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Computer-simulated Plant Evolution

Computers are appropriate tools for testing the inherently statistical hypotheses of evolutionary biology. A desktop computer can re-create the major trends in plant evolution

by Karl J. Niklas

Evolutionary biologists encounter a fundamental difficulty when it comes to testing theories: the hypotheses on which the theories are based often do not make specific and easily falsifiable predictions. Instead they attempt to describe general statistical trends that should be discerned in large populations over long periods of time. In addition both the organisms in question and their environments may have vanished hundreds of millions of years ago—as in the case, for example, of the evolution of the earliest land plants. Therefore when the paleobotanist, the paleozoologist or the geneticist have drawn the evolutionary history of a lineage in great detail, it may still be impossible to give definitive answers to certain basic questions: Why do the observed patterns of evolution exist? How much of what is in the fossil record should be attributed to chance and how much to clearly defined biotic events and selective pressures?

There is, however, an effective tool for testing evolutionary hypotheses: the computer. It can handle large sets of data and do rapid and repeated calculations, and with it the investigator can model complex evolutionary processes. The techniques of computer modeling make it possible to examine many of the intuitive notions formed by biologists about the interactions among organisms and environments. It is this kind of work that has engaged my colleagues Vincent Kerchner and Thomas D. O'Rourke and me at Cornell University. We have been testing the mathematical consequences of various notions about plant evolution.

Computer simulations examine hypotheses by what has come to be known as the hypothetico-deductive method. The first step is to formulate a hypothesis. The various consequences of the hypothesis are then deduced and compared with observational evidence. If the consequences agree with the observations, the hypothesis is partially confirmed. (A hypothesis cannot be "proved" in this way, only made more probable.) If one of the deduced consequences of the hypothesis does not agree with observation, the hypothesis must be modified or rejected. The computer, which can produce a large "population of results" by repeating the same general type of computation many times, is an ideal tool for testing the inherently statistical hypotheses of evolutionary biology.

The first step is to formulate hypotheses: statements about what factors have had the greatest effect on plant evolution. The computer can then be used to model the performance of plants having various primitive characteristics and "score" the relative success of each simulated plant in solving the problems presented by the hypothesized selective pressures. Next, small or large changes ("mutations") that might make the primitive plants fitter, which is to say more able to cope with the hypothesized pressures, can be introduced into the simulated plants. The mutated progeny are themselves scored and are then allowed to mutate further. This process is repeated many times. The final step is to compare the pattern of evolution thus simulated

with the patterns found in the fossil record. If the two are in good agreement, then the operation of the factors that were hypothesized to exert selective pressures is partially confirmed.

This modeling procedure is based on two major assumptions, which can be regarded as the two major tenets of evolutionary biology. The primary assumption is that the genetic character of individuals within a species, and hence of the species itself, changes with time. The second is that there is a degree of genetic continuity between an ancestor and its descendants. The changes within a species are therefore the result of selective pressures applied to many minor variations that arise between parent and offspring.

In order to model the evolution of plants some specific hypotheses must be added to these assumptions. One such hypothesis is that the majority of plants can be seen as structural solutions to constraints imposed by the biochemical process of photosynthesis. Plants with branching patterns that gather the most light can then be predicted to be the most successful. Consequently changes in the plant's shape or internal structure that increase its ability to gather light should confer competitive advantages.

To be effective competitors for light

EVOLUTIONARY DEVELOPMENT of the early land plants is simulated on a computer. This simulated evolutionary sequence is based on the hypothesis that evolution was driven in part by a plant's need to minimize the mechanical stresses inherent in its branching pattern while exposing the maximum photosynthetic surface to the sun. In the simulated sequence, which exhibits some of the major trends in the actual evolution of plants, the most primitive plant (*1*) is low and sparsely branched. (Different colors indicate successive generations of branching; the light green branches are the ones most recently formed.) Later plants tend to have more branches (*2*) and to grow more vertically (*3*); vertical branching patterns present more photosynthetic surface and can grow above the shade cast by such obstructions as neighboring plants. The amount of shade the plant casts on itself is then reduced by the evolution of larger angles between branches, resulting in a plant with fuller growth (*4*). Later plants (*5*) have evolved a single central axis from which many lateral branches grow. The light-gathering ability of this configuration is increased by the evolution, or planation, or flattening, of the lateral branching systems (*6*). The similarity between the trends produced by such a simulation and the trends actually observed in the fossil record is a measure of the accuracy of the hypotheses on which the computerized simulation is based.

weak theory. The ssc will also make fundamental contributions, however, to many other open questions. So far, for example, there appear to be three generations of quarks and leptons. Are there more? Why do the quarks and leptons have progressively greater masses in successive generations? Are the quarks always bound together to form hadrons or shall we ultimately see manifestations of free quarks? Are the quarks and leptons related, and if they are, how? Why do weak interactions show a handedness? Are quarks and leptons really elementary entities or are they built up from some more basic constituents? Does quantum mechanics continue to apply at smaller and smaller scales? Can gravity, as well as the color interaction, be treated in a consistent way by quantum mechanics and perhaps unified with the other known forces?

In the past decade there have been several attempts to extend the partial unification found in the electroweak theory to a grand unification of the electromagnetic, weak and color interactions. Even more recently a development called superstring theory has extended the theory of supersymmetry to a mathematical formalism that may one day bring about an even grander unification: the unified understanding of all four fundamental interactions, including gravity. Out of such grand unified theories has emerged a realization that particle physics has something to say about the earliest epochs in the history of the universe and that cosmology has something to say about particle physics.

Astronomers now believe the universe began cataclysmically in the big bang. In the almost unimaginably hot, primordial universe just after the big bang the full symmetry of nature's laws must have been manifest. Both the study of the very large and the study of the very small thus converge on a common point of view: in order to continue probing nature's underlying unity and simplicity one must build instruments that investigate domains of progressively higher energy. The discoveries in such domains cannot be fully anticipated, but experience teaches us it is often the unexpected discovery that triggers a deeper scientific understanding of the world. The ssc, ambitious yet feasible, would take us to domains of energy never before encountered, where the real discoveries can only be guessed at, and it would give us access to the events that took place almost immediately after the beginning of time. The opportunity and the challenge presented by the ssc will excite all who share our desire to understand the natural world.

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SIMULATED GROWTH of a plant consists of a series of iterated stages. In each iteration the computer decides, based on the plant's inherent "probability of branching," which of the plant's "axes" will branch. It then considers the plant's other inherent characteristics, such as the angles between branches, to determine the directions of the new axes, and it allows each to grow a short distance.

and space, plants must perform certain other tasks. In particular they must be able to stay erect: to sustain the mechanical stresses involved in vertical growth. A second hypothesis, then, might be that the evolution of plants was driven by the need to reconcile the ability to gather light with the ability to support vertical branching structures. A third hypothesis might be tha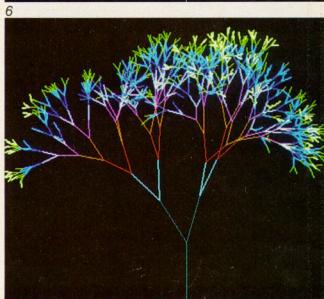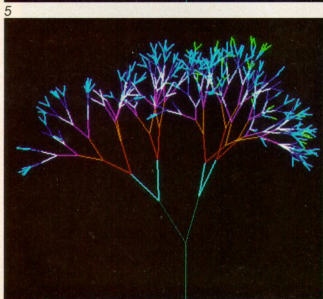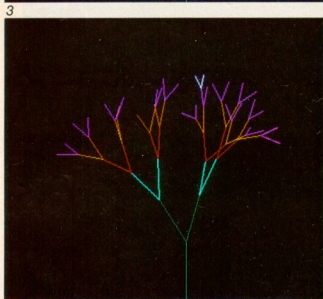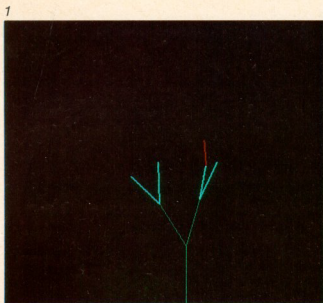t the evolution of plants is driven by the extent to which they are successful at reproduction, placing a premium on branching patterns that allow for better dissemination of seeds or spores.

With this set of assumptions and hypotheses, many of the major trends seen in the early evolution of land plants can be simulated by a desktop computer. The simulations completed so far refer only to the first phase of the spread of vascular plants (plants containing internal tissues—xylem and phloem—that translocate fluids and also help to support the plants' structure vertically). The period simulated is only about 60 million years long, from about 410 million to about 350 million years ago. (In contrast, the diversification of the flowering plants, the most recent group of plants to evolve, took place over a period of about 100 million years.) Hypotheses related to terrestrial herbivores and pollinating insects have not been considered. Such hypotheses would be much more complex to model than those discussed here. With more powerful computers it may eventually be possible to model these features and others that contribute to evolution, such as the effects of climatic changes and catastrophic events.

In order to simulate plant evolution one must develop mathematical techniques for quantifying the competitive advantages offered by various features. One such technique should determine how much a plant having a given structure could intercept. As far as is now known, the first vascular plants, which gave rise to the bulk of the earth's current flora, were leafless, with vertical photosynthetic axes. (Stems, which are axes bearing leaves, evolved later.) The axes tended to grow lengthwise, through the addition of new cells produced by a cluster of cells at an apex, or growing end; they generally added only a small number of new cells to their girth and so had a limited maximum diameter. Branching took place when a single axis bifurcated at its apex into two independently growing axes.

Because many of these plants lacked leaves, the relatively stiff axes were the chief photosynthetic organs. Hence the geometry of a plant's branching and

the way the surfaces of its axes were projected toward the sun were the most important factors in determining the plant's ability to gather light. Unlike the leaves of today's plants, the axes of the first vascular plants could neither flutter appreciably in a breeze nor track the movement of the sun during the day. The light-gathering ability of the early plants can therefore be simulated by programs that determine the total amount of sunlight projected onto a static three-dimensional branching pattern as the sun's position in the sky changes.

Another parameter to quantify is the mechanical stability of vertical axes. Branching patterns that grow mainly in the vertical direction are more efficient at gathering light because they can reach beyond the shadows projected by such obstacles as rocks, hillocks and other plants, but a plant with a vertical posture must be able to sustain the concomitant mechanical loading. The principal load-bearing innovation of modern trees is the woody stem that increases in girth continuously as new cylindrical layers of cells are added internally. Without such secondary wood, the ability of the early vascular plants to sustain

mechanical stresses depended solely on their primary growth: the relatively slender, virtually untapered axes produced when new cells were added only at the tips of preexisting axes.

It is rather easy to calculate the amount of load inherent in a branching pattern, as well as that pattern's ability to sustain the load, if the axes' weights, sizes and orientations are known. The programs that generate branching patterns can also calculate the total strain and bending moment of a branching pattern, as well as the amount of sunlight intercepted. This makes it possible to quantify the factors involved in the tradeoff between, on the one hand, presenting large areas of photosynthetic tissue to the sun and, on the other hand, bearing the resulting mechanical stresses.

Another tradeoff to be considered has to do with shading. Larger and more extensively branched plants have a greater capacity to shade neighboring plants and so gain an advantage over them. This capacity has a negative aspect as well, however: it is likely to increase the plant's tendency to shade parts of itself, thereby reducing its own light-gathering efficiency.
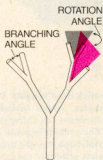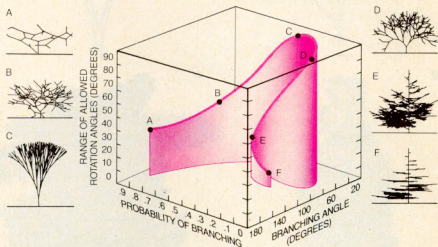
CUBICAL SPACE represents a "universe" of possible branching patterns. Each of the cube's three mutually perpendicular dimensions represents a particular morphological characteristic, and each point within the cube represents a "species" of plant with a unique combination of characteristics. The three characteristics represented are the probability of branching, the branching angle (the angle between adjacent branches) and the allowed range of rotation angles (the angle between the plane defined by a pair of new axes and the similar plane, formed during the previous generation of branching, defined by the axis from which the new axes have grown and that axis's sibling). The computer can simulate an "evolutionary trajectory" (color) within the cube. The computer starts with the plant that most nearly resembles a primitive species. It then examines each of that plant's near neighbors in the cube and determines which is the fittest according to hypotheses selected by the investigator. That neighboring plant is the next point on the trajectory, and the computer then scans all its near neighbors for a fitter plant. The procedure is repeated until the computer has located a plant that is fitter than any other plant in the universe of possible morphologies.

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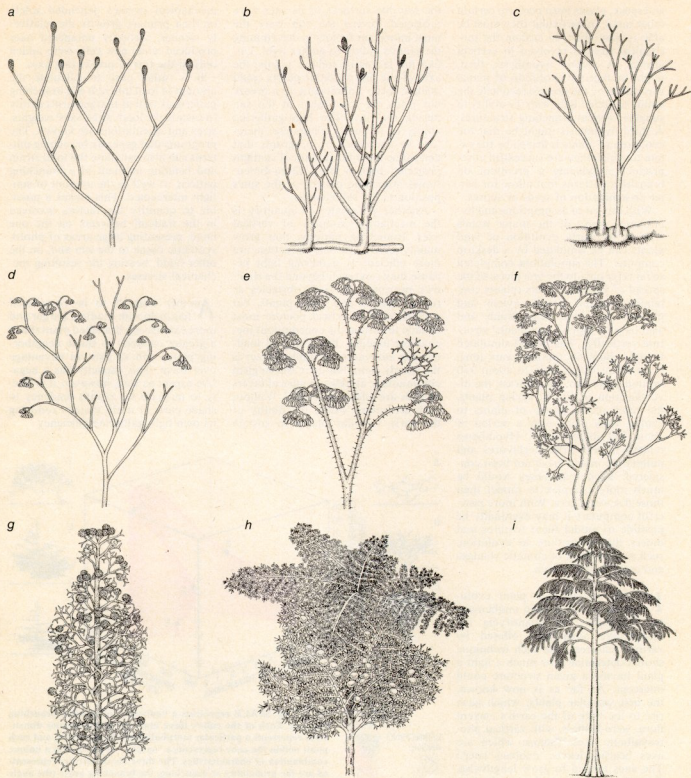
EVOLUTION OF ANCIENT PLANTS shows trends, such as an increase in the number of branchings, the emergence of a main axis and the planation of branching systems, that are also seen in simulated evolutionary trajectories. (Many of the plants depicted are not directly related to one another, and so they illustrate general evolutionary tendencies rather than the history of any particular lineage.) One of the earliest vascular land plants was *Steganotheca striata* (a), a sparsely branched plant that lived about 450 million years ago. *Rhynia gwynne-vaughanii* (b) and *Horneophyton lignieri* (c), both of which have more extensive branching structures than *Steganotheca* has, may have been among its descendants. All three plants are part of the rhyniophyte group. The next major group,

which lived roughly 380 million years ago, was that of the trimerophytes, which included *Trimerophyton robustus* (d), *Psilophyton chariento* (e), *Psilophyton dawsonii* (f) and *Pertica quadrifaria* (g). (The exact taxonomic relations and sequence of occurrence of these trimerophytes are not known, and so they are depicted in a somewhat arbitrary sequence.) The trimerophytes seem to have a main vertical stem; in fact, this apparent main stem is the statistical result of a large number of "unequal branchings," in which one member of a pair of new axes grows in an orientation closer to that of the pair's parent axis. A fernlike descendant of the trimerophytes, *Rhacophyton ceratangium* (h), does indeed have a main vertical stem; it also has planated prefronds, leaflike appendages that mark
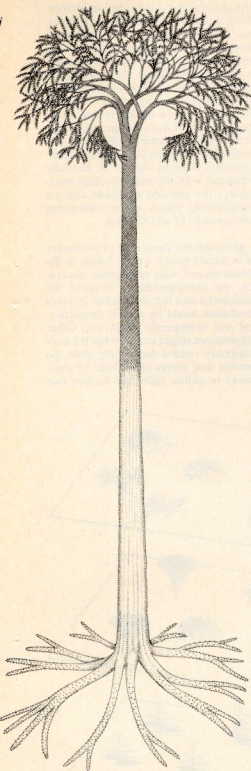
an advancement over planated branches. Another possible descendant of the trimerophytes is *Archaeopteris* (*i*). Plants of this genus had a central trunk bearing lateral branches, which in turn bore leaves. Still another lineage, that of the lycopods, seems to have evolved independently from the rhyniophytes and the trimerophytes, passing through many (but not all) stages characteristic of simulated evolutionary trajectories. Lycopods reached their apex in tree lycopods, such as the genus *Lepidodendron* (*j*).

The hypothesis that light-gathering ability was a primary driving force in the early evolution of vascular plants is certainly a simplification. There is a plethora of shade-tolerant plant species in today's flora, and there is reason to believe some early vascular land plants were shade-tolerant as well. Nevertheless, the fossil record does show long-term trends consistent with the hypothesis that competition for light was primary in the evolution of land plants. Among these trends are an increase in the stature of successively evolved plant groups, a transition to a growth pattern characterized by a single vertical axis bearing lateral axes and the appearance of planated, or flattened, lateral branching systems, which in some lineages mimicked the function of leaves.

These trends have been re-created with more accuracy by simulations in which branching patterns "grow" in ways defined by certain "genetic" characteristics. During each stage of simulated growth, a plant goes through several phases of alteration. First every axis grows a small distance. Then the computer selects on the basis of a predetermined genetic "probability of branching" how many (and which) axes will branch. On those that do branch, the directions of the new axes are determined by two "genetic" factors. One is the "branching angle" between the new axes. The other is the rotation angle: the angle between the plane defined by the two new axes and a plane formed by the previous generation of branching on the parent axis [see illustration on page 81].

In the simplest simulations of branching patterns the branching angle is the same at all branching points; like the probability of branching, it is one of the pattern's "genetic" characteristics. The rotation angle, on the other hand, may vary within a specified range; the range is a characteristic of the simulated plant. Plants that have a large allowed range of rotation angles tend to be full and bushy; in plants where the rotation angle cannot deviate very much from 0, groups of branches tend to fall on parallel planes. After the computer has been used to determine the location and direction of each new axis, all the new axes are allowed to grow a short distance and the process of branching is repeated. The plants are considered complete and their growth is terminated after 10 cycles of branching. A simulated plant in which every axis branches during each of the 10 cycles of growth contains 1,024 axial elements. Larger plants can be simulated, but this would require computers with larger memories. Ten cycles of

branching are enough to mimic the size and shape of the majority of fossil plants under consideration.

The three characteristics—probability of branching, branching angle and rotation angle—define a universe of possible branching patterns that characterizes the morphology of the earliest land plants. The simplest way to imagine this universe is as a cube. Each of the cube's three mutually perpendicular dimensions represents one of the three basic characteristics, and so every point within the cube represents all the plants that have a particular set of attributes. (Because of the random nature of branching, plants having exactly the same mathematical characteristics may be slightly different morphologically.)

For example, suppose the vertical dimension of the cube represents the branching angle. Then any point near the top of the cube would represent a "species" whose branches diverge from one another at a large angle, whereas a point near the bottom of the cube would represent a species that has a small branching angle. One corner of the cube represents a "species" of plant with a branching probability of nearly 0, very small angles between branches and rotation angles that may not deviate much from 0. Points farther away from this corner in any of the three primary directions represent respectively plants that have more branches, those with greater branching angles or those whose branches grow in a greater variety of directions. The combinations of the three variables represented by the sites within the cube include virtually all the branching geometries of early vascular plants.

Naturally the three-dimensional universe is an oversimplification of plant geometry. In reality many more factors than the three described here may influence plant shape. It is possible to simulate multidimensional universes of plant shape, incorporating such factors as the ability to change the length of axes or their girth as well as the ability to produce axes with different probabilities of branching. In particular, a more sophisticated simulation might consider a variable that allows for a phenomenon called unequal branching: at each branching point one new axis may deviate more than the other new one does from the orientation of the axis from which they both grow. In this case there are actually two branching angles, each representing the angle between one of the new axes and the original axis. Multidimensional universes, which incorporate such factors, are hard to visualize, but they can easily be simulated with

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the aid of computers. For purposes of simplification, however, the cubical, or three-dimensional, universe of branching patterns is sufficient to describe the initial phases of plant evolution.

A simulated "evolutionary trajectory" of early land plants can be represented within the cube. First the location within the cube of the most primitive branching pattern (the pattern most closely resembling that of the oldest plants) is determined. Then the computer selects from the plant's nearest neighbors in the cube a species that is more efficient at gathering light. (The light-gathering efficiency of a species is estimated by allowing the computer to grow 10 random samples of the species and find their average light-gathering efficiency.) The process is reiterated until the computer has identified a set of morphological characteristics that is more efficient than any of the species' immediate neighbors in the cube. A line drawn through all points representing the plant species selected by the computer represents an evolutionary tra-

jectory based on competition for light.

It is also possible to produce a trajectory based on balancing the tradeoff between light-gathering efficiency and mechanical stress. In computing such a trajectory the computer, when it scans a plant's near neighbors to determine which species is next in the trajectory, chooses the species that has the highest ratio of light-gathering efficiency to bending moment, rather than simply the plant with the highest efficiency.

The evolutionary trajectories thus simulated, both those based on light-gathering efficiency alone and those designed to reconcile the tradeoff between gathering light and sustaining stress, bear a strong resemblance to trends in the fossil record. The most primitive branching pattern is characterized by few levels of branching, wide angles between axes and nearly vertical planes of branching. The most advanced pattern has planated groups of lateral axes attached to a single main vertical axis.

Intermediate geometries show how the transition from a primitive geometry to an advanced one takes place in

the simulated evolutionary trajectory. First the amount of branching increases. Then one axis in each successive branching grows closer to the vertical than the other axes do and so becomes a central axis. Finally, the resulting lateral axes (the ones growing out from the central axis) come to lie on planes that are close to the horizontal. This sequence represents changes that maximize light-gathering efficiency and minimize mechanical stresses. Coincidentally, it turns out to be virtually identical with the sequence that maximizes the amount of shade cast on neighboring plants while minimizing the amount of self-shading.

A though the simulated evolutionary trends match trends found in the fossil record with reasonable accuracy, the correspondence between the simulated and the real trends in plant evolution could be merely coincidental and biologically irrelevant. Other hypotheses might account for the evolutionary record more fully than the notion that plants are driven by pressures to gather light and sustain me-
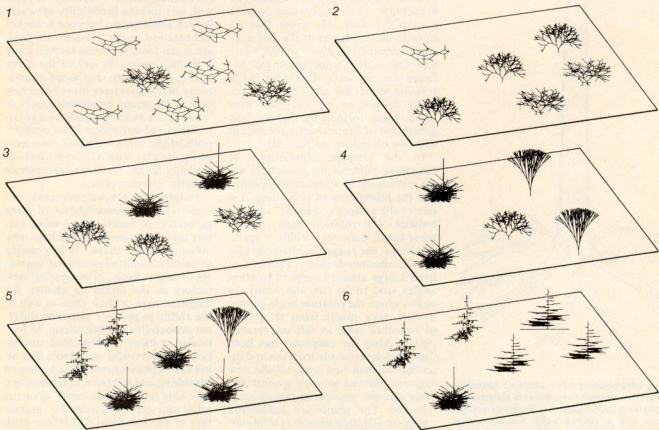
COMPUTERIZED WAR GAME simulates evolution driven by competition among species. The illustration shows six successive stages in the game; in each stage one or more plants of each of three species compete for light and space. The single species in each stage that gathers the least light is eliminated, and the other two are allowed to disseminate spores. Half of the spores from the most successful species mutate, forming a third species to compete in the next stage of the game. The ability to grow depends on the amount of "light" a plant receives (which in turn depends on the amount of surface it exposes and the degree to which it is shaded by itself and other plants). The number of spores a plant disseminates depends on the number of branch ends it has, and the area over which they are distributed depends on its height. Success in the game combines ability to gather light, to shade neighboring plants and to reproduce.

chanical stress. Surely, for example, the success of a species must depend in large part on its success as a reproductive entity. Can the computer examine this hypothesis as well?

To answer the question it is possible to simulate a "war game," in which branching patterns having different light-gathering capacities and reproductive potentials compete with one another in a universe shown on the computer screen. The objective of the game is to declare an "evolutionary winner" on the basis of game rules that are really hypotheses about how evolution might have proceeded.

Each plant is given an area in which it can grow. The area is defined by the plant's ability to cast a shadow over neighboring plants. Each plant is also given an area of a different size, centered on the first, over which it can disseminate reproductive units, which in primitive plants were spores dispersed by the wind. Because many of the early land plants shed spores from the tips of their main axes, the number of spores each plant produces is proportional to the number of branch tips in its branching pattern, the area in which the plant may disseminate its spores is determined by its height. (This is aerodynamically reasonable, because the height from which any light or small object is released is critical in determining the distance a breeze will carry it from its point of origin.) The height of a plant depends not only on the number of branchings but also on the plant's branching angle; plants with smaller branching angles grow taller. Any spores that are distributed in a shadowed area, including the one created by their own parent plant, fail to germinate. (This game rule is reasonable too, because many of the lower living vascular plants can inhibit the growth of their own progeny.)

Plants that have overlapping shadow areas interfere with one another's ability to gather light. Each plant's rate of branching, and therefore of growth, is determined by the amount of sunlight it receives. That depends in turn partly on its tendency to avoid self-shading, partly on how heavily it is shaded by other plants and partly on the amount of photosynthetic surface it presents to the sun.

As the game begins, equal numbers of spores of plants having the three most distinct primitive branching patterns are scattered on a level "playing field" and are allowed to grow. After each plant has grown to 10 levels of branching the computer determines the species whose members gathered the least sunlight and eliminates all plants of that species. The other two

species are then allowed to disseminate spores. Half of the spores from the species whose members gathered the most sunlight are allowed to mutate: their "genetic" factors are altered slightly in ways that increase the growing plant's ability to cast a shadow, to avoid self-shading, to produce spores or to disseminate spores over a large area. The resulting three branching patterns (the two most successful patterns of the previous round and the new, mutated pattern) are then allowed to grow and the sequence is repeated. The game can be made more complex by introducing mutations that are not advantageous, but this generally modifies the results only a little, and it lengthens considerably the time necessary to finish the game.

The game can take a long time to play, even on a computer, because thousands of calculations must be made for even a brief skirmish. The game ends when the last mutation has been selected from the repertoire offered by the trajectory under study. The winners are the species that survive until the end. The game is thus, to be sure, artificially truncated. Real evolution can produce not only changes in the shape of a plant's branching pattern but also changes in the plant's physiology, such as the ability to tolerate shade or to grow secondary wood. Real evolution can also be punctuated by external events such as natural catastrophes, which restart the game with different proportions of players. Nevertheless, even this simple war game generates trends much like those found in the fossil record, and so the rules probably bear some relation to the biology of real plants.

The trajectory emphasizing light-gathering capacity and the trajectory reconciling tradeoffs between gathering light and sustaining stresses are about equally good at indicating which mutations give rise to plants that do well in the war game. In both schemes the most primitive geometry has only a few levels of branching. With sporangia (spore-bearing structures) borne at the tips of its axes, such a plant will have a small reproductive output. In both schemes the most advanced geometry consists of a single tall axis that bears many levels of lateral axes. Sporangia of such a plant, if borne at the tips of its axes, would be numerous and many would be high above the ground, ensuring dispersal over a wide area.

Observations of living plants indicate that the kind of plant that succeeds in the war game is indeed successful in natural competition as well. Studies of the population dynamics of living plant monocultures (cultures of many individuals of the same species)

indicate that larger individuals have an advantage over smaller ones. As the population density of the plants increases, the mortality rate increases as well, but a greater proportion of the small plants die than of the large plants. These phenomena have been observed in many species of plants as well as in the war game.

The same pressures that give rise to these tendencies in living monocultures may well have influenced the early evolution of vascular land plants. When plants first invaded the land, the new habitat was probably sparsely occupied, and so the population densities were low. In time both the number of individuals and the number of species at a site would have increased. Species that grew higher or faster would then have had an advantage. As the density of plant communities increased, individuals and even species may have died out selectively, favoring the survival of taller species.

In this context it is interesting to note a seemingly contradictory point. Because of self-shading, added growth tends to reduce light-gathering efficiency: the plant gathers more light, but it gathers less light per axis. This loss of efficiency is counterbalanced, however, by the tall plant's increased tendency to cast shade on neighboring plants and their spores. The trend toward taller plants may therefore have conferred advantages on a species even though it actually impaired the vegetative performance of individual plants. Apparently, then, the mere presence of many individuals of the same species can give rise to evolutionary trends that will help the species to compete against others.

Computer simulations have shown that the various hypotheses proposed concerning plant evolution have consequences that cannot be verified in the fossil record. One cannot say that the hypotheses have been proved to be correct, only that they have been partially confirmed. Moreover, the simulated consequences of the several hypotheses are virtually identical. It is therefore impossible to determine the relative importance of the various criteria used to produce the simulations; that can be done only when two hypotheses lead to conflicting predictions. Moreover, we have yet to produce simulations modeling such important structural needs as the ability to translocate fluids and to dissipate heat. The general technique of simulation offers great promise as a tool for the evolutionary biologist, but the successful use of any tool requires practice and judgment, and the tool itself must be developed and refined.