Plant Warfare---A Science Classic

Botany—Ecology

Struggle for Domination in the Vegetable Kingdom

OECOLOGY OF PLANTS, An Introduction to the Study of Plant-Communities, By Eug. Warming, assisted by Martin Vahl, prepared for publication in English by Percy Groom and Isaac Bayley Balfour. Oxford, 1909.

The author thus describes his book, which established a new science: "In 1895 I published a Danish work entitled Plantesamfund, which was based upon lectures that I had delivered in the University of Copenhagen. I never imagined that the book would appeal to more than a few readers outside my audience . . . When I wrote it I had no models to study; mine was the first attempt to write a work on Oecological Plant-geography, of which the very name was then all but new. The present book is practically a new one . . . In many places I have felt the lack of definite, detailed, and truly oecological information concerning various questions, and, as in 1895, I must confess that my ideal is far from being realized. The oecology of plants is a subject still in its infancy; numerous investigations must be made before the foundations can be truly and rightly laid, and before a consistent clear, and natural classification of plant-communities is achieved."

HITHERTO we have treated plant-communities as if they were static entities, in a condition of equilibrium and with their evolution concluded, and were living side by side at peace with one another. Yet such is by no means the condition of affairs. *Everywhere and unceasingly* a struggle is taking place not only within the several plant-communities but also between them, so that each of these is continually striving to invade the territory of the others. Moreover, *each slight change in the environment* upsets the condition of equilibrium hitherto existing, and at once occasions *a disturbance and change in the reciprocal relations subsisting. Extremely slight* changes in the environment often evoke remarkably great changes in the vegetation, by favouring certain species and suppressing others. "Rise and fall of the *water-table* should be considered in inches, not in feet," writes the experienced practical man Feilberg. The zonal distribution of vegetation round small lakes and pools that one observes in West Jutland, the distribution of Weber's "sub-formations" of meadow, and that of the several "types and sub-types" of heath, all tell the same tale. Moreover, P. E. Müller shows that minute *climatic* changes suffice to cause forest to give way to another kind of vegetation. From Gräbner we learn that relatively small distinctions in the climate of different parts of the North German plain cause the local floras to be sharply delimited. Attacks by insects or fungi, dry or rainy years, and so forth, may bring about changes. The struggles in question have been the subject of extremely little investigation, so that a wide and attractive field of research lies open.

The struggle between communities is of course dependent upon that between species, to which allusion has already been made. This struggle is caused by endeavour on the part of species to extend their area of distribution by the aid of such means of migration as they possess. "Situation wanted" is the cry in all communities, whether these be human or vegetable. Millions upon millions of seeds, spores, and similar reproductive bodies are annually scattered abroad in order that species may settle in new stations; yet millions upon millions perish because they are sown in places where physical conditions or nature of the soil check their development or where other species are stronger.

Not until recent times was attention drawn to the ceaseless struggle among species. Darwin it was who directed our notice to this struggle, which forms the basis of one part of his hypothesis concerning the origin of the species. Yet other writers had previously noted this struggle in nature; for instance, A. P. de Candolle wrote: "Toutes les plantes d'un pays, toutes celles d'un lieu donné, sont dans un état de guerre les unes relativement aux autres."

The struggle and competition among plants are brought into greater prominence by *changes* that continue without interruption in soil, climate, or other conditions affecting plant-life, including changes in the animal world.

Without such changes the results of the struggle would be neither so distinct nor so rapid. The changes in questions are:

I. Production of new soil.

II. Changes in old soil, or in the vegetation covering it, and in the factors discussed in the first Section of this work, but particularly those caused by man, who is thus responsible for "semi-cultivated" formations. Man intervenes directly when he utilizes the soil for his own purposes, by converting forests into arable ground, or by draining moors, but he also intervenes indirectly when permitting cattle to graze, or when he mows, manures the soil, and so forth.

In regard to the question now under discussion reference should be made to Clement's interesting work, "The Development and Structure of Vegetation" (1904). In discussing the migrations and invasions of plants Clements distinguishes between migration and "ecesis". "Migration merely carries the spore, seed, or propagule into the area to be invaded; ecesis is the adjustment of a plant to a new habitat, it is the decisive factor in invasion, inasmuch as migration is entirely ineffective without it." In discussing invasion he treats of barriers, endemism, polygenesis, also manner and kinds of invasion.

The struggles between communities and the development of these are elucidated in the succeeding chapter.

WHEN new soil arises anywhere it is soon invaded by plants. And it is of deep interest to follow the successive phases in the development of the vegetation. In this way one will acquire evidence of a long series of struggles among the successive immigrants; these struggles sometimes do not end in any decisive result before the lapse of many decades.

New soil arises in the following places: on coasts, where the sea deposits fresh material; at the mouths of rivers; even in river-beds, where masses that have been washed down

are deposited. New soil also arises by the following agencies: action of glaciers, talus, volcanic eruptions, fire that devastates the original vegetation, and human action, but particularly where cultivated land is left to itself. In the last cases the soil is not new to the same extent as in the first cases; it is not barren, but includes a greater or smaller number of seeds and the like. . .

It is difficult to make general statements in regard to vegetation appearing on new soil, because very few detailed investigations bearing on the subject have been conducted. Published work seems to justify the following conclusions:

I. In many cases, possibly always, the first colonists are algae and lichens, as well as mosses (for example, arenicolous algae on the shore, algae and lichens on lava-fields, rocks, and so forth); these prepare the way for Vascular plants. The early vegetation is open. Some time elapses before a coherent covering of vegetation is produced. So far as Vascular plants are concerned, the individuals are at first very scattered, but gradually increase in numbers.

II. The number of species present is small at first; it increases, until after the lapse of a certain length of time it is greater than ultimately. For, at first, many species find suitable spots, but are subsequently suppressed when the vegetation forms a continuous covering and more tyrannous species have entered. Various parts of the recently colonized ground are often clothed with plants in a very dissimilar manner. Gradually the vegetation becomes more uniform and poorer in species.

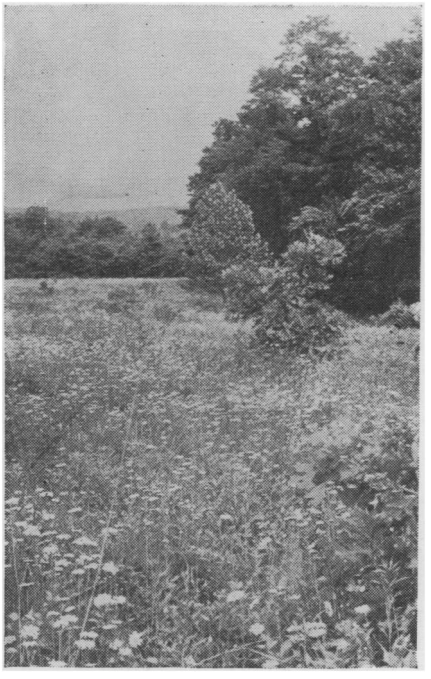
III. Very frequently annual and biennial species are more numerous at first than later on, because on open ground they find the conditions more favourable to them than on over grown ground; many of them belong to the local weed-flora. Afterwards perennial herbs or woody plants preponderate.

IV. The first species to enter are those which occur in the vicinity and possess the best means of dispersal by wind or by birds. Rubble-heaps in the Alps are first colonized by species with wind-dispersed seeds. In Norway, when a coniferous forest is destroyed, the first immigrants are the birch and poplar (with fruits and seeds respectively that are easily conveyed by wind) and Sorbus (which has berry-like fruits).

V. So far as the immigration of trees is concerned, light-demanding trees precede shade-enduring ones; the reverse is impossible. Shrubs are suppressed by trees that enter subsequently.

VI. The differentiation of sharply defined communities proceeds gradually. The earliest commingled individuals in reality belong to different natural communities, which only little by little distribute themselves in the most suitable stations. One can therefore speak of *initial, transitional,* and *final communities.* . . .

THERE is scarcely any biological task more attractive than that of determining the nature of the weapons by which plants oust each other from



Forest invading daisy-field

habitats. Yet we are far from having exhaustively solved the problem even with regard to a single species; for instance, we do not completely comprehend the struggles between the beech and oak, or between other economically important forest-trees. Obviously the matter is not settled by asserting that lack of available space is decisive, or that in the plant world, as in all other communities (including the human race), everything turns on the question of nutrition. Such statements scientifically analysed resolve themselves into a series of the most difficult questions which science could propound, and which could be answered only after many-sided investigations. For instance, there arise such questions as: "Is it lack of one or another nutritive body or water in the soil? Or the excess of another substance? Is it want of heat or of light or of an appropriate combination of these? Or can roots and rhizomes grow so close together as to bar the way to other plants in a purely mechanical manner, or so as to rob them of water and nutriment? And so forth.

We see perennial herbs extinguishing annuals that have settled on ground which was bare but a short time before; but with what weapons the former conquer we cannot say with any certainty. We see silicicolous vegetation of sand (Ornithopus perpusillus, Teesdalia, Spergula, Rumex Acetosella, Pteris aquilina, and others) disappear when the sterile field is supplied with lime (either by special addition of lime as a food-material, or by a change in the lime already present so that this becomes more easily available to plants); and we see this vegetation gradually return as the carbonic acid in the water dissolves and carries away the lime; but we can give no deeper explanation of these phenomena.

Living beings forming a community have their lives linked and interwoven into one common existence in so manifold, intricate, and complex a manner that change at one point may bring in its wake far-reaching changes at other points. In this direction a wide field lies open for investigators. . . .

The general statement can be made that a species has the greater probability of emerging victorious from its struggle the greater the extent to which it finds itself in its *optimal area,* or in other words, the more numerous are the oecological conditions best suited to it. Consequently a species has always to engage in its hardest and most exhausting struggles at the boundaries of its distributional area, if it has here reached the utmost limit of its wanderings as determined by climate. The more suited is the climate to a species, the less exacting is this as regards soil and other conditions, and the more capable it is of competing with rivals. If a species of tree be burned down or felled on a station lying within its optimal area, it will as a rule reoccupy the denuded spot if this be not artificially interfered with; but if it meets with this fate outside the area of its best growth, then it will not reappear, but its place will be taken by a species of tree in whose optimal area the station is situate.