Grassland Climax, Fire, and Man

CARL O. SAUER

Professor of Geography, University of California, Berkeley, California

ECOLOGY has instructed us that plant societies may strike such happy balance with their environment and between their members as to form a stable, indefinitely reproducing order, called a climax vegetation. The concept may have merit at an introductory level of study, when it is good to make the simplest designs of species association. Such simplification of vegetation type and geographic area may be misleading, however, like other regional classifications in which habitat and habit are unified. It becomes seriously misleading if a static view of relation of organisms to environment is substituted for attention to continuing, developing changes in environment, in competition and accommodation between organisms, and in continuity and pace of organic evolution. Both in organic evolution and earth history change is pretty much continuous, and its tempo, direction and divergences are the real object of inquiry.

As a part-time student of climate I have long been interested in climatic limits of vegetation and have become increasingly doubtful of broad climatic-ecologic generalization. In particular, I have misgivings about equating climate and climax vegetation, leaving aside for the moment the question of the reality of the climax. In the first place, so-called climatic regions admittedly are only an introductory device for inspection of moisture and temperature distributions. We make maps on which graduations and irregularities in the weather across the Earth are greatly conventionalized by showing them as a series of areas, delimited by convenient numerical values secured by instrument recordings. Little has been done with an areal climatology that is based on the dynamics of air masses.

The usual classifications of climates derive largely from the old premise that climate and vegetation are pretty much coincident. Actually, therefore, there has been a lot of fitting of isotherms and isohyets to generalized maps of dominant vegetation. The fit is empirical and may be coincidental. Where meteorologic data is wanting, vegetation lines often have been used to delimit climates. Little progress is made in this circular operation of identifying climate by vegetation, and vegetation by the most closely agreeing set of lines that may be drawn for temperature or precipitation. For the most part, critical climatic limits remain unknown as to physiologically limiting weather values for individual plant species. Nor have we much knowledge of the significance of frequency of extreme weather conditions in plant reproduction or survival. It need hardly surprise, therefore, that the cruder the climatic and plant data the more satisfactory the coincidence of the two. One begins, for instance, with the premise that grasslands have a climatic origin, sorts them into tropical and extratropical, semi-arid and humid, and high altitude grasslands, and selects the most closely agreeing climatologic values as their limits.

Also, this sort of manipulation disregards whatever lies behind the contemporary scene of weather or plants. A present plant complex is very much more than a mere reflection of short-term weather, or of plant physiology related to weather alone. Any assertion that under a given climate there will form a stable self-perpetuating plant complex is likely to perpetuate an assumption that arose before there was modern biology and earth science. Plant associations are contemporary expressions of historical events and processes, involving changes in environment and biota over a large span of geologic time. A real science of plant ecology must rest not only on physiology and genetics, but on historical plant and physical geography.

I should like, therefore, to dwell briefly on the last million years, one of the biologically most critical periods of Earth history. We should also regard the possibility that present time still falls within the overall term "Ice Age". It is by now fairly sure that there were within Pleistocene four successive great glaciations, separated by intervals of deglaciation, perhaps longer than the times of glacial extension. Roughly twenty million square miles of land surface were buried beneath ice masses during each glacial stage, and mostly were uncovered during interglacial times. Sea levels fell as ice sheets grew, and rose as they were melted away; continental connections between Siberia and Alaska were made and broken repeatedly.

Far reaching, major climatic changes initiated each glaciation and deglaciation and involved middle and, to some extent, low altitudes, far removed from any ice mass. The Pleistocene was a succession of wide and deep withdrawals and readvances of plants and animals, involving tens of millions of square miles of land, areas far greater than those covered by ice. During ice advances pluvial climates spread across large parts of the deserts and semi-arid lands of the world; during ice retreat, we think that arid and semi-arid conditions resembled the present.

Mountain making, especially about the rim of the Pacific Ocean, was in major swing in early Pleistocene, diminishing toward the present.

The over-all picture is one of maximal environmental disturbance, with a succession of climatic swings in opposite directions by which perhaps only the central tropics remained unaffected. This rarely equalled time of great and rapidly changing tensions for the major part of the organic world, inevitably brought unusual opportunities for natural selection of variant organisms.

An important faunal change needs to be noted. Whenever there were land connections with Asia, dispersals of land animals took place between the Old World and New. Apparently mainly during the second (Kansan) glaciation the New World was colonized by major groups of mammals. At such times there trooped into the New World our great herbivores, the bison, elk, deer, sheep, and elephants, trailed by bears and wolves. The great herd animals became very numerous during the later Ice Age and can be credited with important ecologic shifts in vegetation, as by disseminating seeds along trails and about their bedding grounds, and by exerting selective pressure favoring plants tolerant of browsing, grazing, and tramping. Our later continental history witnessed a stocking of the land with herd animals, perhaps equivalent to present livestock populations.

The latest glaciation (Wisconsin) is thought to have ended about twenty-five thousand years ago, having lasted perhaps three times that span. During this time there were mountain glaciers as far south as the San Francisco Mountains of Arizona and pluvial conditions blanketed the now arid and semi-arid parts of the West and Southwest, with an extension into Central Mexico. The dry lakes of our West and their conspicuous marginal terraces were then freshwater bodies, about which lived herbivorous animals requiring better than desert browse. These lakes in the main were not caused by glacial meltwaters from high mountains, but represent the result of local precipitation. At this glacial time it would appear that aridity had been reduced to minor, detached, low-lying rain shadow basins. The modern general pattern of atmospheric circulation, and hence of modern climates, probably was established with the beginning of the last, great ice retreat. The change from pluvial to arid conditions may have well been rapid, and also the territorial expansion of the organisms capable of living in lands of drought. Shifts in comparative advantage for different species affected most of the United States, least of all the Southeast. Mesophytic types took over most of the deglaciated area, drought tolerant forms much of the West. In each case the race has been to the swift; plants having rapid means of dispersal and pioneering vigor took advantage of the frontier rush.

We are not sure that we are at present in a period of full climatic equilibrium. The general ice recession appears to have stopped about seven thousand years ago. From the states bordering on Canada we are getting, mainly from pollen studies, indication of a sort of climatic "optimum" shortly thereafter. At present, there appears to be in progress a further recession of glacial ice, recorded not only from northern and mountain glaciers, but by a slow, general rise of sea level taking place along the entire Atlantic Coast. At least we have some reason for being cautious about assuming static contemporary climates.

Great changes in climate have dominated the physical world for at least the last million years. It has been a long time for succeeding crises and opportunities for that part of the organic world situated outside of the central tropical areas. It has been, and probably continues to be, a time of marked advantage for mobile and labile forms, for those that are tolerant of environmental change, and those that can change. Evolutionary plasticity pays off at such times. Certainly it has been a time of opportunity for many grasses and herbs as against many trees and shrubs. Fast and heavy seeders, vigorous vegetative reproducers have been favored and thus annuals and plurannuals have had added colonizing advantage. Changing environments have favored survival of mutants. Enforced and invited migrations have brought together previously disjunct forms and multiplied opportunities for successful hybridization. In most respects the balance has been tipped in favor of the lowly and short-lived. The climatic history of the late geologic past supports strongly the view that Pleistocene has been a major time in evolution and dispersal of many grassy and herbaceous forms.

The second great agent of disturbance has been man, an aggressive animal of perilous social habits, insufficiently appreciated as an ecologic force and as modifier of the course of evolution. Man has been in existence throughout the Pleistocene, ranged very widely very early, and during it became the dominant animal over many climates and, it seems, all continents. The earliest human records we have show the familiar use of fire, and they range from England to South Africa. In fact, the most ancient human sites have usually been discovered by finding hearths, broken or crazed stones, baked earth, or accumulation of charcoal. Possessing fire, man was free to move into cold climates, to keep the other predators at a distance from his camp, and to experiment with foods unpalatable in the raw. Fire and smoke became labor saving devices for overpowering, trapping, and driving game, from small rodents to great cattle and elephants. Fire aided the collecting of fallen fruits, as nuts and acorns, and much later was the principal way of preparing land for planting. The earlier human economies collectively may be called fire economies. Often, of course, fire escaped from control and roamed unrestrained until stopped by barrier or rain. The fire-setting activities of man perforce brought about deep and lasting modifications in what we call "natural vegetation", a term that may conceal long and steady pressure by human action on plant assemblages.

In the New World human agency has been discounted because of dogmatic views that man entered America very late. A controversy has been going on for 50 years as to the age of man in the New World. Even the partisans of the late coming of man have been forced to admit an age of at least 15,000 years. It is my considered opinion, however, that the available evidence and the overall probability favor presence of man in the New World for the last third of glacial time. Work is proceeding in so many places and with new criteria so that it should not be long before we have unequivocal evidence instead of emotionally biased guesses. We may have had man in the New World for two or three hundred thousand years with plenty of time for increase in his numbers to the limits of the resources he was able to use. Whenever and wherever man came to live the prospects of a static ecology soon were reduced. With steadily continuing and increasing disturbances of plant associations by him, areas of plant tensions, already existing by reason of climatic shifts, were accentuated and enlarged.

Grasses have fared especially well in the late geologic past and have expanded as dominants in many parts of the world and in many climates. The explanation does not lie as a rule in the unsuitability of such tracts for woody growth. The normal history of vegetation is an accommodation into the plant society of increasing diversity, of forming and filling of ecologic niches by more and more diverse forms. In grasslands on the contrary we have a simplification of plant structure and scale toward minimizing differences in habit and size, simple and ephemeral stems, shallow and fibrous roots. This is a most curious plant sociology, from which the philogenetically most varied woody plants are mainly or even wholly excluded.

Where shallow and fibrous rooting is an advantage, floristic and morphologic impoverishment is understandable, as by adverse soil aeration and temperatures in marshes and moors (though even here woody perennials may be common though dwarfed). Another case is where a tight subsoil at inconsiderable depth stops root penetration. The clay pans of mature soils on flattish surfaces give numerous illustrations of edaphic grasslands. Long continued weathering on old terraces and other old surfaces that have developed senile soil profiles are notoriously disadvantageous for woody growth, especially in pedalfer soils which appear to have less penetrable basal pans than pedocals. These and other special cases of surface and soil formation do account for a number of edaphic types of grasslands, but are quite incompetent to explain the great savannas, steppes, and prairies of the world, commonly above the average in fertility and in invitation to plant diversity.

For these latter the explanation has commonly been sought in climate, especially in an ecology, which from its beginnings has sought climatic explanations for the presence of grasslands and thus arrived at the climatic climax principle. The more we learn of climatic data the less success is there in identifying climate with grassland. There are grasslands with as little as ten inches of rain a year, and with as much as a hundred, with long dry seasons, with short dry seasons, with high and low temperature ranges. In this country they occurred from the drier parts of the Great Plains to the markedly mesophytic Pennyroyal of Kentucky and Black Belt of Alabama. Every climate that has been recognized in which there are grasslands has elsewhere dominance of forests, woodlands or brush, under the same weather conditions.

Grasslands are found chiefly (a) where there are dry seasons or occasional short periods of dry weather during which the ground cover dries out, and (b) where the land surface is smooth to rolling. In other words, grasslands are found in plains, subject to periods of dry weather. They may also extend into broken terrain adjacent to such plains. Their occurrence all around the world points to the one known factor that operates effectively across such surfaces—fire. Recurrent fires, sweeping across surfaces of low relief, are competent to suppress woody vegetation. Suppression of fire results in gradual recolonization by woody species in every grassland known to me. I know of no basis for a climatic grassland climax, but only of a fire grass "climax" for soils permitting deep rooting. For millenia, and tens of them, fires, for the most part set by man, have deformed the vegetation over the large plains of the world and their hill margins. The time of human disturbance is probably long enough, even in the New World, to allow also for evolution of new grassland species and for the development of soils of characteristic profile and structure that are known as "prairie soils", a secondary product rather than cause of grassed surfaces.

A word of reserve may be introduced concerning the assumption that grassland soils are more fertile than forest soils. Grassland soils may be fertile because they lie on plains, are composed of favorable minerals, and are favored by surface as to organic accumulation. They do seem to develop physical-chemical qualities congenial to cultivated grasses, or cereals. By their history prior to cultivation, they may be a self-contained revolving fund of fertility if they are still sufficiently youthful. But, short and fibrous roots in the longer run are at a disadvantage with deeply penetrating roots in carrying up mineral salts from depth. We may over-rate the durability of grassland fertility in our short-term civilized view of time and neglect the importance of deeply feeding trees and shrubs in maintaining a productive Earth.

A drift of vegetation toward more grassland, including probably increased variation in grasses and herbs, has been going on for many thousands of years. This deformation has probably derived its driving force from fires, chiefly a cultural phenomenon. Ecologic assemblages, though not climax nor in equilibrium, have thus been established and maintained. The question now is whether civilized man can or should undertake to maintain grass cover and "forb-herb" ratios about as he found them; in other words, whether the desirable usufruct of such lands will justify or require his use of fire, as it did for his aboriginal predecessors.

In a world increasingly pressed by human needs the symbiosis of stock, grass, browse, and multistory plant cover is an increasingly important problem. Largely the world has lost the better plains for grazing and its shrunken range lands are in mountain, hill, and foothill areas, critical for storing and spreading water for lowland populations. These grazing lands were, I think, primevally strongly modified by fire. In that condition they served well to ease the runoff gently onto the valley lands. What place will be left in them for palatable grasses and herbs under full fire protection? What happens to runoff if grasses yield to shrubs? What is the change in fire hazard as full protection is attempted? What are the risks and returns under controlled burning? Fire, or its elimination, is still a main problem in the applied total ecology by which western foresters and graziers must attempt to work out a durable modus vivendi for man in a non-static environment. The layman can only hope for them that they may resolve this difficult and delicate situation by being permitted to take the longest possible view of beneficial activity by man.