Biological growth functions describe published site index curves for Lake States timber species—Allen L. Lundgren
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"Is it of trees you tell, their months and virtues ...?" 1

Published site index curves for Lake States timber species are widely used to identify potential site productivity based on the height and age of existing trees. In the absence of height-growth functions, they are also used to estimate height-growth of trees and stands. For example, Buckman (1962) and Lundgren (1965) used site index curves by Gevorkiantz (1957e) to estimate height-growth of red pine, assuming that the average tree in a stand would follow the heights traced by the site index curves at various ages.

Both uses require reading values from curves on a graph, and interpolating between lines for those ages, heights, and site indexes not specifically shown. Such readings are tedious and subject to human error, particularly when many readings must be made. Further, repeat readings for the same points may be inconsistent because of the human judgment necessary in interpolation.

To overcome these difficulties and to facilitate using this information in computers, two types of biological growth functions representing height as a function of age and site index have been fitted to 11 published site index curves available for Lake States timber species. In developing these functions, the goal was to closely reproduce existing curves by a convenient mathematical expression. The object was not to replace existing site index curves, but to supplement them with a mathematical function and a convenient table of height factors.

Several mathematical functions have been used to represent site index curves (Stage 1963). Because the available data of height over age are related to growth (although in a somewhat contrived way), biological growth functions appear more appropriate than, say, polynomials. We chose to use two versions of a biological growth function, the monomolecular curve (Richards 1959), to represent height as a function of site index and age.

THE EXPONENTIAL-MONOMOLECULAR FUNCTION

The first and more complex form of the monomolecular function we call the exponential-monomolecular function. The equation form considered was:

\[ H = b_1 S \left( 1 - e^{b_2 A} \right)^{b_3} \]

where \( H \) = Total height of tree in feet

\( S \) = Site index (height at age 50 years)

\( A \) = Age in years

and \( b_1, b_2, b_3 \) are parameters to be estimated

\( e \) = base of the natural logarithms

1 From TO JUAN AT THE WINTER SOLSTICE by Robert Graves, by permission of Collins-Knowlton-Wing, Inc. Copyright © November 1945 by Robert Graves.
The choice of this function was a compromise between simplicity of calculation, both in obtaining the parameters and using the function to estimate heights, and accuracy of fit over a wide range of tree ages. It is similar to the average height-age function used by Brickell (1968). This function has the desirable S-shape with a height of zero at age zero. It specifies that the height at any given age is proportional to site index. It does not specify that the height at age 50 must exactly equal the site index, but the error in predicted height at age 50 never exceeds 0.6 feet for the species considered here. When \( b_2 \) is negative and \( b_3 \) is positive, as they are here, then as age increases height approaches an upper limit of \( b_1 S \).

The parameters \( b_1, b_2, \) and \( b_3 \) were estimated for each species by least squares techniques using a modified form of TARSIER, a nonlinear regression program (Atkinson 1966). The equation was fitted to heights read to the nearest foot from the published site index curves for each species over the range of ages and sites given. Thirty to 60 readings were made for each species.

The data source, range of ages, and range of site indexes for each species considered are given in table 1. For each species the values of the three estimated parameters \( b_1, b_2, \) and \( b_3, \) the \( R^2 \) value, the standard error, and the maximum error of individual observations were obtained by fitting the equation to the observed readings (table 2). Keep in mind that these apply only to the readings made from the curves and not to the data underlying the curves.

As an example, the height equation for red pine is:

\[
H = 1.890 S (1-e^{-0.01979 A})^{1.3892}
\]

For a site index of 60, the height at age 30 would be:

\[
H = 1.890 (60) (1-e^{-0.01979 (30)})^{1.3892} \\
= 113.4 (1-e^{-0.5937})^{1.3892} \\
= 37.14 \text{ feet}
\]

Rounded to the nearest foot, this is exactly the reading of 37 feet obtained from the published site index curves.

The annual height growth (\( \Delta H \)) at any age on a given site can be closely estimated by the first partial derivative of the height equation with respect to age.

\[
\Delta H = \frac{\partial H}{\partial A} = b_1 b_2 b_3 (1-e^{b_2 A})^{b_3-1} S
\]

This equation predicts annual height growth for a given age and site. By substituting in the original equation for height, this height-growth equation can be reduced to a function of height and age:

\[
\Delta H \approx -b_2 b_3 (e^{b_2 A}-1)^{-1} H
\]

For red pine, the annual height growth estimated by this last equation would be:

\[
\Delta H \approx 0.027492 (e^{0.01979 A}-1)^{-1} H
\]

At age 30 the annual height growth of red pine would be:

\[
\Delta H \approx .034 H
\]

We have already seen that the height of a red pine tree at age 30
Table 1. — Species, data source, and range of ages and site indexes used in developing site index functions

<table>
<thead>
<tr>
<th>Species</th>
<th>Data source</th>
<th>Range of ages</th>
<th>Range of site index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red pine (Pinus resinosa)</td>
<td>Gevorkiantz (1957e)</td>
<td>20-120</td>
<td>40-70</td>
</tr>
<tr>
<td>Jack pine (Pinus banksiana)</td>
<td>Gevorkiantz (1956a)</td>
<td>20-80</td>
<td>30-70</td>
</tr>
<tr>
<td>White pine (Pinus strobus)</td>
<td>Gevorkiantz (1957d)</td>
<td>20-120</td>
<td>40-80</td>
</tr>
<tr>
<td>Balsam fir (Abies balsamea)</td>
<td>Gevorkiantz (1956c)</td>
<td>1/20-80</td>
<td>30-70</td>
</tr>
<tr>
<td>White spruce (Picea glauca)</td>
<td>Gevorkiantz (1957c)</td>
<td>1/20-120</td>
<td>30-80</td>
</tr>
<tr>
<td>Black spruce (Picea mariana)</td>
<td>Gevorkiantz (1957b)</td>
<td>20-120</td>
<td>20-60</td>
</tr>
<tr>
<td>Tamarack (Larix laricina)</td>
<td>Gevorkiantz (1957g)</td>
<td>20-120</td>
<td>20-60</td>
</tr>
<tr>
<td>White-cedar (Thuja occidentalis)</td>
<td>Gevorkiantz (1957a)</td>
<td>20-100</td>
<td>20-60</td>
</tr>
<tr>
<td>Aspen (Populus tremuloides)</td>
<td>Gevorkiantz (1956b)</td>
<td>20-80</td>
<td>40-80</td>
</tr>
<tr>
<td>Red oak (Quercus rubra)</td>
<td>Gevorkiantz (1957f)</td>
<td>20-120</td>
<td>40-70</td>
</tr>
<tr>
<td>Paper birch (Betula papyrifera)</td>
<td>Cooley (1958)</td>
<td>20-80</td>
<td>40-80</td>
</tr>
</tbody>
</table>

1/ Breast-height age.

on site index 60 is 37 feet. Using this height in the above equation we find that the expected annual height growth of a dominant red pine on site index 60 at age 30 is 1.3 feet per year.

Note that site index (S) can be calculated directly from an observation of height (Hobs.) at some observed age (Aobs.) by rearranging the height equation:

\[ S = H_{obs.} b_1^{-1} (1 - e^{b_2 A_{obs.}})^{-b_3} \]

This can be substituted back into the original equation to estimate the height (H) at any age (A) from one observed height and age determination in a stand:

\[ H = H_{obs.} (1 - e^{b_2 A_{obs.}})^{-b_3} (1 - e^{b_2 A})^{b_3} \]

The equations for all species except red oak and white spruce have a standard error of less than 1 foot. The maximum difference between observed and predicted heights for individual observations is less than 2 feet for all but these two species. Because it is difficult to read heights from these curves even to the nearest foot, maximum differences of less than 2 feet in using these functions to represent...
Table 2. – Parameters of the exponential-monomolecular function describing published site index curves

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameters</th>
<th>$\beta_1$</th>
<th>$\beta_2$</th>
<th>$\beta_3$</th>
<th>$R^2$</th>
<th>Standard error</th>
<th>Maximum error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red pine</td>
<td></td>
<td>1.890</td>
<td>-0.01979</td>
<td>1.3892</td>
<td>0.9994</td>
<td>0.64</td>
<td>1.4</td>
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<td>Jack pine</td>
<td></td>
<td>1.633</td>
<td>-0.02233</td>
<td>1.2419</td>
<td>0.9964</td>
<td>0.50</td>
<td>1.1</td>
</tr>
<tr>
<td>White pine</td>
<td></td>
<td>1.966</td>
<td>-0.02399</td>
<td>1.8942</td>
<td>0.9996</td>
<td>0.66</td>
<td>1.7</td>
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<tr>
<td>Balsam fir</td>
<td></td>
<td>1.437</td>
<td>-0.02266</td>
<td>0.9381</td>
<td>0.9985</td>
<td>0.69</td>
<td>1.9</td>
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<td>1.637</td>
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<td>0.9784</td>
<td>3.98</td>
<td>9.4</td>
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<td>Black spruce</td>
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<td>0.9993</td>
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<td>1.0895</td>
<td>0.9990</td>
<td>0.66</td>
<td>1.7</td>
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<td>Aspen</td>
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<td>1.480</td>
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<td>0.9377</td>
<td>0.9996</td>
<td>0.41</td>
<td>1.1</td>
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<td>Red oak</td>
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<td>-0.02179</td>
<td>1.0673</td>
<td>0.9955</td>
<td>1.42</td>
<td>4.5</td>
</tr>
<tr>
<td>Paper birch</td>
<td></td>
<td>1.598</td>
<td>-0.01938</td>
<td>0.9824</td>
<td>0.9998</td>
<td>0.32</td>
<td>0.6</td>
</tr>
</tbody>
</table>

1/ Height = $\beta_1$ (Site Index)$($1- e$^{\beta_2(Age)})^{\beta_3}$
2/ Maximum difference between observed and predicted heights over the range of data points analyzed (see table 1).
3/ This function is not recommended for white spruce.

the published site index curves should be acceptable. Most differences will be less than 1 foot.

The function for red oak can be used with confidence on all sites at ages below 90 years, and on sites from SI 50 to SI 65 at older ages. All differences between observed and predicted heights greater than 2 feet occurred only on the lowest and highest curves, and then only at ages of 90 years and older.

The ages given for balsam fir and white spruce are breast height ages; that is, the height for each of these two species at age zero is 4.5 feet. A revised function incorporating an added constant of 4.5 feet was fit to these two species. However, this revised function did not fit the balsam fir curves as well as did the original function and so was discarded.

We recommend using the original function for balsam fir, but only for stands at least 20 years old.

The revised function did give a slightly better fit for the white spruce curves, but both functions gave unacceptably large errors for all but the site index 60 curve. Neither function can be recommended for the published white spruce site index curves.

A SIMPLER MONOMOLECULAR FUNCTION

Most of the published site index curves examined here show heights only for ages 20 and older, and show no point of inflection. Thus the simple monomolecular function, which has no point of inflection, also appears appropriate for representing
these published curves.

The initial equation form considered was:

\[ H = S (a + b_1 e^{b_2 A}) \]

where \( H \) = height in feet
\( S \) = site index (height at 50 years)
\( A \) = age in years

and \( a, b_1, b_2 \), are parameters to be estimated.

This equation provides that the height at any given age is proportional to site index. When \( b_1 \) and \( b_2 \) are negative, as they are here, then as age increases, height approaches an upper limit of \( aS \).

By definition, a necessary condition for any site index curve equation is that \( H=S \) at the index age (50 years for all of the species considered here). To insure that \( H=S \), the parameter \( a \) in the initial equation was replaced by the expression \( 1-b_1 e^{b_2(50)} \). The revised form of the equation fitted to the data by regression analysis was:

\[ H = S (1-b_1 e^{b_2(50)} + b_1 e^{b_2 A}) \]

The parameters \( b_1 \) and \( b_2 \) in this equation were estimated for each species by the same least squares techniques used to fit the exponential-monomolecular function.

After estimating \( b_1 \) and \( b_2 \) by regression analysis, the parameter \( a \) in the initial equation was computed from:

\[ a = 1-b_1 e^{b_2 50} \]

This value of \( a \) was then substituted back into the original equation, together with the values of \( b_1 \) and \( b_2 \) to provide the final equation used in expressing the relationship of height, site index, and age:

\[ H = S (a + b_1 e^{b_2 A}) \]

For each species the values of \( a \) and the two estimated parameters \( b_1 \) and \( b_2 \), together with the \( R^2 \), the standard error, and the maximum error of individual observations were obtained by fitting the revised equation to the observed readings (table 3).

As an example, the height equation for red pine is:

\[ H = S (1.956 - 2.1757 e^{-0.01644 A}) \]

For a site index of 60, the height at age 30 would be:

\[ H = 60 (1.956 - 2.1757 e^{-0.01644(30)}) \]
\[ = 60 (0.62737) \]
\[ = 37.6 \text{ feet} \]

This is close to the reading of 37 feet obtained from the published site index curve.

The annual height growth (\( \Delta H \)) at any age on a given site can be estimated by the first partial derivative of the height equation with respect to age:

\[ \Delta H \approx \frac{\partial H}{\partial A} = S (b_1 b_2 e^{b_2 A}) \]

For red pine, the annual height growth would be:

\[ \Delta H \approx S (0.03577 e^{-0.01644 A}) \]

On a site index of 60, annual height growth at age 30 would be:

\[ \Delta H \approx 60 (0.03577 e^{-0.01644(30)}) \]
\[ \approx 60 (.022) = 1.3 \text{ feet per year.} \]

Note that site index (\( S \)) can be calculated directly from an observation of height (\( H_{obs.} \)) at some ob-
Table 3. – Parameters of a monomolecular growth function describing published site index curves

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameters</th>
<th>2 Standard error</th>
<th>Maximum error</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>b1</td>
<td>b2</td>
</tr>
<tr>
<td>Red pine</td>
<td>1.956</td>
<td>-2.1757</td>
<td>-0.01644</td>
</tr>
<tr>
<td>Jack pine</td>
<td>1.677</td>
<td>-1.8063</td>
<td>-0.01963</td>
</tr>
<tr>
<td>White pine</td>
<td>2.174</td>
<td>-2.5616</td>
<td>-0.01560</td>
</tr>
<tr>
<td>Balsam fir</td>
<td>1.419</td>
<td>-1.3938</td>
<td>-0.02403</td>
</tr>
<tr>
<td>White spruce²</td>
<td>1.662</td>
<td>-1.9864</td>
<td>-0.02198</td>
</tr>
<tr>
<td>Black spruce</td>
<td>1.831</td>
<td>-1.9405</td>
<td>-0.01696</td>
</tr>
<tr>
<td>Tamarack</td>
<td>1.556</td>
<td>-1.6268</td>
<td>-0.02149</td>
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<td>White-cedar</td>
<td>2.020</td>
<td>-2.0630</td>
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<td>Aspen</td>
<td>1.460</td>
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</tr>
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<td>Red oak</td>
<td>1.582</td>
<td>-1.6005</td>
<td>-0.02023</td>
</tr>
<tr>
<td>Paper birch</td>
<td>1.594</td>
<td>-1.5841</td>
<td>-0.01961</td>
</tr>
</tbody>
</table>

1/ Height = (Site Index)(a + b1 e b2 Aob)⁻¹

2/ Maximum difference between observed and predicted heights over the range of data points analyzed (see table 1).

This function is not recommended for white spruce.

Served age (Aobs) by rearranging the height equation:

S = Hobs (a + b1 e b2 Aobs)⁻¹

This can be substituted back into the original equation to estimate the height (H) at any age (A) from one observed height and age determination in a stand:

H = Hobs (a + b1 e b2 Aobs)⁻¹(a + b1 e b2 A)

All species except white pine, red oak, and white spruce had a standard error of less than 1 foot. The maximum difference between observed and predicted heights for individual observations was less than 2 feet for all but these three species. Thus, these equations should be acceptable for representing the published site index curves.

The function for white pine can be used with confidence to represent the published curves. Only one predicted height differed by more than 2.1 feet from the observed reading, and apparently this was due to an error in drafting the curve. Eighty percent of the observations differed by less than 1½ feet.

The function for red oak can be used with confidence on all sites at ages below 90 years, and on sites from SI 50-65 at older ages. All differences between observed and predicted heights greater than 2 feet occurred only on the lowest and highest site index curves, and then only at ages of 90 years and older.

Use of this monomolecular function for white spruce is not recommended.
HEIGHT FACTORS SIMPLIFY USE

Although convenient for computer use, the functions suggested here are not easy to evaluate by hand. To make these equations more useful, the following table of height factors is provided (table 4).

The height factors shown are nothing more than the height per unit of site index at specified ages. The height factor equation is:

\[ H/S = b_1 \left( 1-e^{b_2 A} \right)^{b_3} \]

Multiplying the height factor at a given age by the site index gives the height of the tree in feet at this age. For example, a 70-year-old jack pine on site index 60 would be expected to have a height of 73.2 feet:

\[ H = 1.22(60) = 73.2 \text{ feet} \]

The 10-year growth in height for any species can be estimated by taking the difference between factors for the two ages and multiplying by the site index. Thus, the height growth of red pine from age 30 to age 40 on site index 50 would be:

\[ (.82-.62)50 = (.20)50 = 10 \text{ feet} \]

These factors can be graphed and a curve fitted through the plotted points so that a factor can be read for every age. They also can be used to construct a set of site index curves for any desired site indexes.

For convenience, the tables show factors calculated for ages 10 to 150 years. The range of the data on which these factors are based is outlined in black. Any factors outside this range should be used only with caution, recognizing that they are extrapolations beyond the range of the data.

CONCLUDING REMARKS

Both the exponential-monomolecular and monomolecular functions closely fit the published site index curves for all Lake States species except those for white spruce. In general, the exponential-monomolecular model provides a slightly better overall fit. It passes through the origin, assuring a height of zero at age zero. Also, it is the more flexible function of the two, assuming an S-shape for values of \( b_3 \) greater than 1 but less than 2, and the simpler monomolecular shape for values of \( b_3 \) of 1 or less. Nevertheless, over the range of ages and sites used here the differences between functions are small. Either can be used with confidence to represent the published curves.

Both functions were fitted to heights only within the range of ages shown on the published site index curves. However, extrapolations beyond the oldest age shown on the published curves are consistent with general observations about height growth of older trees. With care such extrapolations may be used in the absence of better information.

Anyone using these functions should, of course, keep in mind the limitations of site index curves. A brief discussion of the use and limitations of site index will be found on the back page of every site index curve publication by Gevorkiantz.
Table 4. - Height factors (F) by species and age for the exponential-monomolecular function;\(^1\) Tree height = F x S, where S = Site index
(In feet per unit of site index)

<table>
<thead>
<tr>
<th>Age</th>
<th>Red</th>
<th>Jack</th>
<th>White</th>
<th>Balsam</th>
<th>Black</th>
<th>Tamarack</th>
<th>White-</th>
<th>Aspen</th>
<th>Red</th>
<th>Paper</th>
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\(^1\) Height in feet per unit of site index = \(F = b_1 (1 - e^{b_2 A})b_3\).
Range of data bounded by black line.
LITERATURE CITED


ABOUT THE FOREST SERVICE . . .

As our Nation grows, people expect and need more from their forests—more wood; more water, fish, and wildlife; more recreation and natural beauty; more special forest products and forage. The Forest Service of the U.S. Department of Agriculture helps to fulfill these expectations and needs through three major activities:

- Conducting forest and range research at over 75 locations ranging from Puerto Rico to Alaska to Hawaii.
- Participating with all State forestry agencies in cooperative programs to protect, improve, and wisely use our Country's 395 million acres of State, local, and private forest lands.
- Managing and protecting the 187-million acre National Forest System.

The Forest Service does this by encouraging use of the new knowledge that research scientists develop; by setting an example in managing, under sustained yield, the National Forests and Grasslands for multiple use purposes; and by cooperating with all States and with private citizens in their efforts to achieve better management, protection, and use of forest resources.

Traditionally, Forest Service people have been active members of the communities and towns in which they live and work. They strive to secure for all, continuous benefits from the Country's forest resources.

For more than 60 years, the Forest Service has been serving the Nation as a leading natural resource conservation agency.