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VEGETATIONAL ADJUSTMENT TO THE INSTABILITY OF THE SITE

BY HUGH M. RAUP
Director, Harvard Forest,
Petersham, Mass, U.S.A.

In this paper I shall present briefly some personal experiences in the study of vegetation. Geographically, these experiences have a wide range, from northwestern Canada and Alaska to the forests of New England, and to the tropical forests of Central America. Having described the experiences, I shall try to say what I think they mean to current thought on the nature and development of natural vegetation, and to our present conceptions of the manipulation and use of native plant life.

The first case history to be presented took place many years ago when I was beginning my first serious field work at Lake Athabaska, in northern Alberta and Saskatchewan. Lake Athabaska is about 200 miles long. Its shores are extremely varied, with shelving sandy beaches, steep rocky cliffs, and broad marshes. The shores have a variety of plant life usually arranged in some kind of zones extending from the open water offshore to the neighbouring uplands.

One of the most commonly used illustrations of plant community structure and succession is the zonation on pond and lake shores. Water lilies and pondweeds in shallow water are gradually building up peat and catching silt and sand around their root stalks. As the muck gradually nears the surface, other plants that like this kind of place, with its peaty substratum and shallower water, gradually take the place of the water lilies. Usually these are cat-tails or some kind of bulrushes. A little nearer the shore-line the sedges and cat-tails have so changed the substratum that they cannot live there any more, and perhaps some grasses can take their place. I described these things in great detail at Lake Athabaska, showing their neat zonal arrangement and the orderly change or succession that was presumed to be going on. My wife was along collecting lichens and mosses, and she quickly found that there was a fine zonation of these plants also. It was particularly evident on vertical cliffs where different coloured lichens made horizontal bands on the rock faces above the water level. Having been taught that wherever possible one should be accurate and have actual figures and measurements, we carefully measured the heights of all the zones above the level of the lake (17, 20).

We went back to Lake Athabaska six years later, seeing again the things we had described, and describing many more. Then we went back a third time, nine years after our first trip. In that field season we discovered that nearly everything we had described previously had vanished completely. Sometime during the three years that had elapsed since we had last seen it, the water level in the lake had risen no less than 9 feet, as shown at the places where we had made our careful measurements. A large part of the watershed that drains into the lake is in the northern Rocky Mountains, where snow and weather conditions had combined to send an extraordinary amount of water into the lake in a very short time. How often this sort of thing happens we do not know with any accuracy. From talking with the oldest inhabitants, the nearest we could come to it was at intervals of forty or fifty years.

At Lake Athabaska, every so often, the whole system of shore vegetation is simply drowned and eliminated, and the plants have to start over again. If there is any succession at all, it is in little fragments that never make any real progress, at least in the way it is assumed that they do. The water lilies had been growing in shallow water offshore, the bulrushes and cat-tails in shallower water, the sedges and grasses on the wet shore itself, each of them for the simple reason that it had found for itself the place best suited to it. These simple observations could be refined to great detail; but to take the next step and say that because the different communities were growing next to each other they were developing from one into the next, would be going beyond the facts, and into pure speculation.

It can properly be asked, "There must have been evidence of such extraordinary high water on Lake Athabaska. Why didn't you see it?" The answer is, "I did see it." I described it and took pictures of it—large driftwood high on the old beaches, and undercut banks high above the existing water level. But I was so entranced with the theory of succession that I bent all these facts around so that they would fit the theory—I thought they were evidence of unusually big storms, or a gradual though permanent lowering of the lake level.

My second case will deal with some observations of tundra vegetation in north-western America. When looked upon as a community of species the tundra is extremely variable in floristic composition and in the forms of the plants that make it up. Nearly all those who try to describe tundra communities attempt to use the familiar methods that have been worked out for temperate zone vegetation. First they try to describe the tundra communities in terms of dominants. But they quickly learn that when they have listed the primary species in a patch of tundra they have put down the names of about half the total flora of the patch, perhaps a dozen or fifteen species. For purposes of description such a method becomes hopelessly unwieldy, and defeats its own purpose. They find that tundra communities commonly do not have clearly defined dominants, but rather are apt to be miscellaneous aggregations of species growing together in what appears to be a disorganized mixture. Recourse may be had to statistical analyses of the frequencies with which species occur, but these often seem only to accentuate the randomization. If competition is present, it has not led to the dominance of any particular group of especially well-adjusted species. If our students want to find different combinations, all they have to do is move on a few feet and they are likely to find them.

Not being able to find dominants, they have still greater difficulty in finding successions of dominants. The seemingly disorganized patchwork of variation will not fit together in any developmental sequences with which they are familiar. With succession so poorly defined in the tundra, the idea of climax becomes almost unusable.

In the early 1930's Dr. R. F. Griggs read a short paper on "The Problem of Arctic Vegetation" at a winter meeting of the Zoological Society of America in Boston (7). Dr. Griggs had the same troubles with the description of tundra communities that others had had, but in his short paper he went a little further and made a simple though highly pregnant observation. He said that in the tundra the plants were acting like weeds in a garden. They seemed to be all jumbled together, with the individual species giving little evidence of dominance. The arctic plants do act like weeds in their community behaviour, and this has been causing much of the difficulty in the describing of the communities. Dr. Griggs did not go much beyond this, except to point out that the weed-like behaviour of the arctic plants constituted a real problem, and possibly a basic one in the study of arctic vegetation.

There exists in the alpine and arctic tundra lands one of those basic natural phenomena that loom so large and are so all-pervasive that they are apt to be missed. It is frost-heaving in the soils, and it occurs with an intensity that is beyond anything we know under temperate climates. Some of the more obvious results of it are the various kinds of patterned ground that are now being studied in detail by geomorphologists (29,30). Not only are there these large manifestations, but also a vast number of small ones, down to those which affect the positions of the least mineral and organic fragment of the soil.

Frost-heaving, and mass movements of soil under the influence of frost, are so common and widespread that they seem to govern the behaviour of most of the plants (8, 18, 21, 22). The roots of the plants are torn loose physically from their soil contacts, and only those that can stand this sort of thing can survive. The frost-heaving is so frequent that it occurs within the normal life spans of all the plants that live in the tundra. Consequently, no small group of species ever gets a chance to develop dominance, and no natural biological succession ever continues long enough to reach any kind of equilibrium or climax.

Dr. Griggs was more nearly right than he knew when he said that arctic plants behaved like weeds in a garden. A garden is mechanically stirred each year by cultivation. Tundra soils are stirred as effectively, if not more so, by freezing, thawing and mass movement. It is probable that some dominance and succession is to be found in the tundra. They are to be expected especially on well-drained soils such as sand and gravel. But even here the successions are apt to be only fragments, so varied locally that they cannot be arranged in any kind of patterns, in either space or time. In short, a basic characteristic of tundra vegetation is that it is essentially unstable. And we have every reason to believe that it has been able to maintain itself under these circumstances for a long time.

The third kind of experience I shall describe took place in Honduras, in Central America. The jungle forests of this region have been for many years an enormous source of wealth, largely because of the presence in them of the so-called rare woods of commerce, such as mahogany, rosewood, primavera, balsa, and Spanish cedar. Most of these fine timber trees are now gone from areas that are accessible, and a large business concern with wide interests in the American tropics has been engaged, during the past fifteen years or so, in an elaborate reforestation programme. It has put some 10,000 acres into tree plantations, and it was only natural that it should concentrate upon the woods best known to commerce. For instance, about 4,000 acres were planted to mahogany.

Wild mahogany is normally found scattered through the older jungle forests, and because these forests were assumed to be ancient and stable, or "climax", it was further assumed that mahogany plantings should be made in the forest, where this species was thought to have been able to come up naturally. Therefore lanes were cut, or rather, "tunnels", through the jungle, and vigorous mahogany nursery stock was set out and carefully protected. These plants refused to grow; they either died or merely languished. To save any of them the forest canopy had to be destroyed by one means or another. At the same time, mahogany that had been planted in the open grew rapidly.

A good many years ago an able naturalist, Dr. Paul C. Standley of the Field Museum of Natural History, made a careful survey of what is known as the Lancetilla Valley in northern Honduras (25). On the high slopes bordering this valley there are some old woods which have been rather carefully preserved because they cover a watershed district serving one of the nearby coastal towns. This forest has long been regarded as very old and stable. It is composed of gigantic jungle trees and a tangle of lesser vegetation; the whole thing illustrating what has been described as the climax. Ranging through this forest, and high on the slopes, Standley found some trees that were practically unknown in Central America outside of cultivation. A corresponding experience would be to find an old pear tree growing in a mixed forest on a New England hillside. He found not only the trees, but by scratching around in the soils he turned up pieces of old pottery.

Another curious fact that can be observed rather easily by anyone who knows a few of the common tropical trees is that in abandoned fields, species that make the rare woods of commerce are apt to seed in naturally. First there appears a dense tangle of shrubs, woody vines, and short-lived trees. Then, scattered here and there, appear individual mahoganies and Spanish cedars. They come into the old fields, along with a lot of other things, much like white pine comes into some New England fields.

Most of the country people in the tropics live by a peculiar kind of agriculture. It is a kind that is widespread throughout both the Old and New World tropics, and is caused by the fact that most of the upland soils are extremely poor in mineral nutrients due to excessive leaching by long-continued heavy rainfall. Agriculture under these conditions becomes a rather temporary affair, semi-nomadic in character. A farmer will cut and burn two or three acres of jungle and immediately plant a crop of corn. But very soon, perhaps within five to ten years from the time he makes his first clearing, he has to abandon that field and clear another patch of jungle.

This sort of thing has been going on for generations of farmers. All one has to do to realize its extent is to look at any landscape in the hill country of Central America. The view shows a patchwork of little farms in all stages of use and abandonment. This is not a modern phenomenon, but is as old as tropical agriculture. It is in the land of the ancient Mayan civilizations of Central America. We know that they were far advanced, with highly developed cultures, at least two thousand years ago; and there is evidence that populations were considerably greater then than they are now (14).

A traveller from the temperate zone has no difficulty in applying the theory of the climax to the high jungle. To his eyes it seems to satisfy the basic requirements of the climax. In spite of great local variation in its composition, as a whole it seems to be remarkably uniform over large areas, clothing hill and valley alike with its dense tangle of trees and climbing vines. Its individual trees are so large that the traveller from the north can hardly conceive of their not being of great age. With all this comes the impression of stability and timelessness. In the situations I have described, however, the facts all point in the other direction, and the supposed ancient jungle emerges as an "old-field forest", the major trees of which came in as pioneers on abandoned agricultural land.

I have no idea how widely this interpretation can be used in tropical America, but I believe it to be prevalent in western Honduras. It should be given some attention in all attempts to work out developmental trends in tropical vegetation.

For my fourth and last case study I come to the forests of New England. There are in New England some fifty commercially valuable or potentially valuable kinds of forest trees. They occur in a great variety of combinations. The Society of American Foresters, in their published descriptions of existing forest cover types, mention between thirty and forty of these combinations of species in the New England area alone, and many more could be described (23). Because the combinations, or communities, are difficult to define, they are even more difficult to map. A realistic map of them would have to be made on a very large scale.

Several generalized maps of New England forests have been attempted, but they do not begin to do justice to the situation (24). It is possible to find, in any one of the types commonly outlined, not only wide variations in its own composition, but also representatives of its neighbours. About the best we can say is that we have an almost kaleidoscopic patchwork of species combinations scattered over our landscape, and that going from south to north we pass by almost imperceptible changes from the oak and hickory forests of southern Connecticut to the mixture of spruce, fir, maple, beech, and birch in northern Maine.

There is some sense to the local distribution of certain types. Every experienced woodsman knows that in central Massachusetts spruce is likely to be found in bogs, and that red maple and yellow birch grow most abundantly in upland swales. He knows that he can expect to find pine in abundance on excessively drained sands and gravels. But these situations are more or less marginal. On the upland loam soils, where he finds the greatest variety of trees and the best growth, there is more of mystery. He knows there are differences between upper and lower slopes, between north- and south-facing slopes, or patchwise without any apparent relation to slope, exposure, or to anything he knows about the soil. He knows that certain readjustments occur following cutting, fire, or clearing, but he quickly learns what they are and what kinds of trees are involved.

The commonest explanation for the extreme variability in these forests is the destructive activity of European settlers in the seventeenth and eighteenth centuries. Between 1620 and the second quarter of the nineteenth century about 40 per cent of the land surface in New England was cleared for agriculture. The most extensive clearing was in the three southern states, in the non-mountainous parts of New Hampshire and Vermont, and in the southern third of Maine. Land that was not cleared was cut over for lumber and pulp, and much of it subsequently burned over. All of the pre-colonial forest has long since been gone from the three southern states, and only isolated and inaccessible fragments of it remain in the three northern ones.

Following prevalent American theory, it has been assumed that the pre-colonial forest was in a "climax" condition—that it had achieved a sort of "dynamic equilibrium" over vast areas as a result of millennia of natural development *in situ*. A certain amount of variation has been allowed in it due to major differences in soils and terrain—"edaphic climaxes" or "pre-climaxes" (15). Shorn of all its technical verbiage, the theory holds that the forest as we know it now is not in a truly "natural" condition, but that each battered part of it is in some temporary, passing stage of slow development toward the more stable and uniform condition that preceded its destruction by the white man. This idea is deeply intrenched in our current ecological and silvicultural thinking. Even the nature of the climax is reconstructed, by invoking the theory of tolerance; from it we learn that hemlock and the so-called "northern hardwoods" (beech, sugar maple and yellow birch) made up the climax in most of New England north of Connecticut and Rhode Island (1).

But when we apply some simple historical methods and find out what the pre-colonial forest actually was, we find that it was by no means in equilibrium, at least not within the carefully worked out concept of what the equilibrium or "climax" should be. In fact, the more we learn about it the more evident it becomes that the old forest was not far different from what we have now. There is every reason to believe that it was nearly as variable over the landscape as it is now, and we believe that its species composition has changed but little. Probably there were more large trees in certain habitats than we now have, though we believe that the number of very old trees was never great. Further, such evidence as we have indicates that individual stands of trees in the pre-colonial forest were essentially even-aged or contained well-defined age-classes, and that the ages varied greatly from one stand to the next (3). Evidence for these things comes from a variety of sources—early descriptions, land-use studies by which old woodlots can be identified, and, most important, studies in the woods themselves.

The complexity of our forests has, of course, gone through a period of intensification due to land use. Historical studies in the "town" of Petersham, Massachusetts, in which the Harvard Forest is situated, show that most of the pre-colonial forest remained essentially intact until the last decade of the eighteenth century (4, 12, 19). Clearing for agriculture then went forward rapidly, made economically feasible by the establishment of inland industrial communities. By 1830 between 60 and 70 per cent of the land surface in the "town" was devoid of forest. Agriculture failed rather suddenly during the third quarter of the nineteenth century, due in large measure to the extension of a transportation system into the rich farm lands of the American middle-west. The result in Petersham, as in most of agricultural New England, was wholesale land abandonment. Abandoned fields in our part of New England usually acquire naturally-seeded stands of white pine, for which seed sources are nearly always at hand. The pine becomes commercially mature in fifty to sixty years. When cut over, as nearly all of it has been in the last half-century, this land does not reseed itself to pine, but is quickly covered by native deciduous trees which have already established themselves under the maturing pine. Analogous old-field sequences, with different timing and different species of trees, are definable in other parts of New England.

Within the matrix of the prevailingly deciduous forest cover of much of southern New England, therefore, are stands of trees growing side by side that have had entirely different histories in the last 200 years. One group contains the old woodlots that were maintained as such throughout the agricultural period. Because of the sprouting habits of our deciduous trees, and in spite of repeated grazing and cutting in these woodlots, we have abundant evidence that their composition has not changed a great deal since colonial times. Immediately adjacent are lands that were cleared in the middle or late 1700's, remained in pasture for perhaps a century, produced a crop of naturally seeded white pine, and are now back in deciduous forest which also has appeared naturally. A striking fact is that unless there are accompanying and sharply defined differences in soil or terrain the present stands, though they differ so greatly in history, are scarcely distinguishable from one another in structure and species composition.

It seems clear that the present complex pattern of species distribution and frequency, even though it has to be interpreted locally in terms of land-use history, is of long standing and must be pushed far back into pre-colonial time. I propose that we should not be diverted from the solid core of fact derived from what we can see now in the New England forests, with all their complicated diversity.

It has occurred to me that the nature and distribution of forest types in New England bears a fascinating resemblance to another kind of vegetation that I have described here—the arctic tundra. As in the tundra, we have a huge number of species combinations scattered patchwise over the landscape. There is no wide expression or continuity of dominance, and our attempts to apply the theories of succession and climax become purely speculative in the face of the hard, historical realities.

In the tundra we have what appears to be a pretty good reason for the lack of organization and continuity in the vegetation. It is the frequent physical disturbance of the site by frost action. Do we have any disturbing influences in our New England forests that could produce the seemingly disorganized patchwork of types and age-classes which now exists and apparently was the rule in the pre-colonial forests as well? In the tundra the disturbance comes every year, or oftener, but there we are dealing with small unit areas and relatively short-lived plants. Suppose we project this to another scale in space and time, with large areas, and with large plants whose life spans reach from 200 to 400 years. Can we find evidence of disturbance in New England that would be effective on this scale?

We have no frost action in temperate zone soils that is severe enough to disturb forest vegetation. In some places soil erosion by running water creates havoc, but there are vast areas in north-eastern America where erosion is and always has been insignificant. Archaeologists who have studied the problem intensively tell me that the New England aborigines were for the most part nomadic hunters. Only in what are now our three southern states was agriculture developed to any extent. Even there it was highly localized, and never extensive. It seems impossible that clearing of the forest for agriculture by the pre-colonial Indians could ever have caused the tangled pattern of forests that existed throughout New England.

Pests and diseases must always have ravaged the forests, but there is a strong argument against their ever having been a major disturbing influence. Evidence in the forests proves that the disturbing agencies, whatever they were, affected all kinds of trees at the same time. Pests and diseases, on the other hand, are always more or less selective, destroying certain species and leaving their immediate neighbours intact.

Wherever coniferous trees make up a considerable portion of the forest, fire is destructive and relatively frequent. Most of the great coniferous forest belt that reaches from northern New England to Alaska has been burned repeatedly, and nearly every stand in it is in some stage of rehabilitation following fire. So far as we now know, there were Indians living in this forest throughout most or all of post-glacial time. Bush Indians whom I have known and travelled with seem to have no particular dread of fire. They do not put out their camp fires; nor, I suspect, did their ancestors. In fact, I believe that with some historical research we could prove that there were many more forest fires in pre-colonial time than after Europeans arrived on our continent.

I shall not explore further the disturbing effects of fire, though I think they are of major significance in accounting for the vegetational patterns in the spruce-fir country. But there are large areas in New England that seem never to have suffered much from fire. In central Massachusetts we can find little or no evidence of general or widespread fires in the recent or distant past.

The great hurricane of September 1938 was enormously destructive to forests in New England, laying waste thousands of square miles of our woodland (2). Most of the damage was done by the uprooting of the trees. In the nature of things, most of the trees that went down were comparatively large, with well-developed root systems. Each root system that was dislodged brought up with it a mass of earth, ranging in volume from one to many cubic yards. Where this mass came out of the ground there is a pit from 1 to 2 feet deep. Some of the uplifted soil has rolled back into the pit; but most of it, with the gradual rotting away of the root system, is being dumped in a mound-shaped mass at the side of the pit and downwind from it. Large areas of land in the path of the hurricane are now copiously sprinkled with these mounds and pits in various stages of development. The mounds, as they gradually form by the disintegration of the root systems, have a characteristic outline and structure. They have buried the pre-hurricane forest floor on which they fell, and this forest floor remains under them as a well-defined humus layer. The pits have a tendency to collect dead leaves which become waterlogged in fall and spring, to form a rather deep layer of unincorporated humus (10, 11).

The hurricane of 1938 was no respecter of species. It destroyed all kinds of trees at the same time, in some places blowing down whole forests, and in others leaving only fractions of them standing, either as individual trees or small groups. Thus our stage is set for the development of even-aged stands, or of stands composed of well-defined age-classes. The fickle behaviour of the wind has given us irregular or patchwork distribution of the damage and of the developing age-classes. Thus the hurricane has left us forest patterns that have some of the major characteristics of the pre-colonial patterns, particularly the even-aged stands that do not seem to be placeable in theoretical sequences of development. Even though it came as a completely unexpected catastrophe, we now know that this hurricane was preceded by others fully as severe (16). Perhaps such winds have furnished the major disturbing agency for which we have been looking.

Having learned to see the mounds and pits in process of formation, we now realize that we have been walking over old ones on the forest floor for years without knowing what they were. A little digging in the old ones exposes the same structures that we see in those formed in 1938 (6, 27, 28). The pits have thick humus layers, the mounds sometimes show ancient buried soil

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horizons, and we commonly find in the mounds themselves remains of the trees that made them. The mounds are especially evident on cleared land that has not been stirred by ploughing. Cultivation easily obliterates them. One of the best demonstrations we have of them is in old trees that are perched on stilt-like roots. These trees grew from seed germinated on the tops of mounds when the latter were fresh, with soil held high in the air by the root systems that were torn up. Roots from the new seedlings penetrated these masses of earth, taking, in the aggregate, the somewhat flattened pyramidal form of the masses through which they grew. Later the upper parts of the mounds were washed away, leaving the roots exposed, often with stones and boulders locked among them.

Again, having learned to recognize them, we have found the mounds nearly everywhere we have looked in the forests of eastern North America. In many places it is almost impossible to walk through a forest without climbing over them. A large percentage of the major trees in any given stand of old woods are found to be growing on the mounds. Almost never do we find them growing in the pits.

At the Harvard Forest Dr. Earl P. Stephens has been investigating the mounds and pits in some detail (27, 28). Much of what I am presenting here is derived from his work. We find the mounds there in great numbers, and they now appear to fall into several well-defined age-classes. Some formed in 1938 overlie others formed many years earlier, and these in turn overlie still others of greater age. Many of them we can date with great accuracy by counting the growth rings of trees growing on them. One of the most prominent age-classes in our woods dates from a major blow-down that we know to have occurred in 1815 (16). We can document, in all, four major hurricanes in the last 500 years.

Here is a source of instability that seems to have been effective throughout our region. Not only have the forests been destroyed or decimated, but also it seems clear that our soils have been physically disturbed to depths considerably greater than our ploughs have ever reached. The extent and intensity of the disturbances are, of course, extremely variable locally due to the vagaries of the wind, and regionally due to the regional distribution of the storms.

In the Arctic the physical disturbance of the vegetation and its habitat is due to frost action, and occurs frequently, even annually or several times within one year. In southern New England it appears to be due to wind, and occurs every century or so. In northern New England and eastern Canada physical instability due to windthrow is probably less frequent than farther south, but fire has had a relatively larger effect. All of these disturbing influences are sufficient to curb the development of dominance, and to halt theoretical natural successions long before they approach climaxes. In both the tundra and the forest they are frequent enough to be within the life span of individual plants, whether the latter be tundra herbs or forest trees.

It is quite possible that the apparent dominance we see in our older, more mature forests has been arrived at, not through any intricate biological competition over a long period of time, but rather because certain trees were able to germinate and grow quickly on mounds of fresh mineral soil formed by the uprooting of their predecessors. Whether they are tolerant or intolerant seems to be of little consequence. Nor is there any implication that the plant community they form is a kind of organism in itself, with a life span involving youth, maturity, or decadence.

We know that there are forest successions in New England, for we have documented them thoroughly in our studies of sequences on abandoned farm land. But again allowing for differences in map and time scales, and considering the poor expression of dominance and climax, it looks as though these forest successions, even though a hundred years in length, are merely fragments like those we find in the tundra.

I have described four cases in which the ideological tools with which I went into the field turned out to be entirely inadequate, or at least so dull and cumbersome that they required more time and energy for repair and adjustment than for use. These tools are embodied mainly in the ideas of the plant community as a more or less finite natural body, developing dominants within itself through competition; natural biological succession among dominants and communities to form well-defined and predictable sequences; natural succession culminating in climax, or dynamic equilibrium, which is thought to remain relatively stable until the climate is altered. I could add many similar cases from my own experience, and I am sure that still more can be gleaned from the experience of other students.

Among the cases described, one aspect is common to all, and I suggest that it has fundamental significance. The ideas of community structure and the expression of dominance, that of biological succession, and finally that of climax, are based largely upon the assumption of long-term stability in the physical habitat. Remove this assumption and the entire theoretical structure becomes a shambles. This is precisely what has happened in all of the cases. In the tundra the disturbing agent is frost in the soil. In the New England forests, both before and after the coming of Europeans, it has been fire and windthrow. In Central America man himself seems to have been a singularly efficient disturber of the tropical forests for at least two millennia. In the little shore communities at Lake Athabaska merely a periodic high water level in the lake was sufficient to undo the theoretical sequence of events. In all of these cases the disturbances have been so frequent and so generally effective that the expected "climaxes", or "equilibria", recede into pure speculation. Natural successions either do not occur at all or are limited to such incomplete fragments as can be accomplished between upheavals.

When I look at these botanical phenomena naively, without benefit of preconceived notions derived from projections of theory beyond the facts, I see the plant community as a relatively loose aggregation of species, visible in the landscape, but not precisely definable in space or time. This is the "individualistic" concept of the plant association propounded by Gleason many years ago (5). I see the community, not as the product of long-term, slow development in a relatively stable physical habitat, but rather as the product of repeated major disturbances by factors largely external to the vegetation. I must think of such disturbances, not as unusual departures from the normal, but as a part of the normal itself.

Such fragments of order as I can see in the changes that occur are then looked upon merely as readjustments within existing patterns. Many of these patterns, even local ones, and even though they may be poorly defined, seem to be remarkably persistent. The species of which they are made seem capable of rehabilitating themselves against devastating odds. When the vegetation is looked upon in this light, its basic unit for study becomes the species or one of the racial subdivisions of the species. Basic plant geography becomes floristic, and basic ecology is the "autecology" of the species. The last is merely sound morphology and physiology applied to the living plant in its natural habitat.

I do not know how far these ideas can be carried beyond my own experience, but I propose that they should be tested elsewhere. There is some evidence that they are widely applicable in eastern North America. Part of this evidence is direct, and comes from field observations (6, 9, 26). More of it is circumstantial, and is derived from the ever-increasing dependence upon statistical methods for the description of communities and the changes that occur in them.

It may be that nothing we, as invading Europeans, have ever done to our eastern forests, short of their complete removal, has exceeded in sheer catastrophic upheaval what Nature herself has done to them repeatedly. There is reason to believe that the rich vigour and variety they displayed to the early colonists were being maintained through recurrent disruption of any trends they may have had toward dominance and equilibrium, and through the recurrent release and enrichment of their soils by fire and windthrow.

My knowledge of our natural range lands is not adequate for proper judgement, but I suspect that the same could be said of them. I had supposed that if stable habitats were to be found anywhere they would be in the grasslands of the Great Plains. But Professor James C. Malin of Kansas University, in a searching review of the natural history of the North American grasslands, has described a galaxy of disturbing factors that seems to have kept that vegetation in a state of flux from time immemorial (13). To express his view he has borrowed a term from the physical sciences, and suggests that the grasslands constitute an "open system" of vegetation.

The application of such ideas in silviculture, and in game and range management, can remove a great many of the shackles that seem to restrict our thinking in these fields. Perhaps we need have far less fear of disturbing balances in soils and vegetation than we are accustomed to. This fear has served to limit many useful experiments in manipulation.

In trying to understand the vegetation I have ceased to expect it to form itself into neat communities that will fit my theoretical constructions. Likewise I do not expect it to follow theoretical sequences of change for which there is no precedent in reality. Rather, I feel the need to know the secrets of its incredible powers of recuperation and persistence in the patterns in which I find it. Greater knowledge of these powers, and better understanding of the way in which they function, should make possible a more efficient use of natural vegetation. Perhaps a long stride in this direction can be taken if the vegetation is conceived of as a complex, fluctuating system wherein there is endless, essentially indeterminate change, and wherein capacity for readjustment, rather than extreme vulnerability, is given primary emphasis.

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DISCUSSION

Dr. Raup explained the techniques used to trace the history of past hurricanes which have blown down parts of forests. It was possible to trace hurricanes as far back as the fifteenth century, and he showed slides to illustrate evidence of wind-blown trees in parts of New England. *Dr. Darling* commented that Dr. Raup's thesis was that the classical notion of ecological succession should not be taken too literally, and that these natural catastrophes could considerably affect our interpretation.

DISCUSSION

Le *Dr. H. M. Raup* (États-Unis) fait l'énoncé des techniques utilisées en vue de retracer l'histoire des anciens ouragans responsables de la destruction de régions forestières. Il est possible de remonter jusqu'au XVe siècle, et, pour illustrer son affirmation, il montre une série de diapositives sur lesquelles figurent des arbres de la Nouvelle Angleterre emportés par le vent. Pour le *Dr Darling*, la thèse de M. Raup semble impliquer que la notion classique de succession écologique ne doive pas être prise trop littéralement, et que ces catastrophes naturelles peuvent considérablement influencer notre interprétation.

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