11.5 m (Figure 6). When all other factors are equal, shorter trees have less crown surface area in NIRM, which in turn predicts slower growth rates, reduced propagule production, and lower timber
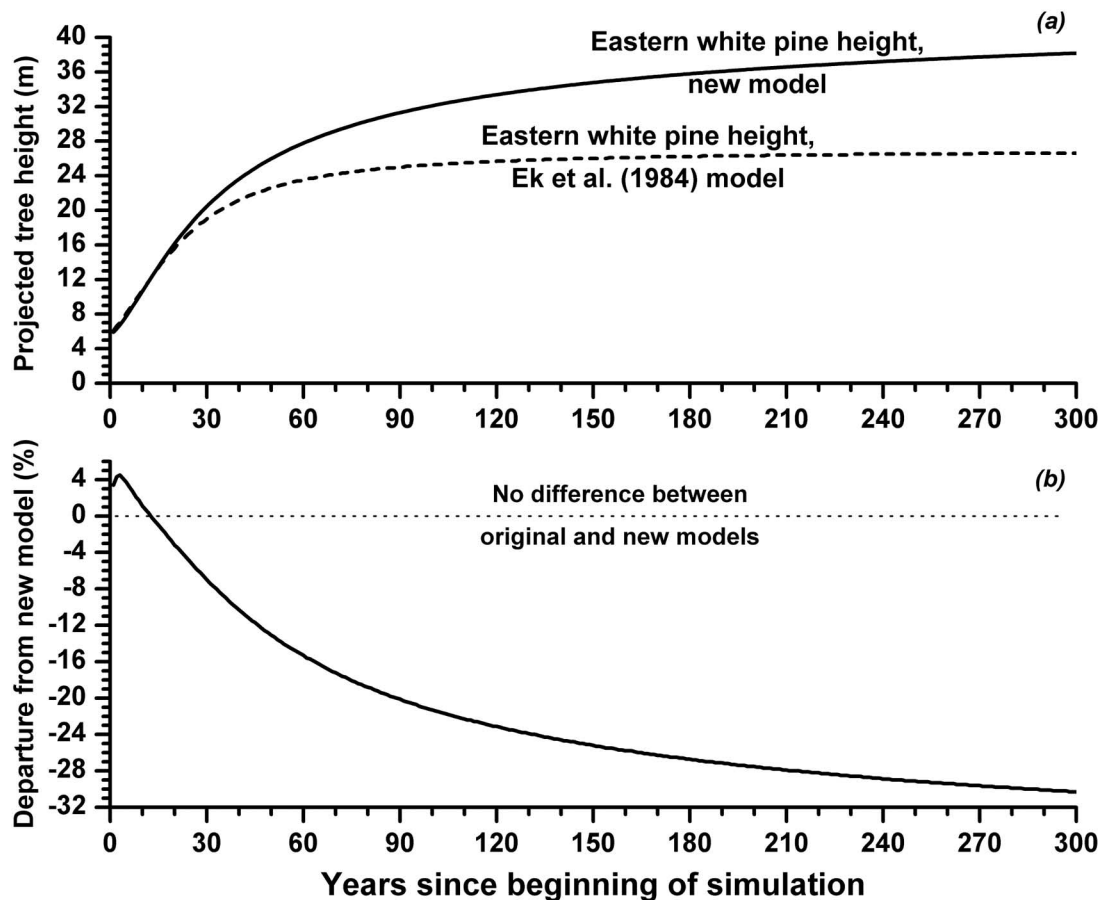

Figure 6. Influence of the original Ek et al. (1984); solid line) and new (dashed line) height functions on predicted tree height (a) and expressed as a relative (percent) difference (b) as simulated by the NIRM individual-based model. Note that these are not given as a function of tree age, but years since the beginning of the simulation, assuming a 6-cm dbh eastern white pine at the start.

yields. For stand-level simulations, this would lower productivity and may create differences in the structural complexity. It may be difficult, e.g., to project the formation of a pine supercanopy over a mature hardwood stand if the height–diameter model is too strictly constrained.

Models (such as NIRM) that use an instantaneous rather than a cumulative or averaging function to predict height must also ensure that abrupt shifts in environmental conditions do not invoke irrational height responses. As an example, unless otherwise constrained, both Equations 1 and 3 would drastically shrink trees if they are suddenly isolated. Think of a 30-m tall seed tree left to regenerate a cleared patch of timber—once the BA of the surrounding stand drops from 20 to 0 m^2/ha, Equation 1 predicts a height of 1.37 m and Equation 3 predicts 15 m. Obviously, unless the top is lost as an immediate and universal consequence of this stand clearing, neither outcome portrays the reality of height accumulation.

Conclusions

Even the best allometric relationship will not account for all of the factors resulting in a real-world tree of a specific dimension. The complexity imbued on individual trees by an ever changing environment, genetic variability, suppression, disturbance-related injuries, and many other factors will always produce inconsistent heights. This helps to explain why studies of modeled versus measured tree heights usually find field measurements superior to simulations (e.g., Bechtold et al. 1998). Some compromises based on the objectives of the simulation and the need for biological realism must be made, as long as the inherent weaknesses of these predictors are recognized and expressed. Ideally, height models should predict trees over the range of potential diameters, especially when incorporated in a system capable of forecasting hundreds of years into the future. If nothing else, a height–diameter model should not systematically bias predictions so substantially as to make simulating natural forest characteristics impossible.

The height model extension technique described in this article is one of several possible approaches and has the potential to extend height equations beyond their fitted range. Although the considerable precision of this approach is an artifact of how the function was fitted, it does permit the heights of very large trees to be estimated in a far more reliable fashion without extensive new sampling. Ideally, a function would be derived from field-measured data and then fit to allow for the best expression of the information. Alternatively, a dbh-based correction factor could also be applied, even though this would also require at least some real tree data to implement. Given the all-to-common circumstances when a height–diameter relationship can not be independently derived across the range of potential heights and diameters, the merger of existing height–diameter equations with reliable and accurate big tree data is a practical means to extend these allometric models beyond their initial size limitations.

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