A simulation in plant ecology

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INTRODUCTION

The purpose of this paper is to present some results from a preliminary study investigating the application of the computer sciences to problems in plant ecology. Results include a model which simulates the growth of a forest in a particular time dependent environment and an implementation of that model using a digital computer and assumed data. At present the model is somewhat restricted in level of detail and range of applicability. It is, however, believed to be a pioneer in plant sciences, and further study will surely suggest directions for refinement in level of detail. The range of applicability is constrained by factors not modeled to a young, growing forest of natural occurrence in a particular environment. Validity is anticipated, not for individual trees, but for the entire forest presented as an ecological system.

Purpose and scope

The general purpose of the model described here is to investigate the feasibility of computer simulation of plant growth processes. The specific model developed devotes unusual attention to adaptability and flexibility in order to provide ready means of incorporating improvements and modifications suggested by plant physiologists or plant ecologists. This approach recognizes the strongly qualitative and descriptive aspects of these sciences and makes allowance for the shortage of quantitative knowledge and relationships required by the model.

The specific model, a young, growing forest of natural occurrence in a particular environment, will allow us to predict changes in composition of a forest as influenced by the ecological interactions. The model includes and accounts for three of the five principal limiting factors in plant ecology, light, temperature, and moisture. The exclusion from consideration of the remaining two factors, soil fertility and soil type, limits the application of the model to forests of natural origin; thus assuring some degree of soil type compatibility for species present. Excluding soil fertility limits the scope of the model to relatively short periods of time during which soil fertility remains relatively constant and uniform in its effect on species present.

It should be emphasized that the model is for growth in a natural environment; consequently, it does not at present encompass such considerations as probability of seedlings started, human intervention, or other extraordinary influences such as fire.

Feasibility

Before embarking on this project, it is appropriate to investigate its feasibility. Toward that end, it would seem that three major areas must prove amenable to computation if the model is to satisfy our general purpose.

First, growth must be predictable from environment.
Given a plant of known heredity and of known previous history, it is possible, by applying the principles of plant physiology, to predict with considerable certainty the physiological reactions which will be evoked in that plant upon its exposure to a given complex of environmental conditions.

Second, ecological interaction must be predictable given a particular flora subjected to a particular environment.
Ecological measurement has been sufficiently perfected to give material aid in predicting the hazards to be encountered in critical areas under various types of land use and management.

Third, the interactions must be "modelable" and "computable."
Important in plant ecology is the principle of limiting factors, which says in effect that the least favorable of conditions present will prove epistatic. In particular, photosynthisis or plant metabolism, will be controlled by the least favorable of soil fertility, soil type, light, temperature, and moisture.

The three above definitive statements were abstracted from the Encyclopaedia Britannica and, together, give strong indications of feasibility for the proposed study.

Basic model structure

1. General flow

A forest, for our purposes, will be defined as two or more established trees that interact ecologically with one another. The first step in the model is to initialize a particular forest (thru observation or assumed data) and measure its initial composition.

The second step is to apply an amount of growth resources (temperature, light, and moisture) determined as a result of a simulated period of climate.

At each time step of the model, the moisture added is allocated to individual trees. The temperature, light, and moisture that would otherwise be available during the climate period are then modified by the influence of neighboring trees. The actual moisture availability determined is based upon moisture evaporation rates influenced by light and temperature, previous moisture present, and potential losses to the subsoil during the period.

Finally, growth takes place at a rate determined by moisture, temperature, and light. Growth rates used vary with individual species and give account of current season and present state of maturity. Moisture used in growing is removed from the soil.

Composition is measured, as requested by input data; the processing of successive climate periods continues until completion.

2. Simplifications and analogs

The particular sample of a forest selected or assumed will be a straight line. In the case of observed data, a strip of some appropriate, but as yet undetermined, width will be selected; all trees within that strip will be assumed to occur on a single straight line. This simplification is believed to be essential to the computational feasibility of the project and causes no significant detraction from realistic representation of the physical world. To simplify calculations the line is chosen in a north-south direction. Thus we will be modeling a "two-dimensional" forest. It should be recalled that we are interested in the ecological system, rather than individual trees. Such a simplification may cause loss of information concerning individual trees, but the loss of information to the overall model should prove to be well within the bounds of significance in the best climate sub-model we can hope to construct, or in the best plant growth models we can conceive.

An important model analogue used is the depicting of shading by an angle, (determined by species, season, and latitude) with shade occurring to the north during the daylight hours within the area of the right triangle, specified by the height of a tree and its shading angle. (Figure 1) The effects of shade on temperature and light (and hence on evaporation and growth) are modeled by analogy. The single angle selected will result in less area of shade than actually exists during the early morning and late afternoon hours; but in so doing, account is taken of the much reduced heat and light intensities occurring at those hours.

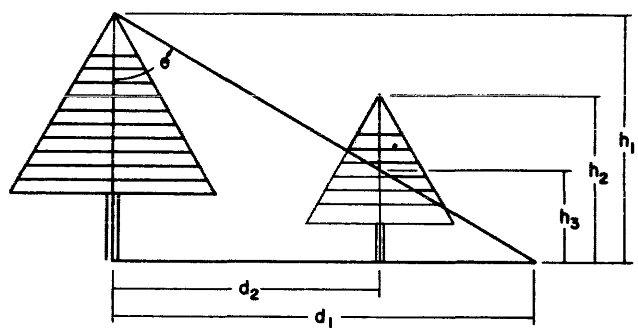

Figure 1—Shade angle

Other simplifications and analogies are, in general, less crucial to the model and are encountered primarily in level of detail.

3. Level of detail

Every reasonable attempt has been made at every point to select a level of detail commensurate with the return of enlightening information and to provide flexibility in model construction and implementation, allowing modular adaptability over a broad range of detail levels. We are unlikely to have achieved an optimum level of detail in this early model. Also, since a major purpose of the study was to investigate feasibility, it has been appropriate in some cases to quite consciously avoid detail that would tend to improve validity but have little bearing on feasibility. An example is that the present model considers all moisture below the surface as a single number for each tree. The number indicates a total amount available without regard to root zones or soil stratification.

The climate model is, at present, a yearly cycle of temperature, moisture, and light means, each quantified as a single number occurring per time period. The time period selected was one month with model runs extending for ten years of simulated time.

Principal model features

1. Climate

During each period of simulated time the climate determines the quantities of additional resources made available for growth. The "model" of climate used here is simply a table depicting typical precipitation, temperature and light during each month.

Precipitation is moisture added in centimeters during the month. Light is the approximate number of hours of daylight per day reduced slightly during months normally experiencing considerable cloud cover or fog. Temperature was entered as a single number determined for each month as follows: Mean daily high and low temperatures for the month were assumed to occur at 1 p.m. plus 20% of time until darkness and 1 a.m. plus 90% of time until daylight respectively. It was assumed that temperature rises and falls linearly from high to low during the day. The positive portion of the above temperature function reduced by 50°F. was integrated between the limits, daylight and darkness, to determine the single temperature input for the month.

2. Shade

During the daylight hours shade occurs to the north of each tree. As noted above, an angle, θ, is used together with the tree height to determine a triangular area in which shade occurs. The shade angle, θ, will generally be smaller for evergreen than for deciduous trees except during those periods of dormancy in which the shade angle is reduced for the leaf shedding deciduous species. If any other tree exists wholly or partially within the shaded area, its light and temperature environment, and hence, its growth rate, is modified. The "shade factor," a number between 0 and 1 indicating the percent shaded, is determined for each tree at each time step by the following procedure.

After resetting all shade factors to zero, perform the following computation for each tree in the system, working from south to north (Figure 1).

1. For tree n, $d_1 = n_1 \tan \theta$.
2. Find d_2 for the next tree to the north.
3. If $d_1 \tau e_2$, begin again at step 1 with tree n + 1.
4. $h_3 = \tan \theta / (d_1 - d_2)$
5. $h_3 = \min(h_3, h_2)$
6. Shade factor = $\max(h_3/h_2$, present shade factor).
7. Return to step 2 above to see if more than one tree to the north is shaded by the present tree.

During each time period, loss of moisture added occurs due to evaporation from the soil at a rate dependent on whether or not the ground is shaded at the center of the "moisture zone."

3. Moisture Zones

The extent of a tree's root system limits the range or distance in each direction in which soil moisture will be available to it. The model assumes that, in the absence of conflicts, all moisture which falls within a distance equal to a tree's present height in either direction becomes available to its roots directly or through capillary action. This distance, or "natural moisture zone," is illustrated in Figure 2 with 45° triangles. (Other angles could be used and varied by species and state of maturity.)

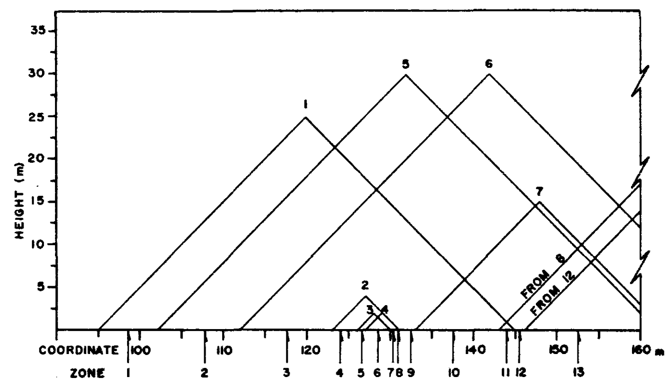

Figure 2 – Moisture allocation

When natural moisture zones overlap, as is generally the case, the trees must compete for the moisture that falls in the overlapping zones. The moisture zone algorithm begins by preparing a table of the starting and stopping co-ordinates of each tree's natural moisture zone. The entire forest is then divided into moisture zones. Associated with each zone is a list of trees competing for moisture in that zone, (Table 1). First we search the table of natural moisture zones to find the tree with the smallest starting co-ordinate. The co-ordinate and tree are entered as the first line of Table 1. We continue by selecting, for each line, the next smallest co-ordinate from the natural moisture zone table and entering it in Table 1. The co-ordinate entered terminates the preceding zone and begins a new one. If a starting co-ordinate is selected, the list of trees competing in the preceding zone is copied and the new tree added to the competition. If a tree's stopping co-ordinate is selected, the list is copied with that tree deleted. Zones of zero length will be subsequently ignored.

4. Moisture allocation

The moisture that falls in each moisture zone will be allocated to the trees competing in that zone by some combination of the following rules. (A weighting factor has been provided as input.)

TABLE 1

MOISTURE ALLOCATION

MOISTURE ZONES*	STARTING CO-ORDINATE	STOPPING CO-ORDINATE	TREES CONFLICTING IN ZONE
1	95	102	1
2	102	112	1 5
3	112	123	1 5 6
4	123	126	1 5 6 2
5	126	127	1 5 6 2 3
6	127	130	1 5 6 2 3 4
7	130	131	1 5 6 2 4
8	131	131	1 5 6 4
9	131	133	1 5 6
10	133	143	1 5 6 7
11	143	145	1 5 6 7 8
12	145	146	5 6 7 8
13	146	162	5 6 7 8 12
14	162	163	6 7 8 12
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* At Time Zero

Rule A allocates moisture in direct proportion to the heights of the competing trees.

Rule B projects with the 45° angle the heights of all competing trees to the center of the zone and then allocates moisture in proportion to the projected heights.

Rule C allocates moisture in inverse proportion to distances from tree basis to the center of the zone.

Results presented later were obtained using Rule C.

5. Growth

Each species has associated with it an ideal growth rate which is a function of height. The growth that actually occurs during a climate period will be determined by reducing the ideal growth by some amount for each unfavorable environmental condition encountered. Ideal conditions for each species, moisture usage rates, and sensitivities, are input parameters.

A tree is selected, and its ideal growth for the period is determined as a function of species and height. If the tree is deciduous and dormant in the present climate period, its projected growth is reduced by an input factor.

The absolute difference in the temperature number that occurred and the ideal temperature is divided by the sensitivity. The sensitivity is the temperature differences that reduces growth by 10%. Thus, from the quotient of the above division, we determine a new growth rate.

The growth is multiplied by the hours of light per day in the current period divided by twelve. If a tree is entirely shaded (shade factor equals one) the growth rate is reduced by the "zero light rate" input factor for that species. If the tree is partially shaded, the growth rate is reduced to a proportionate rate between the zero light rate and the last determined rate.

The moisture needed for growth is determined first, from a usage rate multiplied by height, and then by one plus the projected growth in meters. A subsoil loss is determined as a percentage of moisture present. If the available moisture is greater than that needed for growth and subsoil loss, the moisture is removed and growth takes place. If adequate moisture is not present, the actual growth will be that fraction of the projected growth for which moisture is available.

Preliminary results

At the time of this writing no field data collection has taken place. Therefore the results obtained so far have been the outcome of qualitative model testing. Primarily, this testing has been the operation of the model under extreme conditions such as total absence of some necessary growth resource. Other tests have included such things as operation with and without ecological interference as controlled by spacing of individual plants. A sensitivity analysis has also been performed in order to insure "reasonable" responsiveness to major factors modeled. Validity of basic model structure has now been assumed, since behavior under the tests indicated above is of a form and direction anticipated by initial assumptions.

The output from a typical model run is included below (Table 2 and Figure 3). The forest in this particular example was obtained by random shuffling of data cards representing a deciduous and an evergreen species. (Similar model runs with more than 100 trees have been made.) In Table 2, co-ordinates and heights are in meters. Shade factors and moisture present are described above. The trees at each end are generally in a superior competitive position, and hence "less representative." The third and fourth trees illustrate markedly the effect of changing environment with time. Others illustrate such effects as declining growth rates caused by the increased moisture requirements accompanying increased heights.

This particular, somewhat abstract, forest has been run many times with many variations of model parameters. As a result of the adaptability and responsive-

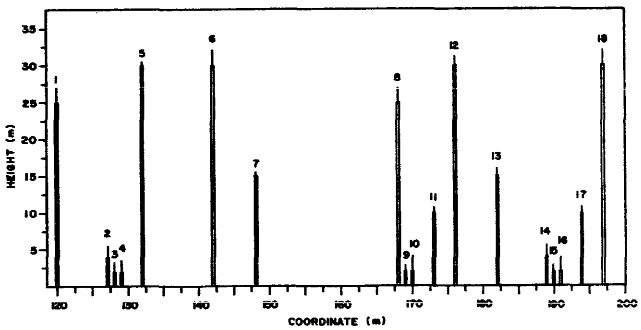

Figure 3 – Results

TABLE 2

RESULTS

TREE NO.	CO-ORDINATE	SPECIES	INITIAL HEIGHT	HEIGHT 5 YRS.	HEIGHT 10 YRS.	SHADE* FACTOR	MOISTURE* PRESENT
1	120	Evg.	25	26.96	28.93	0.00	1259.9
2	127	Dec.	4	5.41	6.76	0.80	58.2
3	128	Evg.	2	3.36	4.12	0.32	0.0
4	129	Evg.	2	3.45	4.11	0.04	0.0
5	132	Dec.	30	30.47	31.02	0.00	60.6
6	142	Evg.	30	31.94	33.57	0.00	50.2
7	148	Dec.	15	15.54	16.25	0.81	31.4
8	168	Evg.	25	26.90	28.52	0.00	51.6
9	169	Dec.	2	2.74	3.16	1.00	0.0
10	170	Evg.	2	4.05	5.45	1.00	0.1
11	173	Dec.	10	10.61	11.36	1.00	41.5
12	176	Evg.	30	31.18	32.51	0.03	0.0
13	182	Dec.	15	15.71	16.39	0.75	65.1
14	189	Dec.	4	5.46	6.56	0.00	70.4
15	190	Dec.	2	2.70	3.12	0.19	0.0
16	191	Evg.	2	3.81	5.15	0.00	0.2
17	194	Dec.	10	10.62	11.25	0.00	228.1
18	197	Evg.	30	32.04	34.08	0.00	1820.6

* At Five Years

ness demonstrated, we are able to conclude that the model will prove valuable in its present form and help to open the gates to a large number of computer studies and applications in the plant sciences.

The future

A step preliminary to future development will be an extensive data collection effort. Data collected over extended periods of time and taken from many different geographic regions for many different species and forest densities will be necessary to properly adjust, or "fine tune," model parameters.

Additional levels of detail may be considered. A stratified soil model seems to be a most promising possibility and would allow for finer accounting of moisture availability, soil type, and fertility in the root zone of individual trees.

A less difficult, but logical, next step will be the ascribing of measures of economic importance to the forest. Such a measure will allow the present model to be used as a "laboratory" for the investigation of many forest management practices. For example, quantitative results concerning the value of thinning to reduce shading could be determined by simply applying the model repeatedly with various thinning criteria applied to the same forest. Such a study made in the physical world, by experimentation, would not only take many years to complete, but would depend on the critical assumption that each forest or subforest under study was completely equivalent and subjected to the very same environmental influences during the entire duration of the study period.

The adaption of the principals and algorithms of the present model to crop plants has already begun. The emphasis, here, must change from one of reaction to natural influences to that of reaction to soil management practices. Also, our attention must focus on the fruit of the plant rather than the plant itself. However, the many similarities make the present model an important first step in this direction.

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