

FOREST SUCCESSION

The study of a woods in New Jersey has yielded a predictive model for the succession of trees in a mixed forest. Two basic factors are the moisture in the soil and the geometry of leaf arrangement

by Henry S. Horn

When a forest has been devastated by man or by a natural catastrophe such as a hurricane, in time a semblance of the original forest returns. The regeneration of the forest goes through several stages called succession: trees that are dominant in one stage of regeneration succumb to trees of other species in the next. Forest succession raises a number of basic questions. Is there an orderly and predictable pattern to the changes? Does succession reach a stable end point if given enough time? Do different patterns of succession lead to the same final stage? Conversely, can one initial stage of succession lead to different final stages? Are some stages of succession more fragile than others? Answers to these basic questions are needed before we can hope to answer more practical questions. Can the natural regeneration of a forest be speeded up by enlightened human intervention? How can succession be controlled in order to keep a forest in its most productive state?

One of the more appealing aspects of studying forest ecology is that basic questions can be explored with a modest investment in technical equipment. Most of my own work is done with a pencil, a notebook and a measuring tape. The one specialized piece of equipment that is essential is an ingenious device for extracting a "core," or cylinder, of wood from a tree. The core provides a cross section of the tree's annual growth rings and hence a record of its age. Although I have access to a full-sized electronic computer, most of my calculations can easily be done with an inexpensive pocket calculator. My laboratory fits into a carpenter's apron.

Forest succession proceeds too slowly for it to be observed directly. Ideally one would like to find several plots of

land with similar physical characteristics but different and well-documented histories. Unfortunately reliable historical records of land use are rare. Some investigators attempt to infer historical patterns of land use from the qualitative pattern of vegetation, arriving at successional patterns with a marvelous but spurious internal consistency. In order to avoid such circular deductions I make a comparative census of the ages of all the trees on various plots of land, all with unknown histories. I then infer successional patterns, and within these hypothetical patterns I measure changes in competition between different species of trees and differences in their growth rate. The empirical patterns I arrive at have led to some theoretical abstractions, which I have provisionally tested with further observations.

Before attacking the general questions about the succession of trees in a forest, I shall document the details of the particular succession I have examined. A 500-acre woods in Princeton, N.J., owned by the Institute for Advanced Study has provided a convenient natural laboratory for my work. A small portion of the woods apparently was never farmed, and the remainder is divided into plots that were last farmed at various times from 35 to 150 years ago. The

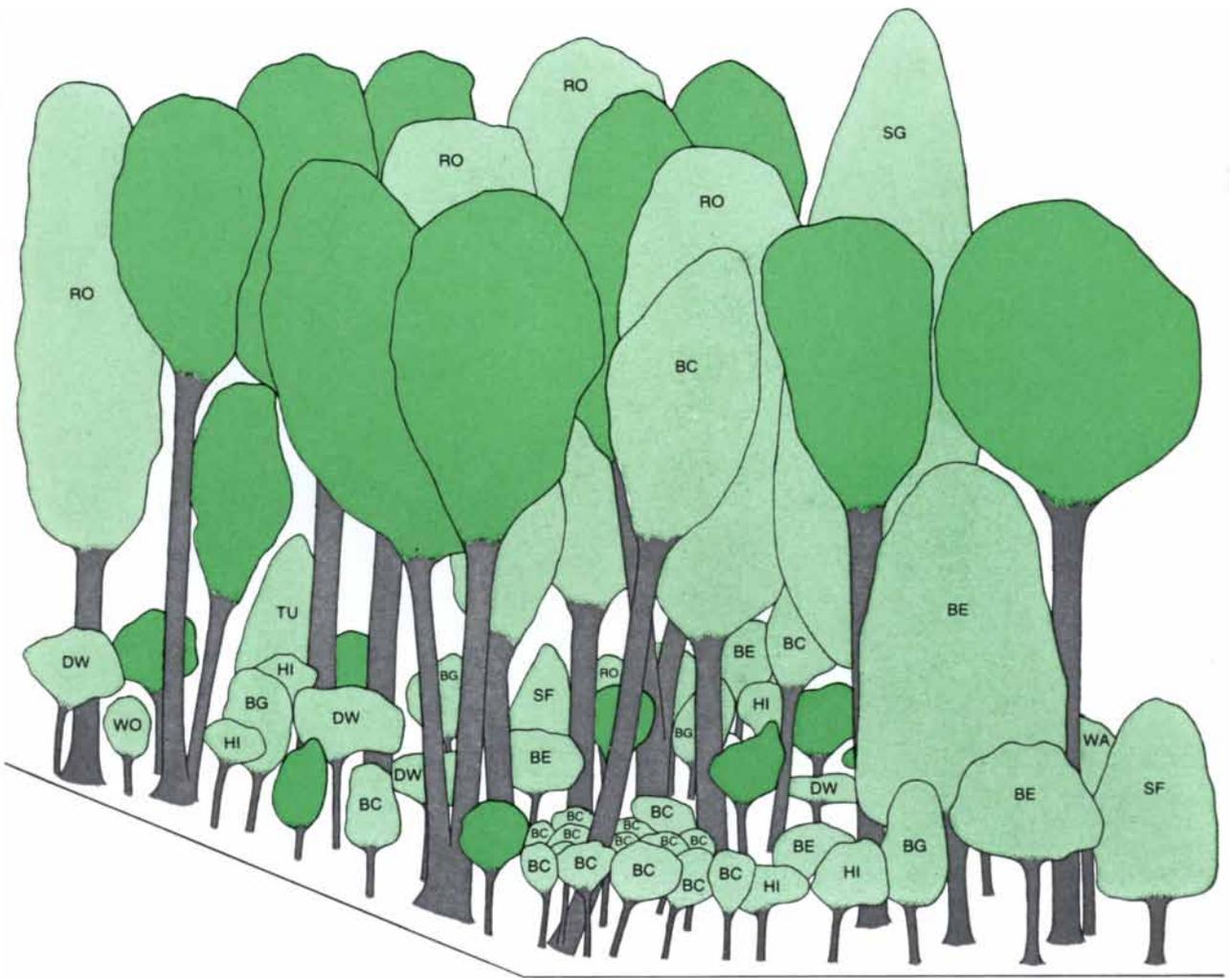
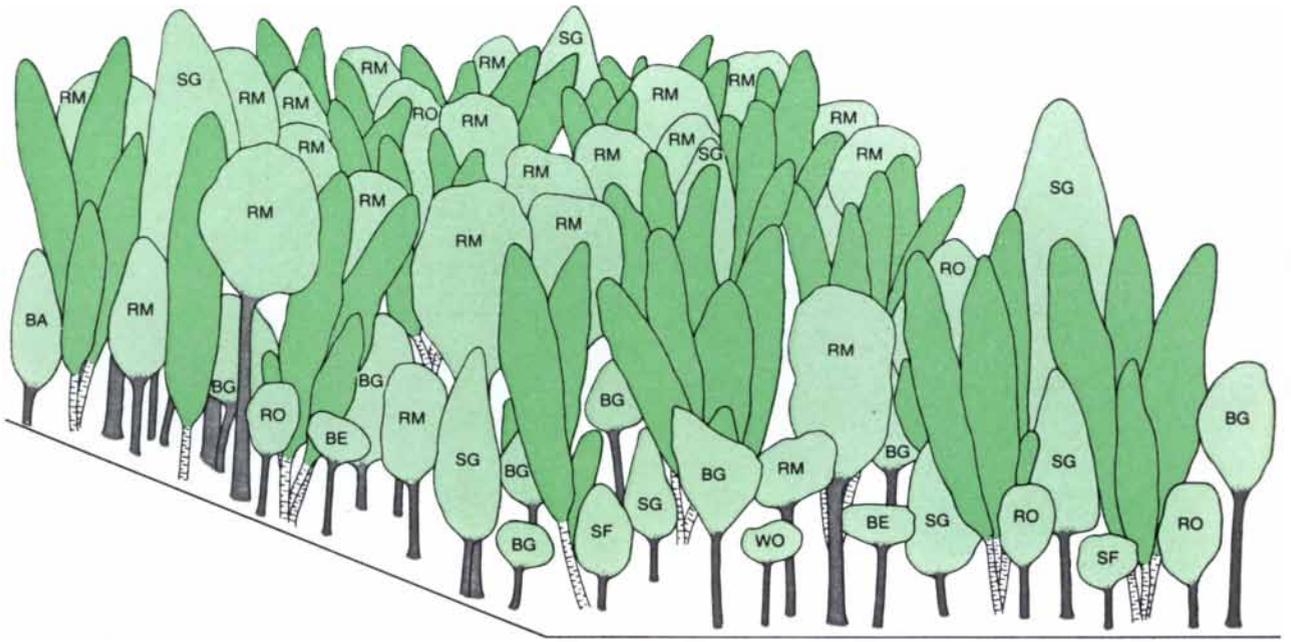
only widespread disturbances were a blight that led to the loss of all the chestnut trees by 1920 and the uprooting of several trees in the hurricanes of 1938 and 1944. Throughout the woods' recent history each of the plots has been within seeding distance of trees that are characteristic of different successional stages.

As a first approximation the stands are ordered by the age of the oldest trees of the dominant species: gray birch (33 years), bigtooth aspen (35 years), sweet gum (37 years), black gum (50 years), red maple (about 65 years), oak, hickory, tulip tree and dogwood (each about 120 years) and beech (about 250 years). For each stand I sought the answers to three questions: Is the stand under invasion by species that are characteristic of supposedly later stands? Is there a senile population among species that supposedly belong to earlier stands? Are the dominant species begetting their kind locally?

One cannot take the first approximation seriously or use the absolute ages of the trees to answer these questions because trees that have rotted away may be well represented by their offspring. On the other hand, the relative age profiles of the various species in each stand will clearly show how well each species will be represented in the near future. An invading species will be represented

FOREST STANDS in the 500-acre woods of the Institute for Advanced Study in Princeton, N.J., are identified by the dominant species of trees in each stand. The dominant species in the six stands on the opposite page, photographed with a "fish-eye" lens, are bigtooth aspen (*top left*), black gum (*middle left*), oak-hickory-tulip (*bottom left*), gray birch (*top right*), sweet gum (*middle right*) and beech (*bottom right*). The three stands at the left are on well-drained soils; the three at the right are on wetter soils. Note that the stands on the wetter soils have a greater number of canopy trees than those on the drier soils. Grapevines festoon the middle story of the bigtooth aspen stand. Gray birch stand has been invaded by the thorny vine greenbriar. Sweet gum has crowded out gray birch, which lies on forest floor. Oak, hickory and tulip are about equally abundant in their stand, which has understory of dogwood.





by many seedlings, a respectable number of saplings and perhaps a few small trees. A locally reproducing species will have trees in several age classes, with a preponderance of young trees. If a stand consists of nothing but older trees, it is senile, and its fate depends on whether other species will invade it before the dominant population reproduces sufficiently for the trees that have died to be replaced.

Analysis of the age profiles of the trees in each stand shows that the gray birch and the bigtooth aspen are senile wherever they occur and that their stands are under heavy invasion by all the other local species. The black gum and the sweet gum are reproducing locally, but their understories are full of red maple, beech, oak and hickory. The red maple is also reproducing locally, but its stand is being invaded by beeches and a few oaks. The oak-hickory-tulip stand is senile, with a few beeches here and there. The beech stand is senile, but its understory is filled with root sprouts, so that the next generation undoubtedly will have an abundance of beech.

The soils in which the stands grow are also a factor in the pattern of succession. The oak-hickory-tulip stand and the bigtooth aspen stand are on coarse, well-drained soil, which is aerated to as great a depth as I can reach with a two-meter soil auger. (The aeration is indicated by the rusty color of the iron oxides in the soil.) In the red maple stand and the beech stand the average water table is within a meter of the surface of the fine, sticky soil. The stands of other species of trees are on intermediate soils.

I have developed a hypothetical successional pattern that is consistent with my observations of the actual stands [see illustration on next page]. Bigtooth aspen invades open spaces readily but

gives way to oak, hickory and tulip on dry soil and to black gum on wetter soil. Gray birch is also an invader of open space, but it gives way to black gum or to sweet gum, depending partly on the history of the plot and partly on some subtleties of drainage. On dry soil black gum succumbs to oak, hickory and tulip, but on poorly drained soil black gum and sweet gum are displaced by red maple. Beech will replace red maple, although a series of dry years enables oak and hickory to invade red maple stands. Conversely, in wet seasons beech slowly invades the oak-hickory-tulip stand.

This hypothetical successional pattern is, of course, an abstraction. It represents what could happen, not what actually has happened or what necessarily will happen. In reality the oak-hickory-tulip stand has the characteristics of a former woodland pasture: compacted soil and a paucity of small trees. The red maple stand consists of sprouts from the stumps of an earlier stand that had been cut. The sweet gum stand has trees of almost uniform age and is just downwind from a huge and prolific sweet gum tree. The black gum stand is in the lee of the tall beech stand and is severely buffeted by turbulent eddies during windstorms. The black gum trees that dominate their stand have had their tops broken off several times and have regrown to their present height.

The only stands that are true to the hypothetical successional scheme are the gray birch, bigtooth aspen and beech stands. The beech trees may even belong to the original forest. Their trunks are free of branches to a great height, and the ground under them still has the mounds and pits created by the uprooting of trees in windstorms of the past, indicating that the land has never been plowed.

Several intriguing patterns arise from the hypothetical successional scheme. It shows that as long as there is enough soil moisture the succession converges on a beech forest. On dry soil, however, the succession either ends or stalls at an earlier stage, with the development of an oak-hickory-tulip forest. The successional sequence of gray birch to black gum to red maple to beech could actually take place on poorly drained soil. The sequence of bigtooth aspen to oak-hickory-tulip could occur on well-drained soil. I am justified therefore in assuming that real successions would show patterns like those I observe among these contemporary stands.

How do successional changes affect the productivity of a forest? Indexes of the annual production of new wood and the standing volume of wood can be calculated from the height, diameter and annual increase in radius of trees that are representative of each age class of each species in a stand. I plotted these "parabolic volume" indexes of the standing crop of wood and the annual production of new wood against the successional age of each stand [see illustration on page 95]. As an open field develops into a forest the amount of standing wood increases steadily, but the production of new wood first increases and then decreases as the forest's composition changes. The decline in the production of new wood is more obvious when production is expressed as the "interest rate," that is, the annual production of new wood divided by the volume of wood in the standing crop.

The geometrical arrangement of the leaves of a tree plays a role both in the tree's productivity of wood and in the successional pattern of a stand. The optimal leaf arrangement for intercepting and utilizing light most efficiently depends on the amount of light that is available to the tree. Leaves are able to conduct photosynthesis at about 90 percent of their maximal rate with as little as 25 percent of full sunlight. At lower levels of incident light, however, an optimal tree should intercept all the available light at its highest intensity. That is achieved by having a single layer of leaves in a shell around the tree. In a crowded stand a single-layer shell can provide no more than one unit of leaf area for each unit of ground area under the tree.

At high intensities of sunlight the tree should have leaves distributed throughout its total branch volume, subject only to the constraint that the interior leaves

BA	BIGTOOTH ASPEN	DW	FLOWERING DOGWOOD	SF	SASSAFRAS
BC	BLACK CHERRY	GB	GRAY BIRCH	SG	SWEET GUM
BE	BEECH	HI	HICKORY	TU	TULIP
BG	BLACK GUM	RM	RED MAPLE	WA	WHITE ASH
		RO	RED OAK	WO	WHITE OAK

DIAGRAMMATIC STRUCTURES of a gray birch forest (*top*) and a red maple forest (*bottom*) are shown on the opposite page. The dominant species in each forest is dark-colored, and the relative heights and abundances of all the species on a 20-by-20-meter plot of ground are given. Although the gray birch dominates the canopy in its stand, it is being challenged by red maple. There are no gray birches in the understory of the red maple stand, but there are scattered young red maples. Beech appears to be invading the red maple stand. If the two stands are indicative of successional patterns, then gray birch gives way to red maple. Since the gray birch stand was originally colonized by both red maple and gray birch at about the same time some 35 years ago, the successional shift from gray birch to red maple is brought about by the late competitive dominance of red maple rather than by invasion.

must receive enough light to balance their own metabolic costs. Leaves need at least 2 percent of full sunlight to pay for themselves metabolically. If the distribution of leaves is optimal, the total leaf area can exceed the ground area under the tree severalfold even in a dense stand. In the open, therefore, the monolayered tree with its lesser leaf area is competitively inferior to the multilayered tree. Conversely, deep shade may prevent the growth of a multilayered tree because its heavily shaded interior leaves do not pay for themselves and must draw their sustenance from the peripheral leaves.

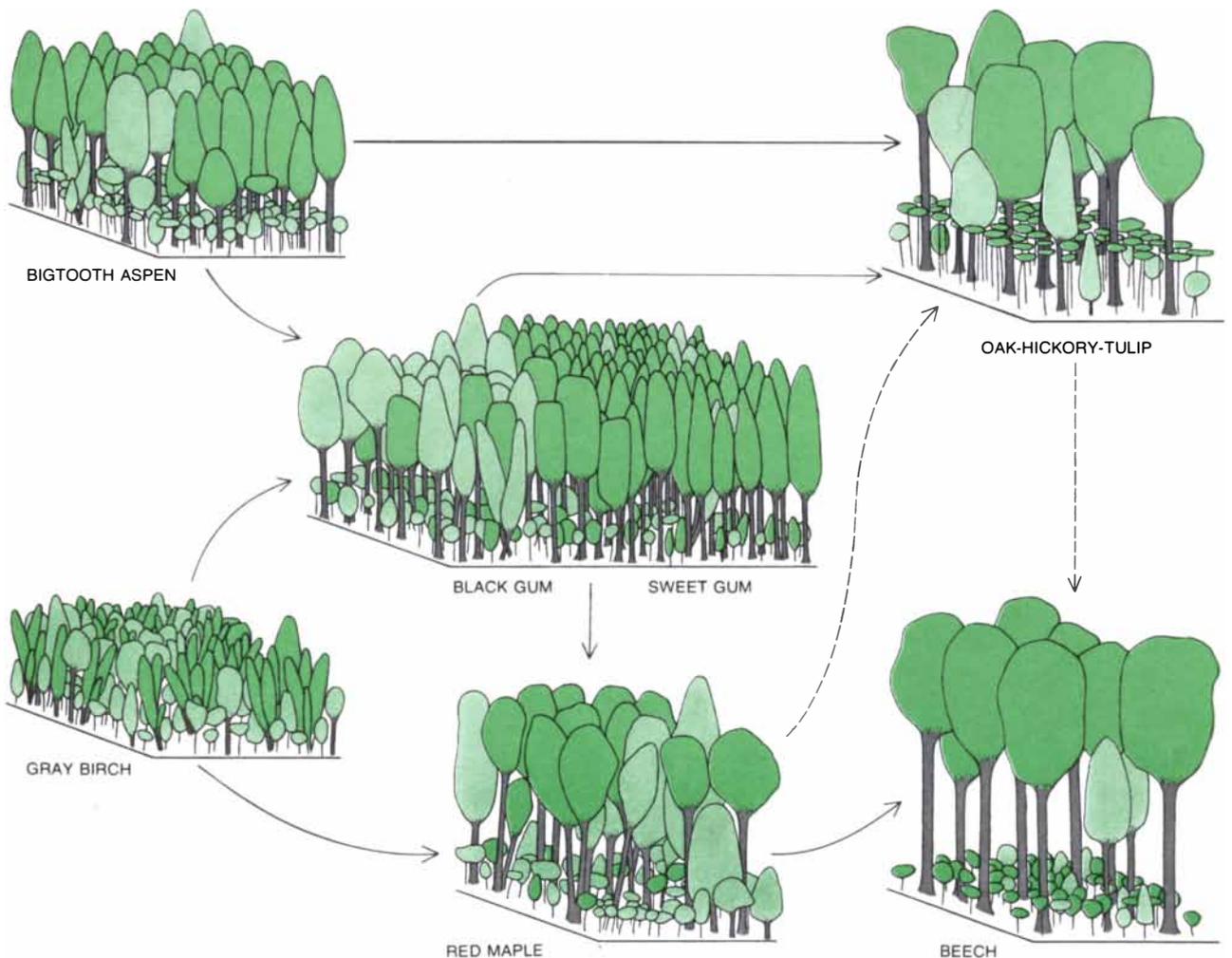
A monolayered tree produces dense foliage at the tips of well-lighted branches. The developmental program for a multilayered tree consists in pro-

ducing lacy foliage at the tips of well-lighted branches and at the tips of any interior branches that are sufficiently lighted or that manufactured a local surplus of sugar in the previous season. An adjustment between dense and lacy foliage can be made by control of the shape and lobing of the leaves, the length of the leaf stems and the spacing of leaves along the twig. For leaves that are spirally arranged along the stem or are set in pairs at right angles, several of the parameters must be adjusted concurrently, but for leaves that lie in the same plane along the stem, either opposite another leaf or alternating with other leaves, only the distance between leaves need be altered.

Why cannot a tree have an adaptive leafing strategy that is flexible, depending on the existing light conditions? An

optimal strategy would require either the ability to predict future lighting conditions or a system of communication between the inner leaves and the outer ones. I have no doubt that I shall eventually locate species of trees that make such an adjustment, but the few examples I have found so far are not convincing enough to warrant discussion. Hence I work currently with the assumption that a species of tree is characteristically either monolayered or multilayered in its arrangement of leaves [see illustration on page 96].

An appropriate and convenient expression of the distribution of leaves in a tree is the effective number of leaf layers within the tree with respect to the leaf area at the periphery of the tree. To obtain it I measure with a light meter the proportion of light that penetrates



HYPOTHETICAL PATTERN OF SUCCESSION has been derived by the author from measurements of primary factors that determine succession in each stand. Dominant species in each stand are dark-colored; other species are light-colored. The capacity of the soil to hold water increases from the bigtooth aspen stand at upper

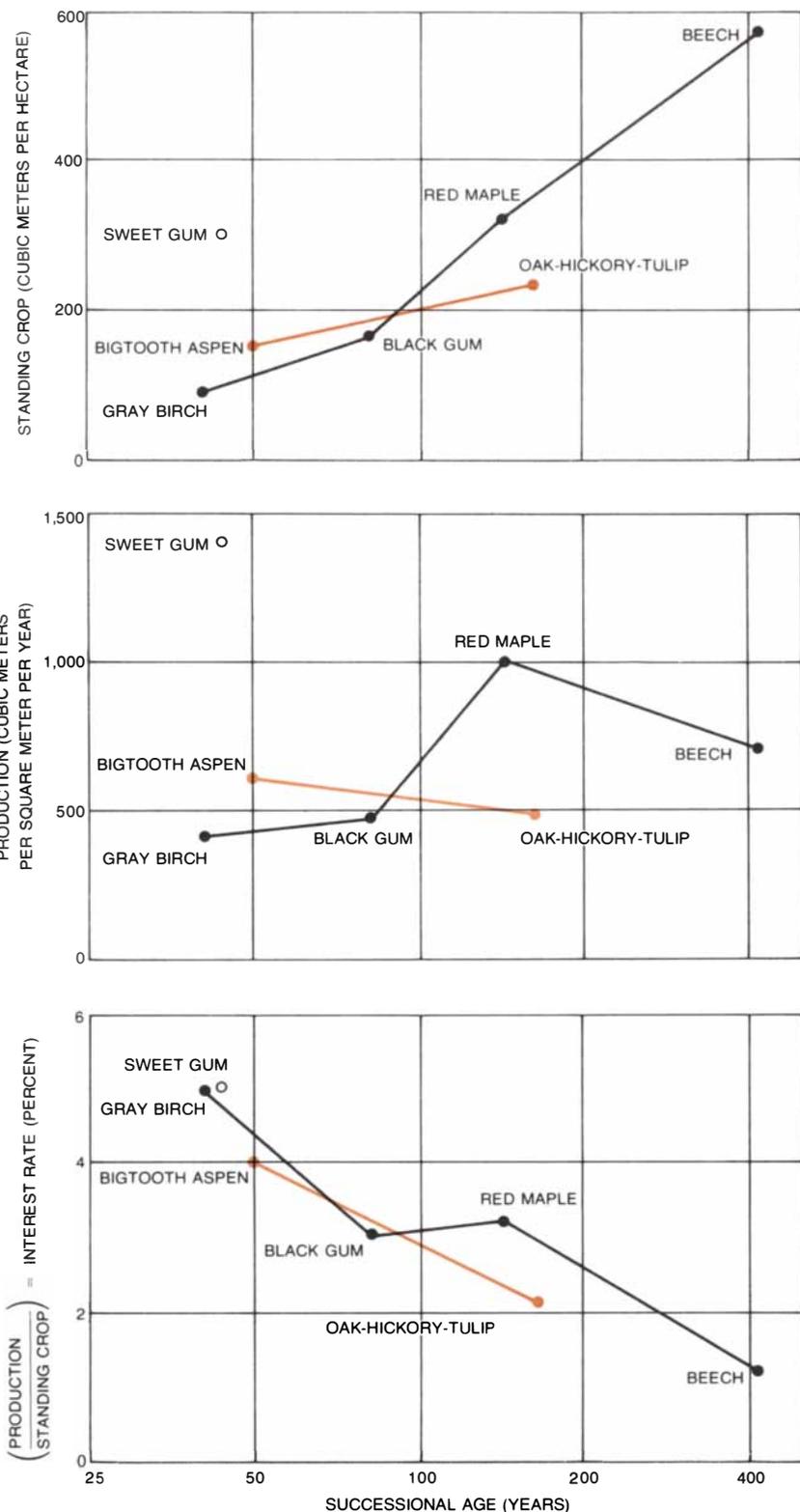
left to the beech stand at lower right. The solid-line arrows represent successional changes that are consistent with the relative age distributions of the species involved. Any of the intermediate stages, except red maple, can be bypassed. There is some evidence that other changes, shown by broken-line arrows, can also occur.

a single densely foliated branch at the outer edge of the tree and then the proportion of light that penetrates through the densest part of the entire tree. From these measurements I calculate how many outside branches it would take to reduce the light to the amount that comes through the tree as a whole. That is done by determining how many times the proportion of light coming through the branch must be multiplied by itself in order to obtain the light intensity coming through the tree. The answer is given by the ratio of the logarithms of the two measured light intensities.

In the early successional stage the number of branch layers is 4.3 for gray birch, 3.8 for bigtooth aspen, 3.8 for white pine and 2.7 for sassafras. In the intermediate successional stage the number of branch layers is 2.7 for white ash, 2.6 for black gum, 2.7 for red maple, 2.2 for tulip, 2.7 for red oak and 2.7 for hickory. In the late successional stage the number of branch layers is 1.9 for sugar maple, 1.5 for beech and 1.6 for hemlock. From these numbers it is obvious that the early successional trees tend to have more branch layers than trees in later stages.

We now have a clue to understanding at least part of the successional pattern in the stands I have studied. Multilayered trees are able to grow faster than monolayered trees in the open environment of early succession, but the shaded understory of these multilayered trees is less suitable for their own offspring than it is for monolayered trees. When monolayered trees eventually reach the canopy, their understory is well shaded, and multilayered trees can live only in the gaps left by the death of large trees.

Several other successional patterns follow directly from differences in the geometrical distribution of leaves. A tree must dissipate the solar heat it absorbs. The heat to be dissipated (and hence the water lost through evaporation) is spread over a greater leaf area in a multilayered tree than it is in a monolayered one. This means that the water loss per unit of photosynthesis is lower for a multilayered tree than it is for a monolayered one. On well-drained soil where water is scarce multilayered trees should therefore be dominant. On moist soil, where monolayered trees eventually come to dominate the canopy by virtue of their competitive advantage in the shaded understory, wood productivity will fall because the monolayered trees are less productive than the multilayered trees they displace. Moreover, the species most



SUCCESSIONAL CHANGES IN PRODUCTIVITY are shown in these graphs, measured by indexes of the standing crop of wood (*top*), the production of new wood (*middle*) and ratio of the production of wood to standing crop (*bottom*). The successional age is given logarithmically. The black line in each graph connects plots of the trees on moist soils, from gray birch through beech. The colored line connects the two stands that grow on drier soils. The sweet gum stand, which grows on soil intermediate in moisture content, is plotted by itself. Note that with increasing age production first increases and then decreases, except for sweet gum, which maintains very high production in a young and densely stocked stand.

adapted to shade should have an unbroken peripheral layer of leaves and thus should cast a shade so deep that not even their own offspring can grow in it. We can expect, then, that undisturbed forests in which monolayered trees dominate the canopy will have little or no new growth and will be senile.

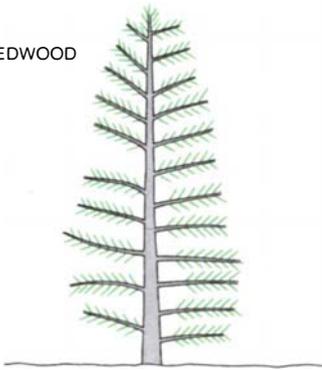
Another potentially important difference between monolayered trees and multilayered trees is their susceptibility to attack by insects. I have often seen

spring inchworm caterpillars defoliate a multilayered tree by eating one layer, lowering themselves on silk threads to the next layer and so on throughout the tree. This behavior is less efficient on a monolayered tree. If the inchworms try to change their foraging position by lowering themselves, they find themselves on the ground and then must proceed to the base of the tree and up the trunk. I have the impression that inchworms defoliate the local monolayered trees

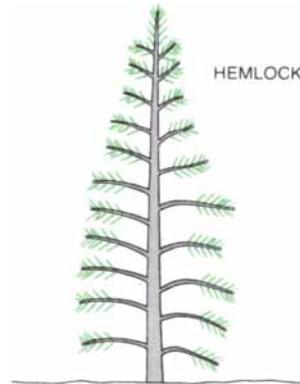
less often than they do the multilayered ones, but the evidence is insufficient to demonstrate that the difference is ecologically significant.

To sum up, interspecific differences in the geometrical distribution of leaves are at least partly responsible for the pattern of succession, for the successional changes in the age structure and productivity of trees and perhaps even for differential predation by some insects. Furthermore, the number of branch layers is a measur-

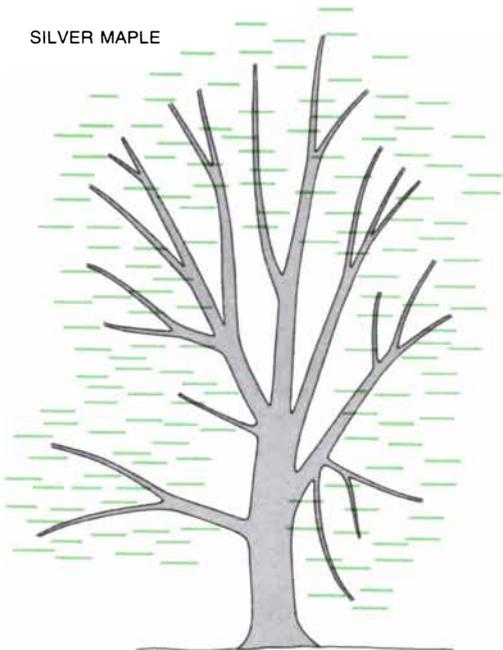
DAWN REDWOOD



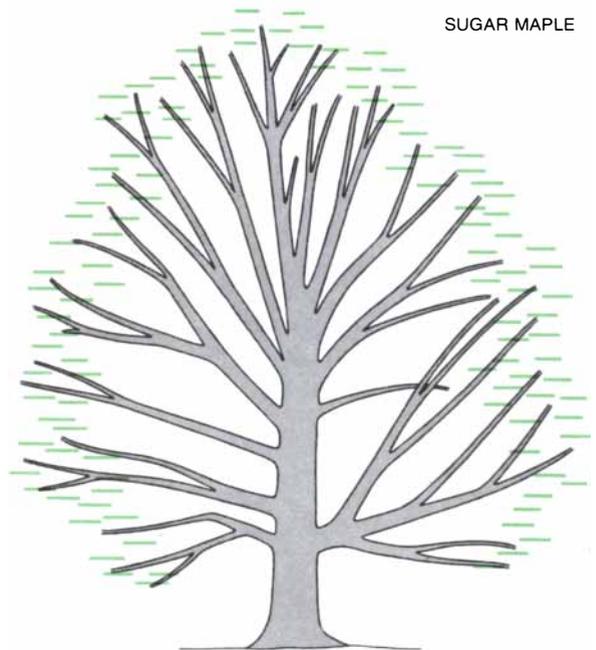
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SILVER MAPLE



SUGAR MAPLE



DISTRIBUTION OF LEAVES in multilayered and monolayered trees is depicted schematically in a slice through the middle of the tree. Dawn redwood and silver maple are typical of multilayered trees, with leaves scattered throughout the volume of the tree. Hemlock and sugar maple are virtually monolayered, with leaves concentrated at the ends of branches. Although the two conifers

have similar branching patterns and a similar pattern of leaf attachment, their total leaf distribution is quite different. The same difference holds for the two superficially similar maples. In open spaces, where the intensity of sunlight is high, the multilayered tree is competitively superior to monolayered tree, but in shaded understory of a forest monolayered tree has the competitive advantage.

able criterion for predicting a tree's rate of growth and its requirements for light and water. I believe predictions based on the number of branch layers could be useful in evaluating new varieties of trees for forests and gardens.

The hypothetical successional scheme predicts that the most aggressive species of monolayered tree will completely eliminate its competitors if given enough time and a favorable environment. In reality many factors other than tolerance of shade will determine the outcome of competition for places in the canopy of a forest. The effect of these additional factors can be taken into account by empirically determining the probability of whether a tree will be replaced by another of its kind or replaced by a tree of another species. I have estimated the replacement probability for each tree in a stand, and from the matrix of these probabilities I can calculate how many trees of each species can be expected to remain in the stand after any given interval [see illustration at right]. The probabilities are estimated by counting the number of saplings of each species under a canopy tree. I then gratuitously assume that every sapling under the canopy tree has an equal chance of replacing that tree in the next generation of the canopy.

When the probabilities for successive generations are calculated, eventually a stationary distribution is reached where the proportion of different species in the canopy does not change. The probability matrix can be weighted to take into account the fact that species differ in longevity and that the generation span is not the same even for trees of the same species. When the actual distribution of trees that form the canopy of the beech forest—the oldest and least disturbed stand in the woods I studied—is compared with the predicted distribution of trees, the prediction is surprisingly accurate [see illustration on next page].

A word of caution is in order. I was fortunate to have found forest stands that began with the invasion of open fields. Later species grew up in the shade of the pioneering species, and the numerical abundance of saplings in the understory proved to be a reasonable predictor of a species' success in reaching the canopy. Other successions might be determined by a race among different species to invade a new gap after a canopy tree has fallen, by biochemical interaction among trees, by changes in the climate or in the soil or by a multitude

	BIGTOOTH ASPEN	GRAY BIRCH	SASSAFRAS	BLACK GUM	SWEET GUM	WHITE OAK	RED OAK	HICKORY	TULIP	RED MAPLE	BEECH
BIGTOOTH ASPEN	3	5	9	6	6	0	2	4	2	60	3
GRAY BIRCH	0	0	47	12	8	2	8	0	3	17	3
SASSAFRAS	3	1	10	3	6	3	10	12	0	37	15
BLACK GUM	1	1	3	20	9	1	7	6	10	25	17
SWEET GUM	0	0	16	0	31	0	7	7	5	27	7
WHITE OAK	0	0	6	7	4	10	7	3	14	32	17
RED OAK	0	0	2	11	7	6	8	8	8	33	17
HICKORY	0	0	1	3	1	3	13	4	9	49	17
TULIP	0	0	2	4	4	0	11	7	9	29	34
RED MAPLE	0	0	13	10	9	2	8	19	3	13	23
BEECH	0	0	0	2	1	1	1	1	8	6	80

NEXT GENERATION OF WHITE OAK = .02GB + .03SF + .01BG + .1WO + .06RO + .03HI + .02RM + .01BE

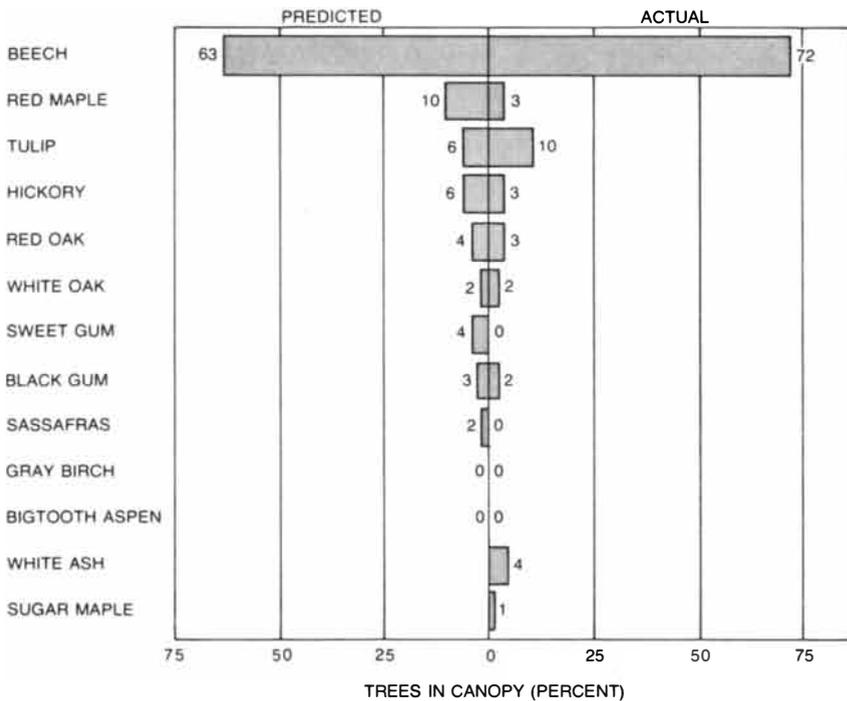
MATRIX OF PROBABILITIES for the replacement of existing canopy trees in a forest by trees of the same or other species is based on the assumption that every sapling under a canopy tree has an equal chance of replacing the tree. Each entry in a row is the percent of the total number of saplings found under a canopy tree of the species listed. For example, under the bigtooth aspen canopy tree 3 percent of the saplings are bigtooth aspens, 5 percent are gray birch and so on. The figures in each row add up to 100 percent. A sample calculation is given for the proportion of the forest that will be white oak in the next generation. The calculation shows that white oak will replace 2 percent of the gray birch, 3 percent of the sassafras, 1 percent of the black gum and so on. The new composition of the forest can then be substituted in the equation, and the composition of the second generation of canopy trees can be calculated. Repetition of the calculations leads to a stationary distribution in which the composition of the canopy remains unchanged in subsequent generations.

of other interactions among plants, animals and the physical setting. Such situations would call for more complex and perhaps technically impossible measurement of replacement probabilities. Nonetheless, as long as the fate of a given spot in a forest is dependent only on its current occupant and a limited number of neighbors, a theoretical representation of succession as a tree-by-tree replacement process is at least reasonable in principle.

The replacement process has several intriguing properties. First, it converges on the same final distribution of trees no matter at which successional stage it begins. This suggests that the convergence is a statistical property rather than a biological one, although there are interest-

ing biological reasons behind both the form of the replacement matrix and the final distribution to which the process converges. When the longevities of different species of trees are taken into account, the relative proportion of each species in the successive stages changes, but no new qualitative properties are seen to emerge.

When a forest that has reached a stationary state is disturbed, it takes longer for it to return to a stationary state if the first species to regenerate perpetuates itself rather than giving way to other species. Local self-replacement therefore slows down the achievement of a stable stationary state. Moreover, if each species' contribution to the next generation is made to be proportional to its



PREDICTED DISTRIBUTION AND ACTUAL DISTRIBUTION of canopy trees in a forest are surprisingly close to each other. The prediction is the stationary distribution that was calculated from the matrix of probabilities in the illustration on the preceding page and the weighted longevities of each species. There are no hidden circularities because the predicted composition and the actual one are based on completely different sets of data.

current abundance, then even small disturbances from the stationary stage may be self-augmenting. There might even be several stationary stages, depending on which species colonize first.

The model I have developed shows that it is dangerous to assign a unique successional status to a species, and that it is ridiculous to determine the successional status of a plot solely by the species of trees that are on it. The final stage of succession is really a mosaic of patches of varying successional age. Some species that are characteristic of early stages of succession, such as the black gum, persist in the late stages, both in the theoretical model and in reality. The age structure of each species within a stand and in several stands must also be taken into account.

The effects of eliminating one tree species or more from a forest can be calculated from the matrix of transition probabilities. Although such calculations are no substitute for real experiments, they may be useful as an aid in deciding which experiments would be worth conducting. One could attempt to find out how to speed or to slow certain successions. For example, the model indicates that patch-cutting, the harvesting of local groups of trees while leaving a large

area of uncut forest around them, should result in a more rapid return to the stationary stage than the cutting down of all the trees or even "high-grading": the removal of all commercially valuable trees.

The dynamic stability of succession must decrease with time, almost by the definition of succession. If a late successional stage is disturbed, the regeneration must pass through a long series of changes before the late stage is regained. That is the exact opposite of the more traditional view that the stationary state of a forest persists as a result of an intrinsic stability of the entire community and that forests tend to resist the perturbations imposed on them by man or by natural catastrophes.

The traditional argument of stability has been invoked to justify the conservation and management of natural areas. A more careful analysis shows that a forest in a stationary state is in fact more unstable than a forest in an early stage of succession. Where natural forests in a stationary state are desirable, perhaps they should be protected not only from disturbance but also from well-intentioned attempts at management.

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