

Potential relative increment (PRI): a new method to empirically derive optimal tree diameter growth

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Abstract

Potential relative increment (PRI) is a new method to derive optimal diameter growth equations using inventory information from a large public database. Optimal growth equations for 24 species were developed using plot and tree records from several states (Michigan, Minnesota, and Wisconsin) of the north central US. Most species were represented by thousands of individuals measured across an extensive geographic region that presumably covered a large range of possible environmental conditions. Thus, it was assumed that the individuals growing at the highest rate for each diameter class represented a reasonable estimate of size-specific optimal growth. Comparison of PRI equations among several hardwood and conifer species of differing shade tolerance indicated that unique patterns of optimal diameter growth result. The PRI methodology is similar to other optimal growth models in both shape and trends of predicted growth, but is easier to calculate and offers more flexibility than many other designs. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Most forest growth models are heavily parameter dependent and require sensible assumptions to provide realistic simulations (Buchman and Shifley, 1983; Vanclay and Skovsgaard, 1997). This is especially true of empirically based models that depend on reliable relationships between eas-

ily measured tree attributes (e.g. diameter at breast height (DBH)) and those more difficult to acquire (e.g. crown size). Extensive work has been done in the development of statistical forest simulation models (e.g. Belcher et al., 1982; Wykoff et al., 1982; Pacala et al., 1993, 1996; Sterba and Monserud, 1997), but the approaches vary substantially and empirically-derived models can be site-specific if not developed for large areas. Improvement in the derivations of growth response to the environment (e.g. Fleming, 1996) makes the task more ecologically mechanistic, but models employing such designs are unlikely to improve

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predictability over strictly empirical models. The intent of this paper is not to establish a set of protocols or benchmarks for diameter increment models (see reviews in Dale et al., 1985; Vanclay and Skovsgaard, 1997), but rather compare a new methodology with existing designs.

Many different equations to estimate diameter growth exist, but only a subset will be reviewed here. JABOWA-FORET gap models (e.g. Botkin et al., 1972; Shugart and West, 1977; Aber and Melillo, 1982; Pastor and Post, 1986; Botkin, 1992) forecast growth as a function of inferred leaf area and tree size. Annual maximum diameter increment for these gap models is calculated as follows:

$$\frac{dDBH}{dt} = \frac{GDBH_t \left(1 - \frac{DBH_t \times HT}{DBH_{\max} \times HT_{\max}} \right)}{274 + 3b_2DBH_t - 4b_3DBH_t^2} \quad (1)$$

where DBH_t is current tree DBH, maximum diameter (DBH_{\max}) and maximum height (HT_{\max}) are estimated from the literature, and the growth parameter (G) equals:

$$G = \frac{4HT_{\max}}{AGEMAX} \left\{ \ln[2(2DBH_{\max} - 1)] + \frac{\alpha}{2} \ln \left[\frac{9/4 + \alpha/2}{4DBH_{\max}^2 + 2\alpha DBH_{\max} - \alpha} \right] - \frac{\alpha + \alpha^2/2}{\sqrt{\alpha^2 + 4\alpha}} \times \ln \left[\frac{(3 + \alpha - \sqrt{\alpha^2 + 4\alpha})(4DBH_{\max} + \alpha + \sqrt{\alpha^2 + 4\alpha})}{(3 + \alpha + \sqrt{\alpha^2 + 4\alpha})(4DBH_t + \alpha - \sqrt{\alpha^2 + 4\alpha})} \right] \right\} \quad (2)$$

where $AGEMAX$ is an estimate of species longevity and $\alpha = 1 - 137/HT_{\max}$. Due to some inconsistencies in the calculation of Eq. (2) for several species, Botkin et al. (1972) approximated values of G and greatly simplified the derivation of the growth increment. Although this procedure seems to predict diameter increment well (Botkin et al., 1972; Shugart, 1984), the complexity of its calculation makes it cumbersome to use. The validity of using variables like DBH_{\max} , HT_{\max} , and $AGEMAX$ is questionable due to their reliance on ‘big’ tree data because these trees are probably not representatives of the conditions experienced by most individuals. Problems may also lie in the method used to determine G since

Eq. (2) was an admittedly arbitrary design (Botkin et al., 1972; Moore, 1989). Moore (1989) proposed the use of open-grown trees to calculate G for his reformulation of the gap increment model (Eq. (1)):

$$\frac{dDBH}{dt} = \frac{GDBH_t \left(1 - \frac{HT}{HT_{\max}} \right)}{274 + 3b_2DBH_t - 4b_3DBH_t^2} \quad (3)$$

Moore (1989) noted improvements in growth model behavior and reliability for Virginia pine (*Pinus virginiana* Mill.), but this modification has not been widely accepted. Finding usable open-grown trees can be difficult in heavily forested regions in which isolated individuals are scarce, or in the case of species that rarely occur in the open. Additionally, as shown later in this paper, the more conservative nature of Eq. (3), when compared with the original gap model version (Eq. (1)) does not represent an improvement in predicting optimal increment.

Another example of a unique growth equation can be found in *SORTIE* (Pacala et al., 1993, 1996). The creators of *SORTIE* followed a different theoretical approach by assuming the primary factor influencing growth in northern hardwood stands is light availability. Unlike many other diameter increment models, *SORTIE* does not incorporate any measure of site quality when determining growth performance. They applied the global light index (GLI) methodology (Canham, 1988) to correlate light availability and growth performance of seedlings and saplings, arriving at the following response function:

$$\frac{dDBH}{dt} = R \frac{g_1 GLI}{g_1/g_2 + GLI} \quad (4)$$

where R is the tree’s bole radius, g_1 is a species’ asymptotic growth rate at high light, and g_2 is the slope at zero light. Pacala et al. (1996) reported that while seedling growth responds geometrically to GLI, this does not apply to larger individuals. To adjust Eq. (4) for the growth of large trees, they incorporated another parameter (g_3) based on the Constant Area Increment Law (Phipps, 1967) to moderate growth performance. Eventually, most species were predicted to experience an annual increment of 1.5 mm for a tree 100 cm DBH.

Zeide (1989, 1993) evaluated numerous negative exponential and power decline functions for their applicability to predicting realized diameter increment. Other researchers (e.g. Martin and Ek, 1984; Shifley and Brand, 1984; Vanclay, 1991), have applied variations of standard growth models like the Chapman-Richards, Bertalanffy, Weibull, Gompertz, logistic, and monomolecular designs to varying degrees of success, but these will not be discussed further because of their links to the work of Zeide (1989) and Zeide (1993). Of the growth models evaluated, Zeide (1993) determined the basic equation forms (reduced versions of most of the designs considered) called the ‘power decline’ (PD) and ‘exponential decline’ (ED) most effectively fit the data:

$$\text{PD: } \frac{d\text{DBH}}{dt} = k\text{DBH}^p a^q \quad (5)$$

and

$$\text{ED: } \frac{d\text{DBH}}{dt} = k\text{DBH}^p e^{qa} \quad (6)$$

where a is current tree age and k , p , and q are species-specific fitted regression coefficients ($k > 0$; $p > 0$, and $q < 0$). These models differ from the ones discussed earlier in this paper in that they are not associated with some measure of resource availability. The equations evaluated by Zeide all share a trend of declining increment potential over time, but require that tree age be known, which is not always available in large forest inventories.

Other approaches to optimal increment have included cross-sectional-, volumetric-, or biomass-based designs. Phipps (1979) produced a growth model based on his earlier work with constant area increment (Phipps, 1967) that predicted annual growth ring width as a function of climate, moisture, and competition. Pan and Raynal (1995) approached increment from a volumetric perspective, in which whole tree volume production was sensitive to earlier growth performance, fertilization, and climate. Maximal growth under either of these designs could be determined if the factors influencing performance were assumed to be optimal. Chertov (1990) created an individual tree model for Scots pine (*Pinus sylvestris* L.) that

constrained optimal biomass growth (I_{bio}) through shading, water supply, or available nitrogen:

$$\frac{dI_{\text{bio}}}{dt} = \min_2\{I_{\text{pe}}, I_{\text{pn}}\} \quad \text{with } I_{\text{pe}} = \alpha K_{\text{E}} B_1 k_{\text{w}}$$

$$\text{and } I_{\text{pn}} = N_{\text{m}}/n_{\text{p}} \quad (7)$$

where α is the biological productivity of needles, K_{E} is a shading coefficient, B_1 is the tree’s needle mass, k_{w} is a value for a simple account of water supply, N_{m} is the available nitrogen in the soil, and n_{p} is the specific consumption of nitrogen. While this subset of growth models represent interesting ecological approaches, they do not readily translate into diameter increment, which is the driving feature of most forest dynamics models. These designs are presented, however, to show that alternative optimal formulations are conceivable and applicable, given the intent of the project.

As can be seen from this sample of optimal growth models, a number of possibilities exist. However, the application of these commits the user to a set of assumptions on diameter increment and growth-modifying factors that may be inappropriate, or could require data (like age) that may not be available. The objective of this paper is to outline a procedure to calculate potential relative increment (PRI, the maximum possible incremental change of a species at a given diameter) in a relatively simple manner independent of age or the factors used to evaluate environmental favorability. This system can then be combined with the appropriate environmental modifiers into a comprehensive diameter growth model capable of predicting increment changes under a variety of scenarios.

2. Methods

2.1. Deriving PRI

The US Forest Service has collected tree and site information for several decades as a part of their Forest Inventory and Analysis (FIA) program. Data are obtainable for most states (and frequently over several remeasurement periods),

allowing the PRI process to be implemented on virtually every commercial tree species in the US. This paper is based on data gathered from state inventories (primarily from Michigan, Minnesota, and Wisconsin) incorporated in the Eastwide Forest Inventory Data Base (EFIDB; Hansen et al., 1992). Species nomenclature follows Harlow et al. (1979) (Table 1).

For all individuals showing some growth (when $DBH_t > DBH_{t-1}$) from each of 24 target species, 5 year actual relative increment (ARI) was calculated from remeasured DBH for each tree:

$$ARI = \frac{DBH_t - DBH_{t-1}}{DBH_{t-1}} P \quad (8)$$

where DBH_t is current tree diameter, DBH_{t-1} is the diameter at the earlier inventory, and P is the remeasurement interval standardization factor (used to adjust ARI into a periodic increment).

Eq. (8) is a version of a simple interest formula (Avery and Burkhart, 1983) that has been earlier applied to calculate tree growth and represents the proportional change in diameter. The ARI values were then classified by DBH_{t-1} and the highest value for every 2 cm DBH class of each species was selected (Fig. 1a). Since the data were collected from several states over 10–15 year for thousands of individuals, it was assumed the highest ARI values represented trees growing at near-optimal conditions. This is a conservative estimate of maximum potential growth rates, as even with the large sample available from the EFIDB there are likely more favorable conditions possible.

A power function was then fit to the maximum ARI data (Fig. 1b) to provide an equation for PRI, which represents the maximum possible growth rate for species at a given DBH:

Table 1

Species for which maximum potential growth rate equations were derived, including the sample sizes (n) gathered from the Eastwide forest inventory database (Hansen et al. 1992)

Common name	Species	Species code	FIA code	n
Balsam fir	<i>Abies balsamea</i> (L.) Mill.	ABIBAL	12	8970
Red maple	<i>Acer rubrum</i> L.	ACERUB	316	10 271
Sugar maple	<i>Acer saccharum</i> Marsh.	ACESAC	318	12 008
Yellow birch	<i>Betula alleghaniensis</i> Britton	BETALL	371	1870
Paper birch	<i>Betula papyrifera</i> Marsh.	BETPAP	375	10 029
White ash	<i>Fraxinus americana</i> L.	FRAAME	541	1002
Black ash	<i>Fraxinus nigra</i> Marsh.	FRANIG	543	6282
Eastern larch	<i>Larix laricina</i> (Du Roi) K. Koch	LARLAR	71	3960
Eastern hophornbeam	<i>Ostrya virginiana</i> (Mill.) K. Koch	OSTVIR	701	998
White spruce	<i>Picea glauca</i> (Moench) Voss	PICGLA	94	2059
Black spruce	<i>Picea mariana</i> (Mill.) B.S.P.	PICMAR	95	7913
Jack pine	<i>Pinus banksiana</i> Lamb.	PINBAN	105	4460
Red pine	<i>Pinus resinosa</i> Ait.	PINRES	125	4787
Eastern white pine	<i>Pinus strobus</i> L.	PINSTR	129	3111
Balsam poplar	<i>Populus balsamifera</i> L.	POPBAL	741	3738
Bigtooth aspen	<i>Populus grandidentata</i> Michx.	POPGRA	743	3292
Quaking aspen	<i>Populus tremuloides</i> Michx.	POPTRE	746	21 859
Pin cherry	<i>Prunus pensylvanica</i> L.	PRUPEN	761	107
Black cherry	<i>Prunus serotina</i> Ehrh.	PRUSER	762	1353
Northern red oak	<i>Quercus rubra</i> L.	QUERUB	833	6906
Northern white-cedar	<i>Thuja occidentalis</i> L.	THUOCC	241	11 141
American basswood	<i>Tilia americana</i> L.	TILAME	951	5276
Eastern hemlock	<i>Tsuga canadensis</i> (L.) Carr.	TSUCAN	261	1739
American elm	<i>Ulmus americana</i> L.	ULMAME	972	1822

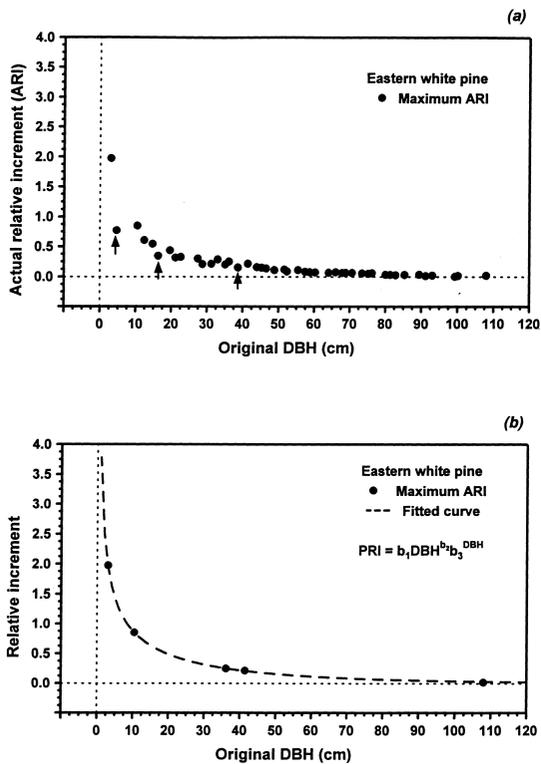


Fig. 1. A nonlinear regression curve fit to increment data for eastern white pine after a subset of maximal ARI values was selected (a). The arrows indicate individuals apparently growing at suboptimal rates (b); which were eventually eliminated as outliers.

$$PRI = b_1 DBH_t^{b_2} b_3^{DBH_t} \quad (9)$$

where b_1 , b_2 , and b_3 are species-specific regression coefficients. The PRI equations were fit iteratively, so that maximal ARI points from specific DBH classes could be dropped under three specific conditions. First, if a point represented an obvious deviation resulting from EFIDB sampling or reporting errors, it was discarded from the maximum ARI data. Second, if a maximal ARI point was noticeably lower than adjacent classes, it was removed from further analysis (arrows, Fig. 1a). Finally, to ensure that prediction errors in upper diameter ranges were minimized, PRI equations were fit closely to the maximum ARI scores for large trees by carefully selecting which optimal points in the smaller diameter classes were retained to achieve optimal regression leverage.

2.2. Analysis of trends and evaluation of the PRI methodology

To determine if there was a relationship between shade tolerance and optimal diameter increment, species shade tolerance scores (adapted from Graham 1954) were compared with PRI values calculated for 20 and 100 cm trees. These size classes were selected because they represented individuals growing during some of the fastest (20 cm DBH) and slowest (100 cm DBH) periods of the tree's life. It was also anticipated that ontogenetic growth patterns would be different for each species, so that those growing most rapidly when smaller may not do so at larger sizes.

Error sensitivity analysis for the PRI methodology was performed by adding $\pm 50\%$ noise to the optimal PRI equation of eastern white pine (*Pinus strobus* L.). This should allow for anticipation of errors arising from a consistent bias in the derivation of the PRI equations, assuming that there is a systematic under- or over-estimation of the fitted curves. Other sources of error will also be discussed in the context of the sampling system and their likelihood to influence the final fitted equations.

For evaluative purposes, optimal 5 year growth response curves for eastern white pine calculated with the PRI method and JABOWA-II (Botkin, 1992) were compared. To derive eastern white pine growth using JABOWA-II, several parameters are required; $G = 141.2$, maximum species diameter ($DBH_{max} = 101$ cm), height ($HT_{max} = 4570$ cm), and age ($AGEMAX = 450$ year) (these were taken from Botkin 1992, p. 56). To further ensure consistency with Botkin (1992), his equation and coefficients to calculate eastern white pine height were also used. Differences in predicted optimal performance were analyzed for their ecological and modeling significance. In addition, a series of constant environmental qualities was applied across the range of diameters (optimal growth, 75% of optimal growth, 50% of optimal growth, 25% of optimal growth, and 5% of optimal growth) to allow for assessment of less-than-ideal growing conditions.

3. Results and discussion

3.1. Regression results

The derivation process resulted in a series of highly significant non-linear regressions (Table 2). Since the intent was to fit an optimal growth curve, the vast majority of ARI values extracted from the EFIDB were eliminated before the final regression. Out of the initial 134 881 individuals sampled from all species, only 208 were actually used to fit the curves (an average of < 9 trees per species). The number of final ARI points by species varied from as few as 3 for pin cherry (*Prunus pensylvanica* L.) to 26 for northern white-cedar (*Thuja occidentalis* L.). The small number of points and the nature of their selection also meant that very little unexplained variation remained for the final regression; R^2 for all species exceeded 0.99 (Table 2). Remember that this is not an

exploratory regression on randomly sampled data, but a deliberate fitting of curves on points selected for their optimal properties, so it is desirable to maximize the precision of the fit. The small final sample sizes should not detract from the reality that tens of thousands of individuals were compared before the end subsets were selected.

3.2. Size-based PRI trends

As expected, species displayed variability in their optimal growth rate (Table 3), with both the 20 and 100 cm DBH PRI scores experiencing substantial dispersion. For the smaller-sized trees (Fig. 2), no statistically significant relationship with shade tolerance was observed ($P = 0.472$). Fig. 3 compares shade tolerance scores with PRI values calculated for 100 cm DBH trees, and once again no statistically significant trend appeared ($P = 0.219$). While some differences in growth re-

Table 2
Fitted potential relative increment (PRI) values by species using Eq. (9)

Species code	b_1	b_2	b_3	n^{*a}	R^2
ABIBAL	2.647020	-0.407958	0.960849	4	0.99997
ACERUB	1.140840	-0.205275	0.977239	4	0.99984
ACESAC	3.521235	-0.798720	0.992414	5	> 0.99999
BETALL	3.119630	-0.784164	0.981528	4	0.99994
BETPAP	2.720950	-0.531016	0.957917	6	0.99962
FRAAME	1.120796	-0.131123	0.970378	6	0.99918
FRANIG	2.773833	-0.703376	0.988433	5	0.99936
LARLAR	3.083610	-0.575280	0.958235	15	0.99525
OSTVIR	4.704480	-1.169317	0.999568	5	0.99876
PICGLA	2.719344	-0.488217	0.975665	7	0.99930
PICMAR	2.699954	-0.786279	0.976055	23	0.99102
PINBAN	4.620040	-0.711505	0.963997	8	0.99982
PINRES	3.292640	-0.358137	0.952945	16	0.99938
PINSTR	3.856766	-0.553002	0.979675	5	0.99994
POPBAL	2.353684	-0.640520	0.989087	5	0.99792
POPGRA	2.977480	-0.539113	0.969068	13	0.99868
POPTRE	4.847405	-0.506860	0.965699	6	0.99972
PRUPEN	5.056000	-0.654914	0.947614	3	0.99909
PRUSER	2.390857	-0.443928	0.969318	6	0.99758
QUERUB	2.241167	-0.506656	0.983046	6	0.99997
THUOCC	1.925890	-0.419270	0.959847	26	0.99832
TILAME	3.467596	-0.616009	0.982476	5	0.99993
TSUCAN	1.749000	-0.436216	0.968043	19	0.99828
ULMAME	2.747876	-0.351470	0.966604	6	0.99974

^a n^* , number of points actually used in the final regression. R^2 values are for the subset of points used in the final regression fitting.

Table 3

Predicted 5 year optimal growth rate (in cm) and potential relative increment for species at 20 and 100 cm DBH (shade tolerance scores adapted from Graham (1954))

Species	Shade tolerance score	PRI 20 cm DBH	Optimal growth rate (in cm) @ 20 cm DBH	PRI 100 cm DBH	Optimal growth rate (in cm) @ 100 cm DBH
ABIBAL	9.8	0.3508	7.0	0.0075	0.7
ACERUB	5.9	0.3892	7.8	0.0443	4.4
ACESAC	9.7	0.2763	5.5	0.0415	4.2
BETALL	6.3	0.2051	4.1	0.0131	1.3
BETPAP	1.0	0.2346	4.7	0.0032	0.3
FRAAME	5.0	0.4147	8.3	0.0303	3.0
FRANIG	2.4	0.2672	5.3	0.0340	3.4
LARLAR	0.8	0.2344	4.7	0.0031	0.3
OSTVIR	9.5	0.1404	2.8	0.0207	2.1
PICGLA	6.8	0.3849	7.7	0.0244	2.4
PICMAR	6.4	0.1577	3.2	0.0064	0.6
PINBAN	1.8	0.2633	5.3	0.0045	0.4
PINRES	2.4	0.4295	8.6	0.0051	0.5
PINSTR	4.4	0.4880	9.8	0.0388	3.9
POPBAL	0.7	0.2774	5.5	0.0411	4.1
POPGRA	0.7	0.3159	6.3	0.0107	1.1
POPTRE	0.7	0.5283	10.6	0.0143	1.4
PRUPEN	0.7	0.2423	4.8	0.0011	0.1
PRUSER	2.4	0.3391	6.8	0.0137	1.4
QUERUB	5.2	0.3490	7.0	0.0393	3.9
THUOCC	5.0	0.2416	4.8	0.0046	0.5
TILAME	8.2	0.3846	7.7	0.0347	3.5
TSUCAN	10.0	0.2473	4.9	0.0091	0.9
ULMAME	4.0	0.4861	9.7	0.0182	1.8

sponse are probably related to shade tolerance, species-based differences appear to dominate growth performance (see Pacala et al. 1996).

Rather than displaying curves for every taxon, a subset of conifers and hardwoods was selected across the range of shade tolerance scores to illustrate differences. The conifer group included jack pine (*Pinus banksiana* Lamb.) (very intolerant), eastern white pine (mid-tolerant), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) (very tolerant), while the chosen hardwoods included quaking aspen (*Populus tremuloides* Michx.) (very intolerant), yellow birch (*Betula alleghaniensis* Britton) (mid-tolerant), and sugar maple (*Acer saccharum* Marsh.) (very tolerant). Potential relative increment responses (Fig. 4) formed declining monotonic curves for both conifers and hardwood species, reaching maximum PRI at the smallest diameters (to accentuate differences in PRI between species, they have been plotted on a log

scale). This is an intuitive result, as it is easier for a very small diameter tree to double or even triple its DBH in 5 year than even a slightly larger stem. One of the most important features of the PRI method is that while PRI approaches zero, it never actually reaches this asymptote (keeping in mind that Fig. 4 is on a log scale and does not use zero as the base value of the y -axis). Most other optimal growth models enforce a zero increment upper bound. Gap models, for e.g. experience no tree growth when $DBH \times HT \geq DBH_{\max} \times HT_{\max}$, and therefore have an artificially constrained maximum possible size.

The rapid decline in PRI value with diameter for all species indicates that relative growth rates drop appreciably with increasing tree size (especially for a species like jack pine). This reflects the limitations expressed by Phipps (1967) and restated by Pacala et al. (1993) and Pacala et al. (1996) that large trees experience disproportion-

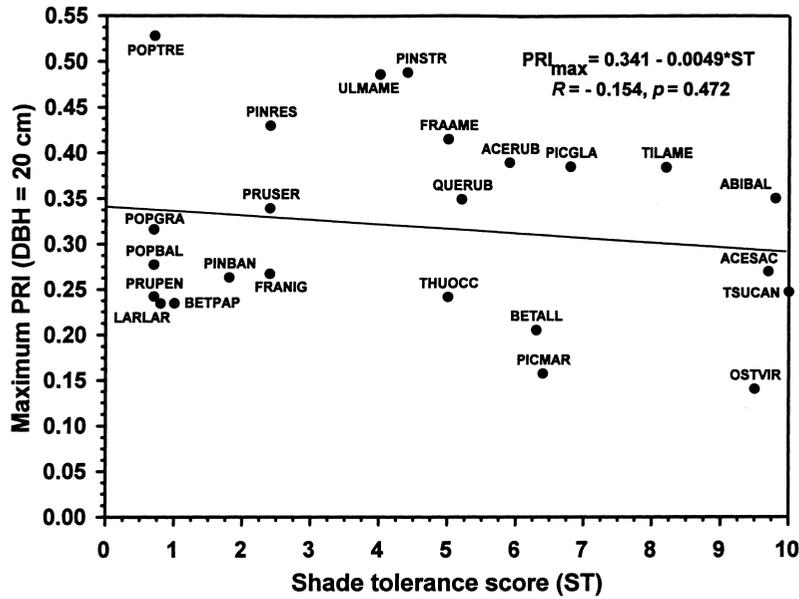


Fig. 2. Maximum PRI values for 20 cm DBH trees as a function of species and shade tolerance score (see Table 3 for species codes). The trend indicated by the solid line is not statistically different from zero.

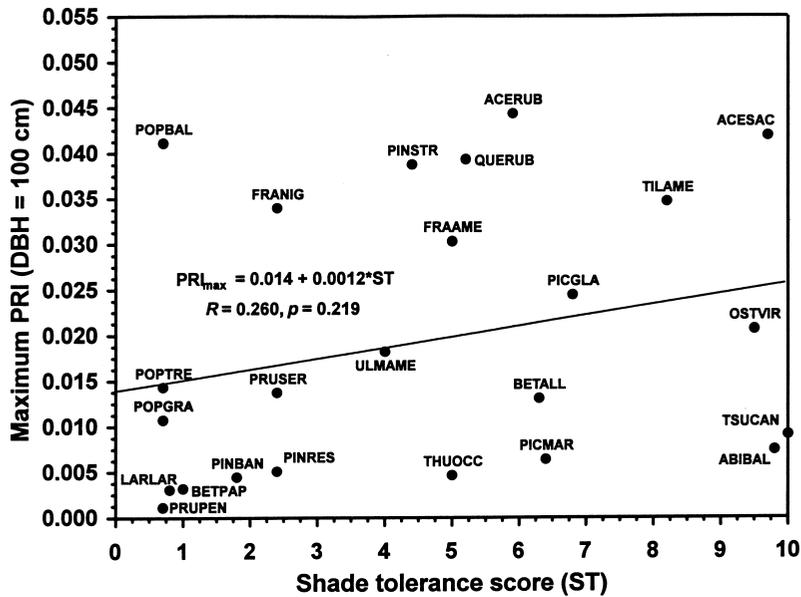


Fig. 3. Maximum PRI values for 100 cm DBH trees as a function of species and shade tolerance score (see Table 3 for species codes). As with Fig. 2, the trend indicated by the line is not statistically different from zero.

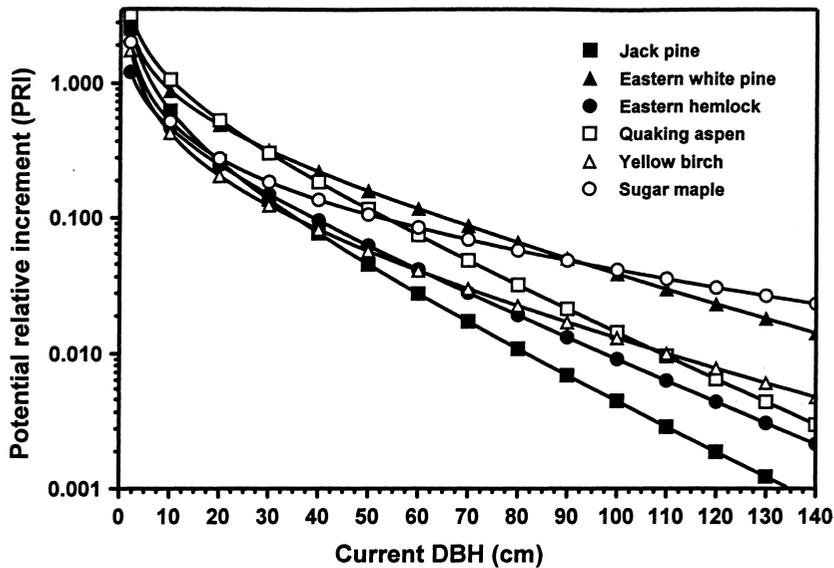


Fig. 4. PRI predictions for conifers and hardwoods of various shade tolerance. Maximum PRI is reached at the smallest diameters with PRI tapering off with increasing tree size.

ately lower rates of diameter change than small trees even though the actual basal area increment may remain fairly constant. What primarily distinguishes the response curves of individual species appears to be the initial PRI rates (i.e. the rate of change of the smallest measured trees; in this case, those ca. 2.5 cm DBH) and the slope of the curves throughout the rest of the diameter range.

3.3. Translation to 5 year optimal diameter increment

Multiplying the PRI equation by the current DBH yields optimal periodic diameter growth (Fig. 5). Note that most species add optimal diameter increment following skewed unimodal curves with maximum diameter growth occurring not at the largest PRI values but at somewhat reduced ones (compare with Fig. 4). Optimal growth is actually the product of PRI and current DBH, so that a slightly smaller PRI score multiplied by a substantially larger DBH yields a considerably greater optimal increment. Table 3 provides a listing of both PRI and optimal diameter growth for the species of interest at 20 and 100

cm DBH. As can be seen in this table, some species grew most rapidly when relatively small while others distinguished themselves at large size classes. At 20 cm DBH, most species were capable of growing at least 2.8 cm in diameter over a 5 year period. Quaking aspen has the potential to add the most diameter over 5 year (10.6 cm for 20 cm individuals under optimal conditions), followed by eastern white pine (9.8 cm), American elm (*Ulmus americana* L.) (9.7 cm), and red pine (*Pinus resinosa* Ait.) (8.6 cm). For 100 cm trees, the most rapidly growing species shifted to red maple (*Acer rubrum* L.) (4.4 cm), sugar maple (4.2 cm), balsam poplar (*Populus balsamifera* L.) (4.1 cm), and eastern white pine and northern red oak (*Quercus rubra* L.) (both at 3.9 cm).

Due to the design of the PRI (Eq. (9)), all species are capable of adding diameter throughout their size range. However, as can be seen in Table 3, a number of species grow very little at large diameters. Some of these species never reach 100 cm DBH in nature, so projecting their increments at this stage is strictly an artifact. The capacity of other species to potentially grow rapidly even at very large sizes may reflect their ability to efficiently utilize available resources under optimal

conditions. This, coupled with the predisposition of some species to slow their growth as they age (due to genetics or other constraints arising from structural integrity or defense against attack), contributed to the disparity in growth performance between species.

3.4. PRI error sensitivity

There are two primary sources of error in the PRI methodology. The first (errors in the data) has already been mentioned in the context of outlier detection in the ARI derivations of eastern white pine. Discrepancies are especially problematic if they occur for small diameter trees, as this tends to greatly exaggerate PRI maximums. The second major source of error occurs when inadequate samples are available for certain size ranges (errors of omission). This could result in suboptimal growth conditions determining the nature of the curves, and is most frequent for the largest size classes where relatively few measurements are available. While it is very difficult to account for either type of error, recognizing that there are conditions under which the trajectories can be

improperly influenced can allow data sets to be optimized post-hoc. Assuming that all problematic data points were removed from the eastern white pine set, the biggest residual source of error lies in missing data ranges. Fortunately, the region of greatest diameter increment sensitivity (roughly from 15 to 60 cm DBH, Fig. 6a) for eastern white pine (and most species), also typically envelops the area of the highest sample frequency (Fig. 6b). In the case of eastern white pine, almost 80% of all samples fell within this range, making it less likely that optimal conditions would be underestimated. However, only slightly more than 8% of all eastern white pine samples were taken from trees > 60 cm DBH, and this is likely the region with the greatest potential for error.

There are some other potential dangers inherent to any regression model. Extrapolating beyond the range of sample data could prove to be a serious problem for diameter increment prediction due to the paucity of very small and very large diameters. Even a slight error in determining PRI values is greatly magnified because of the way increment is determined ($PRI \times DBH$). About

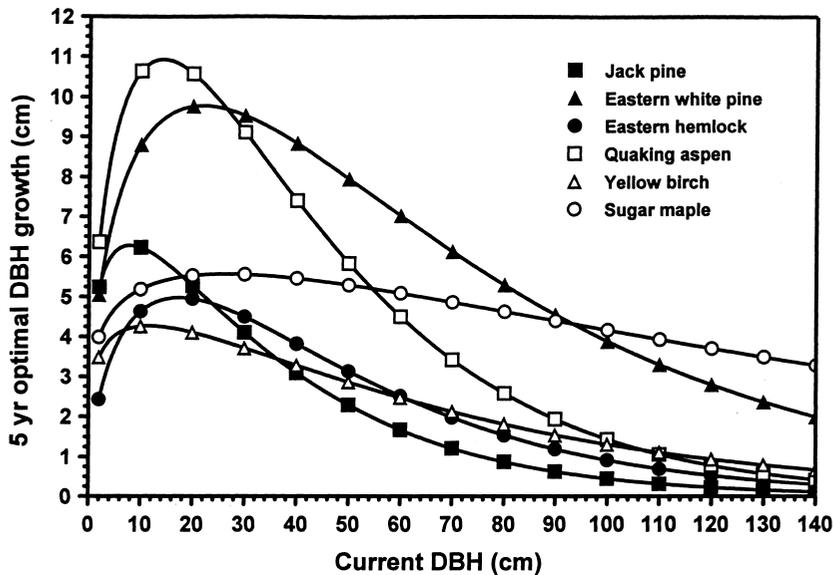


Fig. 5. Converting PRI rates into actual 5 year optimal diameter increment yielding multiple patterns for both conifers and hardwoods. The shift in maximum values results from the nature of growth calculation; larger trees with slightly lower PRI rates generate greater potential diameter increment.

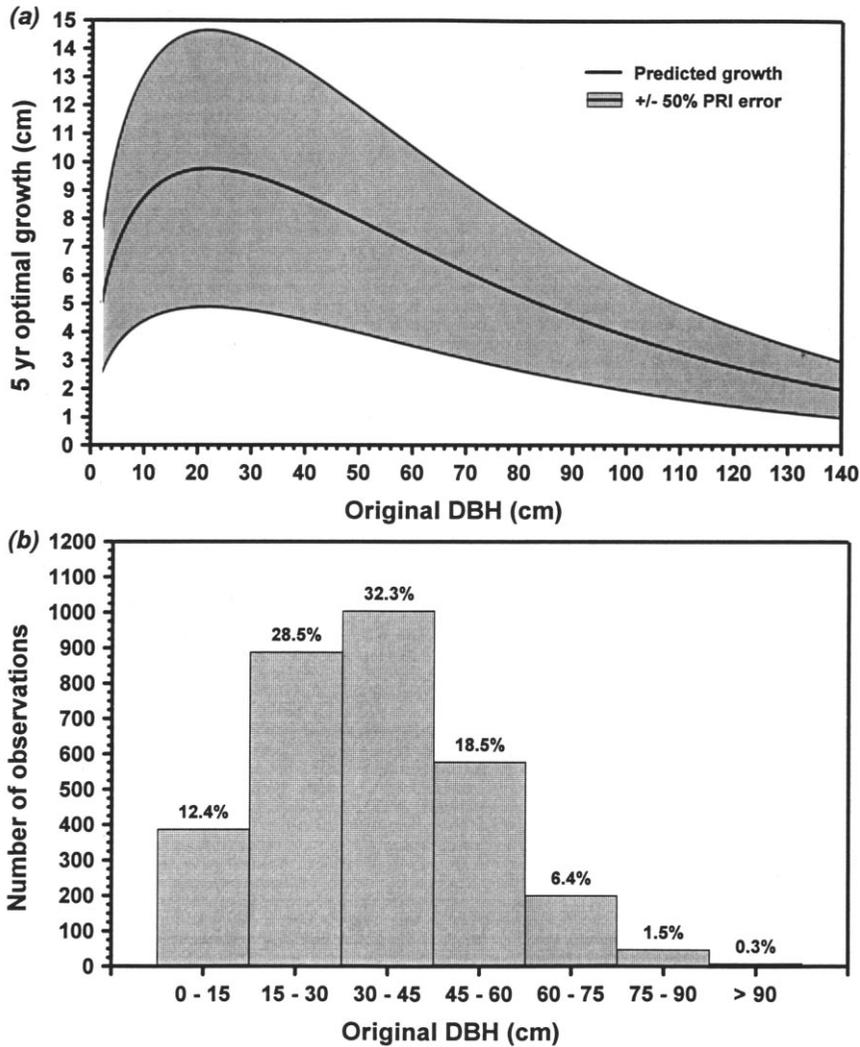


Fig. 6. (a) Error sensitivity (hatched region) of the equation for eastern white pine (solid line). The greatest absolute potential for error (± 5 cm) in predicting eastern white pine optimal growth lies in the 15–60 cm DBH portion of the size distribution, tapering off in both directions. Errors of omission are probably more frequent in the upper diameter classes (those > 60 cm), as they constitute only a small fraction (8%) of the total sample (b).

50% PRI error for large (140 cm) eastern white pines is only ± 0.0037 PRI, which would translate into ± 0.51 cm in optimal DBH growth, while a change of ± 0.0037 PRI at 20 cm DBH would only yield an error range of ± 0.07 cm. Fitting the curves closely to the upper diameter classes further added to the conservative nature of the PRI method, as it reduces optimal increment of large individuals. Another risk comes with the lack of inventory data for some species. While

most species had > 1000 individuals to extrapolate from, only a few dozen pin cherries were extracted from the Michigan, Minnesota, and Wisconsin databases (I recommend at least 100 individuals per species for PRI analysis). When these were processed, the equation for pin cherry predicted unreasonably slow growth at all size classes. Fortunately, additional pin cherry records from several other states (Pennsylvania, New York, and West Virginia) were available and in-

cluded for reanalysis (resulting in a more appropriate set of coefficients). However, species with more restricted distributions and/or limited inventory records could theoretically be represented only by a handful of individuals experiencing conditions far from optimal, and thus produces PRI equations that substantially underestimate actual species productivity. If this is the case, then a different approach to at least the field collection of the necessary inventory information is warranted.

3.5. Comparisons of projected eastern white pine growth from two different models

Both PRI and JABOWA-II predicted the most rapid eastern white pine growth rate at relatively small tree diameters (Fig. 7), though the PRI design estimates maximal increment at a smaller diameter (ca. 20 cm DBH vs. ca. 25 cm DBH). The JABOWA-II design predicts a rapid increase in size until the maximum growth rate is reached, after which it declines fairly slowly until the tree is

ca. 101 cm DBH (when $DBH \times HT \approx DBH_{max} \times HT_{max}$). The PRI method differs in the shape of the response curve and the taper of the upper reaches of projection, with much higher predicted optimal diameter increment than JABOWA-II. This is largely a function of the relatively long time period (450 year, a reasonable estimate of species longevity) JABOWA-II uses to define eastern white pine growth to DBH_{max} (101 cm), which limits the ability of the species to grow rapidly. Furthermore, unlike the JABOWA-II design, PRI does not have an absolute maximum diameter to bound growth and does not require the assumption of zero increment at the species maximum diameter. This better fits with ecological reality, where there is no artificial horizon to limit the ability to predict diameter increment.

However, optimal diameter growth is rarely achieved. Most individuals experience a less than ideal environment that limits their ability to reach maximum increment. Fig. 8 displays the expected growth rates under a range of environmental conditions for both the PRI and JABOWA-II diame-

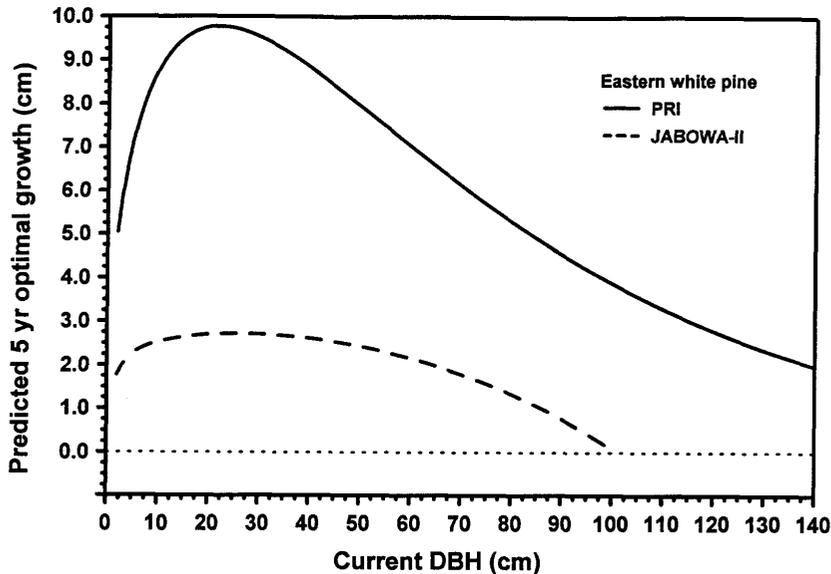


Fig. 7. Comparison of 5 year optimal eastern white pine diameter growth between the PRI methodology and the growth equation in JABOWA-II. PRI predicts optimal growth at a smaller diameter (ca. 20 cm) than JABOWA-II (ca. 25 cm). The PRI methodology anticipates both higher absolute maximal increments (ca. 9.8 cm for PRI versus ca. 2.6 cm for JABOWA-II) as well as across the entire diameter range. The JABOWA-II design also requires an absolute upper size limit, a restriction that does not occur with the PRI methodology.

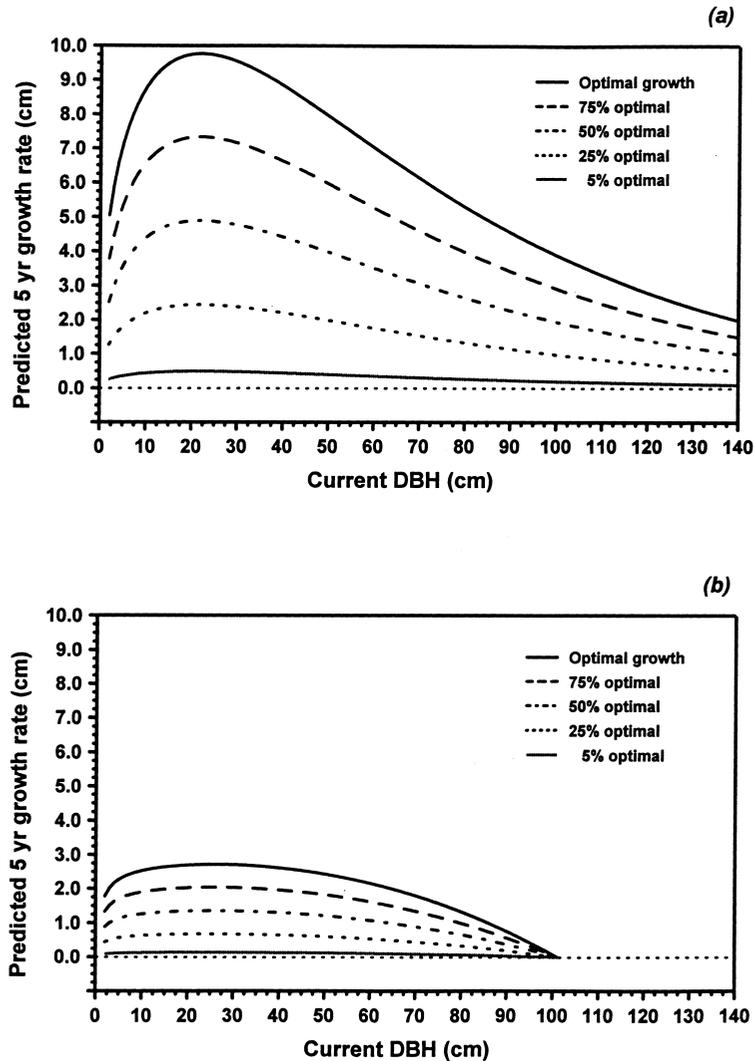


Fig. 8. Five year growth rates for eastern white pine growing under different environments under both the (a) PRI and (b) JABOWA-II models. Under very poor environments ($< 5\%$ optimal), both PRI and JABOWA-II have similar growth patterns, a trend that changes under increasingly favorable conditions.

ter increment predictions. While the PRI and JABOWA-II formulations differ relatively little at very poor conditions, the overall trends to the optimal curves are retained under most circumstances. The ecological ramifications of these differences are substantial. PRI predicts approximately the same increment at 25% of optimal conditions that JABOWA-II does for optimal, which in turn would translate into vastly different growth perfor-

mance for a given individual. Since the JABOWA-II approach is constrained to fit a tree's performance between its initial size and the maximum possible assumed for an individual of maximum age, it is forced to reduce growth at intermediate diameters to ensure that maximum DBH is not reached before its maximum age.

Predicting optimal diameter growth should not require the user to accept constraints based on

questionable ecological foundations. Assigning zero growth and upper size limitations has little basis in theory or reality. More problematic than artificial upper bounds is the constraining impact of metering a finite size over an arbitrary time period. Underestimating growth at the most commonly occurring diameters will significantly influence simulated forest dynamics, which in turn will obscure issues related to stand development. This is especially true in models that rely upon accurate growth estimation to help evaluate treatment effects.

3.6. *Further pros and cons to the PRI method*

The development of a reliable optimal growth curve represents one of the first critical stages in the design of a mechanistic simulation model of forest dynamics; it must be capable of accurately projecting tree growth given the potential of the species and the environmental conditions present. The PRI methodology should prove useful when estimating diameter growth. Its optimal diameter increment curve is very similar to other empirical efforts (e.g. Shifley and Brand, 1984; Vanclay, 1991; Larocque, 1998). Furthermore, the 5 year optimal DBH growth rates shown in Table 3 are comparable to maximum growth rates noted in other sources (e.g. Burns and Honkala, 1990a,b). However, as mentioned earlier, translating optimal growth rates to actual growth rates relies on accurate portrayal of the environmental modifiers.

The empirical nature of PRI derivation has both benefits and problems. While admittedly conservative, the ability to sample very large numbers of trees (almost 135 000 for this study from 24 species) across a broad range of environmental conditions is considerably greater than the small field sampled sets or inferences from other published works often used for this purpose. However, the lack of detail in the originating data sets makes it virtually impossible to reconstruct what actually causes suboptimal growth rates, and there is no guarantee how close the points chosen as indicative of the maximal growth curve fall to the true optimal horizon (even using a data set extracted from a very large area). It is also possible that local selection pressures have influenced

the responsiveness of individuals to their environment, suggesting regional growth curves may need to be fit to avoid biasing the process.

4. Conclusions

The PRI method described in this paper permits the derivation of optimal growth curves for scores of species. Fulfillment of this goal does not necessarily require extensive (and expensive) field sampling, but can be achieved by extracting the information from existing public databases. This system allows for the ‘sampling’ of hundreds to thousands of individuals across broad geographic regions, which in turn encompasses a range of environmental conditions and tree sizes rarely sampled before. While more extensive than most sampling schemes, PRI retains a measure of conservativeness in that it cannot represent the most optimal combinations of conditions under all scenarios, and thus the fitted curves are actually lower than true species optima. The current implementation of PRI (requiring the extraction of diameter data from repeat inventories) necessitates large sample sizes in order to minimize systematic errors in model fitting, but this is not a major issue for most common species in the eastern US.

The PRI system also represents a conceptual improvement in optimal diameter growth modeling. Vanclay and Skovsgaard (1997) recommended a five-point checklist for forest growth modelers (1) the design should be logical and agree with conventional bio-logic; (2) model statistical properties should be valid; (3) model error should be characterized; (4) residuals should be considered; and (5) sensitivity analyses should be performed. With the exception of point (4), optimal increment models that prove robust under these conditions should benefit forest simulation. This paper provides an evaluation of the PRI methodology in this context, and indicates how the system performs given the information available. As convenient as some purely theoretical formulations may be, the ability to correlate growth performance with actual field measurements allows for some measure of certainty to be

incorporated. PRI does not involve the enforcement of an upper diameter limit (for which there is no basis in forest ecology) nor does it bias diameter increment performance of intermediate-sized individuals in order to maintain a specific curve shape and phenology. The capacity to estimate optimal tree diameter growth represents a critical stage in the development of many forest dynamics models, and since this feature has a strong influence on the events that determine the eventual success (i.e. reliability) of the predictions, maximizing ecological reality goes a long way towards ensuring confidence in the results.

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