Computers Track the Path of Plant Evolution

Statistical analysis of branching patterns in early land plants reveals important facets of their initial evolutionary change

One of the most intriguing features about the history of life is the flow of order out of disorder, a phenomenon that must be explained by evolutionary biology. But, as Karl Niklas notes in a recent issue of *Paleobiology*,* before this problem can be addressed properly one must have an appreciation of the contribution of stochastic and deterministic components to the ordered state under consideration. In other words, how much of the observed order is the result of chance and how much the consequence of a tightly choreographed developmental process?

Niklas, who works in the Division of Biological Sciences at Cornell University, has been examining the very early history of plants, specifically, during the late Silurian–Early Devonian (around 400 million years ago), the time when the first terrestrial plants arose. During their first 50 million years on dry land, the major plant groups displayed increased diversity and complexity in branching structure, vascularization, and reproductive organs. In his *Paleobiology* article Niklas describes a statistical technique for analyzing the branching patterns in these early plants. The approach has generated important insights into the pathways of evolutionary change in these simple organisms. "We've been able to make some rather precise mathematical predications," says Niklas, "and we've seen them reflected in the history of plant evolution."

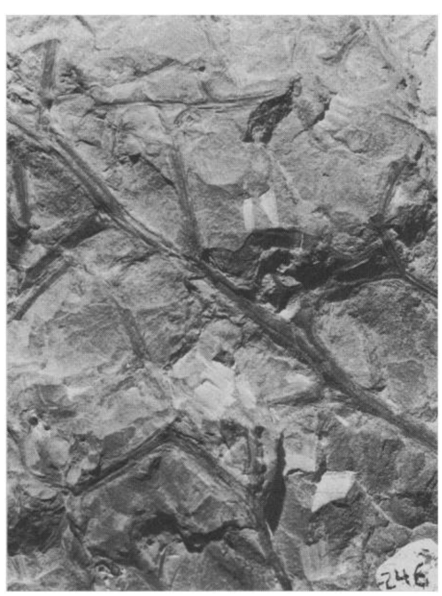
Aside from reproduction, plants have only two major concerns. One of these is the mechanics of growth, a problem made more complicated by their indeterminate growth habit. A branch has to be continuously strengthened throughout a tree's life, for instance, otherwise it will mechanically fail as it grows longer and heavier. The second concern is the need to maximize photosynthetic activity. Quite simply, leaves must be exposed to sunlight as much as possible.

The solutions to these two separate demands result in conflicting pressures on the growing organism, a tug of war, as Niklas describes it. "If you look at the optimal patterns of display for exposure to the sun, they frequently produce maximum mechanical stress in the plant. And many of the structural solutions to problems such as desiccation and continued growth are non-optimal for everything else."

In conjunction with Thomas O'Rourke, a civil engineer at Cornell, Niklas has begun to explore mathematically the architectural solutions to this conflict. "Plants have had millions of years in which to test certain architectural solutions, and we are seeing the results of this in the flora of today." The statistical study of branching patterns in early land plants is an important component of this mathematical approach to understanding the mechanics of modern plants and their history.

Early land plant evolution involved the divergence of two major groups. One is made up of the zosterophyllophytes, which gave rise to the lycopods. And the other is composed of the rhyniophytes, which were ancestral to the trimerophytes and the progymnosperms. This second group was ancestral to the great majority of modern land plants. Both of the early groups—the zosterophyllophytes-lycopods and the rhyniophytes-trimerophytes—appear to have evolved from an ancestral plexus of rhyniophyte-like plants.

These earliest groups comprised rather small, simple plants. The branching patterns, although reflecting a certain similitude between the various groups, have been used by paleobotanists for taxonomic classification. With the passage of evolutionary time, the branching patterns became ever more identifiably characteristic, a progression that has been assumed to reflect some kind of optimization. "We are interested in how plants hit upon these optima and how transitions between major groups occurred," says Niklas.



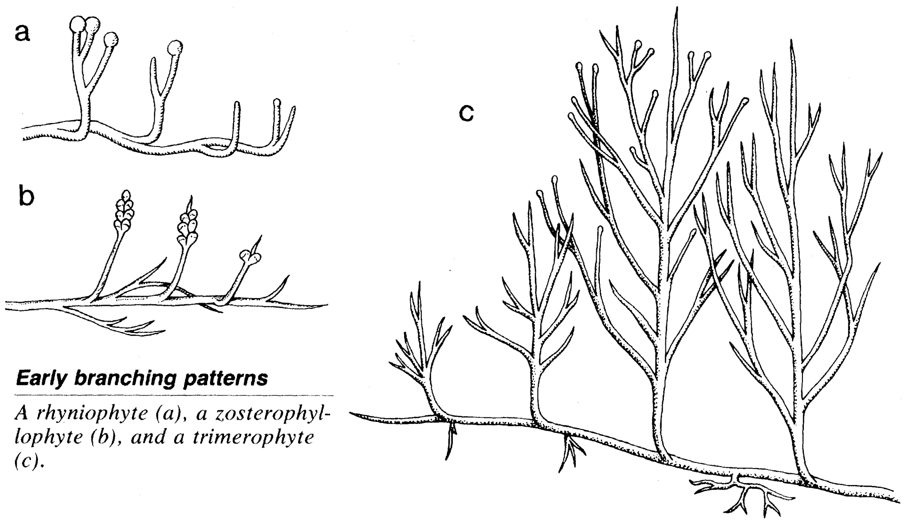
Progymnosperm fossil (× ¾)

The earliest land plants give the impression of being developmentally very plastic and therefore display essentially random branching patterns, but they do have an element of regularity. For a very small plant the consequences of random branching are tolerable. In a large plant, however, the outcome of random branching would be a symmetrical tight bush in which there would be an unacceptably high degree of self-shading. "As plants became bigger they had to diverge from random branching," says Niklas. "One simple solution is to produce tiers of branches, like a pagoda, in which successively higher branches are successively shorter. As the sun sweeps over such a structure, there is a minimum of self-shading." The emergence of this type of asymmetry is precisely what is seen in the fossil record during the first 50 million years of land plant life and beyond.

Niklas needed to be able to quantify the order displayed in the branching patterns within each group. He therefore devised a simple two-dimensional statistical model for axis bifurcation in plant growth. For instance, an axis might terminate, as it would if a spore-containing body were to form; or it might bifurcate. Bifurcation might result in the production of a minor axis that has the same potential for further branching as the major axis; or it might have less branching potential, thus producing an asymmetrical structure.

In a large series of computer simulations, "decisions" about the fate of an axis were determined by reference to one of four probability density distributions. Four different branching models were therefore generated, based sepa-

*K. Niklas, *Paleobiology* **8**, 196 (1982).



Early branching patterns

A rhyniophyte (a), a zosterophyllophyte (b), and a trimerophyte (c).

rately on regular, geometric, binomial, and Poisson probability distributions. Although the shapes of the branching patterns produced are subject to a considerable degree of variability in most models, in general they become more and more asymmetrical as one shifts from regular through geometric, binomial, and Poisson.

With these four branching models mathematically defined, it was thus possible to analyze branching characteristics of fossil plants in order to determine how the groups matched with the mathematics. It turned out that within the two divergent paths of early plant evolution there was a parallel trend, that of increasing asymmetry.

Although the overall pattern of branching within the zosterophyllophytes and the lycopods can be described mathematically by the regular branching model, there is a significant increase in the degree of asymmetry expressed in the lycopods. Similarly, asymmetry increases in the transition from the rhyniophytes to the trimerophytes, and from the trimerophytes to the progymnosperms. Here, however, there is a shift from regular branching in the rhyniophytes to geometric branching in the trimerophytes. The binomial model best describes the branching pattern in the progymnosperms. (None of the branching in any fossil group examined so far conforms with the Poisson model.) Thus, order is being expressed increasingly as these lineages evolve. The question is, where does it come from?

One approach to this question was to run a series of branching pattern simulations in which the decisions about the fate of axes were purely random. If order can flow from disorder, it should be seen here. Niklas reports that, from a run of 100 simulations, each with ten branching intervals, he obtained eight structures that had "a significantly high level of apparent order in their branching patterns." Analysis of these eight ordered structures revealed examples of both regular and geometric branching patterns, but there was no binomial pattern. Niklas also discovered that, if he continued the simulations longer, that is, the program allowed each structure to branch more times, then the degree of geometric patterning increased. There was, however, still no sign of a binomial pattern.

The most dramatic aspect of these results is that, with the exception of the binomial pattern within the progymnosperms, the branching patterns characteristic of the major groups of early land plants can be generated by purely random branching, albeit at a relatively low level (0.8 percent). One might therefore wish to conclude that the evolutionary trends in the two major lineages were governed by purely stochastic processes. However, Niklas's analysis shows that, with the passage of time, there was a steady decrease in variance in the branching patterns within each group. "This is strong evidence that the developmental processes were becoming canalized," suggests Niklas. "The trends we see in the fossil record are the result of natural selection on a finite number of mathematically defined possibilities."

Paleobotanists are of course aware that early plants evolved and developed more ordered branching patterns. The mathematical elucidation of steadily decreasing variance of branching patterns is, however, a significant contribution, particularly as it betokens steadily increased canalization of developmental processes.

The appearance within randomly generated branching structures of ordered patterns that appear, and are refined, in evolving lineages implies that natural selection had ready access to raw material upon which to operate. A frequency of 0.8 percent of ordered structures is, by most standards, a generous supply of apparently suitable variants. The transition from one group to the next must therefore have been relatively easy, involving in some cases perhaps just the general increase in size, with its concomitant increase in geometric patterning. "Increase in size may in fact be a mechanism for canalization," suggests Niklas.

By contrast, the absence of a binomial branching structure within the randomly generated branching patterns presumably implies that the transition from trimerophytes to progymnosperms was not a simple evolutionary change. "The inability to stochastically generate this transition may be taken, tentatively, as evidence for a deterministic rather than random causality," concludes Niklas. He suggests that perhaps the developmental system was perturbed in some way—perhaps genetically, perhaps environmentally—and from this emerged a different form of branching.

Two important features of plant growth, which are apparent among the earliest fossils, are known as reiteration and overtopping. The first, as its name implies, involves repetition of a particular growth sequence, such as a branching pattern. This process can be of value in repairing damage or as a response to certain optimal stimuli. The second feature, overtopping, describes the extreme growth of one branch relative to another. A layered, pagoda-like structure results, which is a good solution to preventing self-shading.

Suggestions of both reiteration and overtopping occur among the branched structures of purely random simulations. Indeed, identifiable reiteration was found in 57 percent of 500 random simulations. Niklas finds that by artificially canalizing such events when they occur during a simulation he can produce structures reminiscent of the true phenomenon. This, again, is a demonstration that structures important in plants today and throughout history would have been relatively easy products of evolution.

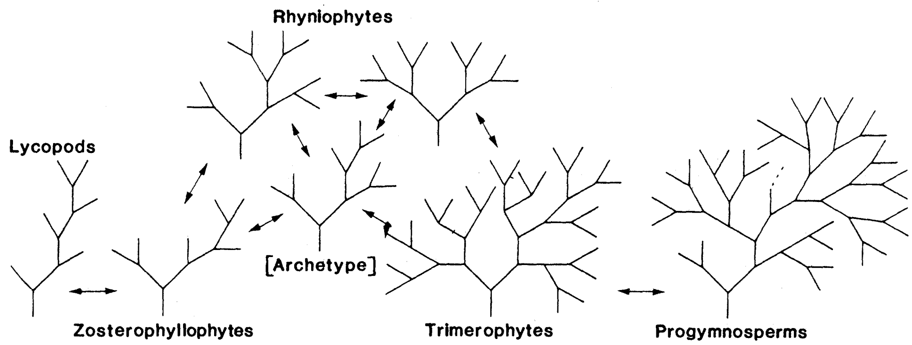
Niklas's mathematical approach to paleobotany might provide aid in tracing more precisely the origin and divergence of an archetypal branching pattern for early land plants, a task with which data on fossils can help only in a limited way. One of the major problems here is that the closer one approaches the archetypal form, the less well defined will be the branching patterns within the separate groups. The mathematical solution to the quest for the archetypal branching pattern is to start with the well-defined branching patterns of later groups and then work back through successive precursors, by the mathematically most parsimonious route for transitions between groups.

Niklas's simulations show that the changes in branching patterns between the lycopods and the zosterophyllophytes and between the progymnosperms and the trimerophytes are distinct. The putative transitions are therefore not in any doubt. Beyond that one finds a plexus of branching patterns composed of certain rhyniophyte groups and a mathematically inferred archetype, which is characterized by regular branching with a certain degree of asymmetry. Exactly which paths ran where at this very early period remain to be established. "We can say, however, that the archetype must have been a plexus of organisms defined on the basis of very plastic branching patterns."

In that Niklas's current model is a two-dimensional representation of growth patterns, it is of course limited in its sophistication. Moreover, it does not take into account the effect of the distribution of sporangia (the spore-forming organs) over the plant, which must influence in important ways the branching patterns that are possible. "The computer analyses do, however, provide a first-order approximation of the random and nonrandom components of branching systems," concludes Niklas.

Meanwhile, Niklas, O'Rourke, and Vincent Kerchner, also at Cornell, are beginning to develop three-dimensional models. "By contrast with the two-dimensional model, you have many more variables to compute: the rotation angle, how does the next branch rotate with respect to the last, and so on. In the model we can also alter the bifurcation angle and the length of successive branches. We are interested in looking at the influence of rotation angle on photosynthesis and on mechanical stability." The upshot is a massive simulation, which, for 10,000 structures with just ten branching increments, would run for 8.33 days on a small computer!

—Roger Lewin



Branching pattern transitions in plant evolution

Analysis of the most parsimonious transitions among the computer-simulated branching patterns shows the trimerophyte to progymnosperm change and the zosterophyllophyte to lycopod change to be distinct and therefore not in doubt. Theoretically the rhyniophytes, zosterophyllophytes, and trimerophytes can be derived from one of several possibilities.

Does California Bulge or Does It Jiggle?

Southern California may be bouncing up and down every few years; could this have been mistaken for the ominous bulge?

First, it was the Palmdale bulge, a 35-centimeter-high, 200-kilometer-long swelling of the ground that reportedly developed during the 1960's. Now, a group of geophysicists is suggesting that some of the same area of southern California may be bouncing up and down every few years, although these apparent oscillations in elevation have never lifted the ground to the extreme height claimed for the bulge. In fact, such rapid but modest oscillations, together with recently discovered measurement errors, may account for most of the reported towering bulge.

In this issue of *Science* (p. 1215), Robert Jachens, Wayne Thatcher, Carter Roberts, and Ross Stein of the U.S. Geological Survey (USGS) in Menlo Park, California, present a 5-year record of three different geophysical measurements, each of which bears on changes in elevation. All three seem to trace the same pattern of uplift and subsidence at Tejon Pass on the San Andreas fault about 100 kilometers northwest of Los Angeles. The ground there seems to have risen and fallen 5 to 15 centimeters twice during the past 5 years. The USGS group reports similar but less striking movement at two other San Andreas sites: Palmdale, which is at the center of the purported bulge, and Cajon Pass, 70 kilometers northeast of Los Angeles.

Researchers keeping an eye on southern California have seen plenty of variations in the crustal properties they have been monitoring (*Science*, 15 February 1980, p. 748), but all too often the anomalous readings have been at different places, at different times, or on instruments whose measurements could not be checked against related observations. Three measurements, gravity, strain, and elevation, were made at each of several sites by the USGS group, and the possible errors in each type of measurement are thought to be unrelated. All three measurements at a particular site tend to record the same episodes of uplift and subsidence. When the ground rises, strain (the distortion of the rock) increases and gravity decreases. That is just what theory would predict if the crust were being squeezed like a sponge. Squeezing the crust would distort the rock, push the ground up, and carry any gravimeter farther from the center of the earth's mass, which decreases the observed gravity.

The concerted behavior of the three measurements impresses many researchers, more so than a glance at the plotted values might seem to warrant. The apparent changes are only a few times larger than the calculated errors, and the statistical correlations among the three are only significant at the 90 to 95 percent confidence levels. Still, the changes appear surprisingly well behaved when compared to the assortment of microearthquakes, bubbling springs, and barking dogs that have often created excitement in California. In addition, the observed elevation changes, which have