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Rationale, Limitations, and Assumptions of a Northeastern Forest Growth Simulator*

Abstract: A cooperative agreement between Yale University and the 1970 summer program of the IBM Research Division resulted in a flexible computer program to simulate the growth of the uneven-aged, mixed-species stands of trees on the 10-meter by 10-meter experimental plots of the Hubbard Brook Ecosystem Study in the White Mountains of northern New Hampshire. Annual increments of tree growth are based on species, tree size, and allocation of available light among the competing trees of the plot. Site quality differences between plots are assigned primarily by the concept of tree-growing degree-days, although soil moisture storage during the growing season and plot rockiness are also considered. Species succession, individual tree suppression and release, and other dynamic properties of forest stands have been successfully reproduced using the program. Additional field measurements are needed to further verify the model and to extend its applicability to nutrient cycling and other aspects of the Hubbard Brook Ecosystem Study. We believe that the simulator could readily be extended to include most other tree species of northeastern North America and also to match data from other sites through appropriate adjustment of program parameters.

Introduction

We have developed a computer simulation of forest growth that successfully reproduces the population dynamics of the trees in a mixed species forest of northeastern North America. The simulator is designed to be used in the Hubbard Brook Ecosystem Study and to provide output in the same form as the original vegetation survey of that study[1]. However, the underlying concepts of the simulation are general. The properties of each species are derived from its entire geographic range and in theory any nonhydrophytic species whose relevant characteristics are known can be entered into the simulation. In the present version of the program, the description of the environment is restricted to those features that have been recorded for the Hubbard Brook Experimental Forest[2], but the relative importance attached to each environmental factor has been influenced by the environmental characteristics of the northeast. It is our hope that a wide dissemination of this simulator will encourage others to test this version with their data and hence lead to later versions of wider usefulness and applicability.

Our basic goal has been to produce a dynamic model of forest growth, a model in which changes in the state of the forest are a function of its present state and random components. This approach has two advantages over the curve-fitting approach to forest growth: First, we can regard the simulator as a repository for an integrated knowledge of the ecosystem; and second, additional hypotheses can be formulated and tested by using Monte Carlo samples of simulator runs and comparing the results with observed data. For example, it would be comparatively simple to operate the simulator to determine over what range and under what conditions its output agrees with the Bartlett Forest birth-death probabilities[3].

The simulation was built step by step, beginning with optimal growth for single trees, the effect of less than optimal light and moisture levels on growth, and the allocation of growth resources among competing trees. We attempted to find the simplest mathematical expression for each factor that was consistent with observation. New factors were introduced only as they were needed, i.e., only when it was clear that the results of the simulation were not consistent with observation and that the differences could be resolved only by the introduction of a new factor. Our primary difficulty in creating the simulation was in finding relevant data regarding the relations between tree growth and environmental variables. Where information was lacking, we tried to choose simple yet reasonable relationships.

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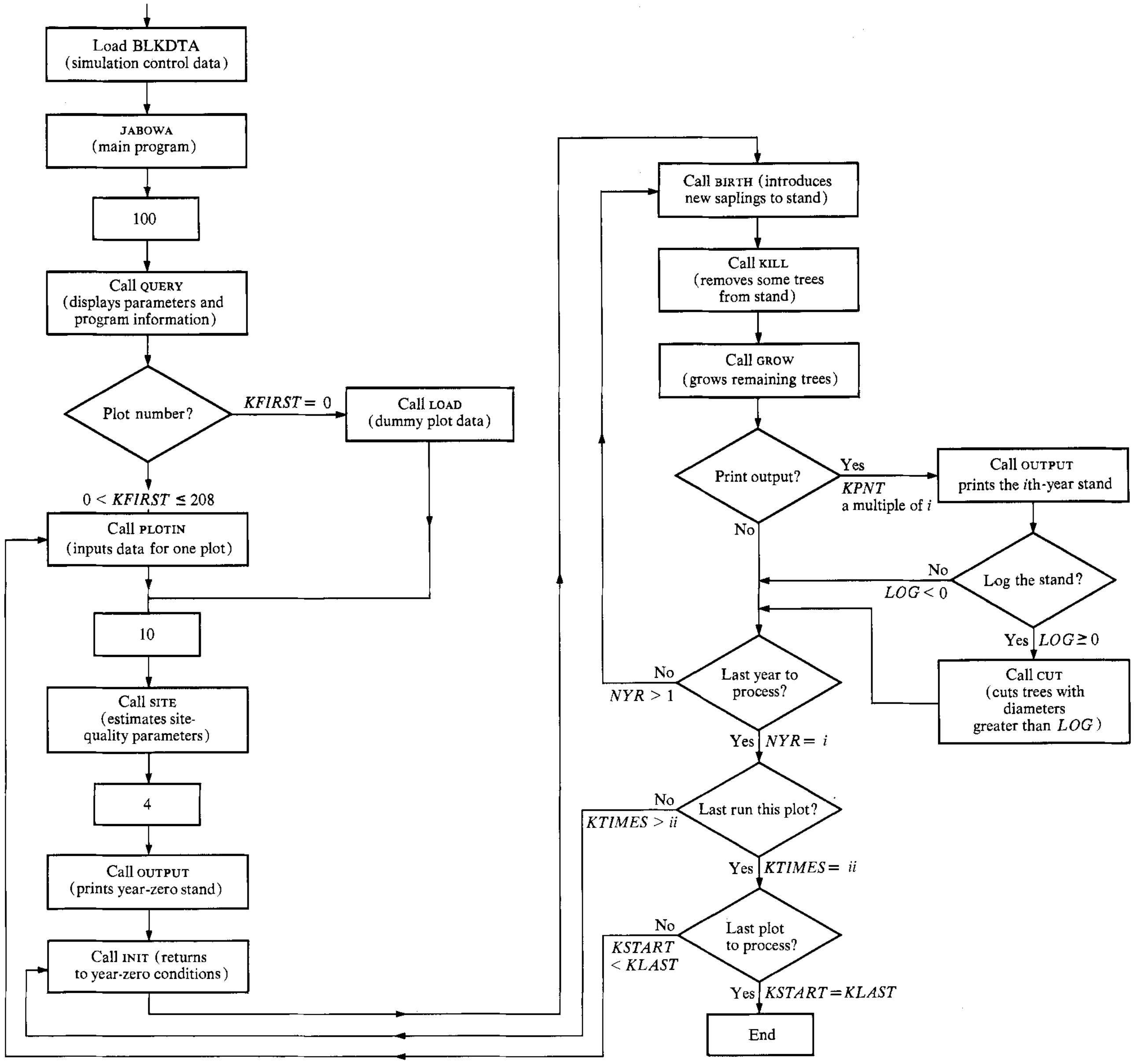


Figure 1 Flow chart for JABOWA version 1.

In the original vegetation survey of the Hubbard Brook forest, the species and diameters of all trees with diameters at breast height (dbh) greater than or equal to two cm were recorded on each of 208 10-m × 10-m plots distributed uniformly over the watershed. Environmental characteristics recorded for each plot were elevation, aspect, slope, percent of the plot surface in rock, till depth, and an index of soil moisture capacity. The simulator was designed to capitalize on these data, "grow" the trees, and allow for manipulation of both stands and site characteristics.

The program is written entirely in FORTRAN IV, using only standard library routines and a good uniform pseudo-random-number generator. A user writeup and listing is available[4] and a flow chart for the main program, called JABOWA, is given in Fig. 1. The program has been successfully operated under the IBM time sharing system (TSS) release 7 and is designed for use with remote terminals and PCS. The remote terminal used was an IBM 2741 and PCS is the TSS Program Checkout System, a command language that allows interrupting the program during execution, displaying and altering values of

Table 1 Parameters[a] for JABOWA version 1.

Species	Shade tolerance ITYPE[b]	Age AGEMX (yr)	dbh D_{max} (cm)	Height H_{max} (m)	Coefficients[e] b_2	b_3 (cm^{-1})	DEGD[f] (degree-days) DMIN	DMAX	Growth constant[h] G (cm/yr)	Leaf-area constant[i] C (g/cm^2)	Evapotranspiration index[k] WMIN (mm/yr)
1 Sugar maple	2	200	152.5[c]	40.11[c]	50.9	0.167	2000	6300	170	1.57[j]	300
2 Beech	2	300[c]	122[c]	36.6[c]	57.8	0.237	2100	6000[g]	150	2.20[j]	300
3 Yellow birch	1	300[c]	122[c]	30.5[c]	47.8	0.196	2000	5300	100	0.486[j]	250
4 White ash	2	100	50	21.6[c]	80.2	0.802	2100	10700	130	1.75	320
5 Mt. maple	2	25	13.5	5	53.8	2.00	2000	6300	150	1.75	320
6 Striped maple	2	30	22.5	10	76.6	1.70	2000	6300	150	1.75	320
7 Pin cherry	1	30	28[d]	11.26[d]	70.6	1.26	1100	8000	200	2.45[d]	190
8 Choke cherry	1	20	10	5	72.6	3.63	600[c]	10000	150	2.45	155
9 Balsam fir	2	80[c]	50	18.3[c]	67.9	0.679	1100	3700	200	2.5	190
10 Spruce	2	80[c]	50	18.3[c]	67.9	0.679	1100	3700	200	2.5	190
11 White birch	1	80	46	18.3[c]	73.6	0.800	1100	3700	140	0.486	190
12 Mt. ash	2	30	10	5	72.6	3.63	2000	4000	150	1.75	300
13 Red maple	2	150[c]	152.5[c]	36.6[c]	46.3	0.152	2000	12400	240	1.75	300

[a]Values not otherwise referenced were developed during the course of this study.
[b]1: intolerant; 2: tolerant.
[c]Ref. 20.
[d]Ref. 18.
[e]H (in cm) $= 137 + b_2 D - b_3 D^2$ (with D in cm).
[f]Obtained by matching northern and southern boundaries from the range maps in Ref. 15 to growing degree-days estimated from January and July mean world isotherms.
[g]Northern strain.
[h]Adjusted for reasonable growth of individual trees in full sun with climate and soil factors equal to one. These values provide for growth to about two-thirds of maximum diameter at one-half maximum age, starting from a 0.5 cm stem.
[i]Leaf area (in m) $= CD^2/45$ (with D in cm).
[j]Ref. 7.
[k]Only one value of $WMAX$ was determined, that being $WMAX = 600$ for white birch (species 11), calculated for the New York City area.

parameters and variables, and dynamically altering the program logic by means of the branch command. Prospective users with similar facilities should have no trouble using the simulator, while those with only batch mode operation at their computing centers should be able to convert the program fairly easily, providing that 50 kilobytes of main storage initialized to zero are available.

It can be seen in Fig. 1 that the innermost loop of JABOWA contains calls to the three major subroutines GROW, KILL, and BIRTH. The other eight subroutines of JABOWA are subservient to these three and to the previously existing Hubbard Brook survey. Discussion of the minor subroutines has been largely eliminated from this paper, as have comparisons between the algorithms of JABOWA and those of prior simulations that have used a less general approach[5].

Subroutines

• *GROW*

This subroutine uses a tree growth model to augment the dbh of all trees on a 10-m × 10-m plot by an amount representing one year's growth. The model consists of a basic growth-rate equation for each species that may be taken to represent the rate of growth of a tree with optimal site quality and no competition from other trees. For each plot-year, this growth rate is decreased by factors that take into account shading and shade tolerance, soil quality, and average climate as measured by the number of growing degree-days.

All growth curves tend to be sigmoid in shape and our final growth equation exhibits this overall property. We realize that some readers may feel that the equations which follow are occasionally based on rather arbitrary assumptions, but we expect that they will concur with us that there is no unique model of forest growth and that many equations based on different assumptions could yield quite similar results.

A tree growing in the open collects an amount of radiant energy roughly proportional to its leaf area. The JABOWA growth-rate equation for a tree growing under optimal conditions has the form

$$\delta(D^2H) = R\,LA(1 - DH/D_{max}H_{max}), \qquad (1)$$

in which D is the dbh of the tree, H is its height (with D_{max} and H_{max} being maximum values of these quantities for a given species), LA is the leaf area, and R is a constant. The equation states that the change in volume (D^2H) of a tree over a period of one year is proportional to the amount of sunlight the tree receives, derated by a factor $(1 - DH/D_{max}H_{max})$, which takes some account of the energy required to maintain the living tissue. The righthand side of Eq. (1) is later multiplied by additional factors to take shading, climate, etc. into account. Values used in JABOWA version 1 for D_{max}, H_{max}, and other parameters are given in Table 1.

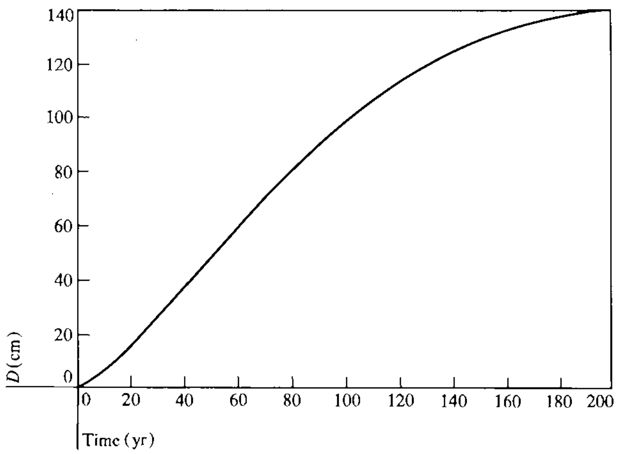


Figure 2 Time-dependent solution of the diameter-growth equation (5), using the parameters for sugar maple (species 1).

The height H (in cm) of a tree with dbh D (in cm) is assumed to be given by the following expression[6]:

$$H = 137 + b_2 D - b_3 D^2. \tag{2}$$

The number 137 represents breast height (4.5 ft) and the constants b_2 and b_3 are chosen for each species so that $H = H_{max}$ and $dH/dD = 0$ when $D = D_{max}$. One finds

$b_2 = 2(H_{max} - 137)/D^2_{max}$ and

$$b_3 = (H_{max} - 137)/D^2_{max}. \tag{3}$$

The rate of change of height decreases with increasing diameter and the actual change in height becomes negligible for large diameters.

JABOWA currently includes no adjustment for the forester's concept of "form factor." It would be comparatively simple to modify Eq. (3) of subroutine GROW to reflect differences in site quality, e.g., how the constants H_{max} and D_{max} vary with measures of growing degree-days and the other requirements for autotrophic plant growth. Field checks would be necessary to reliably quantify such relationships and this was therefore not attempted.

The leaf weight for a tree of species i is taken to be

$$WEIGHT = C_i D^2, \tag{4}$$

where C_i is a species-dependent constant. This equation states that the ratio of leaf weight to stem basal area is constant from sapling age to death of the tree. Data from Hubbard Brook[7] and elsewhere[8–10] indicate that the actual value of the exponent ranges from 1.5 to about 3. The error associated with these estimates is unknown. Assuming that leaf area is proportional to leaf weight, and defining $G = RC_i$, we can write Eq. (1) in the form

$$\delta D = GD \frac{1 - DH/D_{max}H_{max}}{274 + 3b_2 D - 4b_3 D^2}, \tag{5}$$

where δD is the annual diameter increment. A typical curve of diameter (starting from $D = 0.5$ cm) vs time resulting from this equation is shown in Fig. 2.

This particular growth curve corresponds to an unusually large sugar maple and reflects the fact that the simulator should be capable of producing trees of any species as large as have ever been observed. Because of the way trees are killed by the simulator, however, the presence of so large a tree would be an extremely rare event, and the dominant trees produced by the simulator are considerably smaller than the maximum values given in Table 1.

The constant G in Eq. (5) sets the initial rate of growth of young trees of species i [the solution $D(t)$ of the equation is asymptotic to D_{max} as t approaches infinity]. Given a maximum observed age $AGEMX$ for each species, the constant G was arbitrarily chosen so that D/D_{max} was 2/3 for a tree of half the maximum age; this choice of G gives reasonable growth rates for most species.

The growth-rate equation actually used in subroutine GROW is obtained by multiplying the right-hand side of Eq. (5) by the additional factors $r(AL)$, representing the effects of shading, shade tolerance, and actual site insolation; $T(DEGD)$, representing climatological effects; and $S(BAR)$, which takes some account of soil quality:

$$\delta D = GD \frac{1 - DH/D_{max}H_{max}}{274 + 3b_2 D - 4b_3 D^2} \times r(AL)T(DEGD)S(BAR). \tag{6}$$

These three additional factors are discussed in the following sections.

Shade and insolation

By assuming that a layer of leaves is a uniform absorber of light, one can show that the light intensity at height h is related to the light intensity Q_0 above the top of the canopy by[8, 11, 12]

$$Q(h) = Q_0 \exp[-k \int LA(h')dh'],$$

where $LA(h)$ is the distribution with height of leaf area per unit plot area and k is a constant. In subroutine GROW this equation is replaced by

$$AL = \Phi \exp(-k\, SLA), \tag{7}$$

where AL is the available light for a given tree, SLA is the "shading leaf area," defined as the sum of the leaf areas [obtained from Eq. (4)] of all higher trees [with the heights obtained from Eq. (2)], and Φ is the annual insolation in appropriate units. Currently, JABOWA uses a default value of one for Φ; a desirable improvement would consist of a subroutine for generating a value of Φ based on latitude and aspect. The constant k in Eq. (7) is adjusted for reasonable shading beneath a dense canopy, and it has been found that $k = 1/6000$ gives good results for 10-m × 10-m plots.

Version 1 of JABOWA recognizes two types of trees: shade tolerant and shade intolerant. For these two degrees of tolerance, the quantity $r(AL)$ appearing in Eq. (6) is

$$r(AL) = 1 - \exp[-4.64(AL - 0.05)], \text{ shade tolerant;}$$
$$= 2.24\{1 - \exp[-1.136(AL - 0.08)]\}, \text{ shade intolerant.} \quad (8)$$

In each case AL is to be obtained from Eq. (7). The function r, which may be thought of as a representation of photosynthetic rates, is plotted in Fig. 3 for the two degrees of shade tolerance. The constants in Eq. (8) are chosen to give reasonable fits to measured photosynthesis curves[13]. The annual insolation Φ can be expressed in any units if appropriate changes are made in the constants appearing in Eq. (8).

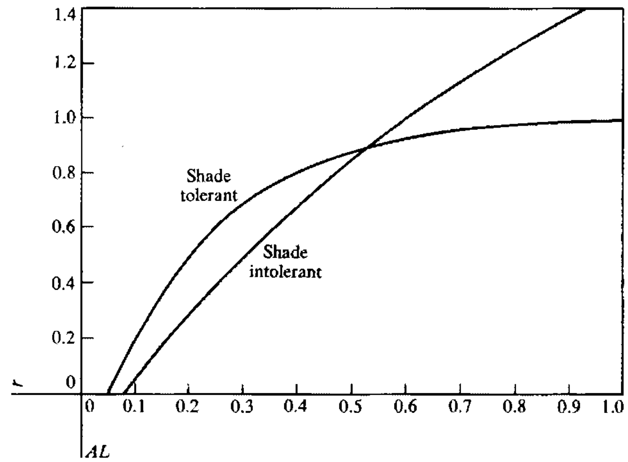


Figure 3 Photosynthetic rate as a function of the available light (fraction of annual insolation) for shade-tolerant and -intolerant trees.

Climate

The function $T(DEGD)$ in Eq. (6) represents an attempt to take account of the effect of temperature on photosynthetic rates. It is assumed that each species will have an optimal temperature, and photosynthesis will decrease symmetrically above and below this optimum. A rough index of these thermal effects is obtained from the number of growing degree-days per year (40°F base) for the site. This quantity is defined as the sum of $(T - 40)$ over all days of the year for which the average temperature T exceeds 40°F. Inasmuch as such detailed temperature profiles do not exist for most forest sites, we used an approximation involving only the January and July average temperatures. If one assumes that the annual temperature profile is sinusoidal, it is easy to compute the number of degree-days using the average annual temperature as a base. If this average is not too far from 40°F, a correction to the 40°F base can be made by approximating the temperature curve by straight lines near the average annual temperature. In this way one obtains the following approximate expression for the number of growing degree-days:

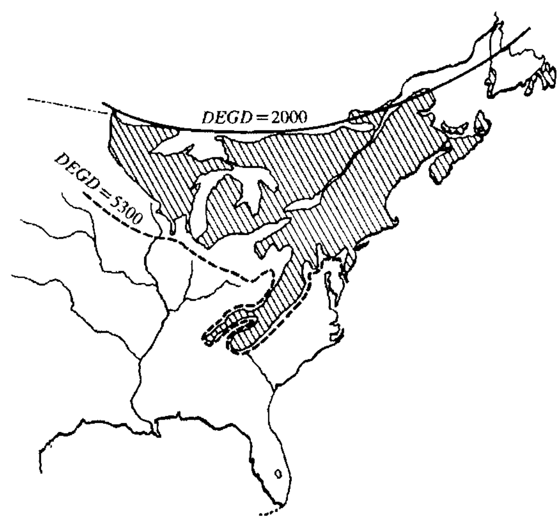
$$DEGD = 365\left\{\frac{T_{\text{July}} - T_{\text{Jan}}}{2\pi} - \frac{40 - (T_{\text{July}} + T_{\text{Jan}})/2}{2} + \frac{[40 - (T_{\text{July}} + T_{\text{Jan}})/2]^2}{\pi(T_{\text{July}} - T_{\text{Jan}})}\right\}, \quad (9)$$

in which all temperatures are in degrees Fahrenheit.

For each species we now set

$$T(DEGD) = \frac{4(DEGD - DEGD_{\min})\,(DEGD_{\max} - DEGD)}{(DEGD_{\max} - DEGD_{\min})^2}. \quad (10)$$

Figure 4 Geographic range of yellow birch and growing-degree-day contours that closely approximate the northern and southern boundaries of this species; range map from Ref. 15 and isotherms used to compute the *DEGD* lines from Ref. 17.



This function is a parabola[14] with the value zero at minimum and maximum values of $DEGD$, and a value between zero and one for any value of $DEGD$ between its extremes. Values of $DEGD_{\min}$ and $DEGD_{\max}$, representing the extremes between which each species will grow, can be obtained reasonably accurately by comparing species range maps[15] with lines of constant $DEGD$ estimated from maps of the January and July world isotherms[16,17]. The comparison of two isodegree-days and the geographic range of yellow birch is illustrated in Fig. 4. It is seen that $DEGD$, a quantity which is in wide use in agricultural studies, is also of use in tree growth analysis. There are admittedly many microclimatic effects, such as exposure to wind and available moisture, that are completely neglected in this approach; however, the number of growing degree-days is clearly a useful measure of gross thermal effects upon plant growth.

Soil quality

Equation (6) contains the factor $S(BAR)$, which is simply

$$S(BAR) = 1 - BAR/SOILQ, \tag{11}$$

where BAR is the total basal area on the plot, $SOILQ$ is the maximal basal area on the plot in which trees will grow, and the function S is a crude expression of the competition for soil moisture and nutrients on the plot.

• *BIRTH*

Subroutine BIRTH enters new saplings into the stand. There are a large number of tree species in northeastern North America that a completely general subroutine BIRTH would have to consider as available for entry in any given year. An additional complication in producing a general subroutine BIRTH is our current inability to specify exactly the optimal light and moisture conditions for the establishment of many of the possible species, or even to make definitive probability statements about the chances of one species relative to another.

The compromise that we selected was to consider only the 13 tree species found on the 208 Hubbard Brook Ecosystem Study plots. Important species such as white pine, hemlock, and red oak were omitted because of this restriction, although these species could easily be included in subsequent versions of the simulator. The Hubbard Brook species were divided into three groups on the basis of their relative tolerance or intolerance to shade.

The tolerant species used by the current version of subroutine BIRTH are

Sugar maple *(Acer saccharum)*

Beech *(Fagus grandifolia)*

White ash *(Fraxinus americana)*

Mountain maple *(Acer spicatum)*

Striped maple *(Acer pensylvanicum)*

Mountain ash *(Sorbus americana)*

Red maple *(Acer rubrum)*

Balsam fir *(Abies balsamea)*

Red spruce *(Picea rubens)*

These nine species do not form a completely homogeneous tolerance class, but the Hubbard Brook data do not support hypotheses for further subdivision. The four species considered to be intolerant of shade by the current version of subroutine BIRTH were subdivided into two groups, namely, the less intolerant

Yellow birch *(Betula alleghaniensis)*

White birch *(Betula papyrifera)*

and the more intolerant

Pin cherry *(Prunus pensylvanica)*

Choke cherry *(Prunus virginiana)*.

Users interested in other species and climates may find that the JABOWA approach to entering new trees needs modification.

More specifically, subroutine BIRTH allows only those species that can grow to be added to the stand. The number of growing degree-days ($DEGD$) available at the site is compared with the species vectors of minimal and maximal values of growing degree-days, $DMIN(i)$ and $DMAX(i)$, and a similar comparison of growing season evapotranspiration $SOILM$ is made against the vector of species requirements, $WMIN(i)$, to produce a list of allowable species. For the nonsuccessional species, i.e., for all but the birches and cherries, a random choice is made from the allowable species list and a random choice of either zero, one, or two new trees of the selected species is added. The diameters of the trees added depend on the parameter $SIZE$ (default value 0.5 cm) and a small random addition.

A random selection of which shade-tolerant tree species to add is not the desperate expedient that it appears to be at first thought. The Hubbard Brook plots show many inexplicable differences in species composition among plots within the elevational bands discussed by Bormann and his coworkers[1]. In addition, on the better sites, with the single exception of beech, the existing plot data do not yield strong correlations among the numbers of trees, saplings, and seedlings of a given species that are present on a plot. At the higher elevations of the Hubbard Brook watershed, the soils tend to be shallower and rockier, and the nonboreal species grow poorly and are subjected to a differentially severe killing (see discussion of subroutines GROW and KILL).

In short, observations of the growth of seedlings and saplings of the major shade-tolerant species indicate that 1) the range of zero to two individual saplings is a reasonable rate of introduction for any one year for a 10-m × 10-m plot; 2) seed germination, growth, and survival of young stems undergo great yearly variations suggesting cycles of three to five years duration; and 3) the occurrence of saplings is not clearly related to light intensity at the forest floor. Therefore a random introduction approximates well our current knowledge. In practice, JABOWA version 1 produces stands that are similar to those observed at Hubbard Brook, although it is possible that this procedure may produce stands that underemphasize the major species, in particular beech, while overemphasizing the importance of the minor-stand components, e.g., red maple. We believe that biasing of the probabilities for species entry should await extensive testing of the present random-choice algorithm. Further field study is clearly necessary to determine the conditions that promote survival of saplings of the shade-tolerant species.

The four relatively intolerant successional species are handled quite differently from the nine nonsuccessional species. It is well known that the germination and early survival of these species are dependent on the openness of the site, but the exact site conditions required for these species are not well known, although the dynamics of one species, the pin cherry, is currently under study[18]. Under proper conditions, pin cherry seeds germinate in great abundance the year following removal of the canopy, but do not germinate in subsequent years.

Birch saplings do not survive under heavy forest shade, and their chances for survival and growth improve as the canopy becomes more open[19]. In subroutine BIRTH we estimate the current weight of leaves present on the plot. The summation *WEIGHT* is based on the moderately well documented assumption that for dominant trees the total leaf area (and hence *WEIGHT*) is equal to a species constant $C(i)$ times the square of the diameter of the tree. Default values for the constants $C(i)$ can be found in Table 1; they are modified and extended from those given by Whittaker[7].

If *WEIGHT* is less than the cherry species cutoff, called *CHERRY*, and the species can grow, then between 60 and 75 new cherry trees are added to the stand. The number of cherry saplings added by the simulator is far below the dense thickets observed in the field. The cherries are a short-lived species and we felt that more realistic modeling would result in an excess of largely unnecessary computation without markedly improving the overall simulation of stand dynamics. In future versions of the program, when the simulation will be used to calculate turnover of water, minerals, and energy, the initial number of cherries will be made to agree with observations. As the program now functions, it starts with too few cherries and gives them a higher probability of survival than is observed, but the average number ten years after a clear cut is realistic.

Choke cherry has a wider geographical range than pin cherry[20], but the latter species is more prevalent near its optimum than is choke cherry. In those areas where both species can grow, a probability parameter *CHOKE*

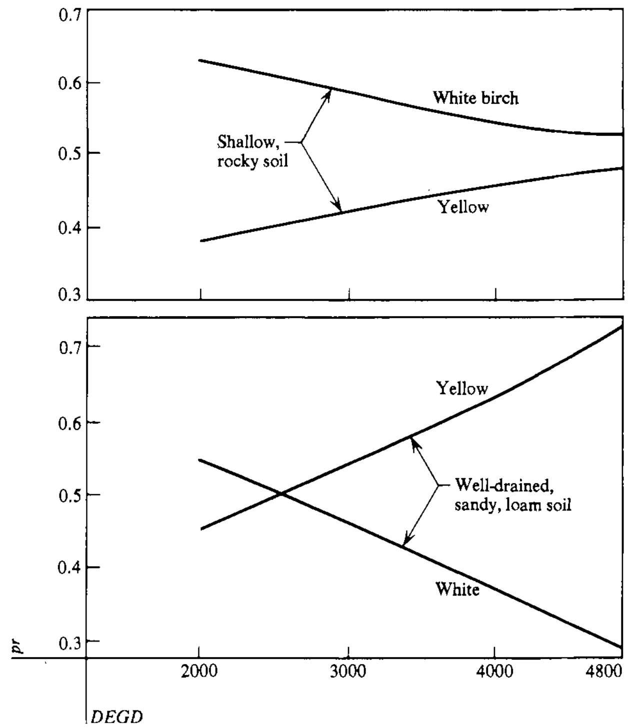


Figure 5 Probabilities that new individual yellow birch and white birch will be entered on a 10-m × 10-m plot by subroutine BIRTH.

is used for weighting the choice between the two cherry species.

If *WEIGHT* > *CHERRY* but the stand is still fairly open, i.e., if *WEIGHT* ≤ *BIRCH*, then in accordance with field observations the two birch species become active candidates for admission to the stand. In the field the two birch species have overlapping ranges, although yellow birch grows much farther south and white birch survives farther north and on much shallower and rockier sites. The algorithm used by subroutine BIRTH reflects these observed differences of birch behavior and allocates the choice between the species as a random choice weighted by site and species constants. Between zero and 13 trees are entered as a random choice weighted by stand density each time the birch option of subroutine BIRTH is exercised.

For the range 2000 to 4800 growing degree-days, in which both species grow, BIRTH biases the probabilities away from a 50-50 allocation. Figure 5 shows the results for the Hubbard Brook area for two soil conditions, a deep, well-drained, sandy loam and a shallow, rocky soil. The bias toward white birch is quite pronounced on those sites with the more extreme microclimates.

- *KILL*

Whether a tree dies each year is determined by subroutine KILL, and the death of a tree can occur by two separate mechanisms. The first is a function of the known maximum age of the tree species, [variable $AGEMX(i)$, where i is the species]. The assumption is made that no more than two percent of the trees of a given species should reach that maximum age. If the probability of death is independent of the age of an individual tree, the probability that a tree will die in any year is

$$pr = 1 - (1 - \epsilon)^n. \qquad (12)$$

If $pr = 0.98$ when $n = AGEMX$, then

$$(1 - \epsilon)^{AGEMX} = 2 \times 10^{-2},$$

or, approximately,

$$\epsilon = 4.0/AGEMX.$$

The program generates a random number between zero and one and if this number is less than or equal to $4.0/AGEMX(i)$, the tree is killed.

If the tree is not removed by this method, the subroutine determines whether the last diameter increment (variable $DINC$) was greater than a minimum value (variable $AINC$), which is 0.01 cm in the present version of the program. All trees whose diameter increments were less than this value are listed in vector $NOGRO$ by subroutine GROW. It is assumed that a tree whose diameter increment falls below this minimum for ten successive years should have no better than one percent chance of surviving those ten years. Then the probability that such a tree will die in any one year is 0.368. A random number between zero and one is generated from a uniform distribution and if this number is less than or equal to 0.368, the tree is removed.

In addition to determining whether a tree dies in a given year, subroutine KILL creates a list of the diameters and ages at death of all trees that have died since the last printout and condenses the live-tree vectors DBH (the list of tree diameters) and $IGES$ (the list of tree ages) by removing all killed trees.

The basic rationale of subroutine KILL is that a tree which cannot maintain a certain minimal growth rate cannot survive for long in the forest, and that, in addition, there are numerous other events, such as severe wind, lightning, parasitism, and defoliation which may result in the death of any tree. While in reality some of these events may be truly random, others are not. The assumption of this model is that even the nonrandom events have only a certain probability of affecting any one tree and that the sum of the effects of all such events approaches a random probability of killing any tree in any year. That such biotic and abiotic factors affect each species differently is represented by the use of the maximum known age of each species to determine the survival probability for any year.

The minimal growth increment that a tree needs to remain an active, healthy member of the forest is, in reality, a species-dependent factor. In our initial experiments with the program, we have found that making the variable $AINC$ species dependent alters the relative importance of the species. We did not find it necessary to distinguish species in this way to produce a successful simulation of the forest.

• *SITE*

This service subroutine produces indices of the quality of the site for growing trees. It is customary for forest site indices to be based on the observed height-age relationship of dominant trees of certain key species that appear on the plot. Such data are time-consuming to accumulate and often quite difficult to obtain for disturbed stands. For JABOWA version 1 we were guided by a different philosophy: We wanted to index site quality not by what was currently growing on a plot, but by estimates of the exogenous influences. We believe that this approach raises interesting questions about the minimal amounts of light and moisture, as well as the optimal levels, that are necessary for tree and stand growth.

To estimate the value of the growing-degree-day parameter $DEGD$ for an individual site, we need long-term estimates of the mean January and July temperatures. It is, of course, axiomatic that this information is not available for most sites where we may be interested in using JABOWA, and we usually have to resort to estimation. Conversion of mean monthly temperatures $BASET$ from a nearby U.S. Weather Bureau first-order weather station is done by subroutine SITE using an average lapse rate for the difference in elevation between the plot height $IELEV$ and that of the base station, $BASEH$. For the growing season months the lapse rate used is 6.4°C/1000 m, while the January minimum used is 3.9°C/1000 m[21]. No attempt was made to account for differences in monthly temperatures that result from differing aspects. All of the Hubbard Brook plots have a more or less southern exposure, and differences in mean monthly temperature associated with aspect were assumed small; for other areas this may not be a reasonable assumption.

Latitudinal as well as coastal influences on climate are pronounced in New England, and we expected that by using data from the closest long-term weather station and adjusting for elevation differences, reasonable microclimatic indices could be developed for nearby sites. Elevational transference should be kept less than 500 m because the growing-degree-day calculation is sensitive to large elevation changes and is not completely linear. Figure 6 shows the result of adjusting the Woodstock, N.H., weather station data for an elevation range of zero to 1830 m, which resulted in values of $DEGD$ ranging from 3828 to 544.

For deep, well-drained, forest soils in New England, it is assumed that soil moisture stress is generally not sufficient to restrict stand growth. However, for shallow, rocky soils it appears that many species may have difficulty becoming established and, accordingly, we incorporated an index of actual evapotranspiration, *SOILM*. This index is developed as a modified Thornthwaite water balance calculation[21]. The maximum available moisture storage *STRMAX* is the minimum value of the soil depth *TILL*, or 10 m, multiplied by the moisture storage per unit depth of the fine soil fraction *TEXT*[22], and discounted by the percentage of rock in the soil mantle. This latter percentage was not estimated for the Hubbard Brook plots, although the percentage of surface area covered by boulders or rock outcrops, *IROCK*, was observed and this was used as a substitute.

Monthly precipitation values are needed for the water balance calculation and, lacking other information, these are assumed to be the same as for the base station, *BASEP*. The only other parameter needed for the calculation of *SOILM* is an estimate of the proportion of the current month's precipitation to be added to *SOILM* if the potential evapotranspiration is in excess of current storage. The default value for this parameter, *EXCESS*, is 0.25. No provision was made to adjust *EXCESS* as a function of *STRMAX*, although such adjustment may later be found to be necessary.

The initial assumption of no moisture restriction of stand growth for New England forests is corroborated by the values of *SOILM* that we obtained. Using the 30-year Woodstock weather data and assuming that $IROCK = 0$ and $IELEV = 305$ m, we found that *TILL* has to decrease below 0.45 m before *SOILM* starts to decrease. At higher elevations there is less heat and hence an even smaller requirement for soil moisture storage. We found that at 1500 m *TILL* could decrease to 0.33 m before *SOILM* started to decrease. Values of *SOILM* as a function of elevation for deep, sandy, loam soil are shown in Fig. 7.

Siccama[23] has reported a "climatic discontinuity" at approximately 762 m, related to the occurrence of hoar frost and possibly affecting the survival of hardwoods at higher elevations. We suspect that something similar to a "wind-chill factor" accelerates tree mortality as the timber line is approached, but the difficulty of quantifying the wind-chill concept with the sparse available data prevented any direct assessment of this factor within subroutine SITE. An indirect assessment of the wind-chill factor has probably been built into the simulator in that only those species that can be grown can be added to the stand. [Tests of *DMIN(i)* vs *DEGD* and *WMIN(i)* vs *SOILM* are made by subroutine BIRTH.] In particular, for shallow, rocky, high-elevation sites the value of *SOILM* decreases precipitously; it is probable that such

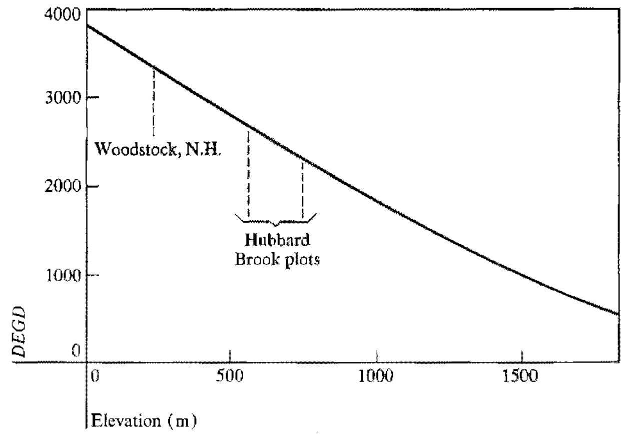
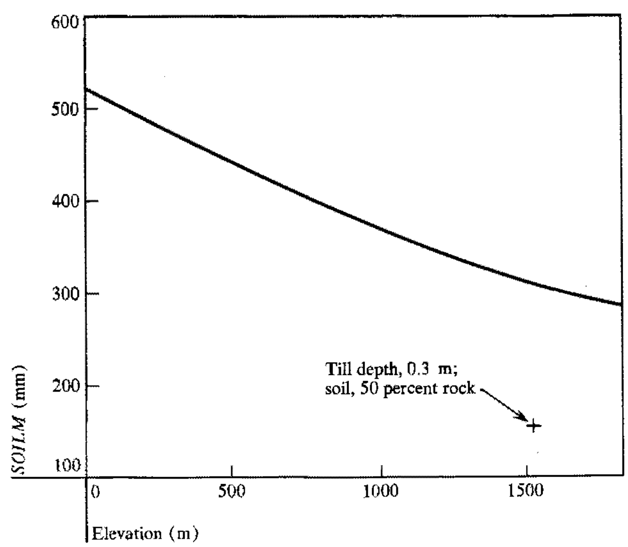


Figure 6 Growing-degree-day values obtained by adjusting mean monthly temperature records from the Woodstock, New Hampshire, weather station (R. Lautzenheiser, personal communication, 1970) with appropriate temperature lapse rates (Ref. 21).

Figure 7 Index of evapotranspiration for deep, sandy, loam soils. The index is a modified Thornthwaite water-balance calculation determined from Woodstock, New Hampshire, weather station records adjusted by the appropriate temperature lapse rate. The point marked with a cross illustrates the lower value for a shallow, rocky soil.



localities form a set that largely intersects the set of wind-chill-factor sites. Later efforts should be directed toward determining whether this indirect assessment of the wind-chill factor is adequate.

The parameter *SOILQ* measures the maximum basal area of a stand of trees under optimal growing conditions for a 10-m × 10-m plot. If rock outcrops reduce the available plot area, the value of *SOILQ* should be reduced accordingly. The parameter *IROCK* is used by subroutine SITE in this capacity; later work may show that this approximation needs to be strengthened.

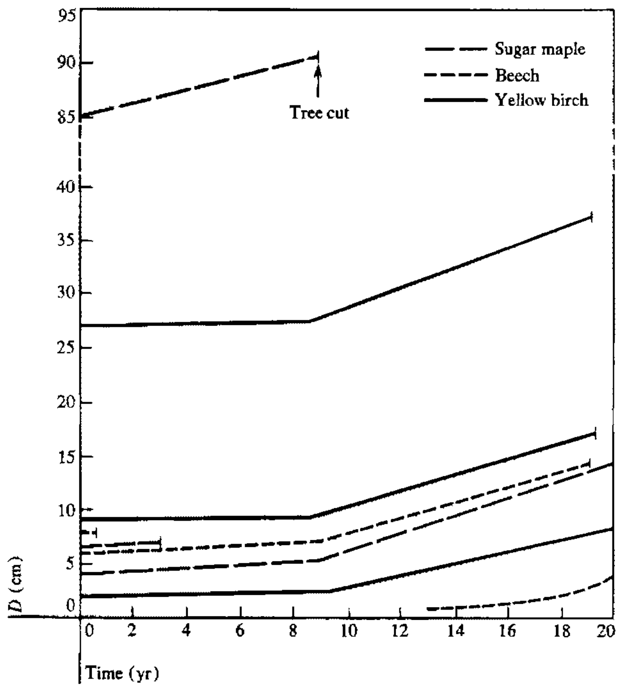


Figure 8 Simulated growth in diameter of individual trees on the same plot. Each line represents a single tree; the end of a line is that tree's death. At year 9 the large sugar maple was removed and the remaining trees, no longer suppressed by the large maple, show increased growth rates.

• *OUTPUT*
Subroutine OUTPUT, a service subroutine for printing current information about the plot, is called by JABOWA whenever the year number is an integral multiple of the parameter *KPNT*.

OUTPUT first checks to see whether any trees are alive; if not, a message to this effect is printed and the subroutine checks further to see whether any trees can grow. If not, OUTPUT gives another message and terminates execution.

If there are live trees on the plot, the subroutine prints the identification of the current year. Then the number of trees and the basal area (in cm^2) and the dbh (in cm), by species, of all living trees are printed. A final line, giving the total number of trees, the total basal area, and the approximate total leaf area (in m^2, obtained by dividing the total leaf weight by 45, which is an approximate conversion factor from leaf weight to leaf area for one plot) are also printed.

OUTPUT next checks the value of the variable *LOG*: If it is non-negative, subroutine CUT, which "logs" the plot (see description in subsequent section), is called. Control is returned to the beginning of OUTPUT, so that the status of the plot after logging is displayed.

If the number of dead trees is zero, either no trees have died since the last printout, or the accounting of dead trees has been suppressed by a negative or zero value of the variable *KAGE*; in either case, OUTPUT returns control to JABOWA. If the number of dead trees is greater than zero, OUTPUT lists the dbh and the age at death, by species, for all trees that have died since the last printout before returning control to JABOWA.

• *QUERY*
This service subroutine is called in the initial phase of JABOWA and is designed specifically for use in an interactive computer environment. The subroutine prints questions on the user's terminal; positive responses to these questions initiate printout of general data, such as a list of species or a list of important parameters and their default values. JABOWA can thus provide the user with a reference table of the parameters he will most likely want to alter with PCS for his particular run.

• *CUT*
This subroutine provides the user with a flexible means of removing trees. CUT enables a user to log a plot, i.e., he can remove all trees with diameters larger than specified minimum values for any or all species. If the user wants to cut all species uniformly, he sets the value of variable *LOG* in the main program equal to the minimum diameter of the trees to be removed. [Species may be logged differentially by adjusting the vector variable *ALIMIT(i)* of subroutine CUT.]

While, obviously, subroutine CUT can be used to simulate a logging operation, it can also be used to simulate other species- and size-dependent natural events, such as the removal of a single species because of a newly introduced disease or the premature death of larger trees due to an age phenomenon (for example, one caused by wind). Logging can be used to simulate a clearing in which secondary succession takes place or to study the population dynamics of a forest less diverse than the real one.

Results
Simulation of competition among individual trees is shown in Fig. 8. In this figure a single, large sugar maple, which itself grows approximately 0.5 cm in diameter per year, suppresses the growth of other, smaller trees on the plot, none of which grows as much as two cm in ten years. When this large tree is cut, growth increases in the previously suppressed trees. The largest remaining tree on the plot, a 28-cm-diameter yellow birch, grows ten cm in the ten years following the cut. Smaller trees, suppressed only by this larger yellow birch, show increases in growth rates consistent with the amount of shading they suffer from larger remaining trees. For example, a nine-cm-diameter yellow birch, which grew one cm before the elimination of the large sugar maple, grows approximately eight cm by year 20.

```
                    THE JABOWA -- A NORTHEAST FOREST GROWTH SIMULATOR (VERSION 1)
DO YOU WANT A LIST OF SPECIES NAMES? REPLY  Y  OR  N
y
THE 13 TREE SPECIES USED ARE THOSE FOUND ON THE 208 EXPERIMENTAL PLOTS OF
THE HUBBARD BROOK ECOSYSTEM STUDY
  1 SUGAR MAPLE       ACER SACCHARUM
  2 BEECH             FAGUS GRANDIFOLIA
  3 YELLOW BIRCH      BETULA ALLEGHANIENSIS
  4 WHITE ASH         FRAXINUS AMERICANA
  5 MOUNTAIN MAPLE    ACER SPICATUM
  6 STRIPED MAPLE     ACER PENSYLVANICUM
  7 PIN CHERRY        PRUNUS PENSYLVANICA
  8 CHOKE CHERRY      PRUNUS VIRGINIANA
  9 BALSAM FIR        ABIES BALSAMEA
 10 RED SPRUCE        PICEA RUBENS
 11 WHITE BIRCH       BETULA PAPYRIFERA
 12 MOUNTAIN ASH      SORBUS AMERICANA
 13 RED MAPLE         ACER RUBRUM
DO YOU WANT INFORMATION ON PARAMETERS? REPLY Y OR N
n
00001
                                      ******************************                            IX =      1065786486
  PLOT   ELEVATION   SOIL   PERCENT   GROWING      INDEX OF
 NUMBER   (METERS)   DEPTH   ROCK    DEGREE DAYS   ACTUAL ET
    0       610      1.2        0     2549.4        423.1

YEAR  SPEC.   NUM.  BASAR.                       DBH
  0
        1  |   4 |   21.991  |    2.000   2.000   2.000   4.000
        2  |   4 |   62.832  |    2.000   2.000   6.000   6.000
        3  |   6 |  130.376  |    2.000   2.000   8.000   9.000   3.000   2.000

              14    215.200    LEAF AREA =    6.681

        DIAMETER LIMITS FOR LOGGING BY SPECIES
             1     2     3     4     5     6     7     8     9    10    11    12    13
           0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0


        ALL TREES WERE CUT
        YEAR    0 NO TREES LIVING

YEAR  SPEC.   NUM.  BASAR.                       DBH
 15
        1  |   4 |    7.234  |    1.890   1.591   1.434   1.024
        2  |   3 |    9.991  |    2.574   1.873   1.608
        3  |  13 |  139.496  |    3.722   3.731   3.722   4.417   3.713   3.717   3.814   4.202   3.368   3.889   3.392
           |     |           |    3.022   3.094
        4  |   2 |    1.347  |    0.970   0.879
        5  |   2 |    0.554  |    0.590   0.598
        6  |   2 |    1.034  |    0.843   0.779
        7  |   4 |  283.334  |    9.625   9.264   9.907   9.172

              30    442.988    LEAF AREA =   22.638

YEAR  SPEC.   NUM.  BASAR.                       DBH
 30
        1  |   5 |  118.857  |    6.675   6.175   5.894   5.088   2.833
        2  |   3 |   40.943  |    5.261   4.860   0.913
        3  |  13 |  795.008  |    9.737   9.746   9.717  10.689   9.673   9.700   9.179   9.891   9.206   8.674   8.771
           |     |           |    1.611   1.609
        4  |   3 |    3.825  |    1.789   1.058   0.744
        5  |   1 |    1.157  |    1.213
       10  |   4 |    4.781  |    1.476   1.564   0.868   0.842
       12  |   1 |    0.688  |    0.936
       13  |   1 |    1.487  |    1.376

              31    966.745    LEAF AREA =   19.433

YEAR  SPEC.   NUM.  BASAR.                       DBH
 45
        1  |   5 |  363.035  |   12.373  11.789  10.492   7.643   1.298
        2  |   4 |  142.066  |    9.172   8.704   3.406   3.066
        3  |  11 | 1926.324  |   16.474  16.476  16.334  17.710  16.210  16.341  16.433  15.584  15.001   5.555   5.547
        4  |   1 |    5.828  |    2.724
        6  |   1 |    2.609  |    1.822
        9  |   3 |   74.750  |    6.713   6.723   2.215
       10  |   7 |   29.539  |    3.370   3.493   2.442   2.399   1.192   0.733   0.609
       13  |   4 |   15.453  |    3.829   1.846   0.766   1.010

              36   2559.603    LEAF AREA =   60.018

YEAR  SPEC.   NUM.  BASAR.                       DBH
 60
        1  |   3 |  604.325  |   17.833  17.154  12.536
        2  |   4 |  167.922  |   12.846   6.395   2.382   1.486
        3  |   9 | 3200.747  |   22.939  22.829  22.485  24.378  22.038  22.166  21.186  20.438   9.194
        4  |   2 |   10.893  |    3.604   0.938
        5  |   1 |    0.736  |    0.968
        9  |   3 |  325.418  |   17.080  11.037   0.887
       10  |   6 |   31.617  |    5.329   2.622   1.690   1.134   0.576   0.710
       12  |   3 |   11.352  |    2.551   1.994   1.993
       13  |   3 |   50.946  |    6.576   4.047   2.291

              34   4403.949    LEAF AREA =  110.214
CHCRW400     TERMINATED: STOP
```

Figure 9 Output of JABOWA version 1 as it appears on the user's terminal, showing 60 years of secondary succession at 15-year intervals on the test plot (Plot 0). In this case the user specified the Elevation and Soil Depth (in m), the minimum size tree to be cut, the number of years of the simulation, and the interval between printouts. Index of Actual ET is an index of growing season evapotranspiration in mm; Spec. is the species number, and refers to the list in Table 1; Num. is the number of trees of each species; Basar. is the basal area contributed by each species; numbers under DBH are the diameters in cm of each tree; Leaf Area is an index of the total leaf area on the 10-m × 10-m plot, and is obtained by dividing the total leaf weight of all species on the plot by 45 (dividing the total index by 100 gives a rough approximation of Leaf Area index on the plot); IX is the number initiating the pseudo-random-number sequence.

```
                    THE JABOWA -- A NORTHEAST FOREST GROWTH SIMULATOR (VERSION 1)
DO YOU WANT A LIST OF SPECIES NAMES? REPLY  Y  OR  N
n
DO YOU WANT INFORMATION ON PARAMETERS? REPLY Y OR N
y
MAJOR PARAMETERS WHICH MAY BE ALTERED BY PCS
  JABOWA.NYR (DEFAULT=500), NUMBER OF YEARS FOR THIS RUN
  JABOWA.KAGE (DEFAULT=-1) POSITIVE FOR DEAD TREE ACCOUNTING
  JABOWA.KPNT (DEFAULT=1), NUMBER OF YEARS BETWEEN PRINTOUTS
  JABOWA.LOG (DEFAULT=-1), TO BE SET POSITIVE TO LOG OVER THE PLOT TO SPECIFIED DIAMETER LIMIT
  JABOWA.KFIRST (DEFAULT=0), FIRST PLOT TO PROCESS, ZERO IS  TEST PLOT ONLY
  JABOWA.KLAST  (DEFAULT=208), LAST PLOT TO PROCESS
  JABOWA.PHI (DEFAULT=1.0), LIGHT LEVEL ON PLOT
  JABOWA.SOILQ (DEFAULT=20,000.0), MAXIMUM BASAL AREA ON PLOT   TO WHICH TREES MIGHT GROW UNDER OPTIMUM CONDITIONS
  JABOWA.DEGD (DEFAULT=VARIABLE), NUMBER OF GROWING DEGREE DAYS  ON EACH PLOT
WANT INFORMATION ON OTHER PARAMETERS? REPLY Y OR N
n
00001
                                   ****************************                       IX =          987643
  PLOT   ELEVATION   SOIL   PERCENT   GROWING      INDEX OF
 NUMBER   (METERS)   DEPTH   ROCK    DEGREE DAYS   ACTUAL ET
    0      1524       0.3      50      965.0         153.7

YEAR  SPEC.    NUM.  BASAR.                      DBH
  0
       1  |    4 |     21.991  |    2.000   2.000   2.000   4.000
       2  |    4 |     62.832  |    2.000   2.000   6.000   6.000
       3  |    6 |    130.376  |    2.000   2.000   8.000   9.000   3.000   2.000

              14     215.200     LEAF AREA =     6.681

        DIAMETER LIMITS FOR LOGGING BY SPECIES
             1    2    3    4    5    6    7    8    9   10   11   12   13
          0.0  0.0  0.0  0.0  0.0  0.0  0.0  0.0  0.0  0.0  0.0  0.0  0.0


        ALL TREES WERE CUT
        YEAR    0 NO TREES LIVING
        THE SPECIES YOU HAVE SELECTED ARE INCOMPATIBLE WITH THE CLIMATE
CHCRW400      TERMINATED: STOP
```

Figure 10 Second example of program output. Major parameters listed are those that the user will most commonly modify. In this example, soil and climate variables for the test plot have been altered to give a severe microclimate. If left to its own devices, i.e., without intervention of subroutine CUT, the program would have killed all existing trees within ten years. Default values for *DMIN* would allow spruce and choke cherry to grow, but default *WMIN* values do not allow the birth of trees of any species.

Because subroutine GROWTH is deterministic, the curves of Fig. 8 are smoother than may occur in nature. Later versions of JABOWA could be modified to allow *DEGD* to be generated as a stochastic process. The properties of a *DEGD* time series have not yet been investigated.

Samples of the program output are shown in Figs. 9, 10, and 11. Simulation of secondary succession at 610 m elevation is illustrated in Fig. 9, which shows 60 years of growth at 15-year intervals following clear-cutting. At year 15, pin cherry (species 7) provides the greatest basal area and yellow birch (species 3) is the only other species contributing more than 100 cm^2 of basal area. By year 30, all pin cherries have disappeared and yellow birch contributes most of the basal area and continues to predominate in basal area through year 60. The importance of the shade-tolerant species increases continuously at each interval. These results are consistent with field observations of succession below 730 m elevation in northern New Hampshire and illustrate a successful simulation of secondary succession.

Figure 10 shows output data for the same tree plot as in Fig. 9 but with the plot now beset with severe environmental conditions: elevation 1524 m and a shallow, rocky soil. The program checks whether the growing degree-days and the index of evapotranspiration are compatible with growth of any of the available species. Default values for *DMIN* would allow spruce and choke cherry to grow if they were present. In this case, however, *WMIN* values are greater than the value of *SOILM* and no new tree of any species can be put onto the plot. The program prints a message to this effect and terminates execution.

Figure 11 shows two 20-year runs of two plots identical except for elevation. Calculated values of growing degree-days and the index of actual evapotranspiration at the two altitudes are printed with the site conditions at the beginning of each run. A change in elevation from 305 m to 914 m results in a growing-degree-day reduction of 1196 (38 percent) and an evapotranspiration index reduction of 88.5 (19 percent). At year zero, the stand of trees on the plot is relatively open. After 20 years at the lower elevation, yellow birch provides the major part of the basal area on the plot and contributes the most individual trees; beech and sugar maple are important; and spruce and fir occur only as small stems. After 20 years at the higher elevation, the initial sugar maple, beech, and yellow birch on the plot have been eliminated and only fir, spruce, and white birch remain, with white birch con-

```
                   THE JABOWA -- A NORTHEAST FOREST GROWTH SIMULATOR (VERSION 1)
DO YOU WANT A LIST OF SPECIES NAMES? REPLY  Y  OR  N
n
DO YOU WANT INFORMATION ON PARAMETERS? REPLY Y OR N
n
00001
                                  ******************************                      IX =          987643
  PLOT   ELEVATION   SOIL   PERCENT   GROWING       INDEX OF
 NUMBER   (METERS)   DEPTH   ROCK    DEGREE DAYS   ACTUAL ET
    0       305      10.0       0     3168.9         471.2

YEAR  SPEC.   NUM.  BASAR.                       DBH
  0
      1  |   4 |    21.991  |   2.000   2.000   2.000   4.000
      2  |   4 |    62.832  |   2.000   2.000   6.000   6.000
      3  |   6 |   130.376  |   2.000   2.000   8.000   9.000   3.000   2.000

            14     215.200    LEAF AREA =    6.681

YEAR  SPEC.   NUM.  BASAR.                       DBH
 20
      1  |   5 |   742.857  |  14.545  14.497  14.444  17.711   1.352
      2  |   6 |   654.477  |  11.664  17.365  17.305   6.972   6.746   1.458
      3  |  11 |  1783.568  |  12.820  12.765  23.569  24.968  14.819  12.633   9.122   8.586   8.992   8.365   8.820
      4  |   2 |     1.887  |   1.112   1.080
      9  |   1 |    11.804  |   3.877
     10  |   2 |     0.863  |   0.647   0.825
     13  |   3 |    38.270  |   6.532   1.643   1.831

            30    3233.727    LEAF AREA =  101.148
                                  ******************************                      IX =      1632522254

YEAR  SPEC.   NUM.  BASAR.                       DBH
 20
      1  |   3 |   251.424  |  14.814   9.991   0.921
      2  |   7 |   774.439  |  11.963  11.927  17.589  17.531   5.723   6.392   3.220
      3  |   6 |  1084.873  |  13.334  25.276  15.623  13.206   8.708   8.386
      4  |   1 |     5.968  |   2.757
      9  |   2 |     4.536  |   1.726   1.672
     11  |   3 |   105.314  |   6.815   6.586   6.653
     12  |   1 |     2.586  |   1.814
     13  |   3 |    14.282  |   3.359   1.802   1.912

            26    2243.421    LEAF AREA =   77.193

                                  ******************************                      IX =          987643
  PLOT   ELEVATION   SOIL   PERCENT   GROWING       INDEX OF
 NUMBER   (METERS)   DEPTH   ROCK    DEGREE DAYS   ACTUAL ET
    0       914       3.0       0     1972.7         382.7

YEAR  SPEC.   NUM.  BASAR.                       DBH
  0
      1  |   4 |    21.991  |   2.000   2.000   2.000   4.000
      2  |   4 |    62.832  |   2.000   2.000   6.000   6.000
      3  |   6 |   130.376  |   2.000   2.000   8.000   9.000   3.000   2.000

            14     215.200    LEAF AREA =    6.681

YEAR  SPEC.   NUM.  BASAR.                       DBH
 20
      9  |   9 |   222.911  |  10.450   8.750   7.338   5.175   2.300   2.188   1.726   1.612   1.331
     10  |   7 |    20.004  |   2.658   2.595   2.826   1.321   0.991   0.695   0.687
     11  |  23 |  1335.297  |  12.480  11.984   9.614  10.276   9.637   9.612   8.796   8.993   9.009   8.823   8.077
         |     |            |   8.126   8.590   8.085   7.595   7.945   7.123   6.821   6.616   7.263   6.459   6.383

            39    1578.212    LEAF AREA =   35.544
                                  ******************************                      IX =        94900730

YEAR  SPEC.   NUM.  BASAR.                       DBH
 20
      9  |   5 |   369.603  |  12.880  11.935   9.440   8.075   2.818
     10  |   9 |    26.896  |   2.354   2.805   2.547   2.256   1.753   1.684   1.419   0.811   0.827
     11  |  32 |  1574.916  |  10.602  10.330  10.346   9.848  10.178   9.747   8.603   8.653   9.429   8.560   8.569
         |     |            |   9.085   7.739   7.773   7.738   7.749   8.023   7.670   7.473   7.428   6.915   6.945
         |     |            |   6.224   6.394   6.962   5.564   5.578   6.227   4.852   4.249   4.626

            46    1971.414    LEAF AREA =   49.703
CHCRW400      TERMINATED: STOP
```

Figure 11 Third example of program output showing two (stochastic) 20-year runs for each of two plots at different elevations.

tributing most of the basal area. Because the plot begins with a relatively open stand, successional species predominate after 20 years. The climax species, sugar maple and beech at the lower altitude, spruce and fir at the upper, are present but have not yet obtained the importance they will have at later stages. These results are consistent with field observations and illustrate that the program successfully simulates altitudinal variations in vegetation.

The pairs of runs at each altitude illustrate the time variation that the program exhibits for identical sites. The

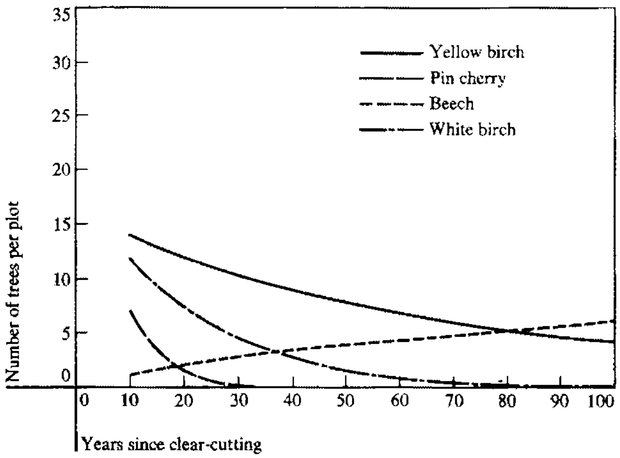


Figure 12 The average number of trees per plot for 100 plots with identical site conditions, $DEGD = 2550$, and deep, well-drained soil.

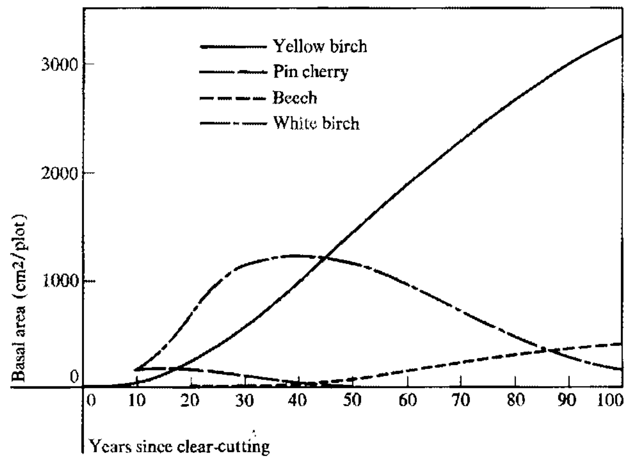


Figure 13 The average basal area per plot for 100 plots with identical site conditions, $DEGD = 2550$, and deep, well-drained soil.

cumulative effect of small, random, annual differences can lead to stands that appear greatly different when viewed at only a single time. For a more complete understanding of the properties of the simulator, one should consider the mean, variance, and skewness resulting from many runs.

Simulations of 100 plots with identical site conditions have been run for 2000 years following clear-cutting. At 610 m elevation ($DEGD = 2550$), the mean number of trees per plot stabilizes rapidly, dropping from 44 at year 10 to 33 at year 20 and remains between 28 and 35 through year 2000. Tree counts on individual plots are much less stable than these averages might lead one to expect, with observed ranges of 5 to 50 not uncommon. Mean total basal area increases from 450 cm^2 at year 10 to 1200 cm^2 at year 20, increases to 5500 cm^2 at year 200 (the time of the yellow birch peak), and then stabilizes below 4000 cm^2. While the mean total number of trees stabilizes rapidly, the numbers and basal areas of individual species change greatly. During the first 100 years following clear-cutting, the average numbers of intolerant, successional species (pin cherry, yellow and white birch) decrease continuously (see Fig. 12) in proportion to their relative maximum ages. The average number drops below one per plot by year 30 for pin cherry, by year 60 for white birch, and by year 200 for yellow birch. The average number of beech increases continuously during the first 100 years, reaching more than five by year 100 and stabilizing between six and eight through year 2000. While the average number of individual trees per plot is greatest early in succession for pin cherry and yellow and white birch, the maximum average basal area occurs at different times for each species (see Fig. 13). The average basal area of beech, which increases slowly to approximately 400 cm^2 during the first 100 years, is 950 cm^2 by year 200, 1400 cm^2 by year 300, and varies between 1200 and 1900 cm^2 through year 2000. At that time, the most important trees in terms of average basal area are (in descending order) beech, sugar maple, red spruce, and yellow birch.

Discussion

JABOWA is a stochastic simulator that attempts to reproduce the random and probabilistic characteristics of a forest. In this sense, the output is like the commentary of an experienced forester or ecologist who can predict the kind of forest that would grow on a particular site, the course of succession on that site, the kinds of tree that would dominate, whether their growth would be vigorous or slow, and so forth, but who would not be able to point to a particular spot and predict whether, in a given number of years, a tree would grow there and what its species and diameter would be.

The success of this simulator indicates that a valid description of a forest ecosystem can be formulated at a level that ignores microscopic details. In this sense, the simulator has attributes like those of thermodynamics, in which the laws governing certain average properties of a physical system are studied without reference to the detailed structure of the system. We suspect that similar macroscopic laws exist for ecosystems and that our simulator can be made to reproduce the behavior of appropriate averages for any forest. By accumulating data from many runs, each beginning with a different initial point for the pseudo-random-number generator, the user can obtain mean values and statistical characteristics of the simulated forest, which he can then compare with statistical measures of a real forest. Because events in a real forest are probabilistic, predictions concerning the population dynamics of trees are limited to such derived population statistics.

While the present version of the program grows the 13 species found in the Hubbard Brook forest, the program is potentially capable of simulating the growth of any nonhydrophytic tree species for which the following data are known or can be estimated: maximum age, diameter, and height; relation among diameter, height, and weight of leaves; geographic range; distribution along a moisture gradient; and tolerance to shade. The environment for any site is currently derived in the program from the mean monthly temperature and precipitation data, the percent of rock on the surface of the plot, the soil depth, and the moisture holding capacity. For forests in locations greatly different from northeastern North America, tree growth may be limited primarily by factors not included in the present version of the program, and modifications would be required.

Hydrach sites and species were deliberately avoided in the version 1 simulator because they do not occur in the Hubbard Brook vegetation survey and because we felt their introduction would complicate the simulation. Expansion of the program to include wet sites would be desirable, as would the inclusion of other environmental factors such as the calculation of light available to a plot as a function of slope, aspect, and the shading of the plot by nearby topographic features.

The major limitation to ecologic simulation is not in finding suitable mathematical models, but in finding sufficient relevant data to allow choice among possible models. We consider the version 1 simulator a first approximation and plan further tests to find out where it deviates from observations. We believe that when users of the program show us where the simulator does deviate from field observations, adjustment of the simulator can be made relatively easily. Two of the weakest links in the data are the relation between tree diameter and leaf weight, which remains imprecisely defined for the majority of the tree species found in the Hubbard Brook Experimental Forest, and the relation between individual tree growth and competition.

Uses of the program

The uses of JABOWA are of two kinds: the first as an aid to the student of forest ecosystems in investigating the implications of his knowledge and assumptions about ecosystem dynamics; and the second as a teaching and training tool in the manipulation of forests and the consequences of man-made or natural changes in the characteristics of the vegetation. Users of the program should have an understanding of the assumptions and limitations of the program and should not accept the results of the program without such an understanding.

Some specific uses include teaching students of ecology about succession and students of forestry about the effects of various cutting regimes on the subsequent makeup of a forest. Any event that can be expressed as a change in basic program dynamics such as growth rate, maximum age, maximum height, death rate, and probability of survival under normal or restricted growth can be illustrated by the program. One can investigate such questions as how much a parasite or herbivore would have to increase the probability of death of a species to make a noticeable change in the importance of that species currently present in the forest, or what the forest composition would be if any of the species were eliminated by a new disease.

The program allows one to investigate what factors are most sensitive in controlling the relative importance of species in the simulation. In our initial tests of the program, results were much less sensitive to changes in the photosynthetic rate vs light intensity curve than we would have thought. On the other hand, the minimum growth that a tree can sustain without significantly increasing its chance of death seems to be a sensitive factor in determining the relative importance of species.

It is our conclusion that the population dynamics of forest trees can be simulated, that such simulation can be done from first principles, and that at present the improvement of simulation is prevented primarily by a lack of data that accurately describe the relation between tree growth and the environment. Attempts to improve this simulation will help to point out crucial gaps in our knowledge about forests and can serve as an open-ended heuristic tool in designing field research.

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