ed by M.H. Nitecki. Academic Press. 1981.

PHYSICAL DISTURBANCE IN THE LIFE OF PLANTS

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The conventional wisdom of our time tells us that the plant life of the world has been disastrously disturbed by the hand of man, and that before this happened it had reached a "steady state" in its relations with its total environment. This state of "balance" or "near-balance" is thought to have lasted for millenia before man's depredations began. This paper proposes that the vegetation had been conditioned to injurious or lethal disturbance by external physical forces long before man appeared, and that the conditioning has been accomplished in large part by the evolution of great diversity not only among its many thousands of species but also among the populations of individual species. The disturbances have been so frequent, varied, and widespread that the supposed "steady state" may never have existed. Diversity has afforded the vegetation a versatility in adjusting to its unstable habitats that may account for its survival -- and ours.

Vegetation forms a very thin rind on the surface of the earth. Parts of it, large and small, have been injured, disrupted, or destroyed by forces from outside itself. Seeing these disruptions in our foreshortened scales of space and time, we commonly think of vegetation as fragile, and the word "irreversible" has been applied to disruptions made in it.

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BIOTIC CRISES IN ECOLOGICAL
AND EVOLUTIONARY TIME

ISBN 0-12-519640-7

But the vegetation has lived its entire life, from its remotest ancestors, at the mercy of the forces exerted upon it by the earth below, the climate above, and by the voracious creatures it lives with. It makes us wonder how it has managed to survive.

The vegetation is made up of myriads of units we call species, each of which has its own line of descent. This in itself gives the vegetation an immense diversity in form and inheritance. Each species is made up of populations of individuals among which there is further diversification. The plants in these populations are so alike in form that we have to group them into single species. They may be genetically uniform, but most are not. They are believed to contain from one to many heritable characters called "biotypes" which have arisen through gene mutations, chromosome doubling, or by processes not yet understood. These characters are thought to be the "raw material" from which environmental relationships are made. In a freely interbreeding population they can be passed around. Groups of them called "ecotypes" are believed to be formed by genotypic responses to particular habitats within the total geographic ranges of the populations (Anderson, 1936; Bradshaw, 1972; Clausen *et al*, 1940; Hultén, 1937; Mayr, 1964; Turesson, 1922 a and b, 1925). Evidence that these ecotypes exist has been found in every species population that has been studied intensively. For example, the Douglas fir of our western forests ranges from northwestern Mexico to northern British Columbia, and in altitude from sea level to 10,000 feet. It is estimated that its ecotypes are so many and so segregated that seed for plantations, if the latter are to be successful, cannot be moved more than one degree of latitude from its point of origin, or to a climatically equivalent altitude (Camp, 1956).

I have lived for many years in a small Massachusetts town called Petersham. It was settled in 1733 by farmers who lived by a subsistence agriculture for about two generations (Raup & Carlson, 1941). The land in the township was completely forested when they came except for a few ponds and wet meadows. By 1790 only about 12-15% of the forest had been cleared, but by 1850 fully 75% of it had been entirely eradicated. Both the population and its prosperity declined rapidly after 1850, and there was widespread abandonment of farms. Only about 15% of the land is now clear.

The presettlement forest was mainly of hardwoods such as oak, ash, maple, chestnut, birch, etc., with a small admixture of conifers such as white pine and hemlock. When the farm fields were abandoned they were naturally seeded to dense, nearly pure stands of white pine which grew to merchantable size in about 50 years. Most of it was logged off between 1900 and 1920. The pine did not reseed itself after logging, but was followed by the same species of hardwoods that the farmers had dug out by the roots a century earlier. This case can be duplicated, using different time periods and species, in most of southern and central New England and in many parts of the middle Atlantic States.

Nobody did anything to help the forest accomplish its rehabilitation after this catastrophic sequence of events. It did so by using only its own capacities. Were the events unique in the lives of the trees, merely aberrant disturbances caused by the advent of European man, or had there been analogous events in the forest's past that had preconditioned it?

The New England hurricane of 1938 was disastrous to the forest economy of the region. Whole stands of mature trees, in all mixtures of species, were destroyed at the same time.

Some trees were broken midway of their trunks, but most were uprooted. The uprooting of a large tree produces a distinctive microrelief feature on the forest floor consisting of an oval mound of loose soil with a pit-like depression beside it (Stephens, 1955, 1956). The pit collects water and dead leaves to form a mass of black semidecayed humus. In succeeding years the relief gradually flattens out. It is easily erased by cultivation, but pasturage does not remove it.

Some 62 of these mound-and-pit pairs were found in a little less than an acre on a wooded slope in the Harvard Forest in Petersham. When dissected and compared they fell into four readily perceived age classes. The youngest were, of course, those of 1938. The next oldest were accurately dated to a hurricane on September 20, 1815, for which historical records were found. The third resulted from a major storm that occurred sometime in the first half of the 17th Century, possibly in 1635 when one was described in the Plymouth Colony. A still earlier series has been dated at sometime in the latter half of the 15th Century. In areas that show no microrelief at all, soil profiles almost invariably show traces of overturned horizons, evidence of much older wind-throws that are no longer visible on the surface.

Having learned to see and interpret the mounds and pits we have found them nearly everywhere we have looked in the forested regions of the Eastern States, southeastern Canada, westward to the western lake states and to the Ozark Plateau (Stearns, 1949; Denney & Goodlett, 1956; Goodlett, 1954; Henry & Swan, 1974). No one has yet worked out historical sequences such as we have in New England, but I have no doubt it can be done.

Some observations resulting from these studies are worthy

of note in the present context. Massive disturbance has been caused by wind in the forests of eastern North America, reaching far back in time. The disturbances have caused the prevalent even-aging found in remnants of the presettlement forests, which had long been an enigma, and they have produced a patchwise distribution of age classes due to the varying paths of storms and to the fickle behavior of the winds in local areas. At least in our part of New England it is probable that no major forest tree has ever lived out its possible life-span. The hurricane history in Petersham has told us that most of the trees seen by the early settlers had to be between 80 and 130 years old, and must have looked much like our older stands do now. Our forests were, indeed, conditioned to violent disturbance long before the coming of Europeans.

The most devastating disturbances the vegetation has had in Quaternary time were the advances and retreats of the continental glaciers. The major effect on plant life in the path of the glaciers was complete destruction. Where whole species populations were in this path the species became extinct. Many boreal and temperate zone species were left with greatly reduced and disrupted populations south of the ice border (Halliday & Brown, 1943). Periglacial climates led to species combinations south of the ice that were unique and no longer exist (Davis, 1969). The same can be said of soils and hydrologies. It is probable that all of the vegetation of the continent was altered to some extent during the Pleistocene. The advancing glaciers destroyed not just a few whole populations, but also large portions of the ecotypic content of a great many more, leaving the latter with limited genetic wherewithal to maintain their habitat versatility. There is a great deal of evidence that the present geographic distribution of the floras of our continent, and their behavior with respect to local habitats, are governed in large measure by what happened to their species populations during the Pleistocene.

Wherever the forests are of resinous needle-leaved trees the principal disturbing agent is fire, started by lightning or by people. The Indians used fire to drive game, or to improve the forage for game, or to produce dry wood for their camp fires. Fire seems to have been universally prevalent throughout the coniferous forest from Newfoundland to western Alaska, south in the western mountains into Mexico, and in the pine forests of our southeastern states from Texas to New Jersey. I doubt that a hole can be dug in the soil under these forests without finding charcoal. The frequency of the fires in any one locality, of course, varies widely. A jack pine forest that I studied in northwestern Saskatchewan in 1935 had been burned three times in the preceding 139 years. We do not know what the boreal forest would be like if it did not burn occasionally. A Swedish forester (Sirén, 1955) studying an analogous forest in northern Finland found that where it had escaped fire for a very long time - some hundreds of years - it had deteriorated as forest and had to be burned in order to restore its productivity.

I have had limited experience in tropical forests such as grow in Central and South America, west-central Africa, and the Indo-Malayan region. For a long time they were assumed to be relatively immune to physical disturbance, but studies in the last 30 years or so have shown them to contain seemingly haphazard patterns of tree forms, age classes and species. A recent student has attempted to explain the distribution of species and tree forms in a tropical jungle by analyses of community and population dynamics (Hubbell, 1979). He found that in order to rationalize the facts as he found them he had to insert a factor of periodic disturbance.

T.C. Whitmore (1975) from studies in the rain forests of the far east has analyzed the growth of these forests in terms of "gap phases". The gaps are openings in the forest made by disturbances of various kinds. The phases refer to stages of tree growth in the gaps, from seedling to maturity and death.

Small gaps may be caused by the death and fall of a single large tree, with a crown 50-60 feet in diameter. The crown might produce a gap of about 1/10 of an acre. Lightning strikes make openings as large as 1½ acres. Some gaps are made by fungal or insect infestations that may kill one or a group of several trees. Mound-and-pit microrelief from the wind-throw of trees is reported as common. Large gaps of up to about 200 acres are known to have been formed by single local storms. Typhoons and tornadoes have destroyed large areas of forest as they have in our country.

Land slips occur frequently on steep slopes during periods of heavy rain. Many can be seen in the landscapes as small areas of bare ground. Soil profiles exposed in road cuts show organic horizons buried by these slips.

In tropical America clearing for agriculture has been going on for at least 7-8000 years, and in Malaya for a much longer time. It has been characterized by a system of shifting agriculture brought about by the low productive capacity of most tropical soils. When a clearing is abandoned after a few years of cultivation it immediately goes back to forest. The result is a random patchwork of little farms in all stages of use and abandonment, and an equally random patchwork of even-aged forests ranging from seedling stages to maturity. Here is a source of tropical forest "gaps" that may go back to the time when man first planted crops.

When I first became aware of the meaning of disturbance to vegetation I thought that if any long-term stability were to be found it probably would be in the grasslands. Then I found the work of the Kansas historian, James C. Malin (1956), who marshalled a formidable array of disturbing influences that had made a vast mosaic of species combinations in the grasslands. The most prevalent disturbances were by fire and wind. Recurring periods of drought so reduced the plant life that the soils, particularly on the high plains, could be blown out by the winds. Much of the soil on these plains is loess, originally deposited by wind. Prevalent fires, started by lightning or by Indians, burned the vegetation and facilitated the movement of the soil. The vast herds of buffalo that roamed the plains continually over-grazed them, trampling the vegetation, breaking the fine-textured soils, and making them even more susceptible to blowing. The vegetation was also destroyed in buffalo wallows and by burrowing rodents such as prairie dogs which formed large communities that often occupied several acres.

Travelers on the plains in the early 19th Century, long before the advent of white settlement, left eloquent descriptions of great dust storms that probably were larger and more frequent than after settlement. Archaeological sites show horizons of occupation separated by thick deposits of loess.

My observations on the physical disturbance of vegetation in the arctic and alpine tundras have been made in several parts of the American Arctic, but I shall confine myself to those made in the Mesters Vig district, in King Oscar's Fjord, Northeast Greenland (Raup, 1965-1971c).

A major limiting factor in the life of the northeast Greenland plants is simple desiccation. There is very little precipitation during the short growing season, and the prevailing winds off the inland ice are dry. Spots that remain wet during the summer are chiefly those immediately below thawing ground or below snowdrifts which linger all summer. Most of the other physical factors deterring tundra plant life are related to the presence of permanently frozen subsoil and to frost heaving. Frost heaving and lateral thrusting are present in all of the soils, varying from almost none in dry gravels and sands to an intensity in some moist finer textured soils that precludes the growth of any plants. Heaving sets up sheering stresses in the soil that are injurious or lethal to roots or rhizomes.

If water is available during the summer to bring the medium- to fine-textured soils to their liquid limit they begin to flow, even on very gentle slopes. They gradually get far enough away from their upslope sources of water to lose their fluidity and begin to pile up. Lobate structures are formed in this way. The vegetation is torn apart and built up as part of the barrier at the front of a lobe which may be only a few inches or as much as 8-9 feet high.

Frost heaving and thrusting have given rise to various forms of patterned ground. Sorted nets and stripes are common in the landscapes. Here the soils get sorted in the process, with coarse fragments in the borders and fines in centers. In active nets the fines usually are so violently heaved that no plants can live in them. Close to the stone borders they are more stable and a few species can survive, but if their roots get into the centers they are heaved out of the ground.

There are many other geomorphic processes in the Greenland tundra that restrict the growth of plants, but most of them are more localized in the landscape than frost heaving and mass wasting. Some of them, though they are of small areal extent, cause total destruction of the vegetation. All that I have mentioned are currently effective, but they must all be seen in another time scale. There is a great deal of rather clear evidence in northeast Greenland that the climate began to be warmer and dryer in the late 1800's or early 1900's. Clayey silt soils near the shores of the Fjord that we know to have supported broad, wet, moss-sedge meadows at that time are now nearly barren, with their soils dried to brittle hardness in summer. Large active mass-wasting structures such as I have described are now found only on the higher slopes of the mountains where they still have abundant water from melting snow and thawing ground. Equally as large or larger ones are found on the lower slopes, but they are completely stabilized by desiccation. Large sorted nets at these lower levels are also stabilized, with centers covered by vegetation. Turf hummock systems, developed on long slopes constantly irrigated by perennial snowdrifts, show progressive desiccation and deterioration in their lower portions, suggesting a general retreat of the snowdrifts. Windblown sand from broad beaches on the seashore has polished adjacent rock faces, leaving only remnants or outlines of lichens that formerly grew on them. Heavy sea ice from the polar basin that comes down the coast in the East Greenland Current began to recede northward in the late 19th Century, opening the northeastern fjord region to shipping (Koch, 1945).

I have mentioned only a few of the physical disturbances that affect the vegetation but they are legion (White, 1979). We have reason to think that the disturbances are not mere aberrations from some relatively stable "steady state". Rather, they are a continuing threat to the survival of the living rind that mantles the earth. They must have presented the same or analogous hazards to the remote ancestors of the present species, and our floras have been at the business of adjusting to them ever since their species first appeared.

We know all too little about how the plants have gone about this. Examples of *what* they have done are abundant, and I shall cite a few, but *how* they have accomplished them is obscure. I suspect that a large part of the answer may be in their evolution of a vast diversity among species, and a kind of "fluid" ecotypic diversity within species.

The jack and lodgepole pines, widespread in the boreal forest, do not open their cones and scatter their seed unless the cones are scorched by fire. Many of our southern pines produce thick, fire-resistant bark on their trunks. In longleaf pine there is a stage in the early growth of its seedlings when they are resistant to fire. The pitch pine, unlike most others in the genus, produces stump sprouts when a tree is killed by fire. A western variety of the white spruce, which seems to have kept its subarctic ecotypes on the foothills of the northern Rocky and Mackenzie Mountains throughout the last glaciation, appears to have spread eastward to the present timberline 2-3000 years before its eastern counterpart, with its depleted ecotypes, could reach the timberline farther east. Nearly all of our many hardwood species sprout prolifically from the bases of their stumps after the trees are cut or burned. Desert species have evolved rather obvious means of living with extreme desiccation, and with wind-blown sand. Arctic and alpine species are geared to extremes of cold, very short growing seasons, long days, and a galaxy of lethal geomorphic processes. Every gardener knows that there is a flora of weeds, many of them with world-wide ranges (Anderson, 1967). They seem to thrive on disaster, administered by sharpened sticks, or hoes, or plows, or bulldozers. They are scarcely known outside the areas disturbed by man.

In the small area of tundra that I studied in Greenland, there was an airstrip, a radio station, a mine, some housing for personnel and about 10 miles of road. All this had been placed there, on an otherwise uninhabited coast, within the preceding decade. Along roadsides, at the borders of the airstrip, and around the buildings there were plants that looked and acted like weeds, but the place was so new that there were no introduced weeds of the kind I just mentioned. What we called weeds had simply moved in from the immediately adjacent tundra or had survived the disturbance in place. In my studies of the tundra plant-habitat relations I had sorted out a group of species that could survive very little frost heaving but were able to tolerate or even thrive in the dry creep of soil on steep slopes, or burial by wind-blown sand, or in the erosion on the banks of small mountain streams, or in occasionally flooded sands and gravels along rivers, or in ground trampled by animals. Most of the species that were acting like weeds came from this group. I sometimes wonder whether our garden weeds were able to come out of ancient floras and take up their abode in ground stirred and trampled by man because they had been conditioned to disturbances of analogous kinds. One might suggest further, that our crop plants may have been chosen from native floras in part because they were already amenable to the kind of treatment the primitive farmers would give to them and their habitats.

It may be that we should build a new frame of reference for the study of vegetation. It should not be based entirely on its present internal structures, physiological processes and supposed communal organizations. Perhaps we should start with the inherited capacities of its species for adjustment to the lethal disturbances that come from outside agents. The frame would have a large element of randomness, but there would be no more randomness than the species have been coping with for a long time.

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COMMUNITY EFFECTS OF INTRODUCED SPECIES

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Though reported species introductions are a biased sample of all introductions, one may nevertheless fruitfully examine their consequences to cast light on community ecology theory. In particular, they would appear to be ideal tests for two broad classes of community models: (1) equilibrium island biogeography, and (2) limiting similarity. Examination of substantial lists of introductions shows little support for either the naive form of equilibrium island biogeography theory or its sophisticated variant, in which species replacement is predominantly within groups of ecologically similar species. Nor is there much evidence for limiting similarity. Both these observations march with similar results drawn from statistical examination of non-experimental systems, and point to the conclusion that interspecific competition, though viewed over at least two decades as the main force structuring communities in ecological time, is very difficult to demonstrate with data at hand.

Individual introductions certainly indicate competition, either between an invader and a resident or between two invaders. But even most of these studies are ambiguous, and for lists as a whole, the main observed effects of introduced species on communities appear to be generated by predation or habitat modification.

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ISBN 0-12-519640-7