SOME ECOLOGICAL CONSEQUENCES OF A COMPUTER MODEL OF FOREST GROWTH

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INTRODUCTION

The complexity of a forest ecosystem makes difficult any attempt to synthesize knowledge about forest dynamics or to perceive the implications of information and assumptions regarding forest growth. Although digital computer simulation seems to offer a potential for creating a complete model of forest growth, little progress has been reported. Computer simulation has been carried out for the growth of trees in even-aged stands of a single species (Mitchell 1969), and for meteorological energy exchange in a forest canopy (Waggoner & Reifsnyder 1968). A specific simulation built directly from Hubbard Brook data has been reported (Siccama *et al.* 1969). Successional change in northern hardwood forests has been predicted from observed birth and death rates (Leak 1970). A conceptual model has been created for the growth of individual tree seedlings from rates of photo-synthesis and the distribution of photosynthates (Ledig 1969). Computer simulation has been carried out for some aspects in a few other terrestrial ecosystems, such as productivity in a corn crop (Duncan *et al.* 1967); but apparently no one has successfully reproduced the major characteristics of a mixed-species, mixed-aged forest from a conceptual basis.

A computer simulation of forest growth is now developed that successfully reproduces the population dynamics of the trees in a mixed-species forest of north-east 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 (Bormann *et al.* 1970). However, the underlying concepts of the simulation are general. The pro-perties of each species are derived from its entire geographic range and in theory any non-hydrophytic 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 Forest, but the relative importance attached to each environmental factor has been influenced by the environmental characteristics of the north-eastern United States. It is hoped 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.

The basic goal was to produce a dynamic model of forest growth, a model in which changes in the state of the forest are a function of the present state and random compo-nents. This approach has two advantages over the curve-fitting approach to forest growth: first, the simulator can be regarded as a repository for an integrated knowledge of the ecosystem; second, additional hypotheses can be formulated and tested 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 estimate over what range and under what conditions it agrees with the Bartlett Forest birth–death probabilities (Leak 1970).

The simulation was built step by step, beginning with optimum growth for single trees, the effect of less than optimum light and moisture levels on growth, and the allocation of the growth resources among competing trees. The aim was to introduce a minimal number of assumptions and to find the simplest mathematical expression for each factor that was consistent with observation. New factors were introduced only when it was clear that the results of the simulation were not consistent with observation. A primary difficulty has been finding usable data regarding the relationships between tree growth and environmental variables. Where information was lacking, simple yet reasonable relationships were chosen.

In the original vegetation survey of the Hubbard Brook Forest, the species and diameters of all trees with dbh (diameter at breast height) greater than or equal to 2 cm were recorded on each of 208 10×10 m plots distributed uniformly over a small watershed. Environmental characteristics recorded for each plot were elevation, aspect, slope, percentage of the plot surface in rock, till depth and an index of soil moisture. The simulator was designed to capitalize on these data, to '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 random-number generator. A complete listing of the source deck can be obtained from the authors 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 was an IBM 2741 and PCS is TSS's program checkout system, a command language which allows for interrupting the program during execution, displaying and altering parameter and/or variable values, and dynamically altering the program logic by means of the branch command. A slightly modified version has also been operated successfully under CMS, The Cambridge Monitoring System. Prospective users with similar facilities should have no trouble using the simulator, while those with only batch mode operation at their computer centre should be able to convert the program fairly easily providing that 50K bytes of core storage initialized to zero are available.

It can be seen in Fig. 1 that the innermost loop of JABOWA contains calls to the three work-horse subroutines (GROW, KILL, and BIRTH). The other subroutines of JABOWA are subservient to these three and discussion of these can be found elsewhere (Botkin, Janak & Wallis 1972).

RELATION TO DATA

The Hubbard Brook Forest under investigation contains thirteen tree species: sugar maple (*Acer saccharum**), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), white ash (*Fraxinus americana*), mountain maple (*Acer spicatum*), striped maple (*A. pensylvanicum*), pin cherry (*Prunus pensylvanica*), chokecherry (*P. virginiana*), balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), white birch (*Betula papyrifera*), mountain ash (*Sorbus americana*), and red maple (*Acer rubrum*). The present forest, which was cut approximately 60 years ago, is dominated by sugar maple, beech and yellow birch below

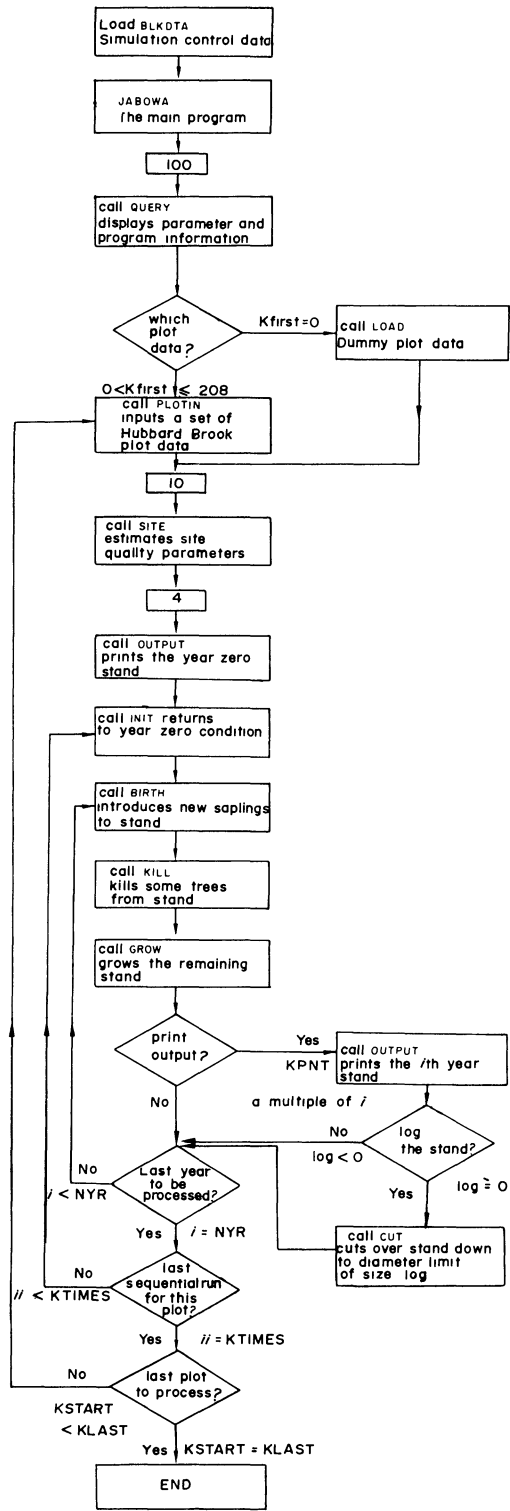* Nomenclature is according to Gleason (1968).

FIG. 1. Flow chart of JABOWA, Version 1 (reprinted with permission from the IBM Journal of Research and Development).

762 m, and red spruce, balsam fir and white birch at higher elevations, although the last three species are also found at lower elevations.

Studies of succession in this area indicate that, in the year following a large clearcutting, pin cherry germinates in great abundance to form dense even-aged stands. Subsequent germination of this species does not occur (Marks 1971). Under some conditions, white or yellow birch may germinate with the pin cherry and continue to enter the stand in subsequent years until light levels become low. It appears that the birches germinate and survive under some shading and can germinate in openings or partial clearings that would not provide sufficient light for the cherry species (Marquis 1969a).

Under heavy shade on the better sites, with the single exception of beech, the existing plot data for the Hubbard Brook Forest do not yield strong correlations between the number 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 non-boreal species grow poorly and are subjected to a differentially severe mortality. Observations of the growth of seedlings and saplings of the major shade-tolerant species indicate that under shaded conditions a number on the order of 0–2 individual saplings may be added in any one year to a 10 × 10 m plot (L. Forcier, personal communication, 1969). The occurrence of saplings of the tolerant species is not clearly related to light intensity at the forest floor, while seed germination, growth and survival of young stems undergo very great yearly variations suggesting cycles of 3- to 5-year duration.

DESCRIPTION OF THE MODEL

In the present, simulator tree species are defined by a few general characteristics: a maximum age; maximum diameter; maximum height; a relation between height and diameter; between total leaf weight and diameter; between rate of photosynthesis and available light; between relative growth and a measure of climate; a range of soil moisture conditions within which the species can grow; and the number of saplings which can enter the stand under shaded, open, or very open conditions. The abiotic environment is defined by an elevation, a soil depth, soil moisture-holding capacity, percentage rock in the soil, a set of average monthly temperatures and precipitation records from a nearby weather station, and a value for the annual insolation above the forest canopy.

Direct competition among individuals is restricted to competition for light (taller trees shade smaller ones, and species with more leaves for a given diameter shade smaller competitors more than other species; under shaded conditions photosynthesis is higher for shade-tolerant species than intolerant ones, and *vice versa*). Species strategy is also invoked by species-specific survival probabilities and by differential addition of new saplings in relation to light at the forest floor. Because the annual probability of survival of an individual is related to the maximum known lifetime of its species, individuals of long-lived species have a better chance of survival in any one year than those with short maximum lives. For each plot year of simulation three major subroutines are called: subroutine GROW, which deterministically provides the annual growth increment for each tree; subroutine BIRTH, which stochastically adds new saplings; and subroutine KILL, which stochastically decides which trees die.

Subroutine GROW

This subroutine uses a tree growth model to augment the dbh's of all trees on a 10 × 10 m

plot by an amount representing 1 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 optimum site quality and no competition from other trees. For each plot-year, this growth rate is decreased by factors taking 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 and the final growth equation used exhibits this overall property. Some may think that the equations which follow are occasionally based upon rather arbitrary assumptions, but it is probable that there is no unique solution to forest growth simulation, and that many equations based upon 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 optimum conditions has the form:

$$\delta(D^2H) = R \cdot LA \cdot \left(1 - \frac{DH}{D_{max}H_{max}}\right) \tag{1}$$

in which D is the dbh of the tree, H 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 1 year is proportional to the amount of sunlight which 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 right-hand side of eqn (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.

The height H (in cm) of a tree with dbh D (in cm) is assumed to be given by the following expression (Ker & Smith 1955):

$$H = 137 + b_2D - b_3D^2. \tag{2}$$

The number 137 represents breast height (in cm), 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:

$$b_2 = 2(H_{max} - 137)/D_{max}; \quad b_3 = (H_{max} - 137)/D_{max}^2. \tag{3}$$

Rate of change of height decreases with increasing diameter (eqn 2), and actual change in height becomes negligible for large diameters.

From the above discussion, it can readily be seen that JABOWA currently makes no adjustment for the forester's concept of 'form factor'. For example, it would be comparatively simple to modify eqn (2) of sub-routine GROW to reflect differences in site quality, if it was known how the constants H_{max} and D_{max} varied with measures of growing degree days, and the other requirements for autotrophic plant growth. Field checks would be necessary to quantify such relationships reliably and this was therefore not attempted.

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

$$WEIGHT = C_iD^2 \tag{4}$$

where C_i is a constant. This equation states that the ratio of leaf weight to stem basal area is a constant from sapling age to death. Data from Hubbard Brook (R. H. Whittaker, personal communication, 1970) and elsewhere (Perry, Sellers & Blanchard 1969; Kittredge 1948; Baskerville 1965) indicate that the actual exponent ranges from 1·5 to about 3. The error associated with these estimates is unknown. Increasing the exponent

Table 1. *Basic parameters*

G = growth constant, C = leaf area constant, AGEMX = maximum age (years); D_{max} = maximum known diameter (cm), H_{max} = maximum known height (cm); b_2 and b_3 are constants in the equation $H = 137 + b_2D - b_3D^2$ relating height to diameters; $DEGD_{min}$ and $DEGD_{max}$ are minimum and maximum degree-days; WMIN and WMAX are minimum and maximum values for the index of evapotranspiration (mm of water per year available for evapotranspiration).

	G[5]	C[6]	AGEMX[9]	Type[9]	D_{max}/H_{max}	b_2	b_3	$DEGD_{min}$[4]	$DEGD_{max}$[4]	WMIN	WMAX
Sugar maple	170	1·57[1]	200[3]	2	152·5[3]/4011[3]	50·9	0·167	2000	6300	300	
Beech	150	2·20[1]	300[3]	2	122[3]/3660[3]	57·8	0·237	2100	6000[7]	300	
Yellow birch	100	0·486[1]	300[3]	1	122[3]/3050[3]	47·8	0·196	2000	5300	250	
White ash	130	1·75	100	2	50/2160[3]	80·2	0·802	2100	10700	320	
Mt. maple	150	1·13[1]	25	2	13·5/500	53·8	2·00	2000	6300	320	
Striped maple	150	1·75	30	2	22·5/1000	76·6	1·70	2000	6300	320	
Pin cherry	200	2·45[2]	30	1	28[2]/1126[2]	70·6	1·26	1100	8000	190	
Chokecherry	150	2·45	20	1	10/500	72·6	3·63	600[3]	10000	155	
Balsam fir	200	2·5	80[3]	2	50/1830[3]	67·9	0·679	1100	3700	190	
Spruce	50	2·5	350[3]	2	50/1830[3]	67·9	0·679	600	3700	190	
White birch	140	0·486	80	1	46/1830[3]	73·6	0·800	1100	3700	190	600[8]
Mt. ash	150	1·75	30	2	10/500	72·6	3·63	2000	4000	300	
Red maple	240	1·75	150[3]	2	152·5[3]/3660[3]	46·3	0·152	2000	12400	300	

[0] Values not otherwise referenced were developed during the course of the study.
[1] R. H. Whittaker (1970, personal communication).
[2] Marks (1971).
[3] Harlow & Harrar (1941).
[4] Climatological ranges in growing degree-days, obtained by matching northern and southern limits of range maps (Fowells 1965) to January and July mean world isotherms.
[5] Growth constants adjusted for reasonable growth of individual tree in full sun with climate and soil factors equal to 1 (values of G will give ~2/3 of maximum diameter at 1/2 maximum age starting from an 0·5 cm stem).
[6] Actual leaf area in square metres is ~$CD^2/15$ for D in cm.
[7] Northern strain.
[8] Calculated for New York City.
[9] Type 1 is shade-intolerant; type 2 is shade-tolerant.

in the leaf weight–diameter relationship (eqn 4) has the effect of steepening this curve for intermediate-aged trees. The exponent could be as small as 1 or as large as 3 without drastically altering the overall shape of the final growth curve.

If it is assumed that leaf area is proportional to leaf weight, and defining $G = RC_i$, eqn (1) can be written in the form:

$$\delta D = \frac{GD[1 - DH/D_{max}H_{max}]}{[274 + 3b_2D - 4b_3D^2]}. \tag{5}$$

A curve of diameter *versus* time resulting from this equation corresponds to an unusually large tree, 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 such large trees would be an extremely rare event, and the usual dominant trees produced by the simulator are considerably smaller than the maximum values given in Table 1.

The constant G in eqn (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 $t \rightarrow \infty$). Given a maximum observed age for each species, AGEMX, 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 (see Appendix).

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

$$\delta D = \frac{GD[1 - DH/D_{max}H_{max}]}{[274 + 3b_2D - 4b_3D^2]} \cdot r(AL) \cdot T(DEGD) \cdot S(BAR). \tag{6}$$

These three additional factors are now discussed in detail.

Assuming that a layer of leaves is a uniform absorber of light, it can be shown that the light intensity at a height h is related to the light intensity Q_0 above the top of the canopy by (Kasanaga & Monsi 1954; Loomis, Williams & Duncan 1967; Perry *et al.* 1969)

$$Q(h) = Q_0 \exp - k \int_h^\infty LA(h')dh'$$

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

$$AL = PHIe^{-k \cdot SLA} \tag{7}$$

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 eqn (4)) of all higher trees on the plot (with the heights obtained from eqn (2)), and PHI is the annual insolation in appropriate units. Currently, JABOWA uses a default value of 1 for PHI; a desirable improvement would consist of a subroutine for generating a value of PHI based on latitude and aspect. The constant k in eqn (7) is adjusted for reasonable shading beneath a dense canopy, and it has been found that k = 1/6000 (in units reciprocal to those of eqn (4)) gives good results for 10×10 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 eqn (6) is

$$r(\text{AL}) = \begin{cases} 1 - e^{-4 \cdot 64(\text{AL} - 0 \cdot 05)}, \text{ shade-tolerant} \\ \\ 2 \cdot 24 \ (1 - e^{-1 \cdot 136(\text{AL} - 0 \cdot 08)}), \text{ shade-intolerant.} \end{cases} \quad (8)$$

In each case, AL is to be obtained from eqn (7). The function r, which may be thought of as a representation of photosynthetic rates, for the two degrees of shade tolerance, contains constants chosen to give reasonable fits to measured photosynthesis curves (Kramer & Kozlowski 1960). Note that the annual insolation PHI can be expressed in any units if appropriate changes are made in the constants appearing in eqn (8).

The function T(DEGD) in eqn (6) represents an attempt to take account of the effect of temperature on photosynthetic rates. It is assumed that each species will have an optimum 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, an approximation is used 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:

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

in which all temperatures are in degrees Fahrenheit.

For each species, is now set:

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

This function is a parabola (see Hellmers 1962, p. 284) having the value zero at minimum and maximum values of DEGD, and a value between zero and one for any value of DEGD between the extremes. Values of DEGD_{min} and DEGD_{max}, representing the extremes for which each species will grow, can be obtained reasonably accurately by comparing species range maps (Fowells 1965) to lines of constant DEGD estimated from maps of the January and July world isotherms (Trewartha 1968; U.S. Dep. of Commerce 1968). There are admittedly many micro-environmental effects, such as exposure to wind and available nutrients, that are completely neglected in this approximation; however, the number of growing degree-days proves to be a useful measure of gross thermal effects upon plant growth.

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

$$\text{S(BAR)} = 1 - \frac{\text{BAR}}{\text{SOILQ}} \quad (11)$$

where BAR is the total basal area on the plot. SOILQ is the maximum basal area of a stand of trees under optimum growing conditions on the plot, and the function S(BAR) is a crude expression of the competition for soil moisture and nutrients on the plot.

Subroutine BIRTH

In each year, new saplings of each species enter a plot on the basis of their relative tolerance to shade and whether the degree-day and soil moisture conditions allow growth of that species. The model is designed in this regard to mimic the specific behaviour of each species and the process of succession described previously. It assumes a seed source available for each species, but only those species that can grow are added to the stand. The available growing degree-days DEGD at the site is compared with the species vectors of minimum and maximum values of growing degree-days $DEGD_{min}(i)$, $DEGD_{max}(i)$, 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 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 single selected species are added. The diameter of the added trees depends upon the parameter SIZE (default value 0·5 cm) and a small random addition.

The idea of a random selection of which shade-tolerant tree species to add is not the desperate expedient that it first appears to be. The Hubbard Brook plots show many inexplicable differences in species composition between plots within the elevational bands discussed by Bormann *et al.* (1970). In addition, upon the better sites, with the single exception of beech, the existing plot data do not yield strong correlations between the number 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 non-boreal species grow poorly and are subjected to a differentially severe killing (see discussion of subroutines GROW and KILL).

A range of 0–2 individual saplings is a reasonable rate of annual introduction for the shade-tolerant species on a 10 × 10 m plot (L. Forcier, personal communication, 1969). Seed germination, growth and survival of young stems undergo great yearly variations suggesting cycles of 3- to 5-year duration, and the occurrence of saplings is not clearly related to light intensity at the forest floor; therefore a random introduction approximates current knowledge well. In practice, JABOWA Version 1 produces stands that are similar to those observed at Hubbard Brook, although the above described procedure may produce stands that underemphasize the major species, in particular beech, while over-emphasizing the importance of the minor stand components (e.g. red maple). However, biasing the probabilities for species entry should await extensive testing of the present random choice algorithm. Further field study is also clearly necessary to determine the conditions that promote survival of saplings of the shade-tolerant species.

The four intolerant successional species are handled quite differently. If the total leaf area on a plot (variable WEIGHT) is below a first threshold (variable CHERRY), between 60 and 75 new cherry trees are added to the stand. The number of cherries added by the simulator is far below the dense thickets observed in the field. Cherries are short-lived trees and more realistic modelling may 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 cherry stems will be made to agree with observations. As the program now functions, it starts with too few cherry stems and gives them a higher probability of survival than is observed, but the number of cherries 10 years following a clearcut is realistic. If the leaf area is greater than the cherry species cutoff but less than a second threshold value (variable BIRCH) then the two birch

species can enter the plot. Between zero and thirteen trees are added as a random choice weighted by stand density, so that the shadier the plot the fewer the trees that are added.

Both the two cherry species and two birch species have overlapping ranges. Choke-cherry has a wider geographical range than pin cherry (Harlow & Harrar 1941), but the latter species is more prevalent near its optimum than pin cherry. Although the two birch species have overlapping ranges, yellow birch goes much farther south than white birch, while white birch survives farther north and on much shallower and rocky sites. In the simulator the choice between cherry or birch species is weighted by site and species constants to reflect the observed ranges.

Subroutine KILL

Few data are available regarding survival rates of trees. Simple assumptions have therefore been made regarding tree death. It is assumed that from sapling age to maturity there are some causes of tree mortality that are age-independent. For actively growing trees, it is assumed that no more than 2% of the saplings of a species should reach the maximum age for that species. This gives a probability, that a tree will die in any year, of

$$p = 1-(1-\varepsilon)^n.$$

If $p = 0.98$ when $n = \text{AGEMX}$, the maximum age of the species, and ε is the death probability, then

$$(1-\varepsilon)^{\text{AGEMX}} = 2 \times 10^{-2}$$

which gives approximately

$$\varepsilon = 4.0/\text{AGEMX}.$$

Trees whose annual increment is below a certain value (0.01 cm in the present version of the program) are subjected to a second death mechanism which assures that such a tree would have only a 1% chance of surviving 10 years in the forest with its annual increment remaining below the minimum (the probability that such a tree will die in any one year is 0.368).

The basic rationale is that a tree which cannot maintain a certain minimum growth rate cannot survive for long in the forest, but 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 at any time. While in reality some of these events may be truly random, others are not. The assumption of this model is that even the non-random 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.

Subroutine SITE

This subroutine produces indices of the quality of the site for growing trees. It is customary for forest site indices to be based upon the observed height/age relationship of dominant trees of certain key species that hopefully appear on the plot. Such data are time-consuming to accumulate and often difficult to obtain for disturbed stands. JABOWA Version 1 involved a different philosophy; it was desired to index site quality not by what was currently growing on a plot, but by estimates of the exogenous influences, growing

degree-days and an index of actual evapotranspiration. This approach also raises interesting questions about the minimum amount of light and moisture that are necessary as well as the optimum levels needed for tree and stand growth. However, in the present version of the program, the soil moisture information is used only to bias the input of new stems.

The growing degree-days parameter, DEGD, has already been described in the discussion of subroutine GROW. To estimate the value of DEGD for an individual site, long-term estimates are needed of the mean January and July temperatures. It is axiomatic that this information is not available for most sites where JABOWA might be used, and so subterfuge may be necessary. 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 3·6° F/1000 ft, while the January minimum uses 2·2° F/1000 ft (Sellers 1965). Note that subroutine SITE expects elevation in feet, rainfall in inches per month and temperatures in degrees Fahrenheit; conversion to metric units is carried out in the subroutine. No attempt was made to account for differences in monthly temperatures which result from differing aspects. All of the Hubbard Brook plots have more or less southerly exposure, and differences in mean monthly temperature associated with aspect differences were assumed small; for other areas this may not be a reasonable approximation.

Latitudinal as well as coastal influences on climate are pronounced in New England, and it is hoped that, by using the closest long-term weather station and adjusting for elevation difference, reasonable microclimatic indices can be developed for nearby sites. Elevational transference should be kept less than about 1000 m, as the growing degree-day calculation is sensitive to large elevational changes and is not completely linear.

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 many species may have difficulty becoming established and, accordingly, an index of actual evapotranspiration, SOILM, an index in millimetres of water per year available for evaporation, was incorporated. The index is developed as a modified Thornthwaite water balance calculation (Sellers 1965). The maximum available moisture storage, STRMAX, is the soil depth, TILL, or 10 m, whichever is the smaller, multiplied by the moisture storage per unit depth of the fine soil fraction, TEXT (Thornthwaite & Mather 1957), discounted by the percentage rock in the soil mantle. The percentage rock in the soil mantle 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 on stand growth for New England forest stands is corroborated by the values of SOILM that were obtained. With the 30-year Woodstock, New Hampshire weather station data, assuming IROCK = 0, and IELEV ≃ 300 m, then TILL has to fall below 0·45 m before SOILM starts to contract. At higher elevations there is even less heat and hence an even smaller requirement

for soil moisture storage, so that at 1500 m TILL can fall to 0·33 before SOILM starts to contract.

Something similar to a 'wind-chill factor' may accelerate tree mortality as timber line is approached, but the difficulty of quantifying the wind-chill concept with the available sparse data presented any direct assessment of the chill factor within subroutine SITE. An indirect assessment of the chill factor has probably been built into the simulator in that only those species which can be grown can be added to the stand. (Tests of $DEGD_{min}(i)$ versus DEGD and WMIN(i) versus SOILM are made by subroutine BIRTH.) In particular for shallow, rocky, high elevation sites the value of SOILM falls precipitously; such localities probably form a set that largely intersects the set of wind-chill sites. Later efforts should be directed towards determining whether or not this indirect assessment of the chill factor is indeed adequate.

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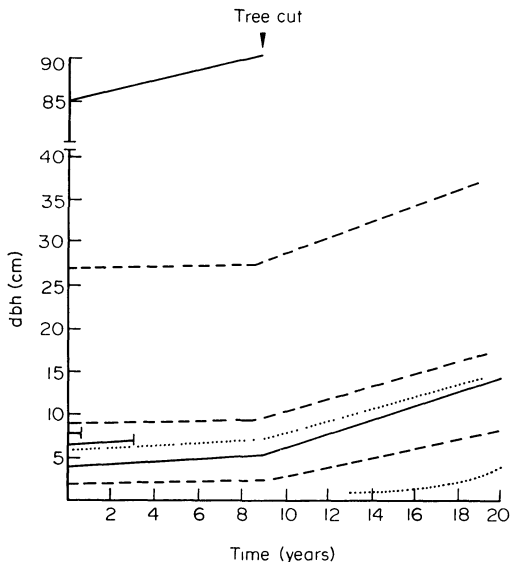

FIG. 2. Simulated diameter growth of individual trees on a single plot. Each line represents a single tree and the end of a line that tree's death. At year 9 the large sugar maple was removed. The remaining trees, no longer suppressed by the large maple, show increased growth rates. ——, Sugar maple; · · · ·, beech; – – –, yellow birch. (Reprinted with permission from the IBM Journal of Research and Development.)

RESULTS AND DISCUSSION

Competition, succession and changes in species composition as a function of time and climate are reproduced successfully by the model. A simulation of competition is illustrated in Fig. 2, where the curves are smoother than in nature because the growth algorithm is deterministic. A single large sugar maple, which grows approximately 0·5 cm in diameter per year, suppresses the growth of smaller trees, none of which grows as much

as 2 cm in 10 years. When this large tree is removed growth increases in the suppressed trees. The largest remaining tree, a 28-cm yellow birch, grows 10 cm in the subsequent 10 years. Smaller trees, suppressed only by this yellow birch, show increases in growth rates consistent with the amount of shading each experiences from larger remaining trees. For example, a 9-cm yellow birch, which grew 1 cm before the elimination of the large sugar maple, grows approximately 8 cm by year 20. Species differences in growth and response to competition for light are also indicated. For example, a beech grows more slowly than a sugar maple of similar size.

Simulation of secondary succession at 610 m elevation is illustrated in Fig. 3. This elevation is well within the hardwood forest, and the simulation shows that 15 years after clearcut pin cherry (species 7) provides the most basal area while yellow birch (species 3) is the only other major contributor to basal area of the plot. All the pin cherries disappear by year 30, and afterwards the importance of shade-tolerant species increases at each interval although yellow birch dominates until year 60. These results are consistent with field observations of succession below 760 m elevation in northern New Hampshire (Bormann *et al*. 1970; Siccama 1968).

The model predicts a general increase in density, or stems per unit area (Fig. 4), and a decrease in basal area (Fig. 5) with elevation. Interestingly, it predicts an anomalous point at 762 m with total basal area lowest at this elevation. During succession density fluctuates more at this elevation than at others. The transition from hardwood to conifer forest actually occurs at this elevation in northern New Hampshire and a study also verifies the model's predictions for Vermont (Siccama 1968). It is important to realize that the model is not artificially constrained to produce this anomaly. The model assumes that the same factors which account for the latitudinal distribution of a species also account for its elevational distribution, and the anomaly at 762 m then occurs as a result of competition and species response to growing degree-days, which is non-optimal for all species at this elevation and latitude.

That the degree-day function could account for so much of the known change in vegetation with change in elevation is a surprising result of the model. The degree-day function was introduced with the expectation that other functions, such as a wind-chill factor to represent the desiccating effects of winter winds, would be necessary. Such additional factors may be needed to predict changes in the volume of trees, but they are apparently not necessary for prediction of stem density and basal area.

The behaviour of individual species as a function of time and elevation is also successfully reproduced. The average basal area per plot for 100 identical plots is shown as a function of time for each of the six major species in Fig. 6. This average decreases with elevation at all time intervals for yellow birch (Fig. 6a), beech (Fig. 6b), and sugar maple (Fig. 6c). The average basal area of white birch tends to increase with elevation (Fig. 6d), while the average basal area of red spruce increases with elevation to 914 m, and then remains constant (Fig. 6e). Balsam fir grows best at 914 m but grows better at 1067 m than at 762 m or lower elevations (Fig. 6f). In basal area, birches dominate the early stages of succession: yellow birch at lower and white birch at higher elevations.

The model predicts an old-age forest that is far from uniform (Figs. 7 and 8); its 'climax' state is best viewed as the most probable state at a point in any area which has remained in a constant climate without major catastrophe for a long time. Simulations carried out at 610 m for 2000 years following clearcut result in a rich forest mosaic, generally dominated by beech and sugar maple, but including plots with a wide range of cover. In two different simulations with identical initial conditions, pin cherry occurred on 1% of

FIG. 3. Output of JABOWA, Version 1, as it appears on the user's computer terminal, showing 60 years of secondary succession at 15-year intervals on the test plot (Plot 0). In this case the user specified the plot's altitude and soil depth, the minimum size tree to be cut, the number of years of the simulation and the interval between print-outs. Soil depth is in metres. Index of Actual ET is an index of growing season evapotranspiration in mm. SPEC. is the species number, and refers to the list above see (p. 850). NUM. is the number of trees of each species; BASAR. is the basal area contributed by each species. Numbers under DBH are the diameters of each tree in cm. Leaf area is an index of the total leaf area on the 10×10 m plot obtained by dividing total leaf weight of all species on the plot by 45. Dividing this number by 15 gives a rough approximation of leaf area index on the plot. IX is the number initiating the pseudo-random number sequence. Major parameters listed are those which the user will most commonly modify.

PLOT NUMBER	ELEVATION (METRES)	SOIL DEPTH	PERCENT ROCK	GROWING DEGREE DAYS	INDEX OF ACTUAL ET			
0	610	10.0	0	2549.4	423.1			

IX = 1065786486

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 30

SPEC.	NUM.	BASAR.	DBH
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	9.746 9.737 9.717 10.689 9.673 9.799 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 45

SPEC.	NUM.	BASAR.	DBH
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 0.938
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 60

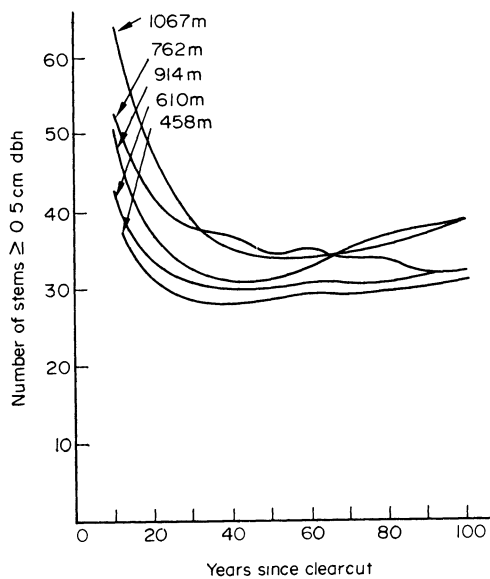| SPEC.	NUM.	BASAR.	DBH
1	3	604.325	17.833 17.154 12.536
2	4	167.922	12.846 6.395 2.382 1.486
3	9	3200.747	22.939 22.829 22.485 24.378 22.038 22.166 21.186 20.438 9.194
4	2	10.893	3.604 0.938
5	1	0.736	0.968
9	3	325.418	17.080 11.037 0.887
10	6	31.617	5.329 2.622 1.690 1.903 1.134 0.576
12	3	11.352	2.551 1.994 0.710
13	3	50.946	6.576 4.047 0.291
	34	4403.949	LEAF AREA = 110.214

FIG. 4. The average total number of stems per plot with dbh $\geqslant$ 0·5 cm for 100 plots with identical site conditions for a range in elevation from 458 m to 1067 m and a deep, well-drained soil.
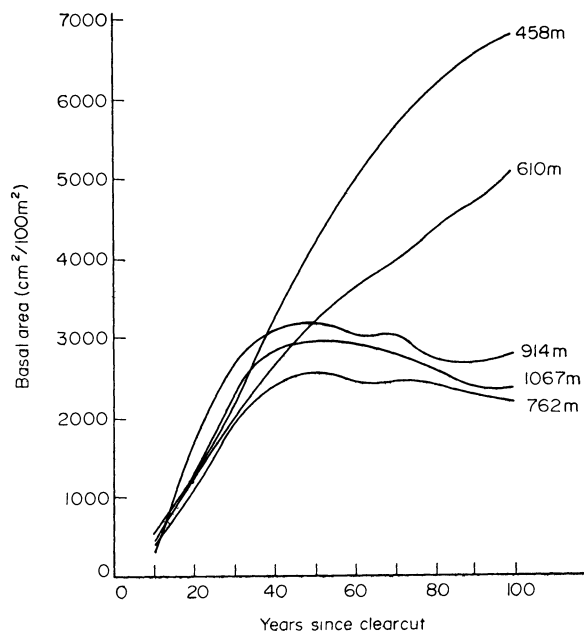

FIG. 5. Average total basal area as a function of time since clearcut and elevation in metres. Each line represents the average for 100 plots at a single elevation with identical site conditions including a deep, well-drained soil.
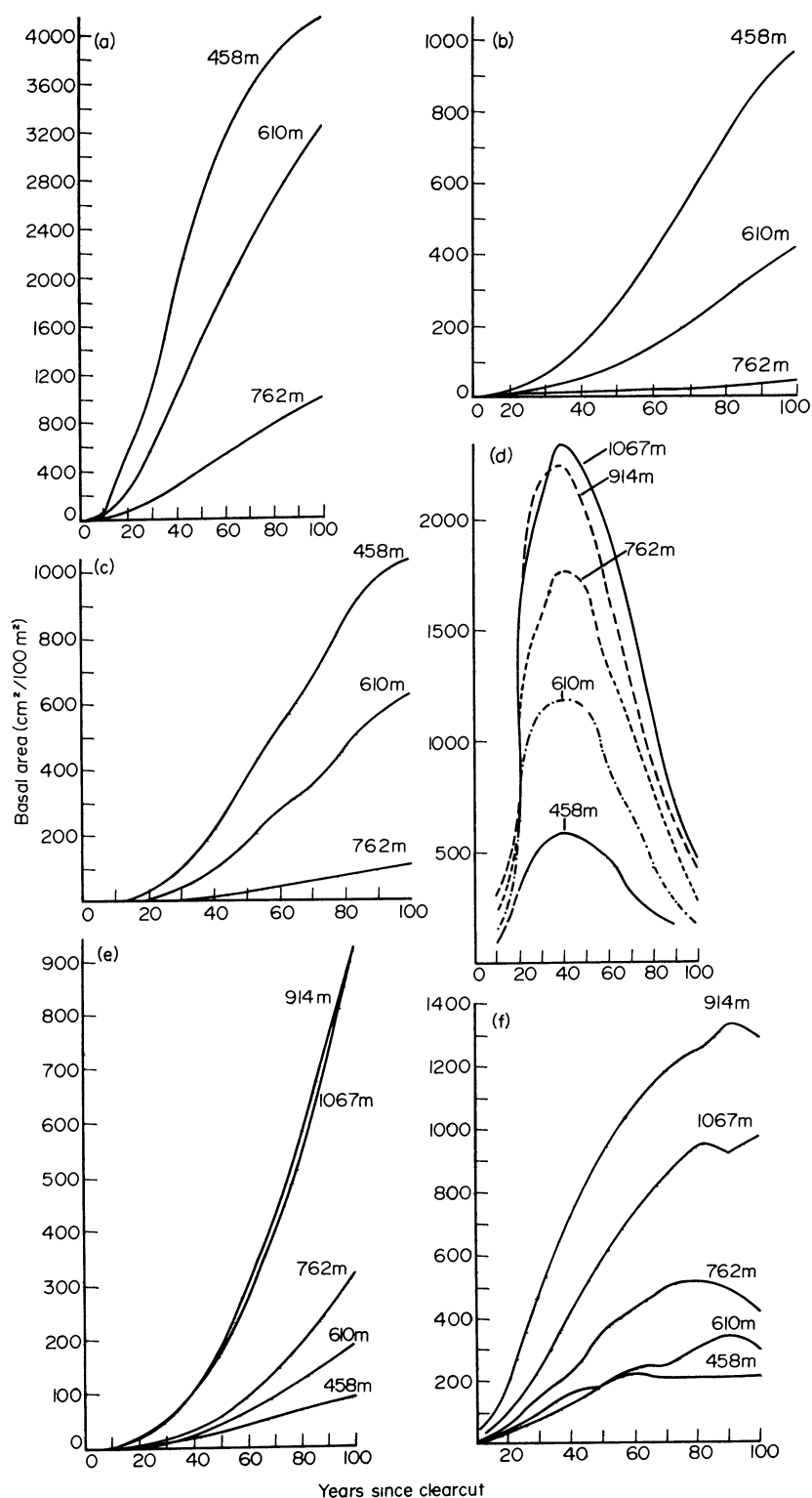
FIG. 6. Average basal area as a function of time since clearcut and elevation for each of the six major species: (a) yellow birch; (b) beech; (c) sugar maple; (d) white birch; (e) red spruce; and (f) balsam fir. Each line represents the average for 100 plots at a single elevation with identical site conditions including a deep, well-drained soil.
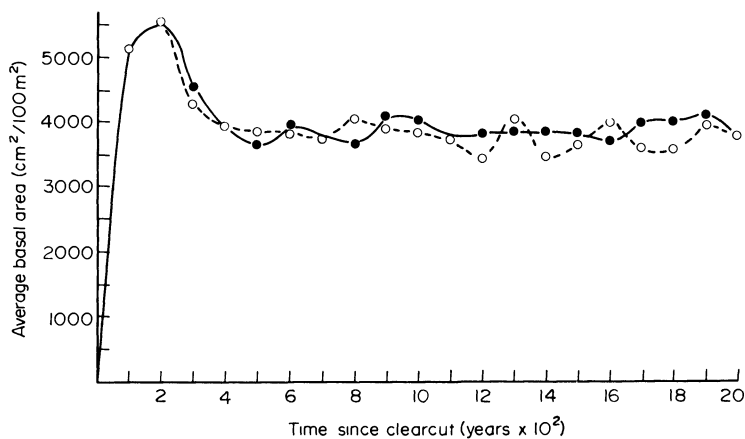
FIG. 7. Two long-term predictions of average basal area per plot of the model at 610 m elevation. Each line represents the average of 100 plots with identical site conditions including a deep, well-drained soil and constant climate, but starting with different pseudo-random numbers.
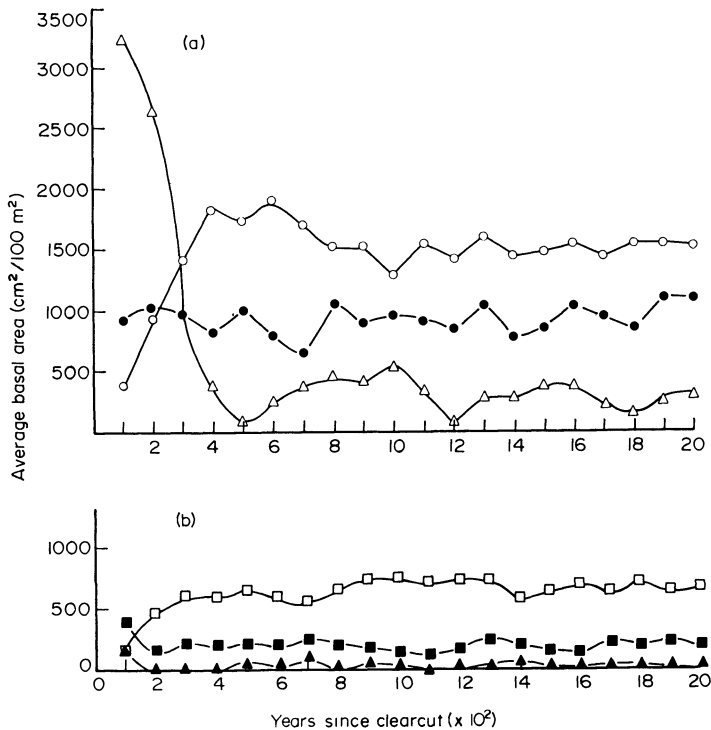

FIG. 8. Long-term predictions of average basal area for six species under constant climate and good, well-drained soil at 610 m elevation for basal area of six major species. (a) Includes those species more typical of the lower elevations: ●, sugar maple; ○, beech; △, yellow birch. (b) Includes those species more typical of higher elevations: ■, balsam fir; □, red spruce; ▲, white birch. Each line represents the average of 100 plots.

the plots after 2000 years. Even in a stable climate openings sufficiently large to permit the growth of pin cherry, solely the result of the 'natural' and nearly simultaneous death of neighbouring large trees, are sufficiently probable to allow a continuing role for pin cherry and other opportunistic species in an old-age forest. Thus, the model suggests a resolution to the long-standing controversy about whether relatively intolerant but
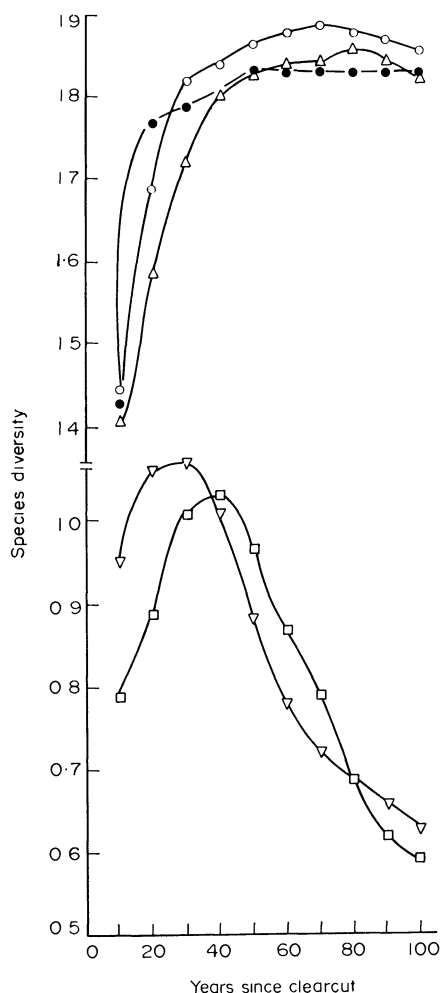

Fig. 9. Species diversity as a function of time since clearcut and elevation. Each line is the mean for 100 plots with identical site conditions including a deep, well-drained soil. ●, 458 m; ○, 610 m; △, 762 m; ▽, 914 m; □, 1067 m.

relatively long-lived species such as yellow birch or white pine could be members of long-undisturbed forests.

The model predicts that an old-age forest will have a smaller standing crop and species diversity* than some earlier stages (Fig. 9). Diversity increases early in succession and reaches a maximum during the first century at all elevations; of course it is much greater below 762 m than above, because sugar maple, beech and yellow birch disappear above

* The Shannon index of species diversity, $H' = \Sigma - p_i \log p_i$, where p_i is the probability of selecting an individual of species i by a random selection process, is used (Pielou 1966).

this elevation, but spruce, fir and white birch, which dominate at the higher elevations, also occur at lower ones.

These predictions are consistent with observed patterns in similar hardwood forests of Wisconsin (Loucks 1970), where peak standing crop occurs approximately 200 years after clearcut and both standing crop and species diversity decrease in older stands. Casual observers of forest ecosystems sometimes suggest that a final or climax state would be reached much earlier. However, it is clear from a conceptual point of view that in any ecosystem the effects of the initial conditions on species composition would be present for a period comparable to a small multiple of the lifetime of the longest-lived major species. (In northern New Hampshire, this lifetime is on the order of 400 years.) The model predicts that the final state could not be said to occur prior to year 400 (Fig. 7) and the final order of importance of the major species is not reached until year 600 (Fig. 8). In light of the high probability of a major natural catastrophe during such a long period, and the variability of site conditions over even small areas in New England, the model suggests that the concept of a climax forest as defined earlier in the twentieth century (a uniform pattern of species composition with wide areal and temporal extent) is untenable.

The long-term predictions of the model must be treated cautiously. The simulator currently uses constant climate, and considers all species that can grow at a site as part of the available reservoir for entry into the stand. Presumably during long periods of excessively hot or cold weather certain species would be removed from the active reservoir, and would be reinstated only when the climate returned to a more normal range. That long-term climatic fluctuations probably exist for New England can be deduced from Landsberg's reconstructed 230-year climatic record of Philadelphia (Landsberg, Yu & Huang 1968). It appears that annual growing degree-days could be adequately modelled using a filtered fractional noise (with $h = 0.8$ and $\rho = 0.4$ (Matalas & Wallis 1972)), but it also appears that the model would then have to be modified to allow for species-specific migration in response to long-term climatic fluctuation.

There are three ways to verify models such as this. The first comprises the reactions of experienced field observers to the predictions. The second involves detailed gathering of all information relevant to the model, and the third is a comparison, where possible, with existing records. That the model satisfies the first kind of verification has already been made clear. Observations regarding the second kind have been carried out, but have not yet been analysed and will be reported elsewhere.

Direct quantitative comparison of the average characteristics of real plots in the Hubbard Brook Forest with the simulated plots described here is difficult because the real plots vary considerably in soil depth and elevation and because this forest has a somewhat complicated and poorly documented logging history. The forest was apparently logged twice, once about 1909 when large spruce trees were removed and again about 1916–17 when hardwoods and the remaining spruce were cut. Analysis of growth rings indicates that the loggers left a forest of scattered large hardwoods of beech, birch and maple and smaller hardwood stems. Although the area was probably not completely clearcut, cutting was sufficient at least in some areas to allow establishment of cherry and birch (Bormann *et al.* 1970).

In spite of the many sources of variation, the mean value for the simulated plots for both years 50 and 60 is within one standard deviation of the mean of the observed forest. Furthermore, some of the Hubbard Brook plots show characteristics very similar to those of the optimal plots of the simulator. For example, a real plot at 553 m elevation,

till depth of 1·5 m and 1% rock had a total of eighteen stems and total basal area of 3658 cm^2. Five yellow birch trees contributed 2376 cm^2, six beech 1005 cm^2, two spruce 89 cm^2, two sugar maple 16 cm^2, with the remaining contributed by understorey species. The average total basal area predicted by the model on 100 plots with identical initial conditions at 610 m is 3250 cm^2 at year 50 and 3660 cm^2 at year 60. By species, the predictions at years 50 and 60 are: sugar maple 200 and 300 cm^2; beech 100 and 150; yellow birch 1400 and 2000.

It is interesting to compare the predictions of the simulator with present conditions of forests in New England and with the meagre accounts available regarding presettlement forests of this area. In its present version, the model predicts that white birch would be present at elevations below 762 m, during early stages of succession and red spruce would be an important member of old-age stands. Although spruce, fir and white birch did not occur in the Hubbard Brook plots below 709 m, these are found at lower elevations in nearby locations, and were apparently more important in the past. An early report (Chittenden 1905) on conditions of undisturbed forests in Northern New Hampshire stated that white birch was found at all elevations but was much more important at higher ones and that red spruce was 'the characteristic tree' of the northern part of this area. Forests between 550 m and 1070 m were 'characterized by the prevalence of spruce in mixture with balsam and yellow and paper birch'. This report attributed an increase in hardwoods to the effect of lumbering. Thus the long-term predictions of the model are consistent with what is known about the original forest cover of New Hampshire.

The one difference found between the predictions of the model and reports of real forests concerns the distribution of stems by size class in stands 50–60 years old. Three reports, one of an old-age stand in Vermont at 488 m elevation (Bormann & Buell 1964), one of a 25-year-old stand in New Hampshire (Marquis 1969b) and the previously mentioned report of undisturbed forests in New Hampshire (Chittenden 1905) agree on the following: stems of size 2–10 cm are more numerous than stems of 10–20 or greater than 20 cm, and the number of 10–20 cm stems is not greatly different from the number of larger ones.

On the other hand, at year 50 and 60, the model predicts the number of stems 10–20 cm to be 4–5 times the number of larger stems although the predictions for stands older than 70 years agree with observations quoted above. If the few observations available are in fact representative of the New England forests, then perhaps the assumptions regarding mortality rates of trees need modification. Further verification is necessary to test fully this possible deviation, and simulations involving modified mortality functions are planned. The model could be easily modified to make it reproduce more closely the observations of these studies, but this would not constitute verification. To verify predictions of this model, records are needed of the actual growth of trees in forests with known histories and clearly specified environmental conditions, but data of this kind are lacking.

CONCLUSIONS

By defining tree species by nine characteristics, and their abiotic environment by seven, the general dynamic features of a forest ecosystem are reproduced. A number of simplifying assumptions were employed regarding tree growth, and detail was added to the model only as required to account for differences between observation and prediction. The existing discrepancies between the present version of the model and observation seem

to relate mainly to the problem of precisely specifying the parameters for the nine species characteristics now in use rather than to the need for entirely new characteristics.

That the general behaviour of an ecosystem as complex as a forest can be reproduced from a few characteristics is itself an interesting and non-obvious result of the simulation. The existing version of the computer program reproduces competition, secondary succession and changes in vegetation that accompany changes in elevation. The existing model appears very flexible in that adjustment of these parameters allows forests to be reproduced with a wide range of characteristics. The model is still experimental and it is hoped that others will use it and help determine its limitations. Detailed field verification of the model is in progress. Further expansion of the model is being made to allow calculation of changes in volume, and therefore biomass and mineral status of the simulated forest. These will require additional species characteristics to relate tree shape to competitive and environmental conditions.

ACKNOWLEDGMENT

SUMMARY

Competition, secondary succession, and changes in vegetation accompanying changes in elevation have been successfully reproduced by a computer simulation of a mixed-species, uneven-aged forest ecosystem of north-eastern United States. As much as the data and understanding allow, this simulation has a conceptual basis. Changes in the state of the simulated forest are a function of the present state plus random components. The program predicts a peak standing crop for the forest approximately 200 years following clearcutting, with a relatively stable, but fluctuating, species composition at subsequent periods. Designed to be used in the Hubbard Brook Ecosystem Study, the program provides output in a form compatible with the original vegetation survey of tnat study and allows a flexible interaction between the user and the simulator.

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APPENDIX

Integration of growth equation

If, by definition, $x = D/D_m$ and $a = 1 - 137/H_m$, the growth equation, eqn (5), is

$$\frac{dx}{dt} = \frac{G}{2H_m} \frac{x(1-x)(1+ax(1-x))}{[1-a(1-x)(1-2x)]}. \tag{A1}$$

The value of G for each species has been arbitrarily chosen in the text so that x is approximately 2/3 when $t = $ AGEMX/2. To simplify determination of numerical values of G, and to study other methods of fixing the value of G, it is convenient to have the integral $x(t)$ of this equation. If x_0 is the value of x when $t = 0$, one has from eqn (A1)

$$\frac{Gt}{2H_{\mathrm{m}}} = \int_{x_0}^{x(t)} \frac{dx}{x(1-x)} \left[1 - \frac{a(1-x)^2}{1+ax(1-x)} \right] \tag{A2}$$

or, from tables of integrals,

$$\ln\left(\frac{x}{1-x}\right) + \frac{a}{2}\ln\left(\frac{1+ax-ax^2}{x^2}\right) - \frac{(a+a^2/2)}{\sqrt{a^2+4a}}\ln\left(\frac{2-(\sqrt{a^2+4a}-a)x}{2+(\sqrt{a^2+4a}+a)x}\right) = \frac{Gt}{2H_{\mathrm{m}}} + C \tag{A3}$$

where C is the value of the left-hand side for $x = x_0$. If $x_0 = 1/2D_{\mathrm{m}}$ (i.e., $D(0) \doteq 0.5$ cm), the value of G giving $x = 2/3$ when $t = \mathrm{AGEMX}/2$ is

$$G = \frac{4H_{\mathrm{m}}}{\mathrm{AGEMX}} \left\{ \ln(2(2D_{\mathrm{m}}-1)) + \frac{a}{2}\ln\left(\frac{\dfrac{9}{4}+\dfrac{a}{2}}{4D_{\mathrm{m}}^2+2aD_{\mathrm{m}}-a}\right) \right. $$
$$\left. - \frac{a+a^2/2}{\sqrt{a^2+4a}} \ln\left[\frac{(3+a-\sqrt{a^2+4a})(4D_{\mathrm{m}}+a+\sqrt{a^2+4a})}{(3+a+\sqrt{a^2+4a})(4D_{\mathrm{m}}+a-\sqrt{a^2+4a})}\right] \right\} \tag{A4}$$

in which D_{m} and H_{m} are in centimetres, and AGEMX is in years.

In some cases, the values of G obtained from eqn (A4) give unreasonable growth rates. This is particularly true of the short-lived species, for which eqn (A4) gives growth rates which are too large, and of beech, for which eqn (A4) gives too small a growth rate. The values of G for these species have been adjusted in the simulator to give more reasonable growth rates.

Probably a much better way of determining a value of G for each species lies in demanding that the maximum possible annual diameter increment given by eqn (5) be equal to some value $\delta D_{\max}$, which could be determined from field observations. One finds that the required value of G is such that

$$\delta D_{\max} \simeq 0.2G\, D_{\mathrm{m}}/H_{\mathrm{m}}. \tag{A5}$$

The value of G for beech used in the simulator corresponds to $\delta D_{\max} = 1.0$ cm, whereas the value of G implied by eqn (A4) for beech would lead to $\delta D_{\max} = 0.7$ cm. The latter value is almost certainly too small; this merely means that the arbitrary assumption that $D/D_{\max} \sim 2/3$ when $t = \mathrm{AGEMX}/2$ is not correct for all species.