LIFE ZONE ECOLOGY

by

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REVISED EDITION

TROPICAL SCIENCE CENTER

SAN JOSE, COSTA RICA

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CHAPTER I

INTRODUCTION

Like a bit of bright blue sky propelled erratically through the forest, a wide-winged *Morpho* butterfly rises and dips and moves rapidly across the varied shades of green and leaf-patterns. Also conspicuous, but on a smaller, slower scale, *Dendrobates*, a bright red frog with dark blue legs hops about on the fallen leaves and bare patches of moist soil. All about, mostly gray-and smooth-barked trees rise up through the heavy shade, some of majestic proportions with huge plank buttresses angling out from the trunks, others with terete or angled boles disappearing above in the general mass of foliage. Tall trees, short trees only a few meters high, long slender-holed palms, some perched low or high on a mass of arching stilts, dwarf palms, banana-leaved Heliconias, feather-leaved seedlings of a legume tree, shrubs, tall, thick- stemmed wild gingers and an occasional tree fern conspicuously marked with leaf scars stand out momentarily to the eye that follows *Morpho*.

But these represent only the framework. Lianas of various proportions rise up near the tree trunks or loop across to a neighboring tree. Trunks, buttresses, vines and fallen logs carry a varied and random assortment of epiphytes, ranging from delicate mosses or lichens, through ferns, orchids and aroids on to huge bromeliads or shrubby epiphytes. While the soil is lightly covered with leaves, a few scattered ferns and other herbaceous plants, far above, the higher branches are densely adorned with epiphytic vegetation.

Just as within a great city, there is so very much to see, yet only a portion of the life and activity is continuously obvious. A group of fast-flying, raucous-voiced parrots land in the top of a small tree and disappear as if by magic, blending immediately with the foliage. Musical or odd sounds reach the ear from unseen birds or insects out of the general weighty silence of the surroundings. Inch-long ants wend their way along the fallen trunks, while crickets and grass-hoppers stand out for a brief moment when they leap to a more distant spot. Most of the mammals, the snakes, tree-frogs and moths are quiescent and hidden now after their forays of the night. The quiet muddy-banked stream nearby teems with fish, shrimp and other life, whereas only a turtle out on a log to sun itself is visible.

Completely hidden from sight also, is a host of other varied forms of life, - in the rotten logs, beneath the leaves, within the soil or under the loose bark on some of the tree trunks. Through all the vegetation and animal life, course the sap and blood streams, translocating raw materials and transforming them into growth and energy.

Here,. in the untouched tropical wet forest, the pressure of life seems overwhelming in its abundance. Here when man wanders alone, he feels depressed, overawed by the multitude of alien organic life-forms. Like the rural man when first he walks the street of a great city, there is an absorbed feeling of a cohesiveness of force and complex organization which sets him apart as a stranger who does not belong.

There is, of course, a real basis for the impression of cohesive force and organization. Each species is settled in a definite niche within the community or association of organisms. Although some animals do no more than prey on other forms of life, and appear to contribute nothing to the community, still they are a part of the balancing forces which maintain an equilibrium within the association.

Such an equilibrium is not a static condition, but rather an averaging out about a status of balance. A few minutes later in a given spot, a different set of nature's actors or animal life may appear on the scene, or moving on a few meters a varied set of tree and plant species may change the makeup of the stage considerably. Over the months and years, the numbers of individuals of given species wax and wane, throwing a portion of the life forces temporarily out of balance until other factors of the life-zone counteract and move this misadjustment back towards equilibrium.

Thus, no given moment in time, nor any given point in space within such a life community may be taken as representing the association precisely. One must read out a picture of the community just as the grocer may read off the weight of an article from the still swinging arm of the scales.

In such a community of life within the tropical wet forest, with an abundance of moisture and heat all through the year, life has attained an exceedingly great diversity and a high complexity of interrelationships. As one moves about the face of the earth, new communities of life with diverse makeups are encountered. These become simpler in structure and number of species as one moves towards the deserts or towards the regions of perpetual low temperatures. What are the relationships between organisms within the community and between the communities around the globe? Are there laws and principles which control the makeup of the natural communities? Are there definite patterns or relationship between the diverse communities of the earth? How were they developed? These are all questions which confront the ecologist in his study of natural communities.

Studies of evolution indicate that the development of the complex communities of today took a long period of time. Like the huge complex cities that man has constructed without a master plan in advance, they could take shape only slowly in accordance with material at hand, with readjustment and reconstruction along the way and with time for occupancy of all the niches or vacant lots within the city limits. We can only sketch out the general process of such an association development.

Given the basic raw materials or chemical elements of the atmosphere and the mantle of soil derived from rock decomposition, with water as an agent for the solution and transport of these elements and with heat and light from the sun or mother star as a source of energy, vegetation has evolved from simple to ever more complex forms capable of transforming the raw elements and solar energy into growth and stored energy.

Parallel with the increased complexity and specialization of species of plants, there has developed also a correspondingly greater complexitv of the vegetation as a whole. Thus, when the plant kingdom in the distant past comprised only algae, bryophytes and lichens, the groupings of the various forms or the plant communities of that epoch were relatively simple. We may still see such simple communities persisting on open areas of glaciated rock or lasting for short periods on bare patches of soil such as road-cuts.

Before the Devonian period was over, various primitive trees of ferns, seed-ferns, scale-trees and the Cordaitales, the fore-runners of the conifers, had evolved and grew together in forest associations, but they were still much simpler in structure than the forests of the present. Subsequently, the cycads and conifers assumed dominance, until following the advent of the Angiosperms or present day flowering plants, the present day forests and other plant communities developed.

The evolution of plants and vegetation thus has given rise to ever more complex unions capable of more efficiently utilizing the raw materials available within the various combinations of heat, light, moisture and soil on the earth. After each successful major step in evolution, which gave rise to a new, more efficient type of plant such as the Angiosperms, there probably followed a period of relatively rapid evolution with the creation of new dominant species, the displacement of less effective previous forms and the occupancy of any newly created niches.

At the present time, the vegetation of the earth is apparently quite stable relative to evolutionary processes, having worked out long since the refinement of species of angiosperms into closed stable communities completely adjusted to or in equilibrium with each set of local environmental conditions. Elements of the various types of previously dominant vegetation either have been eliminated from the list of living plants, pushed back further and further from the more favorable environmental sites or, in some cases, left to occupy special niches for which they were more efficient occupants than any other type of plant evolved to date.

Hypothetically, a new more efficient type of plant than the angiosperm may be evolved in the future and man might study at first hand the evolution of a new set of vegetation and the replacement of a large part of the present flora by quite distinct forms of plant life.

Paralleling the development of plant life, there evolved also the diverse ramifications of animal life Beginning always with plant feeders, long complex chains of predators have developed to take advantage of the original food and energy fixed by plants from the raw elements. Such chains utilize the fixed energy as long and as completely as possible before the chemical elements utilized in life processes are returned once more to the soil and atmosphere through the processes of death and decay.

Although each living organism fits in somewhere within the complex pattern of vegetation or chains of dependent animal life, no area or community of life is static. Variations in the weather pattern which give rise to floods, droughts, hurricanes and like effects are always occurring. These bring about changes in the proportions of plant species and breaks or abnormal numbers in the animal life along a food-chain. The adjustments thereto of species may be numerous or far-reaching as the result of even small changes only, while greater alterations such as the elevation of a mountain range or volcanic peak may offer opportunities for evolution of new species. At any rate, within what is apparently a stable community of plant and animal life, there is an almost continuous change in the proportions and the effects of the component species. In essence, there is a continual fluctuation around a balance, so that from day to day or from year to year, we may never see exactly the same composite picture twice, but rather greater or lesser variations from a theoretical norm.

Such a norm with its average set of components of plant and animal life extends only as far as a uniformity of climatic, edaphic and atmospheric conditions prevail. Such communities or associations are units which may be mapped. Dependent as they are on the formative conditions of climate, soil and atmosphere, some are quite uniform throughout their extension while others may vary across their width with the gradual change of a certain factor or set of factors. As with taxonomic species, sometimes associations are sharply defined while at other times, it is difficult to separate them precisely from their neighbors.

Sets of these associations or communities may be grouped together into life zones or formations, each life zone comprising a definite range of climatic conditions. The same life zone and its associations may show up in widely separated regions, as in different continents. Within two widely separated communities having the same climatic, edaphic and atmospheric conditions, the species of plants and animals may be completely different, but still the general aspect and life-form of the plants and animals be the same.

This repetition of aspect in widely separated areas and with taxonomically distinct material suggests first, that the physiognomy of living organisms follows certain rules in the adjustment of such organisms to given environmental niches, and second, that the evolutionary process moulds whatever material is at hand into the correct form as dictated by the requirements for successful occupancy of an environmental niche.

Interestingly on our planet, Earth, evolution refined the mental capacity and thought processes of man, one of the mammals, to the point where he could understand the cause and effect processes of vegetation and the chains of animal life. With the ability to understand life-processes, coupled with the development of machines and power to supplement his own limited physical strength, man has reached a stage of being the major factor in the alteration of natural associations and the cycles or chains of animal life.

Man is now able to remove the natural vegetation from large areas and to grow or tend thereon specifically selected plants or animals to satisfy his requirements for nutrition or other needs. He is able to remove plants of no value to him, termed weeds, from his plantations of cultivated crops or to remove the animal predators from animal food-chains to produce high yields of food or other products for his own use. Through his ability to understand evolutionary processes, he has learned to alter existent life-forms and to raise their capacity to better satisfy his needs or desires. In sum total, man has been so successful in the manipulation of other organisms, in the altering of the micro-climates of his dwellings and body surroundings, in devising means of locomotion and in controlling his own predators that he has become the one dominant force over most of the face of the earth. As a logical result of all the above controls and his status of dominance, man has augmented his own numbers to thousands of millions of individuals and continues to increase at a fantastic rate.

In fact, man has been so successful to date in feeding and protecting himself, as well as in propagating his own kind that his success in the latter may soon become his main problem. In natural associations, a disturbance of the balance in numbers is followed always by counterbalancing forces which swing the status back towards an equilibrium. However, man through his dominance and control of other forms of life does not necessarily have to follow precisely the rules which are applicable to other life-forms incapable of rational thought. Still, the question remains of how far man may swing the balance in one direction and still be able to maintain an equilibrium with his environment.

At any rate, it is imperative that we understand first, very clearly, the make-up and the causes for differences between the structure and aspect of the natural associations of the earth. We must not only work fast to study the remaining untouched natural communities before they are altered by man, but secure the preservation of sufficient areas of these for future long term study and as banks of life plasm and life-forms for the future needs of man, some of which very likely cannot even be imagined today. At the same time, we must press for early protection also of representative areas of associations which have already been completely occupied by man, but where there is still hope of a gradual return to natural conditions if given sufficient protection and time. With an understanding of the theoretical makeup of such an association, man should be able to assemble the sometimes very scattered remnants within a given protected area and then permit natural forces to rearrange the living components into the original community structure that was developed over the ages.

Secondly, the ecologist must study the long term effects of Man’s dominance of the Earth. He must understand the results that come about from different types of land use and other activities. Only thus, may he arrive at the definitions of proper land use for Each site, know the carrying capacity of each region in terms of human numbers and be sure that he can live happily in harmony with his environment without the need for disasters such as wars, plagues or starvation to maintain a balance.

Thus, the ecologist should not be content with only the study of natural vegetation and wildlife, but must tie all the above knowledge together with information of the results of the activities f the dominant life form of Man. Dominance alone to fulfill the needs or selfish desires of one species at the expense of all other life forms has never been and probably never can be successful. If Man is not to join the ranks of the extinct dinosaurs, who were dominant for many millions of years, then he must learn how to attain and maintain an equilibrium with his environment. Although the task of bringing such an equilibrium falls on the shoulders of political, religious, educational, and other scientific leaders as well as the world’s peoples as a whole, it is still the task of the ecologist to clearly point out the meanings and make-up of such an equilibrium.

CHAPTER II

THE LIFE ZONE

Selection of a basic unit in ecology

One of the major problems in any science is that of determining the basic natural units with which one must work. The biological sciences could not develop far until the invention of the microscope, with which the cell was found to be the basic building block of animal and plant life. Chemistry made rapid advances as soon as a correct identification of the elements was initiated.

In certain fields of study, basic units as discrete as cells or chemical elements do not exist, so that a selection of divisions of equivalent value is more difficult. In those groups where evolutionary processes have been actively involved, there is bound to be some subjectivity, but usually, if the basic unit has been properly chosen, continued study brings about a general agreement as to the correct definition of each unit. An example is the biological species in the field of taxonomy, which may be interpreted differently by individual scientists. The problem of selecting satisfactory units of division in the field of ecology is of a similar nature.

Although some ecologists may still doubt the validity of natural units or groupings of vegetation, most appear to be in agreement that the association or community is the basic natural unit within vegetation masses. However, among plant ecologists, the usual definition of the association has restricted the unit to. a given set of plant species. Such a definition not only places complete emphasis on the vegetation alone but renders difficult the mapping of associations. It automatically implies that the same association cannot be present in different biogeographical regions which are inhabited by essentially distinct sets of species. It even runs into difficulty within one biogeographical region due to replacements of one or a few species along any gradient of simple, but not significant environmental change.

The viewpoint taken in this book is that the association must be thought of as a natural unit in which the vegetation, the animal activities, the climate) the land physiography, geological formation and the soil are all interrelated in a unique recognizable combination which has a distinct aspect or physiognomy. The vegetation comprises a number of life form units which are species, but these do not need to be the same set of species throughout the extent of the association. Similarly to biological species, the range of variation in certain associations will be greater than in others, which may be quite uniform through-out their extension.

Grouping of basic units

When there are relatively few basic units as the chemical elements, there is no special need for establishing larger groups or sets of units in a classification system. However, when the basic divisions are numerous, as in biological species, soils or associations, groupings are needed to facilitate the organization of data and for general comparative work. Ecology has been severely handicapped in the past due to the lack of higher categories of association groupings which would permit the coordination and correlation of studies by individual ecologists.

Differently from biological species, associations cannot be collected and studied in the museum or herbarium. Further, man has been so active in the alteration of natural associations that they are found in the field in a wide array of conditions ranging from the untouched state, when such still exists, to that of having been completely cleared. Due to the diversity of existing states of the associations, coupled with the large number of different associations, it appears extremely doubtful or impossible that larger category groupings could be constructed by working upwards from specific association descriptions.

Although the possibility of defining associations and groupings of these on the basis of taxonomic species is tempting to the local ecologist, such a base is not satisfactory for a global system. The great number of taxonomic species makes it impossible for one to know more than the species of a relatively small region. Names involving species unknown to the reader must necessarily have little significance. Most taxonomic species are units of variable extension, numbers and dominance in the associations. They do not offer precise parameters for comparison.

Furthermore, due to Man’s past wide-spread interference in vegetation, one cannot be sure in many cases whether a species has never been present or has been eliminated by man’s activities. The major handicap to a taxonomic base, however, is the existence of different biogeographical regions in the world. With their predominantly distinct sets of species, the presence of such regions precludes the effective use of species on a global basis.

There remains the possibility of utilizing various environmental factors in a system which can lend itself to category groupings of the natural units or associations. However, a great number of factors enter into a multitude of diverse combinations to produce the wide spectrum of associations. Obviously, to develop a first-order system suitable for world-wide application only those factors which are global in extent may be employed. Furthermore, they must be factors of a wide range in values which can be subdivided into categories.

The above considerations eliminate the edaphic, geological, topographical and many of the climatic factors. This does not imply that these factors are not significant in defining associations, but simply that they do not lend themselves to the establishment of *categories* on a world wide basis. of the remaining climatic factors, only heat, precipitation and moisture, the last dependent on interaction between the other two, appear to satisfy the requirements needed for global categorization. These three climatic factors range from low quantities which are limiting to living organisms to relatively high values. They affect all associations strongly, even though locally, other factors may exert highly significant influences. Their wide range of values offers the possibility of subdivisions into equivalently valued groupings.

Because of the complex nature of each association, it is not possible as yet to differentiate precisely the effects of individual factors on their physiognomy and make-up. Therefore, the specific effects of the three major climatic factors on the associations cannot as yet be separated from the influences of the edaphic and atmospheric factors. However, as one develops considerable field experience in the observation of associations which are determined by various factor combinations over a range of climates, a general picture begins to emerge in one' 5 mind as to the relative effects of the major climatic, edaphic and other factors. Such impressions can be developed more readily where many climates and numerous associations are to be found within small geographical areas. Mountainous areas, in general, and more specifically in the tropical region are excellent for such observations.

From such a still rather subjective base of noting various groupings of associations which appear to correspond to ranges in temperature, precipitation and moisture, the feasibility exists of segregating combinations of associations which coincide with definite climatic ranges. If such numerical parameters of climate are established to provide equivalent-weighted divisions, ecology can eliminate the problems associated with subjective decisions and become a precise science. The definite quantification of climatic parameters for association groupings establishes higher categories than the association unit. In reverse manner, interestingly, once the association groupings are defined precisely by climatic parameters, it then becomes possible to compare associations more efficiently so as to determine the effects of individual factors or various combinations of factors. Methods of selection of associations for such comparisons are explained under the Chapter on Associations.

The objectively defined groupings of associations are called life zones. They are natural sets of associations even though each grouping may comprise a whole catena of landscape or environmental units ranging from swamps to ridge tops. At the same time, the life zones comprise equivalently weighted divisions of the three major climatic factors, namely, heat, precipitation and moisture.

In earlier work with the life zone system, these association groupings had been termed plant formations. The major reason for discarding the term plant formation is due to its specific emphasis on vegetation, whereas it is desired to have the association units and the groupings of associations thought of as comprising not only the vegetation but also the soils, the geology, the topography, the climatic and atmospheric influences and the animal activities.

Although the concept intended here with the life zone is, in essence, similar to that given to the term "biome", the latter term is not precisely defined by climatic parameters. Therefore, since specific biomes have been described or mentioned in the literature of recent years, many of which will not be synonymous with the areas within life zone boundaries, it was deemed advisable to avoid the conflicts that would arise by using the term biome for precisely defined climatic extensions. The term "life zone" had not been used appreciably in recent times and appeared most satisfactory for application to the category of association groupings.

All of this discussion, however, would have little meaning if the life zones or groupings of associations were not natural divisions as defined by the climatic parameters. Since 1947, when the definition of life zone boundaries by specific values of the major climatic factors was set up, the validity of such life zones has been carefully checked. For many years, the most significant positive indication of naturalness of the life zone units was the fact that large areas in Latin America could be mapped largely on the basis of recognition of the life zones in the field. Meteorological stations were too few to serve for more than local verification of conformity. More recently ecological research in Costa Rica supported by the Advanced Research Projects Agency of the U.S. Army Research Office has led to the development of a direct correlation of objective measurements of natural forest stands with the life zone units. Details of methods of measurement and the values are discussed under the section on the Complexity Index.

Past attempts at classification

Ranges in average temperatures and moisture conditions have long been recognized as giving rise to distinct climates, indicated even in common language by the naming of hot and cold regions, or wet and dry sections. The influence of these major factors on the distribution of vegetation and animal life was too obvious to escape notice by even the mind of primitive Man.

Gradually as the natural sciences began to develop, a need arose for more specific definitions of climates. Geographical data and biological collections began to pour into Europe from the far reaches of the earth. In the nineteenth century, climatic classification became a real challenge and before the end of the century, scientists from many fields were attempting to develop a rational system.

The climatologists sought ways of combining various factor data which would provide satisfactory formulas for direct comparison of separate sites or regions. Russian pedologists had noted the existence of some sort of correlation of soils with climates. Thus, the pedologists looked for climatic regime formulations which could be linked specifically with the zonal soils or major soil groups.

Botanists and zoologists were primarily busy with the cataloguing of new species, and in the nineteenth century, the theory of evolution became a major topic of interest. However, biology was broadening out from taxonomy and a few keen minds were attracted to the subject of plant distribution. In 1807, Alexander von Humboldt published his ideas on the relations between climate and plant geography. Especially indicative of the thoroughness of his observations during travels in the Americas is a colored plate showing the altitudinal belts on a volcanic peak in Mexico.

In 1823, J. F. Schouw, a disciple of von Humboldt, published a treatise on the formulation of laws to explain the effects of light, temperature and humidity on the distributi6n of vegetation. Later, in 1855, A. de Candolle published similar studies giving major emphasis to temperature.

Simultaneously, and perhaps stimulated by the increasing notation of vegetation as an indicator of different climatic situations, interest developed in the groupings of plants themselves. In 1863, Anton Kerner, published an early classic on the natural vegetation communities in the Danube Basin. This was soon followed in 1869 by the coining of the word "oekology" by E. Haekel as derived from the Greek word “oikos" meaning home or living site. Subsequently, the term has been modified to "ecology" which may be defined as the study of the relationships between living organisms and their environment.

In 1872, A. H. R. Grisebach published a work on the natural groupings of vegetation over the entire earth. This publication initiated the attempts to treat the total picture of the world' 5 vegetation. 0. Drude in 1890, produced a book on plant geography which was soon followed by two major treatises on world vegetation distribution which have strongly influenced ideas on plant ecology. These publications were Warming's Oecology of Plants in 1895 and Schimper's Plant Geography on a Physiological Basis in 1898, the first originally published in Danish, the second in the German language.

These early major attempts to divide the earth’s natural vegetation into major communities or formations clearly indicated the complexity of the problem. Subsequently, as more data and field experience accumulated, the relations of the major factors to natural environments appeared even more complex and less possible of systematization. Gradually, the concerted effort to set up a rational, precise, climatic classification dropped off. The subject was not forgotten in ecology, but was relegated to a much less important position in the general field.

Considerations of past classification attempts

As seen in retrospect from present times, one can understand why the earlier attempts were not successful. For one thing climatic data were scarce and appreciable coverage was available for only limited portions of the globe. Travel to gain field experience over a wider portion of the world was difficult and time consuming. The major efforts were made in Central Europe where climatic regions are relatively broad in extent so that one could not readily traverse and study an extensive range of climates.

The very circumstances of geography and history must have had a profound effect on the prevention of the European scientists from developing a sound climatic classification. The early efforts to correlate climates and natural environments were carried out largely in the Cool Temperate region. When they traveled somewhat southward, they were confronted with the anomalous Mediterranean climate which constitutes only a relatively local, special climate in several isolated portions of the globe.

Then, when European scientists moved into the tropical region where they might have effectively developed a climatic correlation, historical chance directed most of the scientific effort into the monsoon region of the East Indies and southern Asia. It appears that climatic relations with the natural environment are more obscure there than in the Americas or much of tropical America. The general concentration of precipitation within half the year in monsoon regions tends to lessen the differences in vegetation across the wide range of total annual precipitation.

Subsequent to the early attempts to develop a climatic classification from usually simple data such as temperature and total precipitation, there have been repeated attempts to work out classifications with more numerous items of climatic measurements or with complex formulas to permit adjustments for latitude or other factors. They have rarely come closer to a natural system than some of the earliest attempts.

If a successful climatic classification had been developed in the early years of attempt, undoubtedly it would have led on to a more satisfactory integration of the natural sciences. Lacking that, each field looked less and less for signs of integration and concentrated on specialization within the field.

The geographers have predominantly satisfied themselves with the Koeppen classification, which after considerable modification, gives them a readily applicable system which can be shown on large area maps. The Koeppen system keys out several climatic characteristics to capital or small letters which can be memorized with a little effort This is a handy system for teaching in class and continues to fulfill the needs of geography whenever there is no need for any practical applications of the system in the field. Attempts by other fields to make practical use of the Koeppen system find that it fails to correlate well with natural vegetation or significant divisions of environment.

The zoologists were not early in the climatic classification attempts. Subsequently, Merriam proposed a life zone system in North America which attempted to map out areas of significantly homogeneous animal distribution. This has been utilized considerably by zoologists but is a subjective set of divisions not based on specific climatic parameters. Perhaps, its basic weakness rested on the overemphasis given to the geographical distribution of a relatively few larger animals as compared with the total animal life existent in the area.

Another attempt at taxonomic distribution, but this time with plants, was carried out by Clements in the same continent. Taking over from the idea of formations, he proposed and divided North America, into a set of climax vegetations. Parameters of climate were partially indicated for the various climates, but were not utilized as definitions for the climax areas. Thus, the system was also subjective without any sound base for the equivalence of the units.

Many other ecological systems have been devised, but either fall down on the same basis of lack of equivalence or their definitions are too subjective for scientific application. Beard made a good start in Trinidad and the Lesser Antilles with physiognomic divisions of the natural vegetation. Although basically sound, the definitions were not correlated precisely with climate and again suffered due to a lack of parameters for his units. Based as they were on physiognomic characters of the natural vegetation, the system is not applicable to the steadily increasing areas without or with greatly altered natural vegetation.

The Holdridge life zone classification

After several years of forestry work in the Caribbean region and a specific vegetation study in a mountain area in Haiti, Holdridge became interested in classification systems of climates and vegetation for the express purpose of depicting the relationships of the mountain vegetation to that of the lowlands. After study of many systems, he felt that the earliest attempts had come closest to a satisfactory classification scheme. Working then simply with annual precipitation and temperature values he developed the chart shown in Figure 1.

There was a definite advantage in working on a climatic classification at a relatively late date due to the abundant literature available on past attempts. Furthermore, considerable new information on both vegetation and climatic patterns had been assembled since the earlier attempts of correlation. All this was studied in the light of several years experience of timber cruising which served as a background of intimate knowledge of vegetation. Much of this had been carried out in mountain areas in the tropics where major climatic changes are found in relatively close proximity.

The two major differences of the life zone system from previous attempts at classification are due to a new way of expressing the factor of heat, namely, the biotemperature, and finding that the steps in increasing heat and precipitation which are significant to vegetation form a logarithmic progression.

Biotemperature, which is discussed fully in the next chapter, is a measurement of only the heat which is effective in plant growth. At first, it appeared that a satisfactory biotemperature value could be obtained simply by eliminating all below O^0 Celsius temperatures from calculations. All temperatures lower than O^0 Celsius were considered as O^0 for the calculation of the biotemperature.

Recently, more detailed study in the outer tropics has indicated the desirability of eliminating high temperatures also in the calculation of the biotemperature. Research has not yet established a precise maximum cut-off temperature for vegetation in the open, but observations of vegetation patterns as correlated with temperature indicate that this should be close to 30^0C. Thus, biotemperature is an average of the temperature between 0. and 30^0C. relative to the total period, which on the life zone chart is one year.

The logarithmic progression of temperatures and precipitation values provides a sound theoretical base for establishing divisions of equal weight. Mitscherlich had shown clearly that when an element is a limiting factor in plant nutrition, that additions of that element up to the amount that could be utilized must be increased in logarithmic progression to obtain a sequence of equal increases in yield. In like manner it is only logical, that water and heat as limiting factors would produce equivalent changes if added in amounts which equal a logarithmic progression.

At first, the third set of guide lines was not well understood. Those, which correspond to potential evapotranspiration ratios representing humidity values, were not needed for the classification of any particular site. In subsequent years more attention was given to the humidity values and their meanings. A complete discussion of the life zone chart is given in Chapter 3.

The life zone permits the grouping into natural units of the several hundred or perhaps well over one thousand associations of the earth The life zone chart, considered as a three dimensional representation separates 120 distinct life zones, provided that the sub-units of the Subtropical region and Premontane belt are counted as life zones. As discussed in Chapter 3, there exist locally also some sets of climatic conditions on earth which indicate a few other life zones or extensions of the chart.

Additional grouping of life zones into larger units on a natural basis is possible. The latitudinal biotemperature regions are natural geographical units. Even humidity provinces and altitudinal belts cutting across regions have some natural relations. However, as with the family in plant taxonomy, the life zone unit appears to be the most useful and practical larger grouping of the association units.

What then is a life zone, other than a set of specific ranges of major climatic factors? It may be thought of as a group of associations related through the effects of these three major climatic factors; heat, precipitation and moisture. These leave a definite mark on all the associations even though the group may comprise a quite diverse group of associations. This is true of the mature natural vegetation, the animal activities, the second-growth and the cultural activities of man.

For a rural man especially, the environment where he lives and works comprises more than an association. He knows the look and the feel of the fields, meadows, roadsides, second-growth and the forests of his locality. He includes them all in his surroundings. He knows the appearance and patterns of the sky, the air and the landscape through the day or through the seasons. Such an individual would feel relatively at home throughout his particular life zone.

Undoubtedly, primitive peoples who are essentially a part of the natural environment can recognize the pattern of a life zone much more readily than one who surrounds himself most frequently with the artificial micro-environments of modern civilization. But the latter person also, if he wishes to do so and regardless of the field of his own training, can learn to recognize the life zones readily. This is primarily because a life zone is not only a specific environment but also indicates a definite way of life.

In addition to the aspect and impression of the environment, a life zone is correlated with a set of agricultural practices, a time of planting and of harvesting and in rural districts with types of buildings related to the general agricultural land use. Where agriculture is not developed, then the aspect of the natural vegetation and the animal activities serve clearly to indicate the life zone.

Although this sounds like a subjective system of classification, the' life zone is specifically and precisely defined by the ranges of the three major climatic factors. One working alone may learn to identify life zones by carefully observing the landscape and activities close to meteorological stations which can provide the data to specify the life zone. After that sort of practice with several life zones, one should be able to identify the life zone without the assistance of climatic data.

Early settlement patterns indicate that man had a preference for certain life zones and except for the influence of strong economic or other factors confined his settlement to the preferred life zones. In the Republic of Panama, settlements during the first two or three centuries following the arrival of the Spaniards were confined almost entirely to the Tropical Dry Forest Life Zone. They undoubtedly found the same life zone already settled by indigenous people. The exceptions of settlements outside of the life zone appear to have been only those connected with mining or fortifications at strategic points.

Within the last century, the canal construction across the isthmus and both banana and coffee cultivation finally initiated appreciable settlements in other life zones. These were obviously capital enterprises which overruled the climatic preference of the small farmer and worker. However, during the last few decades, the rapid population expansion has forced emigration out of the Dry life zone with movements into several other life zones.

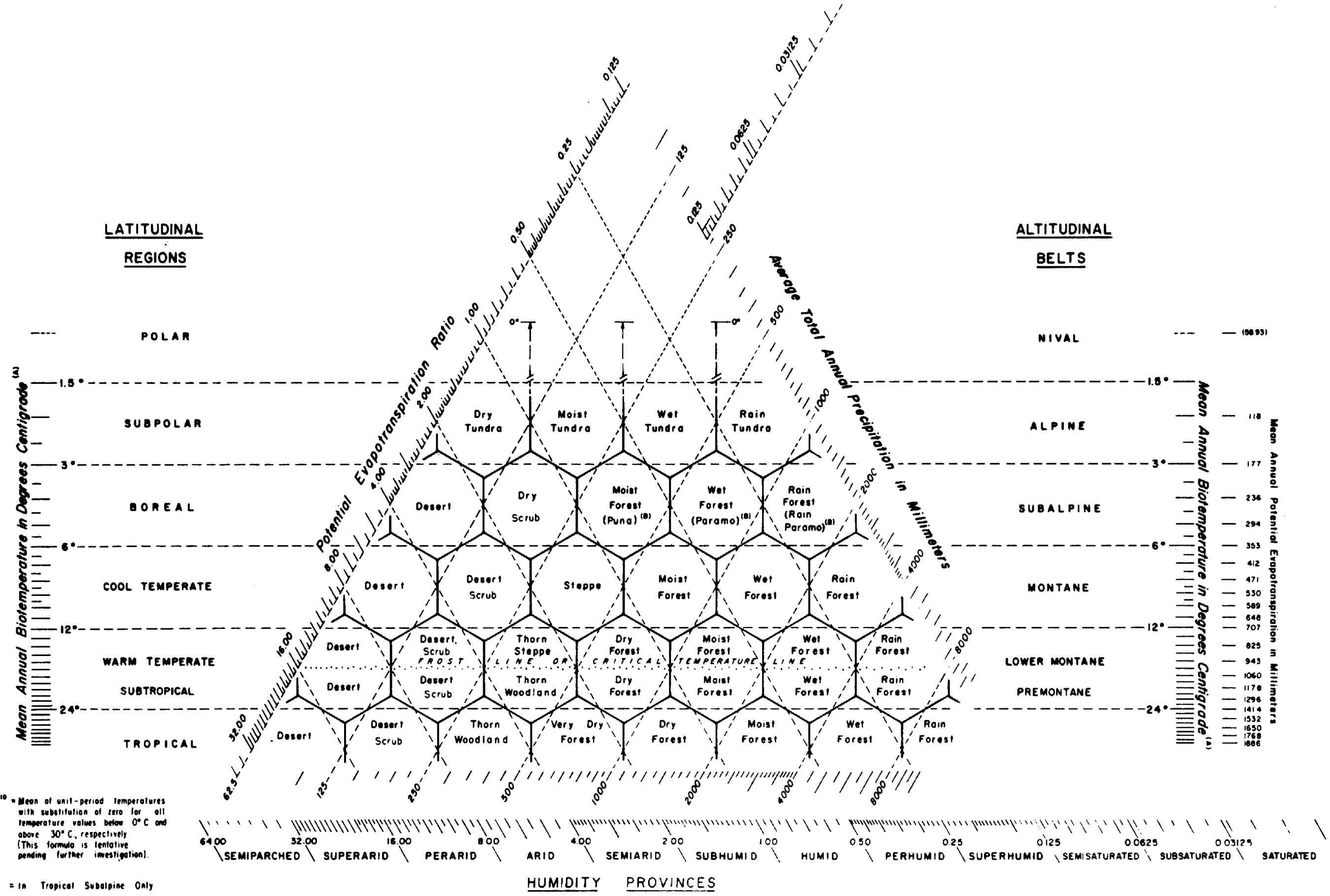
The general pattern of agricultural settlement in the Americas has been similar. The major preference for settlement has been within the two series of life zones next to and on each side of the potential evapotranspiration ratio line of unity. These correspond to the dry and moist humidity provinces. In regions of higher temperature, preference appears to have been given to the dry side of the line.

Interestingly, if the capitals of the twenty-one American republics are plotted on the life zone chart, it is found that nineteen fall within the life zones which are adjacent to the unity potential evapotranspiration ratio line. The two exceptions are Lima, Peru and Santiago, Chile. In the first case, only a *Subtropical desert* life zone location was available for a seaport capital although the Incan capital had been located at Cuzco in a life zone next to the line. In Chile, for a long time after arrival, the Araucarian Indians successfully prevented the Spaniards from moving farther southwards. It is surmised that this delay led to the settling down and establishment of a main base at Santiago which is one life zone removed from the preferable.

This all appears to indicate that Man’s initial agricultural activities probably originated close to the same unity line where a balanced movement of water downwards in leaching and upwards in evaporation would automatically maintain the fertility of the soil. Land clearing and weed control would have been simpler on the dry side of the line, especially in the warmer regions. At any rate, the order of agricultural selection of lands as a basis for settlement probably has always followed the same pattern. Men looked first of all for a satisfactory climate, second for fertile soils and third for favorable topography. Only in these late years of high population pressure has there been any appreciable agricultural movement into the wettest life zones.

FIGURE 1

DIAGRAM FOR THE CLASSIFICATION OF WORLD LIFE ZONES OR PLANT FORMATIONS

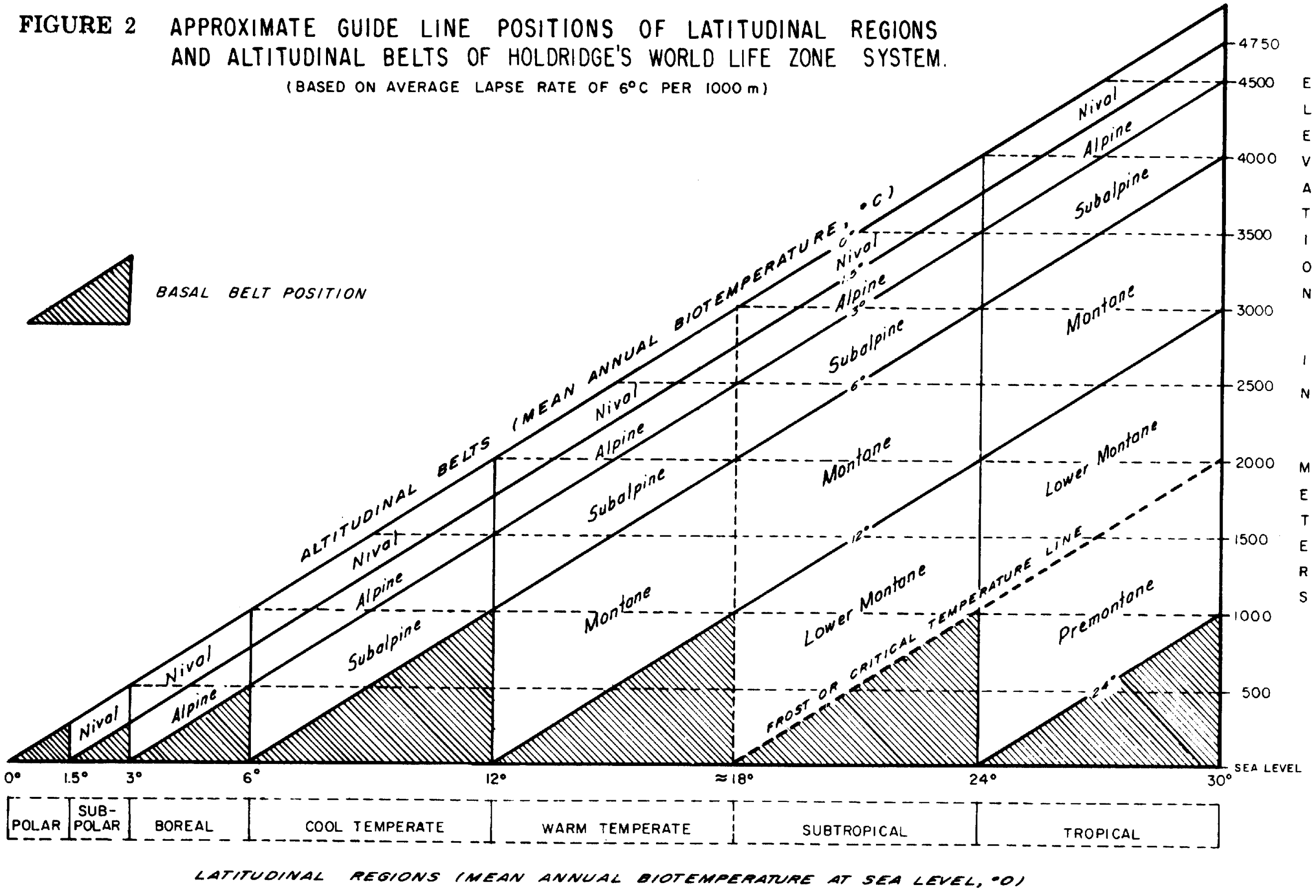


(A) t_{bio} = Mean of unit-period temperatures with substitution of zero for all temperature values below 0° C and above 30° C., respectively (This formula is tentative pending further investigation).

(B) = In Tropical Subalpine Only

FIGURE 2 APPROXIMATE GUIDE LINE POSITIONS OF LATITUDINAL REGIONS AND ALTITUDINAL BELTS OF HOLDRIDGE'S WORLD LIFE ZONE SYSTEM.

(BASED ON AVERAGE LAPSE RATE OF 6°C PER 1000 m)



CHAPTER III

THE LIFE ZONE CHART

The life zone chart shown in Figure 1 is a graphical representation of the most common life zones on the planet Earth The diagram serves equally well for both the northern and southern hemispheres. The chart may be utilized as representing the territory from the geographical equator at the bottom to either the north or south pole of the earth at the top, depending on whether one is interested in or working in the northern or southern hemisphere.

The two- dimensional diagram represents a three- dimensional set of life zones. Considered horizontally, the diagram shows the relative climatic positions of the sea-level or basal life zones on the surface of the planet. Considered vertically, the chart shows the vertical extensions of the basal life zones together with the relative positions and elevational dimensions of the various altitudinal life zones superimposed on or above the basal latitudinal life zones. Thus, the life zone representations may be pictured mentally as a set of six-sided bars extending to the north or south of the equator and curved latitudinally to match the curvature of the earth. when cut vertically at the equator or between regions, such bars would show a hexagonal face as they would likewise when cut horizontally to represent the interception of the bars with the surface of the earth. Each upper life zone is an eight- sided figure, with two vertical hexagonal ends. The basal life zones have a vertical face towards the equator, but the opposite face is a horizontal hexagon. The relative positions of the latitudinal regions, basal life zones and altitudinal belts, but disregarding the latitudinal curvature of the earth, are shown in Figure 2.

The life zones are defined by mean annual values of the three major climatic factors of the environment, namely, heat, precipitation and moisture. However, it must be remembered that within a six-sided bar of the three dimensional life zone figure there may be a whole series of altitudinal and one basal life zone with identical biotemperature, precipitation and potential evapotranspiration range ratios. Additional climatic factors such as day length, atmospheric pressure and seasonal variations of radiation differentiate the life zones within each of those series. Quantitative values of those additional climatic factors are not needed on the diagram because they are correlated directly with mean annual biotemperatures and altitudes.

After acquaintance and work with the system, it is possible to recognize the life zones and their boundaries in the field without dependence on the assistance of climatic data. At least, the latter direct recognition has been demonstrated as possible by several field workers in the Americas. There should be no real problem in doing the same in the Eastern hemisphere.

Heat

Air temperatures, which are the result of solar radiation and movements of the atmosphere at any given point, are measured by means of the expansion and contraction of a column of mercury within a closed, calibrated glass tube called a thermometer. This is the simplest and most practical method of measuring the factor of heat, which is one of the major requisites for life and life processes.

Some ecologists believe that direct measurements of solar radiation give a more precise value for the factor of heat. Direct radiation measurements cannot be taken with a simple instrument like the thermometer. Further, radiation values are available from only a relatively few sites as compared with existing temperature records. However, the main handicap of direct radiation measures for depicting the factor of heat is that they cannot register the significant effects of movements of warmer or cooler air to a given site from adjacent areas. Close to bodies of water or mountains, lateral movements of air masses of different temperature may be considerable. The air thermometer adequately measures the combined results of solar radiation and air movements.

The main dissatisfaction with air temperatures for correlation with vegetation has been due, apparently, not so much because of the inadequacy of the air thermometer, but rather with the methods of calculation of temperature means for correlation purposes. Mean annual or mean monthly temperatures may be readily derived from daily thermometer readings, but it does not necessarily follow that these are the means which are significant to vegetation. Although animal life is less restricted by temperature, especially as reflected in some of the larger mammals, vegetation is selected as the main criteria of temperature effects, because plant life forms the essential base on which animal life depends.

Mean annual biotemperature is the measure of heat which is utilized in the life zone chart. The biotemperature mean is an average of the Celsius temperatures at which vegetative growth takes place relative to the annual period. The range of temperatures within which vegetative growth occurs is estimated to lie between 0^0 Celsius as a minimum and 30^0 C. as a maximum. The positive temperatures within this range must be averaged out over the whole year period in order to make it possible to effectively compare a given site with any other on the earth.

Towards the poles, in the colder regions, there are many days in the year and even several continuous months during which the temperature does not rise above O^0 Celsius. During such periods natural vegetation is inactive, the inactivity being equal whether the thermometer reads -10^0 or -30^0 Celsius.

In the colder regions, a rough mean biotemperature may be obtained by summing up the positive monthly temperature means and dividing by 12, the number of months in a year. Verkhoyansk, in northeastern Siberia may be utilized as an example. The monthly means in degrees C. from January to December are as follows: -50.0, -44.4, -32.2, -15.5, 0, + 12.2, + 13.3, +9.4, + 1.7, -15.5, -37.2 and -47.8, The sum of the positive temperatures of the four months from June to September add up to 36.60**.** This total divided by 12 gives .3.050 as a rough mean annual biotemperature for Verkhoyansk. The elevation there is 100 meters and mean annual precipitation 135 mm., placing Verkhoyansk in the Boreal Dry Scrub Life Zone.

A more accurate mean annual biotemperature is obtained by adding up the daily biotemperatures and dividing that sum by 365, the number of days in a year. At Verkhoyansk$_1$ many days in the year would have a biotemperature of 0^0 because the actual temperature would not surpass 0^0C. during the whole 24 hours of the day.

When both above and below 0^0 temperatures occur within one day, the precise biotemperature for the day is the sum of the positive hourly temperatures divided by 24, the number of hours in a day. However, more frequently, only data on the daily maximum and minimum temperatures are recorded, In that event, one can only use the mid-point between 0^0, corresponding to the below 0^0 minimum, and the maximum temperature. For example, a day with a maximum temperature of 10^0C. and a minimum temperature of - 50 would be considered as having a biotemperature for the day of 10+0 divided by 2 or 5^0 C.

For many years, the biotemperature was thought to differ from mean annual temperatures only in the colder regions of the earth, due to the exclusion of the below 0^0C. temperature readings. More recently, additional investigation on vegetation comparisons between the inner and outer tropics has indicated the need for eliminating high temperatures also in the calculation of the mean annual bio-temperature.

The first implication of this need came about during a life zone mapping project on Hispaniola in the West Indies, It was noticed that the vegetation at low elevations on the island had the appearance of that of a higher elevational vegetation in the inner tropics. Although the mean annual temperature was as high or higher at low elevations on the island than at similar elevations in the inner tropics, the vegetation corresponded to that of a lower mean annual biotemperature on the life zone chart,

A reanalysis of the general vegetation distribution in the Caribbean region indicated that the observations on Hispaniola might well be correlated with the general floral changes between Dominica and Martinique in the Lesser Antilles and in Nicaragua on the mainland. Although there is some overlap of tree species to the north and south of these breaks, the majority of tree species of the inner and outer tropics are distinct.

Previously, plant geographers had considered the water gap of the Nicaraguan-San Juan River break, which joined the Caribbean Sea with the Pacific Ocean in the geological past, as the main reason for the floral discontinuity on the mainland. On the contrary, the life zone mapping work indicated that the floral break may well be due to climate and specifically to temperature effects.

As a general rule, the highest mean annual temperatures are found in the outer tropics rather than closer to the equator in the inner tropics. Since the low elevation vegetation in the outer tropics appeared to correspond more closely to that at somewhat higher elevations in the inner tropics, the obvious conclusion was that there must be some maximum temperature cut-off above which vegetative growth becomes insignificant.

Research in plant physiology has shown that at high temperatures, respiration processes increase faster than photosynthesis, so that a point is reached where net photosynthesis is zero. The main problem is in comparing controlled environment study results with temperature conditions in the open. The most relevant research appears to be that of Gates who has studied leaf temperatures as related to air temperatures and photosynthetic processes. His graphs show significant drops in photosynthesis during the high temperature portions of summer days. Leaf temperatures of exposed leaves reach high values considerably above air temperatures.

From a rough analysis of diurnal temperature changes in the Caribbean region, it was calculated that a maximum temperature cutoff value of 30^0 would result in mean annual biotemperatures which could be correlated with the actual distribution of natural vegetation in the region. The work of Gates appears to confirm a maximum temperature cut-off of that magnitude. Admittedly, this is still probably an approximate value, but will be used in applications of the life zone chart until a more precise value is determined by future research.

The calculation of the mean annual biotemperatures with the elimination of both temperature readings of below 0^0 C. and above 30^0C. has unfortunately become much more complicated than the previous elimination of only below 0^0 readings. This is especially true because temperatures above 30^0 may be reached for portions of days over a considerable part of the year at certain sites. To obtain a reasonably close value, it is necessary to sum up the hourly temperature readings between 0^0 and 30^0 and to divide the total by the number of hours in a year. In effect, temperature readings below 0 and above 30 are eliminated or given a value of zero.

Hopefully, when the significance of the biotemperature to agriculture and other renewable resource land use is appreciated, meteorological stations can be induced to calculate and publish values of biotemperature along with the usual mean temperature values and other data. However, before this request is made to the meteorologists, physiological and ecological research should determine a more precise value for the maximum cut-off temperature.

Biotemperature values representing the heat factor increase logarithmically from the top to the bottom of the chart. The broken horizontal lines corresponding to mean annual biotemperatures of 1.5, 3, 6, 12 and 24^0 C. are the guide lines for the life zone boundaries between the latitudinal regions shown in capital letters at the left of the diagram. The actual boundaries of the life zone hexagons slant back and forth across these guide lines.

The same biotemperature guide lines also determine the altitudinal belts which are shown at the right hand side of the chart. Each latitudinal region can have only those altitudinal belts above the basal region life zones which correspond to those shown on the chart above the low-value temperature limit of that region. Thus, Lower Montane or Montane altitudinal belts do not exist in the Cool Temperate region. Above the Boreal basal region, only the Alpine and Nival belts can be found. Only the Tropical region may have all of the altitudinal belts shown on the chart.

Those who have worked previously with the life zone chart will note one change in each of the regional and altitudinal belt names. Once the new formula for biotemperature had been developed, following the finding of the need for establishing a maximum temperature cut-off, it was decided to substitute "Subtropical” for the previous regional name "Low Subtropical" and "Premontane" for the earlier employed "Subtropical'[1] altitudinal belt. The reason for the change is to eliminate any misunderstanding which appeared possible with the previous similarity of names.

Normally, one knows within which latitudinal region he is working and recognizes any temperature value which is too low for the basal region as pertaining to one of the altitudinal belt life zones. However, with data from sites with which one is not acquainted personally or from relatively low elevations above sea level near the cooler border of a latitudinal region, there may exist some doubt as to the proper assignment to region and belt. In such cases, a plotting of the point of intersection of the temperature value and elevation in meters on Figure 2 will be helpful in assigning any given site to the correct latitudinal region and altitudinal belt. However, since the latter diagram cannot show the overlapping of the temperature lines in accordance with different mean precipitations, it is preferable to learn to work out belts and regions directly from the life zone chart.

The ranges in temperature double in extension progressively in proceeding from limiting to optimal conditions of heat. Theoretically, at the top of the diagram, many more equivalent regions and their corresponding altitudinal belts could be added with additional temperature guide lines at 0.75, 0.375, 0.18125, etc. However, because of the rapidly decreasing areas involved in such classifications and because of the increasing simplicity of living communities in such areas, there exists little present interest or need for continuing such divisions beyond the tundra. Thus, until a need or greater interest develops for more subdivisions, the areas with biotemperatures from roughly 1. 5^0C. to 0^0C. are combined within the Polar region or Nival belt. Nevertheless, such theoretical divisions might become useful if a set of living organisms based on our same carbon-oxygen system of metabolism are found in the future on other planets.

In addition to the logarithmically-spaced biotemperature guide lines which serve to delineate the latitudinal region and altitudinal belt boundaries, there is one other significant heat factor line on the life zone chart. This is the dotted line labeled "Frost line or Critical Temperature line" which partitions the row of hexagons between the biotemperature guide lines of 12 and 24°. The mean biotemperature corresponding to that line should be between 16^0 and 18^0 C., but because the mean is assumed to vary somewhat at the diverse locations in the world where it is found, no attempt has been made as yet to assign a specific biotemperature value to the line.

The frost or critical temperature line represents the dividing line between two major physiological groups of evolved plants. On the warmer side of the line, the majority of the plants are sensitive to low temperatures. They can be killed back by frosts as they have not evolved to withstand periods of cold. Towards the poles or above this line in the Tropical and Subtropical regions, the total flora is adapted to survive periods of variable length of low temperatures, whether as seeds in the case of the annuals or as perennial plants which can withstand the cold.

The line is probably not precisely fixed on the terrain in many places but may advance or retreat during cycles of warmer or colder years. Even without consideration cycles, the line cannot be very precise on the ground because species differ in their sensitivity to occasional low temperatures. Until the line location has received more study areas such as Southern Florida, where the Warm Temperate abuts the Subtropical region, it is tentatively defined as the limit of the area of the cooler region which is subjected to a severe killing frost at least once every three years.

In the wetter districts of the top portion of the Tropical Premontane altitudinal belt and again in the upper portion of the basal belt of the Subtropical region, the author found that the vegetational changes to Lower Montane did not coincide with the lines of killing frosts but are found at lower elevations than the latter.

It is hypothesized that the higher prevailing humidity at such locations tend to prevent the reaching of freezing temperatures, but that even a low temperature of perhaps 2^0C. in combination with high humidity gives rise to an excluding effect on the temperature-sensitive tropical vegetation similar to that of frost. where such double lines exist, the lower elevation or critical temperature line becomes the significant one for vegetational change. Similar conditions may prevail where the Warm Temperate and Subtropical regions abut in humid regions. However, the author has had no first hand experience in areas with that possibility nor has he been able to find references in the literature on vegetational changes in such areas.

The frost or critical temperature line presents the one great anomaly in the regular progression of vegetation distribution from the poles of the earth or the high snow-covered peaks of the tropics to the tropical lowlands. whereas the other significant changes between regional or altitudinal belt vegetations coincide with hexagonal borders along the logarithmically spaced biotemperature guide lines, the frost or critical temperature change crosses the middle of a row of hexagons.

Within the same life zone hexagons, but on opposite sides of the frost or critical temperature lines, the taxonomic lists of plant species are markedly distinct. Cultivated plants are likewise generally different so that land use within a hexagon shows a marked dissimilarity between the two sides of the line. The change in land use in the humid tropics where coffee is cultivated up to the top of the Premontane altitudinal belt and then gives way sharply to dairy pastures or to grain or potato cultivation is a clear cut example of the significance of the line.

Given the importance which man places on the practical aspects of land use and species differentiation, the only logical solution to the classification problem appears to be that of giving separate latitudinal region and altitudinal belt names to the sets of half hexagons above and below the frost or critical temperature line on the chart. Also, this is in accord with past general geographical and ecological denomination of regions and altitudinal belts in the literature. This implies, in addition, that the separate portions of each hexagon in the row under discussion be given a distinct life zone name.

However, from a physiognomic viewpoint, interestingly, the integrity of the hexagons in the 12 to 24^{0}C. biotemperature range receives strong support. The ecological research carried out recently in Costa Rica showed that forests or life zones from the same humidity province in the Premontane and Lower Montane altitudinal belts had the same complexity index. This index which is discussed in detail in Chapter V utilizes data on stand height, basal area, density and number of tree species, which may be considered as significant physiognomic characters of a forest stand.

Thus, although practical considerations appear to justify the separation of the l2~240 row of hexagons into two regions, two altitudinal belts and two sets of life zones, physiognomic evaluation supports the validity of the equivalence of the hexagons of the chart. In essence, this means that the two sets of life zones in the 12-24^{0}C. range are in essence sub-life zones separated for nomenclaturial reasons, but which, physiognomically are really only one set of life zones.

The incomplete hexagons at the bottom of the chart corresponding to the basal life zones of the Tropical region indicate that only a portion of each of those life zones exist on earth. If complete, they would extend on to the next theoretical biotemperature guide line of 48 °C. In actuality, mean annual biotemperatures scarcely exceed 27 °C. in any part of the earth. Thus, considerable areas in the tropical region even at sea level fall within the lowest transitional triangles of the second row of hexagons. At present, these extensions into the tropical region are being identified as Tropical Premontane.

Altitudinal and Latitudinal Ranges of Vegetation Zones:

A rough approximation of the ranges in elevation of altitudinal belts in meters is given in Figure 2. These values must not be taken too literally, but are helpful in working transects in given areas. Specific locations of the biotemperature guide line values change with latitude and are affected locally by such factors as air drainage or prevailing winds, slope exposure, topography and changes in precipitation.

A logarithmic progression of 500, 1000 and 2000 m. is evident in the range of elevations between the successive pairs of biotemperature guide lines 3° - 6°, 6° - 12° and l2° - 24°. The basal belt of the tropical region attains to an elevation of at most around 1000 meters. This is due to the fact that only a portion of the basal tropical biotemperature range is found on the earth. If this were extended to the next theoretical biotemperature guide line of 48 °C., we could expect a basal belt of 4000 meters in elevational range.

Theoretically also the alpine belt between 1.5 ° and 3° should have an elevational range of 250 meters and the remaining areas between biotemperatures of 1.5° to 0° should also extend for another 250 meters in elevation.

In actuality, the theoretical elevational ranges tend to expand considerably at higher altitudes and especially so with increasing latitudes. of course, minor variations in temperature become relatively more influential when related to narrower ranges of temperature between the guide lines. However, the primary reason for this expansion in elevational ranges must be due to the changing relation between the decreasing height of the vegetation and our standard method of measuring temperatures at a given height above the ground.

At higher elevations, the plants which grow to heights of less than a few centimeters are much more intimately affected by the temperatures of the top soil and superficial stones than to the standard air temperatures taken above a meter from the ground. Thus man finds some tundra plants extending on for a great elevational range in mountain areas such as in the high Himalayas and the slopes of the Brooks range in Alaska. Even more exceptional cases may be found such as lichens growing on exposed rock outcrops in the mountains only a few miles from the South Pole. Obviously, in the last example, only the heating of the rocks during short periods of the year creates a positive biotemperature in a very superficial layer on the rocks. It would be doubtful that a standard temperature station would register any positive air temperature at such a site.

The ranges of the regions in degrees of latitude are more irregular than the ranges of altitudinal belts. The regional widths are affected strongly by the diversity in shapes of the continents, ocean currents, interior lakes and rivers or mountain ranges in relation to prevailing winds. Nevertheless, the general principle of a logarithmic progression of degrees of latitude between the biotemperature guide lines is indicated. Also, as similarly found with the ranges in meters of the altitudinal belts, there is only a partial development of the tropical basal region and a broadening of the actual regions where relatively low temperatures prevail.

In order to show the theoretical pattern of latitudinal ranges of the regions for comparison with the actual diversity of the regions, an attempt is made in Table 1 to quantify the regional ranges in degrees of latitude. admittedly, this is only a table of estimated values presented for the purpose of stimulating further thought and study of latitudinal region distributions.

Table 1. Approximate theoretical extensions of vegetation regions in latitudinal degrees.

Region	Range of Biotemperature between Guide Lines	Range in Latitude	Range in Degrees of Latitude
Nival	0˚ to 1.5°	9° to 67°22.5’	22°37.5’
Subpolar	1.5° to 3°	67°22. 5' to 63°45’	3°37.5’
Boreal	3° to 6°	63°45’ to 56°30’	7°15’
Cool Temperate	6° to 12°	56°30’ to 42°	14°30’
Warm Temperate	12° to 17°±	42° to 27°30’	14°30’
Subtropical	17°± to 24°	27°30’ to 13°	14°30’
Tropical	Above 24°	13° to 0°	13°

Precipitation

The second major factor utilized as a climatic determinant of the life zones is precipitation. The value used is the mean annual total of water in millimeters which falls from the atmosphere either as rain, snow, hail or sleet. Water which condenses directly upon the vegetation or ground, such as dew, is not included even though locally such moisture may sum up to a quantity which has an appreciable effect on the vegetation. The primary reason for the exclusion of such water from the precipitation total is that standard meteorological stations do not include this water in their records, which are compiled as precipitation caught in an above ground container in an open space free from higher vegetation. The water condensed from dew or mist when appreciable is considered as a factor of atmospheric association conditions.

The mean precipitation values increase across the diagram from left to right. Guide line values of mean annual precipitation cross the chart from lower left to upper right at an angle of 600 to the horizontal biotemperature guide lines. Again as with the temperature, such guide lines do not coincide with life zone boundaries but rather determine with other guide lines the mid-points of four of the sides of each life zone hexagon. The values of such guide lines increase logarithmically across the chart.

Meteorological data from occasional sites show mean annual precipitations which are either too low or too high to fit within any of the life zone hexagons on the chart. Because the areas involved are ordinarily quite limited in extent, the symmetry of the chart has not been altered to include these. However, precipitation values and humidity province names have been extended beyond the main body of the hexagon chart to permit plotting of specified points and the nomenclature of any life zone.

Thus, a low elevation site in the Warm Temperate region with only 40 millimeters of mean annual precipitation at a mean annual biotemperature of 150 could be called the Warm Temperate Superarid Desert to differentiate it from the Warm Temperate Perarid Desert shown at the left edge of the diagram. At the other extreme, a site at an elevation of 600 meters above sea level with a mean annual biotemperature of 5^0 and a mean annual precipitation of 2500 mm could be termed the Cool Temperate Subalpine Sub-saturated Rain Forest life Zone to differentiate it from the Cool Temperate Subalpine superhumid Rain Forest life Zone presently shown in the border position on the right hand edge of the chart. In work in local regions where sometimes only a portion of the life zone chart is utilized, it would be possible to make the necessary extensions of the lines and set of hexagons to include any such life zone which falls outside of the diagram shown in Figure 1.

Moisture

The third and final climatic factor which determines the boundaries of life zones is humidity. Some confusion in the literature has arisen from associating humidity directly with precipitation. Although there is a direct correlation of humidity with precipitation along a given temperature line within a latitudinal region or altitudinal belt, the same correlation cannot be generalized over the total world environment. The same mean annual precipitation which gives rise to wet humidity conditions in the Subpolar Region or Alpine belt results only in arid conditions when it falls in the lowland tropics. The reason, of course, is that humidity is determined by the relation of temperature to precipitation, leaving aside considerations of other sources of moisture.

There appears to be no possible meteorological or climatic measurements presently feasible which can give directly a suitable set of values to be utilized as the third or humidity coordinate of the life zone chart. The value which does work adequately is termed the potential evapotranspiration ratio. Potential evapotranspiration is the theoretical quantity of water which would be given up to the atmosphere within a zonal climate and upon a zonal soil by the natural vegetation of the area, if sufficient but not excessive water were available throughout the growing season. A more detailed discussion of this theoretical value and attempts to measure or derive it are presented in the chapter on atmospheric water movements. Once both evaporation and transpiration are directly correlated with temperature, other factors being equal, the mean annual potential evapotranspiration in mm. at any site may be determined by multiplying the mean annual biotemperature by the factor 58.93.

The potential evapotranspiration ratio is determined by dividing the value of the mean annual potential evapotranspiration in mm. by the value of the mean annual precipitation in millimeters. since potential evapotranspiration is the total of water which potentially could be utilized by the normal natural mature vegetation of a climatic site and the precipitation is that quantity of water made available for potential use in transpiration by the vegetation or evaporation, then it can be understood that the potential evapotranspiration ratio is a definite measure of humidity which may be utilized for a relative comparison of distinct sites.

The values of the potential evapotranspiration ratio increase across the diagram from right to left even though this increase in ratio actually signifies a decrease in effective humidity. The potential evapotranspiration guide lines are placed on the diagram crossing both the temperature and precipitation guide lines at angles of 60°. Again as with the other values, the ratio lines help determine the midpoints of the sides of the life zone hexagons where they cross the precipitation and temperature guide lines. Thus, all of the planes of the life zone polyhedron, both latitudinal and altitudinal, are precisely determined or fixed by intersections of the planes located by the three types of guide lines.

The latitudinal and altitudinal regional strips between pairs of potential evapotranspiration guide lines are humidity provinces. The names of these are placed in their corresponding positions at the bottom of the chart. Names of regions, altitudinal belts and humidity provinces have been selected to conform most closely with general scientific usage, although where this was not possible names were made to conform with the general pattern of the chart.

Determination of the life Zone from Climatic Data

In order to determine from climatic data to which life zone a particular site belongs only the mean annual biotemperature, the mean annual precipitation and the elevation above sea level are needed. The biotemperature logarithmic scales are in vertical columns at both the right hand and left hand edges of the figure in half degree intervals from 1.50 to l2 and beyond that at one degree intervals. By placing a straight edge across the chart from the correct value in each of the vertical temperature scales the line of biotemperature is located.

Next, the same is done utilizing the precipitation scales at the bottom and at the right of the block of hexagons. The precipitation scales vary from intervals of 25 mm. at the drier end to much larger intervals at the wetter end. The point where such a line drawn between the precipitation values crosses the established biotemperature line for a given point is the location of that specific site on the life zone diagram. The potential evapotranspiration ratio value could be calculated also and a line drawn between its value on the corresponding scales at the left and the bottom, but this is not necessary as only two lines of crossing are needed to determine the precise location of the site being plotted.

Even with the location of a point within one of the hexagons, the correct life zone is still not determined. Because the chart represents a three dimensional figure, it is still necessary to define the life zone as belonging to the basal portion of the region at the left or to an altitudinal belt at the right of one of the warmer regions. Roughly, the maximum range of altitudes of the basal regional formations or of their corresponding altitudinal belts indicated at the right between the same temperature guide lines are as follows: Tropical 1000 meters; Subtropical 1000 m.; Warm Temperate 1000 m.; Cool Temperate 1000 m.; Boreal 500 m.; and Subpolar 250 m. with the undifferentiated regions on to 0^0 C. of unlimited range.

A station with a mean annual biotemperature of 8^0C. and a mean annual precipitation of 350 mm. would fall within the hexagon labeled Steppe opposite the Cool Temperate region and the Montane altitudinal belt names. If the elevation were only 200 meters above sea level, this would obviously be a basal life zone and the correct name of the life zone would be that of Cool Temperate steppe. Had the elevation above sea level accompanying the same values of temperature and precipitation been 1200 meters, then the elevation would be above the total elevational range of the Cool Temperate basal belt so that it could not be a basal life zone of that region.

One method of determining the correct life zone for an elevated point is to calculate the temperature at sea level below the point. This can be done by considering a rough equivalence of 6^0C. for each 1000 meters of elevation. In the above case of 1200 meters this calculation would be 1.2 x 6= 7. 2 which added to the actual temperature of 8^0 would equal 15.2^0**,** the supposed temperature corresponding to a sea level temperature at that point. The sea level point would correspond to the Warm Temperate region and the elevated site would fall in the Warm Temperate Montane steppe life zone.

Another way of making the same determinations would have been that of lining up the values of temperature and elevation on Fig. 2 which would automatically show the 8^0 and 200 meters as crossing in the stippled basal region of the Cool Temperate region and the 8^0 and 1200 m. as crossing in the Warm Temperate Montane altitudinal belt. However, as stated previously it is preferable to memorize the maximum altitudinal ranges corresponding to each region and do the determination of the correct life zone on the same life zone chart.

The dark heavy hexagon lines are the borders of each life zone. As may be noted on the diagram the various guide lines of temperature, precipitation and potential evapotranspiration ratio mark out 6 separate triangles in each hexagon. These are zones of transition. Within each triangle two of the three climatic factors correspond to the same region, province or strip as the remainder of the main body of the hexagon but one of the factors essentially corresponds to that of a neighboring life zone' s temperature range, humidity province or precipitation strip. This is sufficient to give rise to a transitional nature of the association located within that triangle.

Frequently, when collectors of plant or animal specimens refer to an especially interesting location for collection, it turns out that their collecting station was located within the general area of the three triangles where three life zones join. Also, when one is mapping life zones in the field where few or no meteorological stations exist, one encounters areas which at first are difficult to assign to a life zone and which on further examination usually turn out to be one of the transitional triangle areas.

One of the advantages of the life zone chart is that when two or more stations in the same general region are plotted on the diagram the relative climatic relations of the points are obvious and one can visualize the life zone lines which must be crossed in the intervening territory between such stations. This gives one an opportunity to predict the life zones to be encountered before crossing such intervening territory.

As an example of this, on my first visit to Mexico City, we were scheduled to make a trip the following day out to a fish hatchery site in the mountains. Available climatic and elevation data showed that the latter was located in the Subtropical Montane Wet Forest life zone whereas Mexico City falls in the Subtropical Lower Montane Dry Forest life zone. A glance at the chart shows that two intervening life zones are placed side by side between such a pair of points and the route would obligatorily pass through either the Montane Moist Forest or the Lower Montane Moist Forest life zone in going from Mexico City to the fish hatchery. As it turned out the precipitation increased proportionately faster than the temperature was lowered so that the route passed from the Lower Montane Dry to Moist and then crossed into the Montane Wet. Knowing which of the two possibilities to expect made it relatively easy to follow the changes in the species and physiognomy of the vegetation.

CHAPTER IV

THE ASSOCIATION

Division of a Life Zone into Associations

The life zones comprise only the first order category of environmental divisions**.** Even though the natural life zones are extremely useful for broad comparisons and generalizations, subdivisions are necessary for more specific analyses and for inclusion in the classification system of second order environmental factors such as soils, drainage, topography, strong winds, mists and various patterns of precipitation distribution.

However, the major factors of heat, annual precipitation and moisture, utilized in the differentiation of life zone units, are still the dominant causes controlling the environment. Often workers within a regional localization develop a belief that the second order environmental factors are just as important or more so than the major climatic factors of heat, moisture and total precipitation. For example, the correlation of mangroves with the soil conditions of tidal estuaries becomes so strongly linked in the mind of the tropical worker that he forgets that there are multidudinous examples of tidal estuaries in temperate regions with other types of vegetation than mangroves. Though soil conditions are indeed important, they are still secondary to the broad climatic factors.

Utilizing significant ranges of variation in the second order factors, each life zone may be subdivided into ecosystems which comprise less extended sets of environmental conditions, each occupied, under natural conditions, by a group of evolved organisms which are adapted to and feel at home within those conditions. Such an ecosystem corresponds to a natural community.

The important point to remember is that a distinct community of organisms, under natural conditions, is associated with a specific range of environmental conditions within a life zone. Thus, the logical name for such a specific range of conditions appears to be that of association. This permits the assignment of a specific environmental unit name and the mapping of a fixed, relatively permanent area, regardless of whether the natural, undisturbed associated community of plants and animals is still in existence or has been removed or significantly altered by man's activities.

In other words, the association is here defined as an area with a definite range of environmental factors which under natural undisturbed conditions is occupied by a distinctive community of organisms. Such communities must be or must have been significantly distinct to set the association apart from the surrounding associations of the life zone. There is no need to go beyond the specific life zone concerned to determine the criteria of distinctivity, because any associations in other life zones are automatically distinct because of differentiation due to the gross climatic factors.

Whereas the first category division into life zones was made by establishing definite ranges of climatic factors which are universal on the face of the earth, associations are determined by factors of the environment which are usually more restricted in extent. For example, the inversion of the normal pattern of rainfall during the warm season to one of rains in the cold season and drought in the warm period of the year known as the Mediterranean climate is a condition which is found only in a few places on the earth. Other common examples are monsoon climates, areas where the clouds frequently contact mountain slopes, elevated water tables, areas of limestone or serpentine rocks, or areas of excessive salinity

The different associations within a life zone are usually more readily distinguished by recognition of the distinct sets of organisms which occupy the areas. Because of their lack of mobility the units of vegetation are more easily observed even though they are not necessarily more characteristic of the community than the animal life or the environmental conditions. All too often the feasibility of recognizing a few plant species has led to the designation of an association by a nomenclatural combination of two or three of the dominant plant species. Although this is a procedure which is helpful locally in naming associations, it cannot be applied on a global basis.

With the exception of a few organisms which have circled the globe in their natural distribution, most species are confined to a specific biogeographical region. Thus, the use of specific names for the identification or classification of associations is not considered suitable for a world wide system of classification. Combinations of specific names of two or three dominant plant species might better be used as synonyms or local common names for the associations.

On the other hand, an association of a life zone comprising a specific but unique range of environmental conditions will comprise a set of niches which may be identical in two or more biogeographical regions. Through the long process of evolution, local species have been developed from available material to fill the niches of the association. Given the wide range of plant material in the world, very likely there are few unoccupied niches for plants with the possible exception of certain isolated local sets of conditions such as oceanic islands or isolated tall mountain peaks. With animal life and especially with the larger forms, there appears to be a greater number of unoccupied niches even in relatively large land masses.

Plant species which occupy a specific niche in a specific association have the same aspect of physiognomy even though they may be quite unrelated taxonomically. Striking examples of this are the Cactaceae of the Americas and the

Euphorbiaceae of southwestern Africa growing in the same dry associations or the "frailejones" of the Compositae in the high Andean paramos which match the Asclepiadaceae plants in similar situations on Mr. Kilimanjaro in Africa.

With plants, physiognomy goes with the niche, but in animals the niche is basically one of activity. Thus, although this is often accompanied by a characteristic physiognomy which matches the niche, this is not a nearly universal correlation as in the plants. Actually, there has been too little study of the correlations of combined plant and animal life in specific associations in two or more biogeographical regions to permit more than speculation at the present time. Furthermore, the identification of associations by specific names only prevents their comparison through the literature, as there can be no certainty from such names that the same association is meant in each case.

Even within the same life zone within a biogeographical region, the utilization of lists of species from associations clouds their distinctness. Many plant and animal species may range through several associations or even two or more life zones. As a listed species, such evidence may be of no help in classification whereas the physiognomy of a plant species or the activities of an animal may be quite distinct in separate associations.

As an example of this in plants, consider Rhizophora Mangle, the red mangrove which occurs commonly in tidal swamps along the coasts of the Americas. Specifically, this would appear to be the dominant tree which characterizes one association. Yet, if the height of the stand in the various life zones is considered, then obviously the association in each life zone is distinct from that of the others. Very likely careful study of such associations would turn up many specific differences in addition to the obvious one of the height of the canopy.

As an example of animals, the black bear of the north may carry on very distinct activities in different associations of the same life zone. Sometimes the bear will be feeding on beech nuts on the ridges where Fagus is common, whereas at other times it will be in the cedar (Thuja) swamps feeding on frogs. One may say that the bear is a common element of both associations differentiated by the niche it occupies in each.

The Association Unit

A definition for a natural undisturbed association may be stated as a range of environmental conditions within a life zone together with its living organisms of which the total complex of physiognomy of plants and activities of the animals are unique. The same association may be found widely separated on the face of the earth in different biogeographical regions and composed of widely differing sets of species.

Considerable debate is present in the literature as to whether there is a distinct unit corresponding to an association and concerning the characteristics of the same. The problem is essentially the same as that of determining species.

Sometimes species and associations are clearly distinct from all others. In other cases just where to draw dividing lines is debatable and differences of opinion are possible. Nevertheless, in the same way that species delimitation is essential for the science of taxonomy, so also ecology must develop an adequate system for classifying associations or ecosystems if it is to be made into a definite science.

However, the natural associations are becoming increasingly more disturbed with the ever expanding alterations of natural life caused by man. Thus, it is imperative to learn to define and to name the associations by the ranges of environmental factors within the life zone so that these areas can be delimited as permanent areas regardless of the actual cover or land use. These latter cover aspects are subject to change over relatively short periods of time. The cover or land use aspect enters the classification system as a third category defining the natural or artificial status of the plant and animal life within the fixed association. The second category, that of associations, is defined by ranges of secondary environmental factors within the first category of specific life zones, as determined by ranges of the broad climatic factors.

Less attention has been given to associations by animal than by plant ecologists. However, since animals are tied to the vegetation at the bases of all food chains, the same association which is obvious to the plant ecologist should be the unit for animals. At first glance, this appears too restrictive in area, because the larger and more conspicuous animals and birds work through several adjacent associations or even life zones. Still these represent only a minor portion of the total animal life of an association. The insects, spiders, worms and animals of other orders are not only tremendously more numerous but are less conspicuous and much more restricted in their movements.

Thus, although some of the plants and animals occupy the same or different niches in more than one association, still the complete set of organisms as well as the environment will differ from one association to another. A niche is here considered as an opportunity for space and food within a community. Through their mobility, larger animals may take advantage of several small or temporary niches scattered over a considerable area. However, a bird or animal of such nature should be considered a part of the community even though it may be a transient which arrives for only a short period each year to take advantage of a specific fruit. The alternative of trying to define more extensive areas for the larger animals would result in variously shaped and overlapping areas which could not be systematized.

Classes of Associations

The associations may be grouped in four basic classes, although there do exist various possible combinations. The four types of associations are climatic, edaphic, atmospheric and hydric.

A climatic or zonal association is the area occupied by a plant community growing on a zonal soil in a zonal climate. From this it may be inferred that no other environmental factors in the area complicate the first order broad climatic factors which determine the life zone. Obviously, there can exist only one climatic association for each life zone. Because this association is the most representative of the life zone, the name of that community is placed in each hexagon on the life zone chart.

The climatic associations offer the best opportunity for observing or studying the regular pattern of the effects of the major or first order environmental factors on the physiognomy of the vegetation, the activities of the animals and the nature of the soil. By utilizing a triangular block of life zones on the chart, three linear sets of climatic associations can be selected so that in each set one of the three, major climatic factors will be constant throughout while the other two factors are varied. As this can be done for each of the three factors, it should be possible to analyse from field measurements in each climatic association the precise effects of each of the individual major climatic factors on the community and its soil.

An edaphic association is the area occupied by a community on an azonal or intrazonal soil. Most of the variations tend to affect the water balance or humidity balance and thus give rise to effectively drier or wetter associations than the corresponding climatic association. For example, sandy soils drain and dry out more rapidly giving rise to a drier site whereas a raised water table provides more effective moisture than that furnished by rainfall alone and results in a moister community. The results are effectively the moving to the right or to the left of the climatic association conditions at that point.

However, there are other cases where the variations are more complex. The presence of a hardpan in the soil results in a less well-drained, wetter condition during the rainy season and a drier condition in the dry season. Less fertile soils and saline soils affect the physiognomy of the vegetation in like manner.

An atmospheric association is the area occupied by a community in an azonal climate. Examples of azonal climates are the Mediterranean climate, the monsoonal climate, that of cloud forest areas and that of especially windy areas as on ridges between peaks or in some coastal regions. As with edaphic associations, most of the variations in physiognomy of vegetation indicate effectively moister or drier conditions because of the atmospheric variations. Monsoonal climates ar~ those where the rainfall is concentrated in a shorter period of the year than would be typical of a zonal climate, Thus, in a wet forest life zone, where the average dry season in climatic associations would extend for two months or less, the monsoonal conditions give rise to wetter conditions in the rainy season followed by a long dry season atypical or azonal for the quantity of annual precipitation.

A hydric association is an area occupied by a plant community growing in shallow water where the soil is covered with water for all or nearly all of the year. This classification includes fresh, brackish and salt water areas but excludes all deep water areas. In the latter, which are of most interest to the animal ecologist, there is a need to develop a scheme or chart of deep water life zones as a basis for any classificatory system.

Associations may differ from the climatic because of both edaphic and atmospheric conditions which affect the same area. Examples of such edapho-atmospheric associations would be a cloud forest area growing over limestone so that neither the soil nor the climate would be zonal, or a beach thicket community growing on nearly pure sand and exposed to strong salt-burdened winds. Since the types of soils under shallow water vary from mud through sand to gravel and rocks,-even within the same life zone, bottoms which were not considered normal for the area would also have a double classification as edapho-hydric associations.

In addition to the one climatic association, the life zone may have several edaphic, atmospheric or hydric associations. Various combinations of these may be found in one life zone in one area or region, but it is not impossible also that a life zone with only one association may be found, especially in mountainous areas where a life zone may be very restricted in extension.

Naming of Associations

Except for the climatic association, the classes of associations cannot be utilized for specific association names. This is due to the fact that there may be several edaphic, atmospheric and hydric associations within a given life zone. The names applied must adequately differentiate the numerous associations in the latter classes while, at the same time, indicate the class to which they belong.

Also, there are two good reasons for not utilizing the names of dominant species in the nomenclature of the associations. The first is due to the fact that even with identical environmental conditions in different biogeographical regions, the dominant species which have evolved will be taxonomically distinct. Since an ecological system should permit global comparisons for a clearer understanding and satisfactory dispersal of knowledge of successful land use applications, association names should preferably be based on environmental factors rather than species.

Second, because of the wide-spread interference by man in the natural communities. of plants and animals, the utilization of dominant species in association names becomes inadequate. In spite of the fact that environmental conditions may be the same in many areas, the actual cover may vary from crops through pasture or various stages of succession to natural undisturbed vegetation.

Furthermore, even in considering only natural mature communities, names based on dominant species mean little to most workers in another biogeographical region. In such cases, specific names not only signify little or nothing in reference to the environmental conditions, but also cannot even be visualized.

In order to permit global comparisons, to arrive at a precise environmental classification regardless of the present state of cover and to present a comprehensible idea of the conditions involved, names of associations, in all cases other than the climatic association, should include, as briefly as possible, those edaphic, atmospheric or hydric characteristics which are essential to distinguish an association from all others of that particular zone.

As an example, within the Subtropical Moist Life Zone in Thailand, one may cite the shallow or Excessively Drained, Moderately Infertile Residual Soil, Dry Atmospheric Association. The association name thus includes information concerning the moisture conditions, fertility and formation in place of the soil plus the added dryness of the air due to the extended dry season in a monsoonal climate. The name clearly indicates that this is an edapho-atmospheric association.

Depending upon the past history of burning and cutting the association may be encountered varying from a fairly complete stand of trees through open savannah-like parkland to practically open grassland with some bush. However, the conditions of cover do not affect the association name or boundaries, but would enter in the third category of classification, which covers the actual cover conditions or land use found within the association limits.

At the present time, this association is part of the so-called Dry Dipterocarp Forest which extends also into the Subtropical Dry and Wet life Zones. Although the general soil factors are similar, the physiognomic and taxonomic differences indicate clearly that the Dry Dipterocarp name is too general and that the associations in the three life zones are distinct•

Another example which may be cited is the Low Fluvial Terrace, *Seasonally* Fresh-water Flooded, Fertile Soil Association in the Tropical Moist life Zone *in* Darien Province, Panama. The geomorphological information in the name indicates *that* these are deep alluvial soils with a fluctuating water table.

This is the cativo forest, predominantly of Prioria copaifera, but the association may be found also in cultivation or in second growth. The actual status would be depicted under the third category classification.

The above cited association names represent our present thoughts on how to classify and catalog satisfactorily the diverse vegetation and cover conditions which one encounters on the land surfaces of the globe. Refinements in the terminology and abbreviations can be developed with more extended use of such a classification. However, the aim intended, which appears feasible, is to provide in a three category classification, a clear cut definition of an area.

The association examples cited above utilize knowledge of the geomorphology, moisture conditions, soil fertility and special atmospheric conditions. In cases where the nature of the parent material is such that an intrazonal soil would be formed, then geological information such as Serpentine Rock or limestone would be added to the Association name. Also, when animal activities are a significant causal factor for the maintenance or the nature of the association, this factor should be added to the association name.

One problem of association mapping or nomenclature is that caused by the presence of a mozaic pattern of two or more associations within the same general area. A frequently encountered example is that of broken topography where one association occupies the narrow ridge tops or crests, another occurs on the lateral slopes and a third is found in the better-watered, more fertile bottoms of the intervening valleys. Foresters have usually solved the problem of correct sampling of such a mosaic of associations by running their cruising strips or sampling lines at right angles to the topography.

This is the sort of situation that has made many ecologists despair of developing a sound classification scheme of associations. On the other hand the same situation demonstrates how precisely the associations show the environmental conditions. In ecological classifications, such situations must be described as mozaics, with an explanation of the pattern of distribution and a description of each of the component associations.

Association Description Methods

How best to describe or characterize an association is still a moot question. A great number of systems have been proposed and utilized which more clearly than anything else indicate that the correct answer has not been found. Systems vary from the spectrum idea of Raunkier through various numerical systems enumerating percentages of constancy, frequency, coverture, etc., based on species, to diagrammatic representation of the elements of the community, to the actual sketching of the trees on a narrow long plot showing their height to scale as first suggested by Davis and Richards.

The best of the methods utilizing species and the most practical is that developed by the foresters which through judicious sampling and relatively simple measurements determines the distribution of species by diameter classes and basal area in addition to determining the quantity of lumber or wood by species. When they go on to measure the relations of height to diameter of specific common species in order to map out sections as different site classes, they get into the use of physiognomy very adequately as a means of measuring site productivity. Their eminently practical systems have received very little attention from the ecologists probably primarily because the latter have not been pressed to show the basic importance of ecological work to land use planning or other practical applications.

Of the systems that are not tied directly to species identification, Raunkier’s spectrum system is one of the most interesting. Regardless of the difference in frequency numbers of each species in the actual vegetation, he counted each species only once, assigning it to a given life form and thus had a different set of numbers for each association which was known as its spectrum. His scheme would very likely have been esteemed much more if there had existed a classification scheme for major ecosystems within which the arrangement of his spectra could have been demonstrated.

Dansereau partially combines Raunkier's system with frequency measures, has developed interesting figures to represent the life forms and places them in a diagram such as that of Davis and Richards, but not to scale. Actually, each species is not counted once but rather groups of similarly formed species are lumped together, and their frequency is roughly indicated. Obviously, too much mental calculation must be carried out to interpret such diagrams and there is a real question as to the ecological validity of his groupings. Raunkier had wisely avoided that problem by accepting the results of natural evolutionary processes as the best indications of natural units.

Of all systems for complex forests, the actual scale diagrams of Davis and Richards, which were used so effectively by Beard and other workers, gives one of the clearest ideas of the physiognomy of a forest community. It is a troublesome task to make a single diagram but once done it stands as a real monument to the association depicted, especially valuable in these times when so many forests are being rapidly cleared for additional agricultural areas.

However, the most serious fault of the design is that it depicts a very narrow strip in the forest which represents only one particular section of the association. Such a narrow strip must be selected subjectively as being representative of the association, a very difficult task and especially so for one not thoroughly acquainted with the community. Further since it shows the species as they actually are, it includes usually several individuals which have not yet attained to mature size. One can never be sure whether or not a given tree species is not larger at maturity than the biggest one shown in the diagram. Thus a great deal of effort is spent in duplicating other specimens of the same species without even then necessarily showing the mature stature of that tree species. Even then, the representation is of a chance historical picture of the development of the association which, if the plot had been taken a few meters away in any complex association, might show a considerably different picture. Even though the general aspects of physiognomy should be fairly comparable the set of species in their various stages of maturity might be considerably altered.

The need for more precise methods for the characterization and portrayal of the structural and physiognomic make-up of associations was given considerable attention on the ARPA financed research in Costa Rica. Several forest associations in 10 different life zones of the tropical region were studied intensively. From the data assembled, a new complexity index was devised which appears very helpful in characterizing natural mature forest stands. After the development of that index, the objective data of the components provided a satisfactory base for the development of an idealized profile which is believed to give a clearer picture of the physiognomy and structure of a stand than those of previously utilized profile systems.

The Complexity Index: Even though it has been well known that vegetation becomes more luxuriant and more complex with both higher temperatures and greater precipitation, there has been no general agreement on how best to quantify such complexity nor as to actually what factors contribute to the complexity other than a list of the species which are found growing together. Perhaps the concept of complexity can be most clearly expressed by citing a few examples.

When one pauses on a highway next to a fruit tree orchard, one is ordinarily observing a stand of evenly spaced, relatively even-sized trees of one species of a low, nearly uniform height. Within a very few moments one obtains a very clear mental picture of such a simple stand.

In an intermediate situation, one might observe similarly a natural forest stand comprising a mixture of only a few coniferous species, The greater height of the stand which the eye must span, the variable spacing and range in size from small to large trees make it necessary to look at the forest with greater care and for a longer period of time before obtaining a clear picture of the association, Such a stand is considerably more complex than the fruit orchard.

In wet areas of the tropical region, one may encounter highly complex associations with stands of appreciable height, numerous tree species in several stories together with a wide assortment of sizes and spacing. One must study such a stand for a much longer period than the other examples given even to obtain an approximate mental image of the complex forest.

There is no doubt that other components such as vines, epiphytes, shrubs and herbaceous plants also add to the complexity of a forest. However, if a complexity index is to be of practical use for comparison, the factors to be measured must be reduced to the minimum possible. But with such reduction there is a greater need to select those universal physiognomic characters of a forest stand which are most significant.

The important factors of density or number of trees per unit area and basal area of the stems are usually taken in ecological studies. Other than these two factors the height of the forest and the number of tree species per unit area appear to be the two other most significant physiognomic features of a natural forest. The former is not always recorded in ecological studies and the latter is rarely utilized.

The formula derived for the complexity index is as follows:

$$C, I. = 10^{-3} \text{ hbds}$$

Where

h = height of the stand in meters, For stands with an irregular canopy, the heights of the 3 tallest trees per tenth hectare plot are averaged out to secure the value.

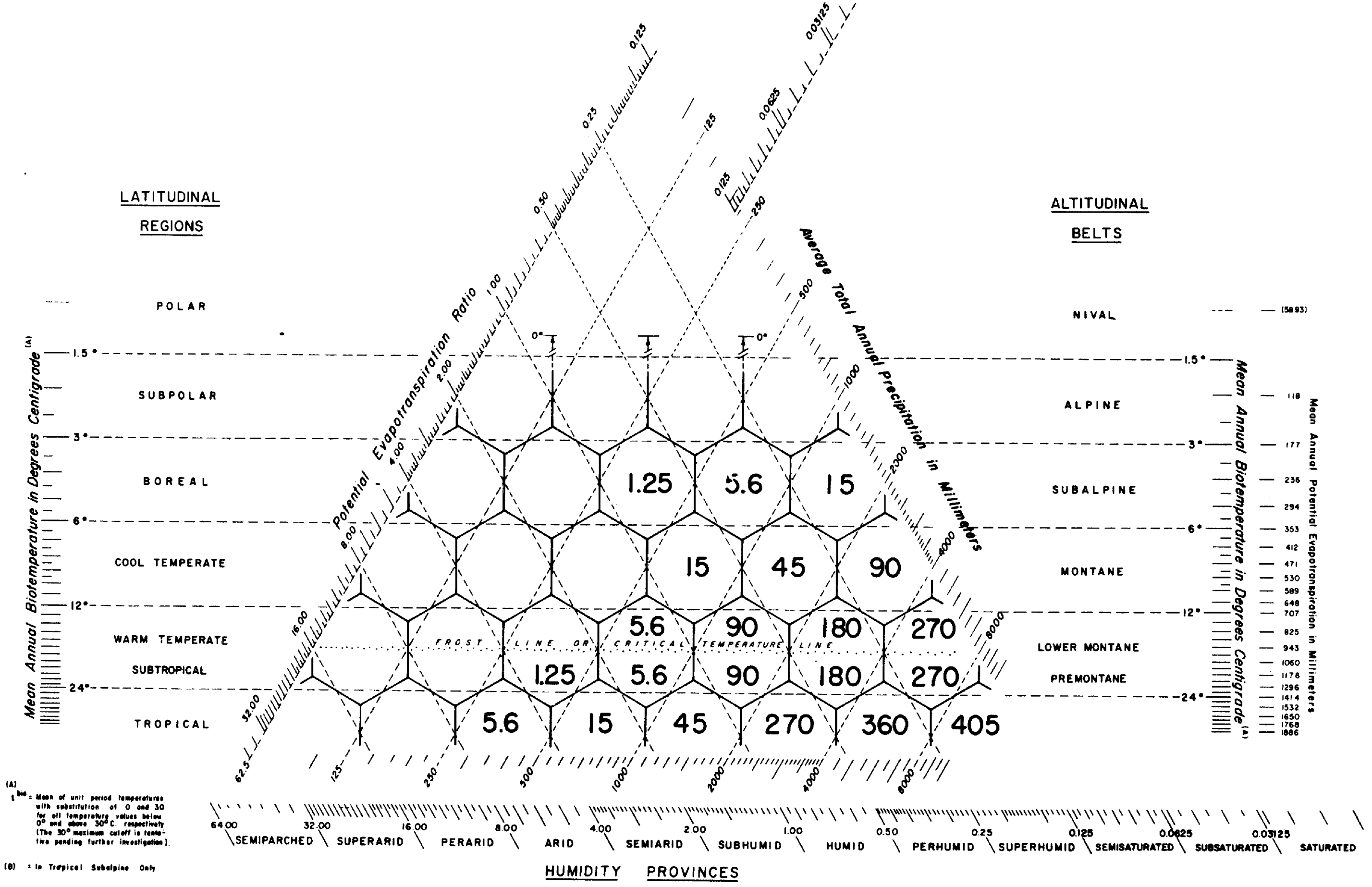
b = basal area in square meters calculated from diameters of trees 10 cm. or over in diameter at breast height (1.37 meters) per one tenth hectare,

d = density or number of tree stems of 10 cm. in diameter or greater per one tenth hectare,

s = number of species of trees of 10 cm. in diameter or greater per one tenth hectare, The division of the product of these four values by 1000 is carried out to reduce the number to a smaller relative Size.

No research has been carried out to determine the optimum size for complexity index plots. Working in the complex forests of the tropical region where larger plots require too much time, we derive the index from rectangular plots of 100 meters in length by 10 meters in width which permit good control of the plot borders. Plots are taken at random within mature, natural forest, but avoiding any exceptional blow-down or intervention by man. At least three plots, from which an average complexity index may be obtained, are desirable for each association.

FIGURE 3 COMPLEXITY INDEX VALUES FOR MATURE NATURAL FOREST STANDS WHERE NO STRONGLY RESTRICTIVE GROWTH FACTORS ARE PRESENT —



(A) t_{bio} = Mean of unit period temperatures with substitution of 0 and 30 for all temperature values below 0° and above 30° C. respectively (The 30° maximum cutoff is tentative pending further investigation).

(B) = In Tropical Subalpine Only

Once the values of the climatic associations of a few tropical life zones had been obtained, the pattern of relationships of the indices was observed and the series extended to all of the natural forested life zones of the world. The values for the hexagons are shown in Figure 3.

The index needs extensive testing, but preliminary data from life zones not found in Costa Rica have indicated that the predicted values are substantially correct. This implies that the complexity indices for a given hexagon are the same in various regions, as 90 for the Cool Temperate, Warm Temperate Montane, Subtropical Montane and Tropical Montane Rain Forest Life Zones.

Also, the complexity index value for a hexagon remains the same across the whole range of the life zone, provided that one does not change to a more, or less favorable association. Values where the life zones meet are an average of the values of the two abutting life zones. The abrupt change of complexity index values is in marked contrast to the impression of a continuum which is obtained by working with the distribution of taxonomic species.

Values of the complexity index do vary greatly within a life zone by associations. This increase or decrease in value due to edaphic or atmospheric influences may very well offer a promising approach to the quantitative evaluation of the effects of the limiting or favoring factors on vegetation growth. This variation is especially strong in the life zones along the unity potential evapotranspiration line where changes in effective soil moisture are especially important to vegetation.

Another interesting finding is that the frost or critical temperature line which separates the latitudinal Warm Temperate from the Subtropical Region as well as the altitudinal Lower Montane from the Premontane Belt does not affect the complexity index values of that row of hexagons. Even though very marked changes In floristic composition are found in crossing the line, apparently the physiognomic characters utilized for the index are the same on both sides of the line within any given hexagon.

The Idealized Profile: Due to their taxonomic and physiognomic complexity, most forest associations of the tropical and subtropical regions are extremely difficult to describe verbally in any manner that will adequately convey a composite picture of the stand. Some graphic illustration is very desirable to show the space and size relations of the various components. Photographs help to convey impressions but rarely show with clarity the basic structure of a forest. The forest profile diagram employed first by Davis and Richards (1933) and since utilized by various workers has proved to be of great value in depicting the general structural features within a single illustration.

In that system, after clearing out the shrubs and trees below 10 to 15 feet in height or simply disregarding them, the space locations and verticle profiles of all trees remaining on a rectangular strip of usually 25 by 100 feet are drawn to scale based on visual estimates or actual stem and crown measurements. The resulting sketches are assembled in a readily comprehensible scaled diagram which shows clearly the major features of the stand at the transect location. Species are usually indicated by letters which are keyed to taxonomic names in an accompanying list.

In utilizing the system of actual profile diagrams in Costa Rica, we have encountered two problems. First, due to the great complexity and local variability of stand composition and structure, the selection of the strip to be portrayed is difficult and subject to considerable bias. Separate workers would rarely choose the same area as being most representative of the forest type or association under study.

The second problem is due to the dynamic nature of a forest, which is continuously replacing those portions where individual trees or groups of trees have died or fallen. The resultant replacement pattern, comprising young and immature trees, varies throughout the stand so that, as a general rule, no two diagrams from the same forest would be alike. Furthermore, as Newman (1954) has pointed out, the presence of immature trees tends to obscure the fundamental layered structure of the forest.

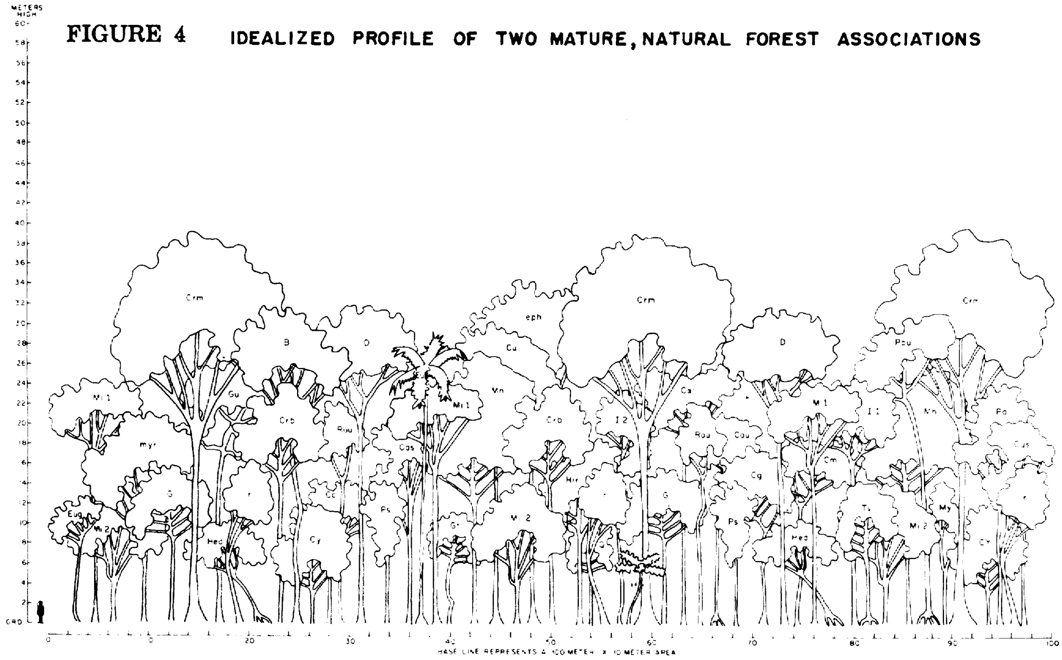
The diagrams for recording vegetation structure proposed by Dansereau (1951) pose even more problems. Not only do they have the same disadvantages pointed out for the actual profile system, plus the cumbersome requisite of interpretation of symbols, but they carry subjectivity still farther in the arbitrary establishment of groupings based on man's judgement of the relative significance of specific ranges of structural characteristics. Dansereau does include lianas, shrubs, herbaceous material and leaf characteristics, but does not give species identification of any of the components.

In the Costa Rican forest ecological research sponsored by the Advanced Research Project Agency of the Dept. of Defense, which has been carried on during the past two years, a different system for drawing up forest profile diagrams has been devised. The same parameters used in calculation of the complexity index for any forest association may be utilized for preparing an objective, idealized profile diagram which will generalize the basic structure of a forest stand more precisely than the actual profile diagram of Davis and Richards. The diagram is termed "idealized" because it attempts to represent the total mature structure which has been partly attained and towards which any immature portions of a forest are developing.

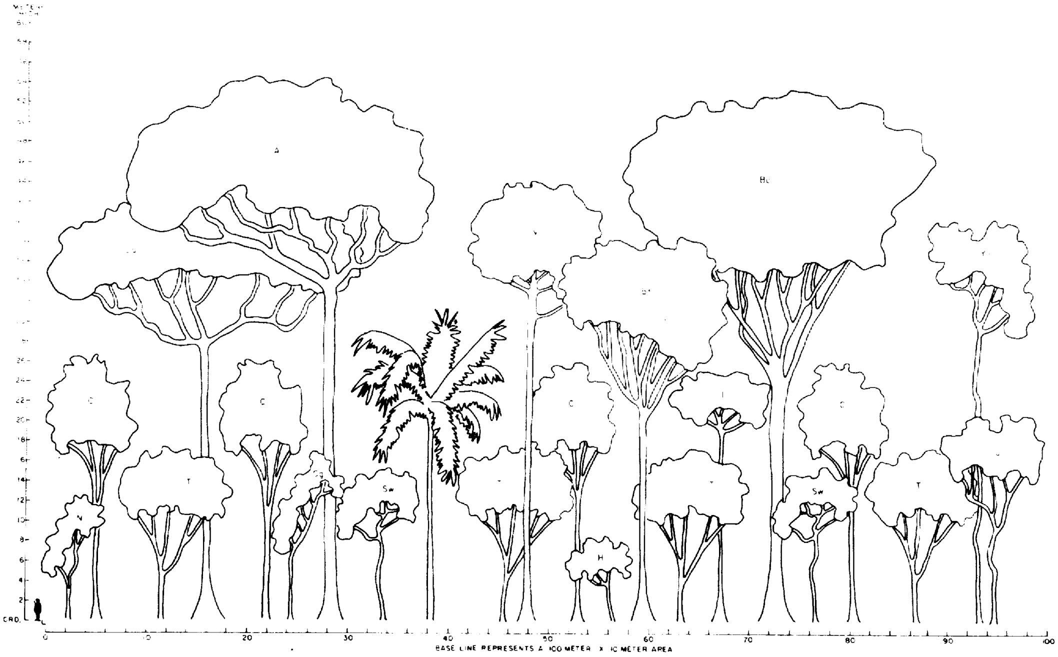
A tally of all trees having diameters of 10 cms. or more at breast height, by species, on rectangular plots of 10 x 100 meters provides basic data for calculating average density, proportional composition by species and basal area, The tenth-hectare plot size also facilitates conversion to a hectare basis for other comparative studies. Plots are distributed at random in the stand under study.

The average number of tree species per plot indicates the number of species to be placed in the scaled profile diagram representing 10 x 100 meters or a tenth-hectare. The actual species up to that number to be included in the diagram are those which are of greatest average frequency in all the sample plots taken.

FIGURE 4 IDEALIZED PROFILE OF TWO MATURE, NATURAL FOREST ASSOCIATIONS



CLIMATIC ASSOCIATION IN TROPICAL PREMONTANE RAIN FOREST LIFE ZONE, VALLE ESCONDIDO COSTA RICA



MONSOONAL ASSOCIATION IN TROPICAL MOIST FOREST LIFE ZONE, POTRERO GRANDE, COSTA RICA

Fotos\Figure4.bmp

After examining several individuals of each of these species, inside or outside the plots, one can then select one tree of each, the form and size of which is most characteristic of a normally full-grown or mature individual of the species. The diameter, total height, breadth and depth of crown are measured with instruments and a profile sketch to scale is made of these. Individuals with the greatest diameter are not necessarily selected. This measurement and sketching completes the field work needed for the idealized profile diagram.

The product of the average density of number of individual trees per plot times the average basal area in square meters per plot provides another objective value to be equalled or closely approximated in the profile diagram. At base camp, the product of the number of trees sketched and their combined basal area is compared with the average product obtained from the plots. Calculations are then made by adding duplicate individuals of the more frequent species in accordance with their proportion in the stand until the product of density times combined basal area equals or closely approximates the product obtained in field sampling from the plots. The final frequency distribution of the selected species should be very close to that of the plot tally averages.

sketches of the trees with the requisite duplication of those of frequent species are then assembled in a single scale profile diagram. Species may be lettered and keyed out as in the actual profile diagram. The examples of profile diagrams shown here in Figure 4 were results obtained by this method in forest associations in different life zones in Costa Rica.

As shown, the idealized profile diagrams are intended to depict the end result of growth in those specific associations. The results are almost completely objective, choice being confined only to the selection of sample mature trees of the species for measurement and representation. This assumes, of course, that the sample plots are selected at random and with sufficient sampling intensity within natural stands of a mature forest association. At any rate, very similar profiles should be expected, even if made by two different crews working in distinct portions of the same association. The system may be of value in temperate regions as well as in the tropics.

The most frequently-voiced objection to such an idealized profile diagram is that it represents an artificial combination of all-mature trees which would infrequently be encountered over any extensive area under natural conditions. This may appear to be a valid criticism but the advantages of a model of a stable all-mature stage lend strong support to the idealized profile diagram. First, it is a model for an association that can be duplicated by separate workers even with little or no previous knowledge of the association. Second, by utilizing models representing a standard, ultimate stage of stand growth, precise comparisons can be made between forest associations without the added complication of variable stages of growth as in the actual profile diagrams. similarly to architecture, one may compare structures with blueprints or artist sketches of completed buildings more accurately than if given only actual sketches of these in various stages of completion.

Animal Activity in Association Descriptions

Earlier, mention was made of the need for including significant animal action in the description of associations. This is not always possible, but there are certain cases where omission of such an item would leave out a valuable designative character of the association. One example that comes to mind is the presence of earth mounds erected by termites in certain savannas. The mounds are not only conspicuous but also they represent an appreciable movement of soil from lower strata in the earth to the top surface, an action which is bound to have considerable influence on the texture and fertility of the surface soil.

In the tidal swamps of Darien in eastern Panamá, another interesting case of the influence of animals was observed. There along the estuaries of the Rio Tuira, an association is found almost exclusively occupied by one species of tree, Aviceunia bicolor. In general appearance this tree is very similar to A. nitida with the numerous pencil-like pneumatophores protruding vertically from the soil as the most striking characteristic. However, A. bicolor has much wider leaves than A. nitida, very likely due to its inhabiting similar edaphic sites in the Tropical Moist Life Zone where the atmospheric conditions are more humid than those associated with the drier life zones in which A. nitida is found.

In the drier life zones, the predominant movement of water upwards to the surface of the soil maintains the high salt content of the surface soils even though tidal inundations are usual only in infrequent higher tides. In the moist life zone the predominance of precipitation over evaporation from the soil would tend contrariwise to remove salt from the surface soil and one would expect this stand to convert rapidly to a forest of Mora. That it does not, but remains stable for relatively long periods is very likely due to the activities of countless fiddler crabs which make their homes in the soil of this association. Although small in size, their habit of continually excavating muddy soil from lower depths and depositing it above the soil surface to one side of the hole results in an effective counteraction to the predominant leaching effect of the high precipitation. The bluish color of the soil casts or deposits indicate that it is brought from below the median water level. It is supposed that these humble animals by their combined efforts are the main reason for the maintenance of this particular association long beyond what would be its normal duration in the primary succession by their inadvertent movement of salt with the soil from lower to upper levels.

Association Niches

If an association is considered as a set of niches for plants and animals, then it is understandable that there should be competition within the community for the niches. This, in a sense is more noticeable amongst animals because activity of fighting is more obvious than the slow relentless competition between plants. In animal life, this competition seems more noticeable between units of the same species supposedly because their activities are the same and thus result in competition. On the small ponds in the tropics where abundant bird life may have built up, one notices that several different species work over the area with each carrying out a some-what different activity because they are looking for different kinds of food. Much more frequently in such a situation there is a chasing and squabbling among the individual units of the same species.

The overlapping of niches of different species can be analysed for the carnivores but rarely shows up as contemporaneous attacks on the same prey. When one considers all of the animals which prey on the little forest hare of the American tropics one realizes that there can be a great amount of overlapping of the various activity niches of the predators. The results of such competition are very difficult to observe or analyze. Because of their very distinct physiognomy these various predators are not usually thought of as competing for the same niche.

In the above case, the total food gathering activities of each predator, ranging possibly from the large cats to the bushmaster snake are probably quite distinct. The fact that all may prey on the hare implies some overlapping, but this may be distinct both by season and by the percentage which the hare comprises of the total food of each. Again, one predator may take only the young, another only weakened individuals and a third the fully active adult. In essence, then we have a debatable point as to whether the little forest hare comprises one niche for which various predators compete or whether the hare may be considered several different niches.

In the case of plants the lack of mobility renders it more easy to consider any overlapping of niches. This has been well recognized, Gams having introduced the term synusia, meaning a group of plants of similar life form and filling the same niche in the community. Saxton called it an aggregation of species or individuals making similar demands on a similar habitat. In addition to the taxonomic considerations, this is another of the points which has given rise to doubts as to the validity of associations.

If we think of only trees, the synusia are usually thought of as those in the same size or height group. The big question is whether or not the trees of such an apparently natural grouping are really making similar demands on a similar habitat. In the tropical forest one of the most interesting aspects is the great diversity of species and the continual change of their frequencies as one moves over a larger area in what offhand appear to be identical conditions. Naturally, according to the taxonomic definition of an association the resultant mosaic looks like anything but a true recognizable community.

However, the grouping of tree species as a physiognomic group, simply because they are of the same height, is apparently simplifying the field of physiognomy of trees too much. Although to an inexperienced observer these may appear monotonously similar, just as Richards speaks of the tropical forest looking like so many species of laurel, actually there is a great variation in the same height group of other physiognomic characters such as type of leaf, leaf size and texture, branching habits, etc.. What we probably have is a great number of niches in the tropical forest and a questionable degree of overlapping, just as in the case of the predators of the little forest hare.

If the tropics were only a special climate so favorable to evolution that several species could have evolved in the same region to occupy the same niche, then there would doubtfully exist any forest of only one or a few species. This has often been interpreted as due to unfavorable site conditions. However, some of the highest basal areas and largest trees are found in such supposedly unfavorable situations. On the other hand, the same aspect of one or few species could just as well be interpreted as a reduction of niches to one or only a few.

Common examples of such simpler structured forests in the tropics are the swamp forests, both fresh or saline, especially those due to not only a high water table but also to periodic flooding. Obviously such periodic flooding eliminates the possibility for different niches due to water abundance everywhere at the same time that it distributes the fertility of the soil uniformly. In addition, since these are usually forests on deep alluvial soils there is no variation of consequence in the depth of the soil available for the plants.

If we consider a series of climatic associations within a humidity province as for example the moist or wet life zones from the lowland tropical region towards perpetual snow and ice on the mountains the numbers of tree species in all strata are reduced as temperatures and precipitation are reduced. This would indicate that there are a greater number of niches as temperature and precipitation increases.

since potential evapotranspiration increases with rises in the mean annual biotemperatures, then it should be apparent that the greater range in quantity of water that is available for actual evapotranspiration in the progressively warmer and rainier series permits a greater number of combinations of water availability in the climatic associations. Other factors could be listed also. The potential for soil formation being faster, the potential for leaching being greater, there are more combinations of soil depth and soil fertility feasible, the warmer and rainier the region within the same humidity province.

Apparently then, the species have been evolved to fill different niches. In many parts of an association the general overlapping of the niches results in the haphazard scattering of the species through an area because their distribution is partly due to chance capture of a particular space. However, whenever a particular niche becomes more common in an area the particular species adapted to that particular niche may become relatively more abundant. Unless this abundance becomes sufficiently distinct to permit recognition and mapping of appreciable areas then it is more practicable to consider these endless variations about a norm as one association.

Of course, as one moves through even the same biogeographical region it is possible for species to be replaced by another with the same relation to the same niche. This is often true of species of the same genus and with the same life form. Although sometimes this is due to the frequent carrying out of taxonomic collections and study on a political rather than an ecological ecosystem basis, sometimes the truly distinct species are obviously due to local evolution to fill niches in what may have been separate regions in the distant past.

At the present stage of ecology, we are still too far behind in general association descriptions and mapping, especially in the tropics, to spend much present effort on the definition of each of the niches in the complicated associations. We should perhaps assume for the present that each of the species of the dominant vegetation in an association represents a niche and utilize the number of species of similar life form occupying closely related niches as part of the essential physiognomic description or definition for a particular association.

Physiognomic Data needed for Associations and Subdivisions

The subdivision of the association ecosystem into smaller units may become much clearer as a sufficient number of association descriptions have been compiled. That such further subdivisions are practicable and how they will be separated has been indicated already by work in Finland and perhaps in other places. In Finland, the foresters have started already to subdivide the natural association of spruce or fir into divisions which have a different rate of forest productivity. These can be identified and separated by the subordinate vegetation of shrubs and herbs under the forest. Because of that indication, it is thought desirable, until much more research data has accumulated, to confine the physiognomic diagrams of forest associations in the tropics to only the tree strata. Perhaps the vines and epiphytes which share space with the trees should be included but there is need for experimentation as to how these may be shown in a diagram to the scale of the trees.

As to what the physiognomic data of such a forest association should comprise, in review, some of the major data are the total number of tree species, the number of strata, their heights and the number of tree species in each. The character of buttressing may be important and should be included. The number of species which are deciduous and the period of time out of leaf is important although we have had little available data on such phenological information because of the stiff requirements of not only knowing the species but of covering the area with observations over several years in order to get an average of the lengths of the periods involved.

Other physiognomic data will undoubtedly be important but research is needed before definite statements may be made as to their validity. For example, Tasaico in making leaf measurements at four altitudinal belts in Costa Rica in climatic or close to climatic associations of the wet humidity province found that the average leaf tip length of the species in each belt was a definite and equal percentage of the average leaf length. since the relation of leaf length appeared to have a straight line correlation with the temperature, the long drip tips which have been pointed out as a characteristic of tropical "rain" forest turned out to be only the same proportionately lengthened tip on a relatively longer leaf.

since the width also showed a similar percentage average of the length of the leaf blade then supposedly the length, the width, the area and the length of the leaf tip are all related and that even though they may all be indicative as physiognomic characters there is no need for making more than one of these physiognomic measurements. This however was a research project carried out as an exploratory assignment. Before we can be absolutely sure of such relations more disperse projects should be carried out on the same relations with the application of statistical analysis.

What is needed in addition to the vegetation physiognomic measurements are notes or data on the activities of the animals which may be significant for the association description as well as geological, pedological and meteorological measurements. Relative to soils, the vegetation association appears to correlate with the soil series. The more detailed separations done by soil mappers into types will probably eventually be shown to correspond to the subordinate ecosystems within the association, as mentioned previously, which may be determined by the character of the brush and herbaceous vegetation in forest zones. However the ecologists are behind on association work and have not taken the desired lead in clarifying the association ecosystem for the soilsmen. This has resulted not only in relatively weak practical ecology but has prevented the pedologists from setting up a clear cut system of classification in their own field.

CHAPTER V

SUCCESSION

Definition

As the name of the process implies, succession is a series of phases of vegetation growth of successively more complicated structure and composition. The term is applied to a community of plants and not to the growth of individuals. In reality, as a vegetation community develops so also there are corresponding changes of the animal communities which inhabit the area. Further, one of the most marked changes of the environment is the development or change in the soil. Thus succession involves a broad development of the ecosystem in any given area. succession may be defined as a series of developments of the ecosystem in any given area leading progressively towards a more complex structure and composition of the association.

There are many types of succession depending on whether or not the development covers the complete chain from the bare lithosphere or deep water or repopulates variously reduced sections of an existing community. With the increase in man's influence on the face of the earth, with the correlated destruction or removal of natural communities from vast areas, the study of succession has taken on an importance far outweighing the study of natural untouched communities. However, by the same token, a knowledge of the mature natural state has also become increasingly important as indicating the end goal towards which succession is proceeding.

Evolutionary Succession

The natural evolution of organisms on the face of the earth has comprised a long chain of succession up to the present time. When life first emerged from the sea and started the conquest of the above sea-level regions of our planet, it encountered a very inhospitable environment. The surface was of bare rock or rock particles alternately wet by precipitation and dessicated by solar heat. Long epochs were to pass before this could be converted into a covering of soil which could support a luxuriant vegetation and an appreciable animal community.

The first invaders of the solid surface were the class of plants known as the Thallophyta, comprising the algae and the fungi. Most of the algae and the fungi thrive best in moist conditions as they are too thin and delicate to resist drying out.

However, the combination of an alga capable of manufacturing food by photosynthesis and a tough fungus coat furnishing protection to dessication, known as a lichen, was an evolutionary adaptation to the problem of invading such inhospitable sites. Such lichens are in evidence today on bare rocks, playing the same role of helping to break down the rock surface and holding a thin layer of rock dust and organic matter in place.

The Bryophyta or mosses and liverworts comprise the next advanced class of plants in the evolutionary scale. Some of the mosses are just as effective as the lichens in forming a primary invasion of an open rock surface. These are thin leaved and delicate also but are able to dry out and then return to a vigorous growing condition with the first wetting by the drops of rain. In more humid areas, where the lichens and the resistant mosses have accumulated a thin layer of soil, less resistant mosses are able to establish colonies and grow. The more luxuriant the moss growth the faster the incipient soil can be built up although normally, this is a slow, lengthy process. Most of the liverworts grow on moist soil and are less resistant to dessication than the mosses. Apparently they were not as important as lichens and resistant mosses in early attacks on the rock surfaces. Not all land surface is bare rock, under "desert" conditions it is mostly particulate.

Just as today some of the larger herbaceous plants which follow the mosses in colonization of a rock surface are ferns or fern allies, the class of Pteridophytes followed the mosses and liverworts in evolutionary development. Fossil fern records stretch back to over three hundred million years ago. The ferns and the forerunners of our present club mosses of the genus Lycopodium were larger plants. Already, there had been considerable progress in the development of plant communities from the early symbiotic beginnings of algae and fungi. From that time on the Pteridophytes evolved into two separate chains, the Cycadofilicales and the Cordaitales. These two branches of plants developed, along with the ferns and fern allies, the great swamp forests of the Carboniferous period from which the coal beds were formed.

Soil, at least in alluvial deposits, had developed areas of depth where vegetation of appreciable complexity could grow. Animal life in the form of insects, vertebrates and others were finding an increased number of niches available for their own evolution. Always, there was a slow steady succession towards more complicated ecosystems. From the Cycadofilicales were developed the Benettitales and the Cycadales of which only nine genera represent the latter in the tropical and subtropical regions of the present. The Cordaitales branched into the Ginkgoales and the Coniferales. Cf the formerly large group of the first, only one species remains, Ginkgo bioba of Eastern Asia which is widely planted in temperate zone parks and gardens.

The Coniferales persist in many genera and species. Coniferous forests still cover appreciable regions of the cooler parts of the earth.

Subsequently, the great modern group of plants, the Angiosperms, arose with its two classes, the Monocotyledons and the Dicotyledons to largely displace the Coniferales from the warmer regions of the earth and to push them back on to colder and less favorable sites. This process may or may not be finished but the cultural activities of man have so changed the natural vegetation of the earth that even if this successional trend had been operative until recently, it may have been stopped now.

This great chain of succession working through the whole period of evolution of plants on the earth is one of a continually improving environment as far as the development of soils go. The plant fossil record indicates a greater extension of tropical and subtropical climates in the past, but the major difference in the environment must have been the gradual improvement of soils. Each subsequent, more complicated community of plants was apparently able to more fully utilize the potential capacity of the site and correspondingly enriched the soil productive capacity still more.

Interestingly, the earliest divisions of plants to have evolved have persisted to the present time whereas several of the intermediate groups in the long succession have gone out completely or left only a very minor remnant, such as the one species of Ginkgo. According to size records from fossils those extinct groups were of large dominant species. When more efficient groups of plants evolved, the previous dominants were doomed to extinction. There may be a parallel therein with the animal succession through geological time as the fossil record is also full of large animals such as the dinosaurs and the mammoths which were dominant animals during certain periods.

The present day conifers appear to offer the clearest understanding of the forces at work in the major chain of succession. Where Angiosperms are the present day dominants as in the Tropical to the Temperate regions, the conifers are largely restricted to the sites of inferior soils. Only on such sites and possibly due to their symbiotic relations with root micorrhiza are they able to still compete satisfactorily with the Angiosperms. From this it may be inferred that the conifers evolved to occupy such sites when poor soils were widespread on earth. Perhaps even the inferior sites which were satisfactory for conifers were an improvement over the soils where previously the Cordaitales and the Cycadofilicales were dominant.

Primary Succession

There is an expression in biology, namely, "Ontogeny recapitulates phyllogeny" pointing out that the development of the embryo of the individual higher animal passes through a series of stages retracing the long past evolutionary history of the species. In a sense, present day succession on a rock surface in the cooler regions also traces the history of the long term evolution of vegetation.

As pointed out previously, the early lichen stage is followed by mosses and then ferns although at that point too some of the more modern grasses and other herbs enter the picture. The extinct groups naturally cannot enter the present chain, but conifers may take over and eventually with further development of soil and improvement of the site give way to broadleaf trees. This chain of succession of vegetation recapitulates the long term phyllogeny of the development of the plant community.

Such a succession may be observed in various stages of development on granite ledges where the last extensive glacial movement in the north removed all soil and previous vegetation in the relentless push of the ice southwards. In the lowland tropics, a comparable situation may be found on areas previously covered over with lava flows although in the latter region the conifers may be completely absent from the successional chain.

Another long succession frequently described in northern ecology textbooks is that of the gradual filling in from the borders with the development of a firm soil and an advanced community on sites formerly occupied by glacial lakes or ponds. Perhaps the comparable situation in the tropics is that of the development initiated by mangrove formation on the shores of estuaries and bays. However, the same filling of fresh water ponds or small lakes occurs in the tropics also and many times at a much faster rate. Usually such bodies of water were formed by landslides or lava flows although the same may be observed in artificial ponds or lakes created by man.

Examples of the development of land by mangroves are very common in the tropics. The speed of the process depends largely on the movement of suspended material in the streams which flow into the tidal estuaries or bays as well as the depth of the water in the latter. Where the hinterlands are areas of high rainfall the movement of soil seawards is tremendous.

An excellent example in the Americas may be observed in the Gulf of Darien and its estuaries in Eastern Panama. Above La Palma on the Tuira River, the tides affect the height of the water for even several miles upstream on both the Tuira and Chucinaque rivers. During the rainy season most of the upstream tidal rise is due to damming of the fresh water by the salt water tide entering the mouth of the Tuira River. During the dry season the salt or brackish waters penetrate much farther upriver and natives report seeing schools of jelly fish on the Chucinaque.

Near La Palma, all colonization of developing silt flats is carried out by the viviperous pointed fruits of Rhizophora Mangle. Due to the tidal range of up to 7 meters in height, this mangrove develops a truly impressive set of stilt roots. Trees attain to 30 meters or more in height. Once established, a stand of mangrove rapidly accumulates silt around the roots and builds the soil up to high tide level. Up to this stage only a limited number of other plant species enter the association with the red mangrove. The only tree is Pelilciera Rhizophorae of the Theaceae with a much widened base consisting of thickened bark over thin buttresses. The fern Acrostichum aureum establishes itself here and there within the mangrove forest as soon as the soil is elevated sufficiently.

From this stage of the mature Rhizophora stand there are three routes of succession possible. If the tidal waters become less saline, the Rhizophora stand may convert directly into a forest of Mora oleifera locally called "alcornoque". This is a one-species forest of less canopy height than the red mangrove forest. Where the succession has taken place in recent decades, one may observe an almost pure stand of alcornoque overtopped by an occasional isolated red mangrove, remnants of the previous stage of succession. This succession is almost universal at the head of the smaller estuaries which head into small valleys where the land rises fast. When the Mora is changing leaves, the yellow color of the foliage before dropping clearly shows up to the traveller in a plane as a thin border between the dark foliaged red mangrove forests and the sloping-land forest of various shades of green and less uniform canopy height.

If the land continues to rise but the tides still at least occasionally bring saline water over the soil, the red mangrove goes over to a pure stand of black mangrove, Avicennia bicolor, where as mentioned under associations, the fiddler crabs help to maintain the stand by continually bringing salty soil up to the surface from lower depths. Such stands are not too extensive in the Tuira River valley but last for considerable time. An overmature stand was observed which was dying out. Here the spaces caused by tree death were being regenerated exclusively by Avicennia bicolor indicating that this stage of succession may endure for at least more than one tree generation. The association is on a difficult site as the stand has less height than either the red mangrove or the alcornoque and the basal area is less. Eventually, when the red mangroves have marched farther seawards and less saline tides are combined with some washing off of salt by the rains, this stand will probably convert to a Mora oleifera forest.

The third possibility takes place perhaps through accident or more usually when the red mangrove stand disintegrates before conditions are suitable for the Mora. In that case, the Acrostichum fern may capture appreciable areas. This forms a very dense herbaceous stand about two meters tall which effectively bars any floating seeds such as the Mora from entering. Even though the site is ready for the successional stage of Mora, the capture of the site by the latter appears to be a time consuming process involving shading at the borders and a gradual encroachment from all sides.

The Mora oleifera stand remains pure until there is sufficient elevation of the soil by further deposition of silt to lessen the intrusion of brackish water tides or until the stands are effectively moved farther from the mouth of the river by the development of mangrove stands so that the tidal waters become fresh. As this takes place the Mora stand is replaced by a pure stand of cativo - Prioria copaifera. The cativo stand is a vigorous, tall-canopied, high basal- area forest reflecting the abundant water and rich soils. The site is adverse only to the extent of occasional flooding by fresh water but to a species which is adapted to that situation the site is not adverse.

With additional deposition of silt and elevation of the site, this stand eventually is gradually replaced by a mixed forest of the alluvial fresh water plains with a high water table, but only very rare flooding for short periods of time. Cativo still forms a part of the stand of such a forest but is not the only dominant as at the start of its successional stage. Although the stages of succession have been described as changes of species the physiognomic stages of the various stands are just as striking, if not more so, than the difference in taxonomic character.

This is the general picture of the successional stages in filling in an estuary of a bay by continual silt deposit. Coincidentally, another series of stages of succession are in operation along the river banks. Up river from the red mangrove areas, shrubs of the white mangrove border the river banks along with Tabebuia palustris as far as the river may transport fairly brackish waters in the tides. The silt banks then give way to a dense stand of the tall herbaceous Montrichardia arborescens which attains to heights of about six meters. This reaches its richest development in sections of a meandering river which is cutting back and forth across the alluvial plain. The Montrichardia establishes itself on the newly deposited silt on the slip-off banks which are found on the inside curves of the meanders. On the opposite or cut-off *banks,* theriver is undercutting the established stand of Prioria. It is supposed that the currents of the river with strong down stream flow along the cut-off bank and quiet or upstream-tending flows along the slip-off bank bring a brackish tidal water to the latter areas.

The Montrichardia stand starts well down towards the low tide level next to the river and gives way to Mora where tidal inundation is very slight at the top of the long-sloped bank. At the shallower edge, young seedlings of Mora establish themselves within the Montrichardia stands and on development shade it out completely. Often when seen laterally, the Mora stands show a curve or gradually rising height of the canopy back from the Montrichardia edge.

This in brief is an example of major successional processes where land is being formed and slowly elevated. The process is considerably more rapid than developments on an open rock surface because the soil is not formed in situ but is captured from that transported from upstream by roots and stems of vegetation. Thus, the soil is essentially fertile and deep even though it does not have a well developed profile in the earlier stages of succession. In many other rivers of the tropics flood conditions may establish new islands well away from all tidal influence. In such cases the succession is somewhat similar to that following removal of vegetation for temporary cultivation.

However, the series of successional stages in the development of alluvial lands outlined above have counterparts in other parts of the world. What is happening is a change of the soil conditions sufficiently to result in a series of distinct plant associations. The climate in such cases does not change. With development, the living community becomes progressively more complicated in some cases, but in others, as with the intermediate stages of black mangrove, Acrostichum fern areas and the Mora forest in the series outlined above, certain steps in the succession may be less favorable or productive than even previous ones such as the red mangrove forest.

There are other series where the complexity and productivity continue to increase. Examples in the eastern U.S. A. are well known. One of these is the improvement of a site with an oak-hickory association onwards towards a much higher development of fertility and water holding capacity of the soil reflected in the maple-beech stand. A similar soil improvement process occurs where conifers invade old abandoned fields where the soil has become run-down and has little fertility or water holding capacity. Once the conifer stand has developed and added considerable organic material to the soil, where fires have been excluded, then hardwood or broad-leaf stands enter and take over from the conifers.

This rather long-term succession leading to improved soil conditions and a more complex association of vegetation was the base for Clements picturization of all vegetated areas developing the site towards a climax vegetation. The trouble with such an hypothesis is that such successional trends only work in a limited portion of the land surface of the world. In other places a series of associations which lead progressively on to a higher association do not occur. There still exist several terminal associations within each life zone dependent on the nature of the underlying geological structures, topography, etc., which prevent the attainment to one specific climax in each climatic zone. Even though it might be supposed that eventually a several thousand foot layer of limestone or sandstone might be eroded away, ecology can not afford to depend on a system which takes such a long stretch of time into consideration.

Up to this time consideration has been given to associational succession. One example of this was the evolutionary development of vegetation over the ages which produced new groups of organisms capable of most adequately utilizing the greater complexity of the ecosystems and the increased number of niches in these. Another is a similar but briefer development with existing plant species with a succession of stages following each other on an extensive area of exposed rock. A different set of associational succession was depicted as a chain of development in tropical tidal estuary conditions where new land surfaces are being formed. Here conditions are not necessarily progressively better but fall into distinct associational steps dependent on various factors which successively become dominantly influential on the ecosystem. The associational changes which were influential in the proposition of the Clementsian climax hypothesis are essentially only the end portion of the second set of associational succession changes mentioned.

Secondary Succession

Different from the interassociational successions listed above a more commonly observed succession is that of the intra-associational succession which goes on continuously in natural conditions and has been greatly augmented by man's cultural activities. Within natural forest stands, openings are continually being created by the death and fall of dominant trees, whether of individuals only or groups, caused by tornadoes, cyclones or other restricted natural phenomena. In such cases there is little actual change of the conditions of the site beyond the temporary removal of the taller elements of the vegetation. The area is temporarily subjected to somewhat higher temperature conditions and receives more light, but redevelopment of the same association is usually so rapid or the area so limited in extent that one cannot adequately consider this as a succession of associations.

This succession may most clearly be observed in a small abandoned agricultural clearing in the tropical forest where the size of the opening is great enough to see the full development of the changes, but the area is small enough so that abundant seed material of the mature community is available on all sides. Such isolated agricultural clearings are also usually abandoned due to weed competition long before there is any appreciable deterioration of the soils. Succession proceeds rapidly through a series of stages towards replacement of a mature stand of the association.

The first stage is the brush stage which lasts from only a few months to two years. This is a combination vegetation of herbaceous plants, shrubs, vines and young seedling trees of invading species. This is a period which one might term “the machete stage” as it is practically impossible to traverse the area with any degree of comfort without opening up a narrow strip in advance with a machete. Many of the herbaceous plants form thick mats up to two or three meters tall. These are large ferns, Heliconia, wild gingers and the like. Shrubs of the Acanthaceae, Piperaceae, Solanaceae, Compositae and Rubiaceae, to cite the most common taxonomic groupings, intermingle their branches and stems with the herbaceous plants and the seedling fast-growing trees while all of these are criss-crossed, interwoven and overtopped by a mass of herbaceous and woody vines.

Depending upon the humidity of the site and the fertility of the soil, before long, the fast growing trees begin to emerge from this low tangle and form a canopy above a man's head. The species common in the American tropics are the balsa - Ochroma lagopus, Cecropia spp., Trema micrantha, Schizophyllum, Belotia, Mortoniodendron, Jacaranda and several others. They are characterized by their fast, vertical, monopodial growth with large compound or lobed leaves or, if of small simple leaves, by branch deciduousness. All are dispersed readily by wind or birds and, as to be expected, are abundant fruiters. These species are dispersed in the natural forest association where they hold on sufficiently long in closing openings to furnish seed for newly developed openings. They also find a rather permanent set of clearings, or rather a narrow strip, along the banks of streams and rivers. In such conditions in the natural forest, the weak-crowned non-vigorous tree offers very little resemblance to the vigorous offspring it gives rise to in an open site. Paul Slud found a different set of birds inhabiting the second growth stands as compared to the community within the natural forest. Again these seem to build up in numbers like the vegetation wherever there may occur any appreciable area of the second growth successional stages. Probably also these birds exist in small numbers in the natural forest travelling from opening to opening.

Once the rapidly growing trees clearly emerge from the brush and become dominant they start exerting an inhibiting effect on the generally lower mass of vegetation. Before long it is possible to traverse the stand without a machete even though with still some difficulty from the strands of vines. With the fast developing stands of these species the forest develops considerable height, the soil is once again well protected and cooler and the addition of organic matter to the cycle of overturn becomes appreciable. With the stand eight to ten meters tall, the soil improved and the forest floor much freer from superficial competition, new tree species begin to emerge as seedlings underneath the rapidly elevated canopy.

These species are surely less competitive than the pioneers in the open conditions and do not need as much direct sunlight for their development. They may possibly be somewhat deeper rooted than the pioneers but little or no investigation is known concerning that aspect of their development. These more numerous species continue to grow up towards the canopy where, as the shorter-lived pioneers begin to die or disintegrate, they take over and form a taller, denser and longer-enduring canopy.

The final dominants may comprise a part of this second canopy or enter the association still later with the still more improved soil condition. The pace of change gradually slows down and there is more difficulty in distinguishing such a late stage of succession from the random chance portion of a mature natural forest. The rate of development is correlated closely always with the condition of the site. Wherever deterioration of the soils has been appreciable the return to a condition approaching the natural forest may be considerably delayed.

In the preceding notes, a relatively little changed and small area was considered. As cleared areas become extensive another factor enters the picture. That is the availability of seeds from natural forest. Usually, under such conditions, the set of species which form the invaders are abundant. In fact they may have been built up so that in some cases one or only two species may almost dominate the first canopy. But the prime change in the pattern of succession occurs when natural forests are so distant that few seeds are available for the later stages of the canopy. These are usually less likely to be readily transported as the seeds of the invader species and are usually less prolific fruiters. Such a situation may give rise to a marked change in the succession with often a development of a set of intermediate species distinct from that which would be found in a small opening in the natural forest.

One of the problems in terminology within successional development is that caused by the different growth rate in the different temperature regions or belts and in the different humidity provinces. Whereas under tropical humid conditions, the stages succeed each other rapidly and can properly be thought of as stages of succession, in temperate regions the pace may be so slow that certain stages, even of the early ones, persist for several years. On a long term view they are also stages of succession but from the practical standpoint they are usually thought of as being associations themselves and a distinct part of the vegetational picture.

Because successional stages are usually of relatively short duration, they must be treated in ecological classification in the same manner as actual land use, which may change from year to year. Following the subdivision of an area into life zones and associations, both based on ranges of environmental factors, the next logical step in classification appears to be to set up a third category level of actual vegetation cover or land use. Thus, a given association area might feasibly contain several subdivisions such as mature natural forest, various stages of succession, cultivated crops, orchards, pasture, house-lots and roads.

Long term stages of succession in cold climates, because of the duration, may have to be classified as associations, but could be termed successional associations. On glaciated areas with shallow soils, long term successional development may go through associational developments very similar to the set of associations in succession following long term agricultural use with degradation of soils caused by man. However, such problems may actually cause few terminological difficulties for the ecologists working in such areas.

Succession in Land Management

This is especially important because man's land cultural activities primarily deal with the control of natural succession. In agricultural practices, the land user establishes an artificial association and then is concerned with preventing natural succession from taking place. This latter is usually called weed control because any plant not desired in the artificially established association is considered a weed even though the same plant might be of intrinsic value per se and even be cultivated and tended in some other artificial association.

Foresters and water management or wild life management men work essentially in managing succession rather than preventing it. However, the forester may be especially interested in maintaining a particular successional stage association because its specific components are of greater economic value than a subsequent natural phase. The best known example of such a case is the pine or coniferous forest which tends to progress naturally with site improvement to a mixed hardwood stand of less economic value. This is most effectively accomplished by controlled burning of the stand site at intervals of proper spacing to kill out invading hardwood seedlings and to impoverish the top soil sufficiently to render it unfavorable for the hardwoods, but not sufficiently to slow down the growth of the conifers to any appreciable extent. Long periods of controlled burning are followed by harvesting and a period of exclusion of fire during which the conifer is regenerated and brought up to a size where burning may be accomplished without killing the young trees. Such conifers and even some hardwoods such as teak indicate their ability to withstand this type of successional management by the thick protective bark formed at the near-ground level section of the bole.

As the young seedling and bush growth of early successional stage associations furnish more abundant browse for such game animals as deer and abundant seed production for certain game birds like the partridge, the wild life manager is also especially interested in managing his area to have a satisfactory balance in the series of successional stages. Where both lumber production and game management aims are essential, the forest manager can plan his cutting operations at intervals and with the correct distribution of cutting areas to satisfactorily meet both aims.

Land management for water production is especially concerned also with successional stages. This research is becoming especially important as water becomes one of the limiting natural resources for man in several densely populated sections of the earth. Since earlier stages of succession utilize less of the precipitation for transpiration than mature stands, ideal water management involves the maintenance of successional stages sufficiently dense to adequately protect the soil from erosion and to provide the maximum absorption and storage in the soil compatible with the least transpiration. Where distinct uses are to be combined, as water production, wild life management and timber production at the same time on the same area, this requires a thorough knowledge of the series of successional stage associations and methods of manipulation which produce the best balance of conditions to satisfy all requirements to the best possible degree.

More primitive agriculture in areas of not too dense populations and on soils which may not be dedicated permanently to agriculture because of topography, structure$_3$ low fertility or any combination of these, is one of shifting cultivation which utilizes the land for a few years followed by a long fallow period during which the successional processes of soil improvement return the soil to a condition satisfactory for renewed use in agriculture. This is a satisfactory land use for a low level culture or where transportation prevents any other form of utilization of the natural resources of the area.

Future Research Needs

The soils men are interested in fitting soils into classification systems. Most of the successional stage association soils are classified as series types or phases without much consideration as to how sets of these form series. They at least have clearly brought out the fact that the soil portion of the ecosystem undergoes considerable changes due to man's cultural activities or as affected by the redevelopment of natural vegetation on any given area. These two sets of knowledge of the soil and vegetational categories must be linked up by scientific studies and correlation of data. Further the animal ecologist must add his information on the successional changes of animal communities through the various successional stage associations of a series.

Throughout the literature, successional development, as with associations in a more mature stage, have been described and traced out taxonomically. It is still difficult to give any examples from the physiognomic point of view. This is clearly unfortunate and must be remedied in the future. Again we will not be able to exchange notes and knowledge across separate biogeographical zones until we can do so on a physiognomic basis. There are many indications in nature that this will be feasible.

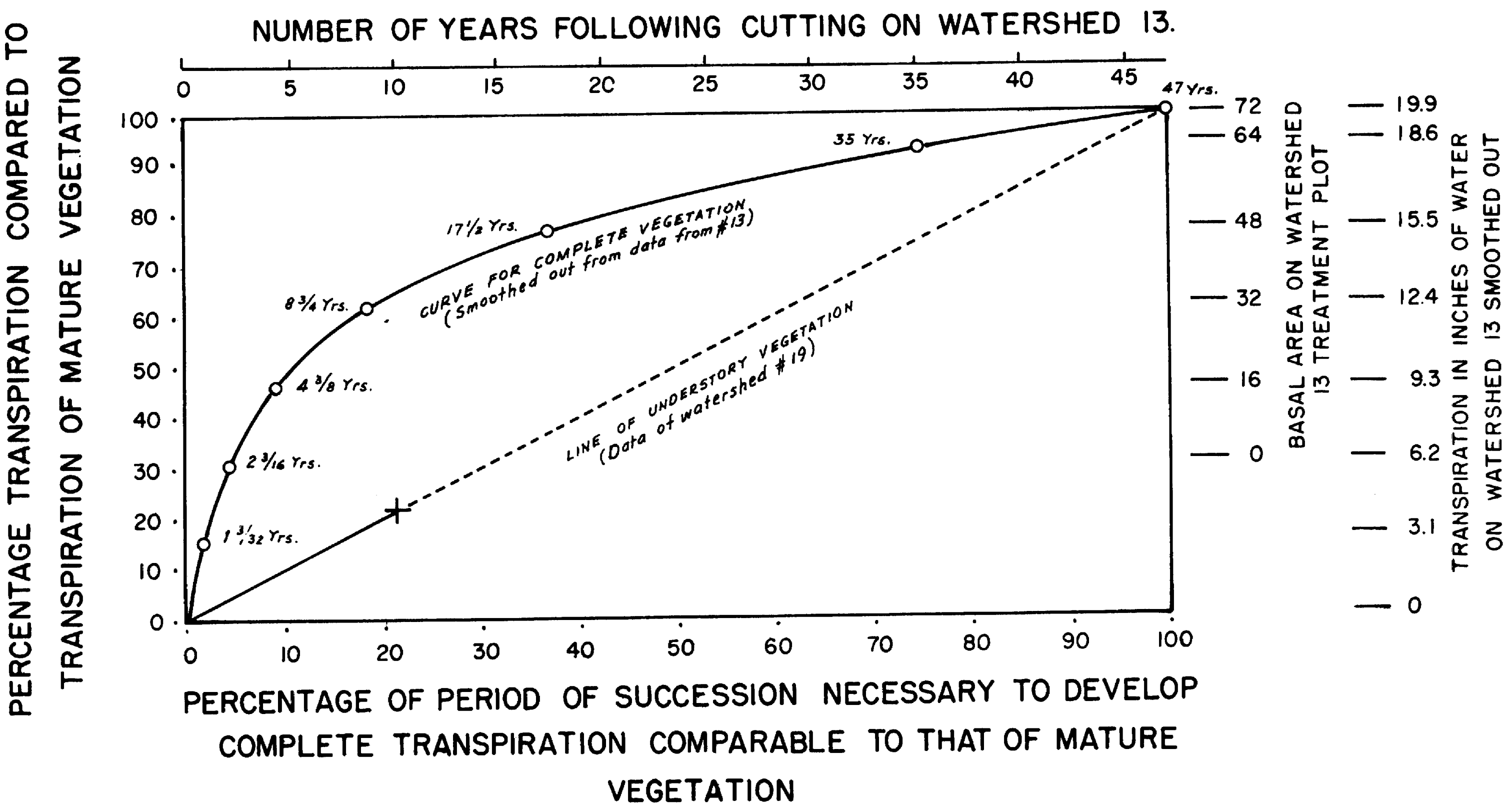
As an example Figure 5 shows the data from a series of successional stages in a watershed study area at Coweeta in the U.S.A. Although these data were taken specifically for the purpose of water run-off studies, they represent an interesting case of development measurements in succession. If these data are plotted with different logarithmically spaced intervals as shown in Figure 5 then a very interesting curve is obtained. With a successively doubled period of time the development of the vegetation follows a clear curve and the time periods correlate very well with the height of the vegetation and the basal area development. We need many more such studies on vegetation development in different associations. They do not necessarily have to be tied in with water production studies.

Another fertile field which the successional stages of vegetation offer is that of potential productivity of a site or association. For comparisons of this aspect, mature natural vegetations are too complex and constitute too great a mass of material to handle. Mature vegetations have only to grow sufficiently to replace their losses, in other words to maintain a static condition of balance. Thus, their production of new material does not necessarily represent their potential productivity in any given period of time. We also cannot measure productivity satisfactorily by removing the vegetation and growing thereon a standard crop. Unfortunately, such comparisons have been utilized in the past so that the tropics are considered of low potential productivity as deduced from the yield of corn as compared with corn production in an Iowa field.

Strictly defined, the potential productivity of a specific ecosystem ought to be set as the weight of dry matter per unit area which may be produced in a year’s time. Whether or not the material produced is of present importance to man may be an important economic consideration, but is not a basic criterion of potential productivity. This productivity might well be measured relatively by weighing the total dry matter produced on small plots of a series in a relatively uniform set of succession conditions and comparing the results. A more complete discussion of the measurement of productivity is given in Chapter XI.

FIGURE 5

TRANSPIRATION PATTERN AT COWEETA FOLLOWING TREATMENTS



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CHAPTER VI

THE SOIL

Soil as a Part of the Ecosystem

The soil is an integral part of every ecosystem. It represents the foundation or base within and upon which every terrestrial community of living organisms has developed. It is the transitional zone between the geological crust of the earth or lithosphere and the atmosphere or hydrosphere. There are, of course, areas where the geological mantle makes contact directly with the atmosphere or superficial waters, but usually there is a soil cover of variable depth between these.

Soil not only supports and provides part of the food and living space for the animals and plant communities, but is also partly developed by and from that same community. The various facets of climate continually act on the lithosphere to produce more of the raw constituents of the soil. It may be formed and remain in place or may be moved about on the surface of the earth by gravity, by water or ice and atmospheric movements. Thus, it may be built up from below, from the top or have been transported laterally from other sites.

The soil, which forms a definite part of any terrestrial ecosystem comprises only a relatively thin, superficial layer on the lithosphere. The surface rock layer disintegrates and develops into soil not only due to the effects of climate, but also to the mutual interactions between the soil and living organisms. In certain desert districts, where climatic effects have broken down surface rocks into masses of granulated rock particles, the effective lack of water prevents the growth of living organisms so that a soil is not developed. In any case, time for the accumulation of effects is an essential element for the development of a soil and a soil profile.

When biological assays of a soil are made, demonstrating the abundant populations of Protozoa, fungi and other forms of life which are an essential part of the soil, then the idea of the soil as a living community becomes comprehensible. But when one considers turther all the plant roots which traverse and feed in the soil as well as the many animals which move above ground and also burrow into the soil, then it is obvious that the above and be low surface organisms, the soil and the atmosphere above are all part of one living community and environment, the ecosystem.

This is obligatorily the viewpoint of the ecologist. The whole environment comprising the atmosphere and the hydrosphere, the living organisms, the soil and that portion of the lithosphere which is close enough to the atmosphere or hydrosphere so that there is a mutual reaction between the rocks and living organisms must be treated in unity, as making up together distinct sets of ecosystems.

Attempts to Develop Soil Classification Systems

The pedologists were among the first scientists to become interested in the broad relations between climate and soils. They found that with the exceptions of certain types of parent rocks, a given climate produces in place, from many different classes of rocks, the same kind of soil. Such soils were termed zonal soils. This paralleled the findings of early ecologists that major areas of vegetation, called formations, with a relatively uniform physiognomy could be correlated with climatic provinces.

As with the ecologists, data accumulated with additional study brought to light more and more exceptions to a clear-cut pattern of correlation of soils with climate. Little was apparently done to try to correlate soils with vegetation and gradually the pedologists turned more and more to chemical and physical analyses of the soil as their basis for classifications. At present, soils classification schemes have become increasingly complicated and less convincing.

In order to develop a satisfactory classification system of soils for the world, undoubtedly it will have to be one which fits precisely with a natural classification of ecosystems. The previous discussion of how the soil integrates with the other constituents of the ecosystem makes that appear logical.

With a unified approach, it appears possible that the nature of the soils in a given area may be interpreted from the physiognomy of the vegetation. If enough soil observations were to be made where natural vegetation could be examined to permit the development of a scheme of soil variations with physiognomy, it should be possible then to tell from the soil in areas completely deforested just what the original vegetation was like as to physiognomy.

Without question there exists already a wealth of soil measurements, descriptions and analyses from all over the world. Most of these were taken, however, either from areas where the original natural vegetation has been greatly altered or if not, then without correlated notes on the physiognomy of the vegetation. All of this wealth of soil data rather than lead to a natural system of classification has given rise to a general feeling that such a classification is impossible.

As a matter of fact, there appears to have been too much busy work of analyses, descriptions and measurements and too little thought given to the general soil picture for the purpose of learning what data should be taken in order to develop a classification system.

Originally, the zonal soils were correctly thought of as soils which were the direct result of a specific climate and the vegetation which could be correlated physiognomically with that climate. Some strikingly different soils were described and set forth as zonal soils. However, pedologists soon departed from the basic idea of a zonal soil by including more than one soil from a given climate. The best example is that of the northern prairie soil and grey-brown podsolic soil which may be found relatively close together under one set of climatic conditions, depending on the nature of the vegetation. No one appeared to realize that the mixed hardwood forest of the grey-brown podsolic soil was the natural climatic vegetation and that the prairie was a result of long continued burning with a resultant capture of the area by tall grasses.

This is perhaps understandable as a desire on the part of the soil scientists, just as with the early ecologists and vegetation, to have clear-cut, distinct units with readily recognized characters. Once the idea of clearly distinct zonal soils had been well implanted, the soil scientists were completely unprepared to understand the soils of the tropics. Thus, although they had found several zonal soils across the Cool Temperate region, they could only distinguish one or two in the whole breadth of the tropics. The result was the description of one or two broad zonal soils across several climates and several distinct vegetations. Of course, by the time the soil scientists began to look seriously at tropical soils, major soil classification emphasis had swung to the characters of the soil and soil profile so that climate and vegetation were not considered of any special importance.

With that misinterpretation of the original, logical idea of zonal soils, there is little wonder that subsequent attempts to develop logical and natural higher categories of soil classification were doomed to result in disappointment. Such categories were the order, suborder and great soil groups. Based as they were on correlations with an erroneous set of zonal soils, they could not emerge as natural groups.

The only sound division of higher category status was that of the division of all soils into pedalfers and pedocals. This was a logical division because it separated land surfaces into the two climatic provinces of moist and dry. Apparently, the dividing line coincided with the unity potential evapotranspiration line where potential evapotranspiration equals precipitation. Unfortunately a category of only two divisions is of little or no practical assistance in the classification of the complex array of soils in the world.

Soil Series

Contrary to experience in the higher categories, the classification of smaller local units has been much more satisfactory. Such units are the soil series, with subdivisions of types and phases. Perhaps the greater naturalness of such divisions is due to the fact that they were the actual units which field men found could be differentiated and mapped in the field. At the same time, of course, the dependence on scattered groups of mappers for the decision of the range in each category would be expected to result in some disparity of interpretation.

As defined in the 1938 U.S. Yearbook of Agriculture, a soil series is: "A group of soils having genetic horizons similar as to differentiating characteristics and arrangement in the soil profile, except for the texture of the surface soil, and developed from a particular kind of parent material". Obviously the phrase in the definition: "- - similar as to differentiating characteristics - -" left considerable range for interpretation and depended on how many characteristics were taken into consideration.

In 1949, Ricken & Smith commented as follows on the evolution of the concept of a soil series:

"The current concept of soil series is markedly different from that of earlier years. It will be recalled, for example, that at one time the Marshall series was broader in some respects than even the Prairie great soil group. Through the years, the series has come to mean a landscape unit that has a narrow range of soil properties, most of which are significant to agriculture. It has been possible to develop the series concept only through increases in the basic facts of soil science. It is to be expected that further development and revision of the concept are likely to follow as additional knowledge is gained. In summary, the series is a unit of soil classification which recognizes the maximum number of fundamental features of the soil profile. Hypothetically, the series is the largest landscape unit and also the highest categorical unit of classification about which all features and properties relevant to soil formation are distinguished.”

Soil Type

The soil type has generally been employed for subdivisions of a soil series differentiated primarily on the basis of the texture of the surface or plow layer of the soil. According to Ricken and Smith previous practices of mapping many types within a series have been changed to a narrower definition of a soil series including a specific range of texture and thus reducing the number of types as well as bringing the concepts of soil series and soil types closer together. They cite as examples the present recognition of loamy sand and fine sandy loam types, silt loam and silty clay loam types and silty clay and clay types as three separate soil series as compared with a previous single soil series with several types based on these various texture groupings.

A further subdivision, the soil phase, is a division of the soil type based primarily on significance to man's use of the soil rather than to any soil genetic significance. The general genetic properties of the soil phase must then be within the range of those of the soil type and soil series. Examples of situations favoring subdivisions of type into phases are those where different degrees of slope and degrees of stoniness occur, which would influence management practices for control of erosion in the former and the use of farm machinery in both cases.

Correlation of Soils with Vegetation

When the various discussions of these minor soil classification categories are carefully considered, one realizes that the soil scientists working primarily with soil characteristics alone, have come out very close to the natural ecosystems as defined also by the distribution of vegetation. Considered from a broad scientific view, the most unfortunate aspect indicated is the dearth of collaboration between soil scientists and vegetation scientists towards setting up a uniform ecosystem classification which would have been of use to both groups as well as providing separate data for mutual and more satisfactory resolution of problem cases. Taxonomic classification of plants based on several characters has been fortified considerably by checks from other scientific approaches such as serology, wood anatomy and more recently biochemical analyses. There is no doubt that both vegetation and soil classification systems would have benefitted mutually by collaborative research on a uniform ecosystem classification.

Apparently, the soil series should coincide with the plant association of the ecologist and with the forest type of the forester, wherever tree growth is possible. However, the lack of an integrated approach to the problem in the past renders it difficult to state categorically just how they do correlate in actual field practice. Further, the soils scientist has been concerned primarily with open agricultural areas to which the forester and association ecologist have been least attracted for their work and research.

Because of the primary importance of the soil to agricultural practices, the soil scientist needs to extend his classification system to a considerable degree of refinement in order to satisfy practical needs of management scheduling. Further, this becomes even more complicated because soil classification needs to denote the effects of soil deterioration caused by poor past management of soils.

Management of forests, range land and watersheds does not as yet require such a detailed soil classification as that essential for intensive agricultural use. Where these other uses require only extensive management plans, the soil series or the plant association appears to be satisfactory as a basic unit. In more intensive forest management, the site class as a division of the association or forest type is utilized. This is essentially a productivity classification. Site classes are determined physiognomically by the height-diameter relation of the same species. It is possible also that the same might be established physiognomically on the basis of the understory of smaller plants. Possibly the same could be done on areas from which trees have been removed for pasturing or in non- arboreal associations.

Correlation of Classifications in various Disciplines

In order to facilitate interdisciplinary studies and work on the classification of ecosystems and their soils, it would be highly desirable although not obligatory to use common terms for each classification in a satisfactory name for the major landscape units corresponding to the plant and animal community, the soil series and the forest type.

Where needed, the secondary division into smaller ecosystems might well be termed natural types. These would correspond to some of the present soil types as well as the site class of the forester. The ecologists do not have a satisfactory name for such a unit. As this is very often a variant due to a soil difference, the correlation of the name with that of type used in soil classification appears appropriate.

The use of the word "natural" to qualify type is suggested to permit a ready distinction from those soil types which are due to long agricultural use or abuse. These might well be termed cultural types. The term soil phase for still finer subdivisions of soil types is of major importance to the pedologist alone. The present use to indicate stony areas or range of slope gradient appears to be useful and satisfactory. For the most part this will have less significance outside of agricultural use.

The soil scientists could satisfy their needs for larger classification categories by adopting the life zone climatic unit which at the same time would give them a category division to correspond precisely with the divisions in other sciences. Such a category would automatically give the pedologists over 100 divisions for the land surface of the world. Since no soil association or type could be common to more than one life zone, their classification system would immediately become manageable and much simpler to apply.

Zonal Soils

Further, there is only one possible ecosystem within each life zone with a zonal or normal climate and a zonal or normal soil. This corresponds to the climatic association. Although I have utilized the term climatic association in previous publications, perhaps it would be preferable from an interdisciplinary point of view to term this the zonal association corresponding to either the soil, the vegetation, the fauna or the climate.

If the soils of the climatic or zonal associations from sets of contiguous life zones were studied and compared, the patterns of changes with increasing temperature or precipitation would undoubtedly emerge. Such true zonal soils could then serve as references for the study and analysis of azonal and intrazonal soils within each life zone. All this could lead to objective analyses of the effects of special rock bases, drainage conditions and the like.

As indicated by the soils of the climatic associations of the basal tropical life zones, true zonal soils in the tropics are not strikingly different in appearance. The majority will have the same structure and texture as these will have been derived by the uniformity of high temperature conditions. The essential differences will be those correlated with changes in water movement in the soils due to a uniformly significant increase in precipitation and humidity from the desert to the rain forest.

From the unity potential evapotranspiration ratio line to the desert, there will be an increasing tendency for water to move upwards in the soil for evaporation at the surface. From the unity line to the rain forest, the opposite tendency, that of water movement downwards through the soil with correlated leaching will increase. Thus, the pH and the fertility in the upper layers of soil will be significant characteristics.

Also, the vegetation becomes increasingly more exhuberant from the desert to the wet forest after which due to the excessive rainfall and leaching, it becomes less impressive in the rain forest. Thus, up to a certain point, more organic matter is added to the top of the soil as rainfall increases, but in inverse ratio, once broken down, the products will be leached from the soil more rapidly.

In moving towards lower temperatures, the zonal soils will be noted as having a slower breakdown of organic material. However, this brings up a very interesting question, namely that of the podsols under boreal coniferous forests. The conifers, as mentioned under Succession, represent the remnants of a previous world wide vegetation which has not been completely replaced by the more recently evolved Angiosperms. In the Boreal region, it is very possible that a climatic or zonal association of Angiosperms does not exist. Therefore, the zonal soil under the present climatic association may show a distinct break in continuity of the pattern of zonal soils from the warmest to the cold regions.

Aging of Soils

The effects of time or aging are said to bring in another interesting complication in soils. This is especially important in the tropics where the benign climate may effectively speed up the process of aging. Geologically recent volcanic soils appear to fall outside regular classification systems. Often they are rich in minerals, have excellent structure and high fertility and do not show the regular profile of older soils. Such soils permit successful agriculture and grazing in areas with high rainfall which would not be satisfactory on older volcanic or other soils.

After a long period of time, such volcanic soils attain to a normal condition. Later, according to Mohr, soils become senile, as a result of aging. However, because long, geological periods of time are involved and little is known of the history of use of such areas, the subject of senility of soils needs much more study. We do know that volcanic and alluvial soils eventually develop into less fertile or more normal soils. That change in alluvial soils may be observed on old river terraces.

If there is some change of fertility and structure of such soils to a more normal profile and soil characteristics, it is possible that even normal soils would become poorer in fertility after long periods of time. This idea must be weighed against the general opinion that mature natural vegetations are in complete equilibrium and that the soils would be maintained in balance providing there is no intervention by the cultural activities of men.

There are many soils which have obviously been deteriorated by the cultural activities of man. Extensive areas in the tropical region, known variously in the Western Hemisphere as savannas, llanos or campos are the result of long continued burning with a corresponding deterioration of the fertility of the soil. Fires favor the grasses and eliminate most of the bush and tree species with the exception of a few fire-hardy species such as Curatella americana.

The growth of the previous year which has not been grazed is converted during the dry season into an ash cover on the soil. If this is not blown off by the winds the first rains of the wet season may carry much of the fertility to the streams along with the run- off. Leaching during the rainy season carries fertility down to the water table where it may become fixed as a hard-pan. Once this is formed there can be no fertility moving up from greater depths and the top layer becomes more impoverished each year through burning and loss of ash.

Most of these savannas are to be found in the Tropical Dry Forest Life Zone but areas of savanna exist in the Moist Forest Life zone also. Usually, these were lighter or less fertile soils genetically so that they dried out sufficiently to permit burning. Following long continued burning, they become very infertile.

Shifting cultivation with a long period of fallow permits the rejuvenation of the soil. However, once population pressure becomes heavy, the fallow period is successively shortened so that the soils become less productive and less able to rejuvenate rapidly. This process is becoming more and more marked as population increases in the tropics.

Thus, with more and more people to support, the general picture in the world is that of increasing areas of degenerated soils. As population increases, expansions or colonization of less and less productive ecosystems is taking place. Whereas the native populations of the Chimaltenango valley in Guatemala have continued to produce corn annually for at least several hundred years without any obvious deterioration of the soils, some of the recently colonized areas in the tropics have been abandoned in periods of less than 20 years.

Knowledge of such degraded areas in conjunction with comparisons of yields of corn in the tropics with those of Temperate regions has given rise to a wide spread opinion that tropical soils are not very productive. Nothing could be farther from the truth. What is needed is a fairer comparison and a more satisfactory measure.

Productivity

Once one is acquainted with successional or second growth development in both tropical and temperate regions, he becomes aware that growth is much more rapid in the tropics. This is due in part to the longer temperature growing season in the tropical region, but is proportionately much greater even if growing seasons are weighted proportionately. The average temperature during the whole growing season must be taken into account. Very likely, production is proportional to the mean biotemperature, but we do not as yet have sufficient data to decide whether this mean biotemperature would be annual or the mean of the temperature growing season.

To calculate productivity for any area, the factors to be taken into account are temperature, length of temperature growing season, portion of temperature growing season with adequate moisture, fertility of the soil and any other factors which would favor or detract from growth. Obviously, there are too many factors and too little knowledge, at present, of the relative weights of each environmental factor to permit satisfactory calculation of productivity in that manner.

The number of tree strata or stories is not well understood and is very often difficult to note with clarity in the natural forest. In the moist and wet forest life zones, this may be considered as 4 for the tropical region, 3 - warm temperate region, 2 - cool temperate region and 1 for the boreal region. Apparently these numbers are not exceeded in nature.

One way suggested for checking the number of stories is that of dividing the stand height in meters successively by 2 and finding the number of results greater than 5-meters which is considered as the minimum height for trees. Thus a redwood stand of 84 meters in height successively divided by two would give: 84, 42, 21, 10.5 and 5.25. This potential of 5 stories is greater than the maximum possible 3 of the Warm Temperate region. The nearly complete dominance of redwood in such a stand is also a clear indication that it is a one-story stand. Thus, since the redwood stand falls in the Warm Temperate Moist Forest Life Zone where the climatic association should have three stories, the relative height of the redwood stand is 84 m. divided by three or 28 meters. Such a site is not as productive as a stand of 30 meters height with three stories in the Tropical Moist Forest Life Zone.

The number of stories diminishes also with less humidity within the same region. Again, the successive division by 2 of the total stand height gives one a clear idea of how many stories are possible. Apparently, the maxima in the Tropical Region are 3 stories in the Dry Forest and Rain Forest Life Zones, 2 in the Very Dry Forest Life Zone and 1 in the Thorn Woodland Life Zone.

In all likelihood, the subject of story analysis will turn out to be somewhat more complicated than the hypothetical calculations mentioned in the preceding. In actual fact, there has been practically no study of this aspect of vegetation association physiognomy. Until many artificial diagrams are made, as discussed under associations, we will not be able to read out the true significance of forest stories. Again there is an indication that the number of species should double in successively lower stories within climatic or zonal associations. Variations from that hypothetical normal pattern may need to be taken into account in the determination of relative productivity as well as of actual evapotranspiration.

The assumed productivity of a site is often low because man attempts to produce a crop completely different from the crop which evolution over the ages had established as the most productive unit for the site. Thus, man can expect to capitalize very little on the potential productivity of a site when he replaces a vigorous forest stand of 4 stories of hardwood trees in the tropics by a stand of corn only 2 meters tall or a grass pasture of only 1 meter in height.

CHAPTER VII

THE ATMOSPHERE

Composition of the Air

The mixture of chemical elements in gaseous form which is held to our planet by gravity is known as the atmosphere or air. Apart from the water vapor and dust content which varies from place to place and from time to time near the surface of the earth, the atmosphere is quite uniform in composition. The usual make-up of dry air in percentages is as follows: nitrogen -78.09, oxygen - 20.953 argon -0.93 and the remaining 0.03 percent mostly of carbon dioxide with traces of the rare gases neon, helium, krypton and xenon along with negligible quantities of free hydrogen, methane, and nitrous oxide.

The percentage of carbon dioxide may be increased considerably in the vicinity of volcanoes during the eruption of gases from the earth's interior. The same is also augmented over cities and industrial establishments where man's activities are responsible. The progress of widespread burning of fossil fuels in the present industrial age has even led to some conjecture on the possible effects of man's changing significantly the composition of the atmosphere.

The physical composition of the air continues up to a great height. Between about 15 to 30 K. above the earth, there is found a layer with a high content of ozone, comprising oxygen molecules with 3 rather than 2 oxygen atoms. Although high above the earth, the stratum is of considerable biological importance due to its absorption of ultra-violet rays which are harmful to organic life.

Density and Height of the Atmosphere

The total mass of the atmosphere of the Earth is relatively small, being equivalent in weight to a layer of mercury 760 mm. in depth. The atmospheric pressure, measured with a barometer, is normally expressed in its equivalent height of a column of mercury.

Stumpff describes the air mass in the following terms: "As the specific gravity of this liquid metal (mercury) is 13 times as great as water, the atmosphere's mass is therefore equal to a sheet of water of corresponding area with an average depth of 33 feet (slightly under 10 m.). But even at sea level - where it is most dense - atmospheric air weighs about 800 times less than water. If the air were a liquid of constant density, that is to say, if it were as dense throughout as it is at sea level, then its surface would be at an altitude of 26,000 feet (nearly 8000 meters) and the peaks of the Himalayas would form islands up to a height of about 3000 feet (just over 900 meters) above this homogeneous atmosphere".

Actually, the atmosphere thins out with elevation and extends far beyond 8 kilometers. At the top of Mt. Everest, the highest land surface on earth, the atmospheric pressure is only about 230 millimeters or less than one-third of the density at sea level. At 400 kilometers above the earth, the atmospheric pressure is only one three millionth of a millimeter with density only one ten thousand millionth part of its value at sea level. In spite of the low density there, it still contains many million times as many molecules as the estimated density of 1 atom per cubic centimeter in space.

Water Vapor Content of the Atmosphere

Although all terrestrial plant and animal life, with the exception of certain anaerobic forms of lower life, depends on the carbon dioxide and oxygen of the atmosphere for existence, these are not limiting factors at lower elevations over the whole planet. It is the temperature and the moisture content of the air, which, in their variations over the planet, cause the notable differences in plant physiognomy and animal activity as per the divisions into life zones, and associations.

Where climates and soils are normal or zonal, the quantity and pattern of annual precipitation in combination with mean temperatures give rise to predictable humidity conditions of the atmosphere. Groups of life zones with the same humidity conditions form humidity provinces, wherein the range of the potential evapotranspiration ratio is the same. The different life zones within a given humidity province have distinct ranges of mean precipitation and mean biotemperature, but the various combinations of these result in the same humidity range throughout the province.

Just as in the case of edaphic conditions different from zonal soils, so also, variations in the pattern of precipitation from that of a zonal climate have produced significant changes in vegetation physiognomy and animal activity to necessitate the establishment of atmospheric association categories in ecological classification. The major atmospheric variations are discussed in the following notes:

Monsoon Climates: In parts of the tropics and especially noteworthy in southeastern Asia, the reversal of prevailing winds during the year produce an abnormal precipitation, the duration of the rainy and dry seasons may be the same, about six months each, so that the vegetation and animal activities have been evolved to adapt to variable quantities of rainfall during the rainy season, followed by long, continuous dry seasons.

However, monsoon climates are variable. Not always is there a relatively even division of the year into dry and rainy seasons. The following precipitation data are from three stations in Costa Rica which fall within the Tropical Moist Life Zone. Of the ten year records, the monthly means of less than 100 mm. of rainfall are underlined in order to indicate the approximate length of the dry season. One must take into account also the amount of storage moisture in the soil to obtain the true length of the dry season.

	Chase	Río Incendio	Esparta
Month	Baja Talamanca	Golfito	Puntarenas
Dec.	249	140	23
Jan.	209	52	5
Feb.	195	71	7
Mar.	122	46	2
Apr.	124	138	42
May	215	294	310
June	167	294	303
July	236	305	328
Aug.	206	405	325
Sept.	79	360	329
Oct.	151	533	544
Nov.	209	378	189
Total	2162 mm	3016 mm.	2402 mm.

The ratio of the dry to wet portions of the temperature growing season is shown at the bottom of Fig.5. In the Tropics, where the temperature growing season is 12 months long, the ratio figures correspond to months. For the Chase and Esparta mean annual precipitations, a normal or zonal dry season would comprise a 3 month period and for Río Incendio slightly over 2 months. If a rough figure of one month for drying out of the top layer of soil is assumed the effective dry seasons for the three stations are: Chase - 0 months, Río Incendio - 2 months and Esparta - 4 months. Río Incendio is the only one of the three stations with a normal precipitation pattern or zonal climate. Esparta is definitely a monsoon climate with a one month longer dry season than normal. This would correspond to a dry atmospheric association. Chase, without an effective dry season, demonstrates the opposite of a monsoon climate. The area corresponds to a moist atmospheric association.

Comparative physiognomic studies on series of dry atmospheric, zonal and wet atmospheric associations in specific life zones apparently have not yet been undertaken. Observations in the dry season in Costa Rica indicate that the dry atmospheric associations of the tropical moist life zone appear much like the associations of the tropical dry life zone at that time whereas the moist atmospheric associations superficially appear to belong to the tropical wet life zone. The relations are apparently similar to the appearance in the range of dry edaphic, zonal and moist edaphic conditions within one life zone.

Study of the literature indicates that the region of southeastern Asia has such extensive monsoon climatic areas that a specific flora has evolved to fit the conditions. So far, observations have not confirmed this in the Americas. Perhaps the monsoon climate areas in this hemisphere are not of sufficient extension to have fostered the evolution of specially adapted species. On the other hand a knowledge of the conditions produced by such atmospheric variations does permit an understanding of some odd distributions of tree species.

For example, in Costa Rica, Tabebuia guayacan, is a large Bignoniaceae tree which Is one of the characteristic species of the Tropical wet life zone climate and related associations. The leafless crowns covered with a mass of bright yellow flowers show up clearly from a plane at the time of initiation of the rainy season. Surprisingly, when first encountered, the same species is also a normal component of the dry atmospheric association of the Tropical Moist life zone. On comparison of the precipitation data, however, it is obvious that the species is subjected to similar monthly mean rainfalls during the rainy season in both life zones. Since the tree is deciduous, it simply passes through the severe dry season of the dry atmospheric association in a long resting period.

A corresponding odd species distribution with extension of range into the moist atmospheric association of the Premontane Wet life zone is that of Chaetoptelea mexicana at close to sea level elevations inland from Limón, Costa Rica. This large tropical elm tree is a common component of the Premontane Rain life zone in Costa Rica at medium elevations, primarily between 1000 and 1500 meters above sea level. The year long moist atmospheric conditions near Limón permit it to thrive far from its typical habitat. However, since it is also associated with a high water content of soils in the Premontane Rain life zone, it may only be able to grow in the moist atmospheric association of the Premontane Wet life zone where extra water is available in the soil. The examples observed were located at the foot of slopes adjacent to alluvial plains where extra ground moisture would be available.

Mediterranean Climates: Another series of special atmospheric associations is found frequently within the Warm Temperate region. The condition corresponds to a reversal from the normal climatic pattern of heavier rainfall during the warm season of the year, to that of major precipitation during the months of low temperature, with drought during the warmer months. These special conditions were first encountered by scientists in Southern Europe and around the Mediterranean Sea, hence the designation as a Mediterranean climate. The same atmospheric conditions are also common in Chile, southern Australia and in the south-western U.S. A..

The lack of coincidence of a favorable humidity growing season with the most favorable temperature growing season for the latitudes has given rise to the evolution of vegetations of very distinct physiognomy and usually of distinct taxonomic species. Leaves are, in general, more sclerophyllous and the height of the vegetation is less than would be encountered in zonal climates of the same biotemperature means.

The distinctness of the vegetation physiognomies has given rise to specific common names such as “chapparal” in southwestern U.S.A., "maqui" on the Mediterranean coast and "malee” in Australia. These appear to be best known in the Desert Bush, Thorn Steppe and Dry Forest life zones of the Warm Temperate region. Very few descriptions of altitudinal belt vegetations from such regions are accompanied with the necessary climatic data to permit correlation with the life zones of the chart. The heavy snow areas in Californian mountains may correspond to upper elevation Mediterranean climates.

Fog or Mist Belts: One moist atmospheric condition of wide occurrence in local areas is that of extra humidity above normal caused by the frequent occurrence of fog or mist, in contact with vegetation. One of the most commonly encountered examples of the condition is that at frequent cloud levels in areas of orographic rainfall.

The contact of cloud belts with mountains is often found in the Tropical and Subtropical regions. This has resulted in the erroneous utilization of the term "cloud forest as indicating a definite association or vegetation. This is a case where two striking characteristics, namely, the abundance of epiphytes and the impressive aspect of mist curling through the trees have been given undue emphasis in vegetation characterization. Other physiognomic characteristics, such as the height of the vegetation may have more physiognomic significance, but being less noticeable than the epiphytic growth are often not even mentioned in vegetation descriptions.

In reality, cloud forests occur in all tree belts in the tropical region, so that the range in physiognomies and sets of species are considerable. These can be specifically assigned to moist atmospheric associations of life zones of the altitudinal belts. The condition is most commonly encountered in the Moist to Rain forest life zones in the Premontane and Lower Montane altitudinal belts of the tropical region.

The moist atmospheric condition caused by cloud or mists also occurs outside of the tropics. One of the well-known associations of this condition is that of the redwood - Sequoia sempervirens in northwestern California. Even with the considerable natural height of that species, the stature of the trees is increased by the addition of extra water to the soil in the form of drip from condensation on the foliage. The stagheadedness of some redwoods or the dying back of the terminal point of the trees probably is caused by cyclic variations of a few years duration of the quantity of mist reaching the stand or of precipitation.

This increase in stature of the vegetation in all except the most humid environments is an interesting physiognomic characteristic of the moist atmospheric associations. One of the most striking cases is found along the Pacific coast in Peru, where the clouds press against the hills which rise above the surrounding desert. Being a Mediterranean climate, without the mist, the natural vegetation would be low chaparral. Although the original vegetative cover of the "lomas" has been almost completely destroyed by man’s activities, a few remnant trees in certain localities indicate that the extra moisture derived from condensation of mist and dropping to the soil made possible a tree forest cover.

Artificial forest plantations established at one area in the “lomas” suffered from a lack of equilibrium between their crowns and root systems and the variable moisture available over periods of years. The same phenomena of die-back at the tips and subsequent regrowth, which may be observed in the redwood forests was very strongly marked in the “lomas” plantations. A more detailed exposition of the “lomas” vegetation with discussion of the possibility that epiphytes help to maintain an equilibrium in such moist atmospheric associations is presented in the appendix.

Simply stated, the hypothesis on regulation by epiphytes is that they can respond to differences in moisture by new growth faster than the supporting trees. Thus in periods of increased precipitation or drip from moisture condensation, expansion of epiphytic coverage lets a smaller proportion of available water drip through to the soil, whereas the contraction of epiphytic growth in drier periods results in a proportionately greater amount being available for tree growth. The net result may well be an equilibrium in growth of the tree vegetation over periods of cyclic variations of weather.

The data on water caught in a rain gauge tinder a tree as compared with a gauge placed in the open at the same site indicate the possibility of considerable difference in mist deposition dependent on the height and leaf surface of the vegetation. At any rate, areas of mist or cloud condensation may be of special importance to hydrology because the removal of natural vegetation may have a considerable adverse effect on stream flow at lower elevations. Since water is becoming an increasingly limiting resource in several tropical mountain areas, more research on the relations of vegetation with condensation moisture is needed.

Strong Winds: Normally, there is continuous movement of the atmosphere, but general low velocity of such air motion exerts no significant effect on vegetation physiognomy. However, there do exist several types of air movements, which produce effects of sufficient significance to place the resultant vegetation in an atmospheric classification.

One of the most obvious of such conditions is found in the high mountains, on exposed ridge tops, or in coastal areas where frequent strong, steady winds blow. These give rise to a generally pruned-appearance towards the wind with greater extension of branch and tree growth to leeward. Less obvious, because it can only be determined by comparison with the same vegetation in sheltered sites is the lower stature.

The actual cause of the lowered and compact vegetation surfaces exposed to the winds must ordinarily be due to excessive evaporation from any irregularly exposed surface. However, actual wind pressure is also involved in the form of individual trees, while along sea-coasts, salt spray carried by the winds may be a contributing factor to alteration of tree growth. Even in the cloud belt of Rain Forest life zones, exposed ridges in the Caribbean islands carry a low sheared vegetation. On El Yunque, in the Caribbean National Forest of Puerto Rico, the leeward side of the peak carries a dense closely-spaced forest of only a few meters height. Britton and Gleason referred to this as the mossy forest due to the predominant epiphytism of mosses and moss-like lichens. On the exposed side of the peak the vegetation is reduced down to a meter in height. Although wind pressure and evaporation during a relatively restricted portion of the year must have some influence on the reduction of vegetation height on El Yunque, the predominantly saturated air can scarcely be the basic limiting factor. Probably, the general high saturation of the soil with moisture is the major limiting factor. Again, as in the Peruvian Lomas the epiphytic mosses may play an important role by slowing up the drip from the trees to the soil and offering a greatly expanded leaf surface for evaporation and transpiration.

A somewhat similar condition of strong winds, but in less humid conditions, is found in the saddles or passes between volcanic peaks in Guatemala. There, the stronger trade winds of the dry season are funneled through the passes. Not only do the winds affect the vegetation within the pass, but exert a strong drying influence for quite a distance down the leeward slopes. Supposedly, the evaporation caused by air movement is further augmented by the greater absorptive capacity of the air as it drops towards lower elevations and warms up.

Sufficiently strong winds to fell individual trees or stretches of forest are associated with hurricanes or typhoons, more localized tornadoes or the local gusts which precede thunderstorms or rainclouds. Where appreciable areas of natural forest are felled, a higher percentage of an association area may be found in successional stages. The results of the gusty type winds are less noticeable and give rise to natural associations with smaller basal areas and a relatively greater number of smaller diameters.

Other Atmospheric Conditions

There exist other localized conditions of the atmosphere which are not as well documented or which have received little attention. For example, the landward effects of the Humboldt current are much less marked in Ecuador than in Peru. However, the Pacific lowlands are subjected to long continuous periods of day-long, dense cloud covers which must exert some influence on the vegetation. This may be no more than an effect of relatively lower temperatures for any given elevation, but only careful study and comparisons with the vegetations of other tropical regions can determine the actual effects.

Cold air drainage into the lowlands in valleys which drop rapidly from high mountain areas is another atmospheric phenomenon which may produce significant differences in vegetation composition and physiognomy.

CHAPTER VIII

WATER

Water, as essential for Life

Originating in a water medium, life has from the beginning utilized that liquid as a base for solution and internal transport of all the chemical elements and their combinations which are essential for the life processes of organisms. Understandably then, the evolutionary movement of living organisms from a water medium to above-water environments made requisite the development of structure and function which could permit the maintenance of a satisfactory supply balance of liquids between the internal parts of the organism and the external environment.

Water is a chemical compound of specific physical characteristics. It is abundant on our planet, and exists in the solid, liquid or gaseous state within the ranges of temperature and pressure which are found naturally on earth. Although through a considerable temperature range it shrinks in volume with cooling like other materials, on freezing or solidifying, water expands in volume.

Water has not only an unusually high heat capacity, i.e. ability to absorb heat, but also remarkable, are its high latent heats of fusion and evaporation. It is exceptional in its capacity as a chemical solvent, and comes nearer than all other substances to being a universal solvent.

Except only for mercury, water has the highest known surface tension. Its cohesion is such that the tensile strength of a column of water approaches that of steel. This, of course, applies only to a column of water without structural flaws such as bubbles. Water also adheres strongly to many substances, this character giving rise to some of its important natural movement in soils or roots known as capillarity. Its rise to great heights in trees is due to the creation of a vacuum at the leaf by transpiration, which in combination with cohesion, capillarity and root pressure move the water upwards against the forces of gravity.

Given its physical characteristics, together with its relative abundance on our planet, water enters intimately and decisively in those natural processes which we lump together as climate. Water is continuously being evaporated from open bodies of water and other moist surfaces. This water vapor is subsequently condensed into clouds or locally deposited directly on land and other surfaces as dew or mist condensation. From the cloud cover, water returns to the planet surface as precipitation.

Water is not only extremely important in soil formation and soil transportation processes but fills a vital function as a solvent for the transfer of most of the needed chemical elements to the vegetation from the soil. Through their root systems, the plants take in rich solutions, extract the elements needed for growth and other processes, and then give off water vapor to the atmosphere through their stomata in the process known as transpiration. The whole process of absorption, translocation of the solutions through the plant tissue, the extraction of chemicals and transpiration from the stomata of the leaves is in a broad sense comparable to movements of food materials through the alimentary tracts of animal organisms.

Thus, water not only shares a major role with heat in developing a range of climates, but is an essential part of living organisms. On the life zone chart, heat as biotemperature, water as total precipitation and the combination of those two as effective moisture obviously constitute the major climatic factors. With water entering intimately into living processes also, it may be surmised that the physiognomy of vegetation and correspondingly, the activities of animal organisms must have a direct relation with the climatic distribution of water.

In a general way, it may be noted that the luxuriance of the vegetation increases as water becomes increasingly more abundant in the form of precipitation in moving away from the deserts where water is definitely a limiting factor. In other words, with more water available, more vegetation can grow on a given unit of area with a correspondingly greater transpiration. Also, the availability of water depends not only on climate alone, that is, precipitation and moisture of the atmosphere, but also on the water holding capacities of different soils and the nature of the topography with Its effects on drainage or collection of water. Again, these differences of the soil as well as certain special characters of the atmosphere, such as especially strong winds or the contact of clouds with mountain slopes affect the moisture content of the atmosphere.

Thus, although there is a rough general correlation of vegetation and correspondingly of transpiration with the major factors of climate, there are secondary variations caused by minor climatic factors, soils and local atmospheric conditions which altogether constitute a wide range of complex situations of water return to the atmosphere from land surfaces.

Measurements and Attempts to Measure Atmospheric Water Movements

Climatologists and physicists have long attempted to find a practical way to predict or calculate water movements, other than precipitation, from measurements and the assignation of proper relative weights to the various major and minor climatic factors. However, since soils and vegetation are variable factors which have a definite influence on such water movements, calculation of the latter from climatic factors alone is impossible. The only feasible approach to such a problem is through natural vegetation which reflects all the climatic and soil factors and its own capacity to transpire water.

Before proceeding with discussions as to how vegetation may be utilized for determining water movements, the various movements of water in liquid or vapor form should be considered. A definition of precipitation, the prime movement of water from the atmosphere to the earth, has been presented already in the chapter on life zones. The other water movements are defined in the following paragraphs.

Evaporation is the movement of water into the atmosphere from surface areas without passing through living cells in the process. The surface areas include open water, snow, ice, soil, rock, man’s constructions and vegetation. In vegetated areas, part of the precipitation is intercepted by the above ground vegetation, of which some drips to the soil or flows along the vegetation to the ground and another portion is returned to the atmosphere from the moistened surface.

Transpiration is the movement of water into the atmosphere from and through living plant cells. Most of this comprises water vapor passing out through stomata of the leaves but would also include any movement of water to the atmosphere through cell walls or as drops of liquid in the rather insignificant process of guttation. Many animals give off water to the atmosphere through perspiration and respiration, but the quantities involved are relatively small and usually not considered.

Evapotranspiration is the sum of evaporation and transpiration. This is often referred to as actual evapotranspiration. Run-off is that portion of the precipitation on an area which moves by gravity over the surface or far enough into the earth to become unavailable for use by the vegetation of the area or for subsequent evaporation from the soil surface.

The preceding defined terms along with precipitation comprise the actual natural water movements. Precipitation may be measured directly with standard rain gauges. Run-off may be measured with much more difficulty, but only for complete watershed units. This is done by measuring the outflow through a weir from a catchment basin over several years. By surveys to measure the surface area of the catchment basin, the run off per unit area may be determined. This can be done with accuracy only where there is certainty that the basement rocks under the watershed do not permit seepage and all run-off passes through the measuring weir.

The total actual evapotranspiration may be determined indirectly in such a watershed by placing several rain gauges through the catchment basin, calculating the total precipitation which falls on the area and substracting the run-off from the precipitation. Again this may be determined per unit area of land surface.

There is no direct way to measure either evaporation or transpiration separately from extensive areas. However, in a few watersheds this has been done indirectly. In the preceding paragraph, the method of determining actual evapotranspiration was indicated. After a few years of measurements in the watershed, an average annual value of total actual evapotranspiration is obtained. In certain experiments, after such a watershed calibration is made, a portion or all of the watershed may be treated artificially to remove all living vegetation. If this is only a portion of the total calibrated watershed, a separate complete segment of the watershed must be controlled and its run-off measured in a weir.

In this manner, transpiration from the area is stopped. The difference between the calculated precipitation which falls on the area and the measured run-off should correspond to actual evaporation from the area. This is not too precise a figure but gives a very clear idea of the percentage of evapo-transpiration water which is utilized in evaporation. There is, of course, no way of knowing whether or not the removal of the vegetation, by adding suddenly a considerable amount of extra litter to the soil surface, affects the value of evaporation as compared with evaporation as a part of evapotranspiration from the vegetated area.

Water movements to the atmosphere or run-off are measured also from small artificially controlled areas. One of the commonly utilized meteorological instruments is that for measuring evaporation from an open pan of water. When these are open above, precipitation must be included with the loss of water to obtain a net value for evaporation. This is evaporation from open water, but still can not match even closely the evaporation from a natural pond or lake as the enclosing pan complicates air movements and more seriously, the water in a shallow pan heats up more than in deeper natural water where more mixing is usually to be found.

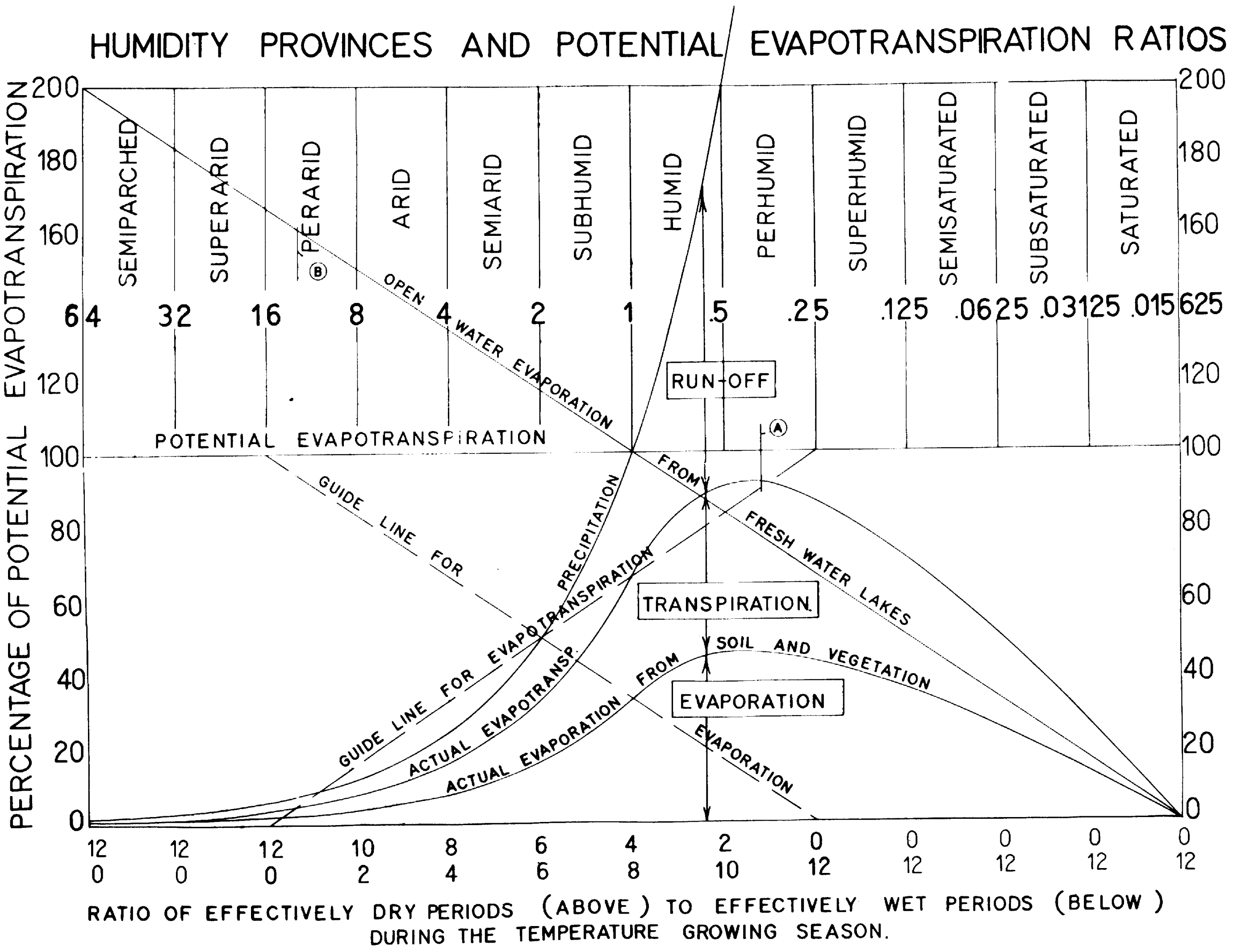
The livingston atmometer comprises a spherical porous clay bulb connected by a tube to a jar of water with special devices to keep rain water from entering the jar and to allow air to enter to replace the evaporated water. Instruments are calibrated at the factory so that the resultant measurements are satisfactory if the bulb is kept free of algae, but gives only a relative measurement of evaporation from a porous clay bulb in different environments. It cannot give a direct reading of evaporation from the natural site.

Open topped tanks filled with soil and planted with crops, called lysimeters, may be used to measure rim-off. Again, as in watersheds, evapotranspiration may be determined from the differences. However, they are essentially expensive methods of obtaining artificial figures from small areas. The problem in all the preceding instruments is primarily the lack of precise data from natural conditions to permit calibration of instruments or the development of a satisfactory correction factor.

The need for a standard value of water movement to the atmosphere for relative comparisons led Thornthwaite, a climatologist, to set up a hypothetical value which he named potential evapotranspiration and to develop a method of calculating that value from mean annual temperatures with corrections for latitude. Holdridge defines potential evapotranspiration as the amount of water which could be transpired under optimum conditions of soil moisture and vegetation on a zonal soil in a zonal climate. The potential evapotranspiration ratio is the quotient of the annual potential evapotranspiration divided by the mean annual precipitation.

In the development of a diagram with logarithmically spaced value lines of temperature and precipitation to determine world plant formations or life zones, Holdridge (1947) found unexpectedly that one of the three requisite sets of parallel boundary guides for the hexagons was potential evapotranspiration ratio lines. This made possible the extrapolation from the diagram of a value of annual potential evapotranspiration for any station which had been located on the chart by the plotting of mean annual data for bio-temperature and precipitation.

FIGURE 6 WATER MOVEMENTS IN CLIMATIC ASSOCIATIONS



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Subsequently, Holdridge (1959) (1960) found from his plant formation diagram that the same value for potential evapotranspiration could be deter-mined with greater ease and more precisely by simply multiplying the mean annual biotemperature in degrees C by the factor 58.93.

Further consideration of the interesting direct relation between biotemperature and potential evapotranspiration, coupled with observations of vegetation over a wide range of conditions in the western hemisphere, has led on to the derivation of the nomogram for atmospheric water movements from areas of climatic vegetation associations, as presented in figure 6, and of formulas for other types of vegetation associations given in the text of this Chapter.

The correlation of height of vegetation with evapotranspiration signifies that the mechanisms of the physiological process of moving water up and through vegetation are governed or limited by climatic parameters, by soil moisture conditions or by both in combination. Furthermore, because natural forest vegetation is made up of one to several stories comprising various species of different heights at maturity, generic characteristics of the species must be involved.

Species such as Ceiba pentandra, which grow well in three or four life zones attain progressively greater heights in succeedingly moister humidity provinces in the same temperature belt, even when soil drainage conditions are similar. This appears to indicate clearly that moisture is a climatic parameter which governs height of trees. The climatic effect in such cases could be exerted through either the atmosphere or the soil or both in conjunction.

Many tree species grow to a greater height in cove situations, i.e. in the valleys, than farther up the slope. Due to their close proximity, the difference in height growth cannot be attributed to climate but must be due to the soil.

In general, the same species of trees within the same life zone grow to greater heights in those areas where clouds or fog bathe mountain slopes. This is a climatic effect but again exerts influence on both the humidity of the atmos-phere and, through drip and reduction of evaporation, the humidity of the soil.

In these three cases of increased height of identical species, additional moisture in the soil is clearly indicated in one example while in the other two, either moisture of the atmosphere or the soil or a combination of the two could be the cause of the increase in stature. Evaporation is increased if the atmosphere is less humid, but evaporation alone except in windy areas should have little direct influence on vegetation height.

Transpiration

Transpiration, on the other hand, is a cell process. It is primarily the movement of water vapor through the cell wall of turgid leaf mesophyll cells into the stomatal cavities and thence through the stomata into the atmosphere. The turgidity of the cells is possible only when there is sufficient available water in the soil. Movement into the stomatal cavity and out through the stomatal openings would depend however to a great extent on the humidity of the atmosphere and air movements. This exit of water vapor regulates the movement of water through the mesophyll cell walls which provides a large part of the force required to move water up through the trunks of the trees against the force of gravity.

At first glance, it would appear that the transpiration mechanism would work more efficiently in drier atmospheric conditions. On the contrary, the evolutionary adaptations of species indicate several adjustments to counteract the effects of dry atmospheric conditions. The mechanism of the stomatal opening with its sausage-shaped guard cells is such that when conditions are moist they are held open while in dry conditions they close. Thus, stomata are open early in the morning or in moist periods of the day. Under more arid climatic conditions stomata are often sunk into the leaf tissue, which slows up water movement of transpiration.

In wet tropical forests, only a few consecutive days without rain causes considerable leaf fall from evergreen species, another way of reducing transpiration. In drier climates, the trees drop their leaves for the duration of the dry season thus completely eliminating transpiration during those periods.

As a general rule then, it appears that transpiration is a relatively rapid process. Because of the many mechanisms for reducing the movement of water vapor out from the leaf, obviously the limiting factor must be the arrival of water to the leaves. Again, since the translocation of water up through the plant stem to the leaf is primarily produced by transpiration, the speed of transpiration must be controlled within a species by the availability of water in the soil.

The process of absorbing water from the soil, transporting it up to the branches and the movement of water vapor into the atmosphere as transpiration is a complete, unified system. However, the system can work at topmost capacity only when there is sufficient water in the soil and the atmosphere is humid enough so that the governing mechanisms for slowing down transpiration are not brought into operation.

As with most such governing mechanisms, it is likely that they are effectively operative only within a certain limited range with the one exception of deciduousness. The latter, however, is not exactly a governor control, but more a closing down of all operations for the duration of the dry or cold season. Since each species has its own particular system of transpiration control, it may be assumed that such a system of control is adequate for regulating the plant’s water system within, the range of variations of the soil-atmosphere moisture content through the natural range of that species.

Transpiration causes a vacuum in the leaves which, given the strong cohesiveness of water, is the major factor in moving water up through the trunks of tall trees. Thus, the transpiration rate in a broad leaf species must be correlated with its potential stature. However, its actual height in any given ecological environment within its range will depend primarily on the moisture conditions of the soil. The tree can increase in height towards its maximum until the variations of moisture in the soil during the growing season are too great for the transpiration governor systems to handle satisfactorily in correlation with the force necessary to maintain cohesion of the water columns.

When that point of stature is reached, further growth of the tree upwards cannot possibly be maintained. It is possible, of course, that during a moist cycle, a monopodial tree will put on some additional height. This may be observed in the Californian redwood forests where frequent stag-headedness or the dying back of the upper few meters of height of the tree may very likely be attributed to a return to normal or average moisture conditions following several years of an over-average cloudiness or higher rainfall.

In the formulas for the determination of actual evapotranspiration from heights of forest stands, the number of stories in the ideal forest are also taken into consideration. A single-storey stand may be twice the height of a two- storey or three times the height of a three-storey forest. Apparently, the multi-storey forest with multiple root systems in the same soil profile can bring on soil water limitations much faster than a single storey root system. We know relatively little about root systems in complex associations, but if the roots of different species primarily obtain their water supply from different levels then it would logically follow that in a one species stand water would move into its root zone level from other levels, greatly postponing water shortage, whereas multi- level root systems would prevent this and bring on water limitation much faster.

Conifer stands, such as pine forests, are frequently of only one storey. Often a pine stand grows on less fertile, drier sites right beside a lower stature hardwood stand. Only by dividing the height of the pine canopy by the number of stories in the hardwood stand can one obtain relative heights more in line with the water holding capacities of the respective sites.

Although conifers, in general, are taller than broad leaf species of the same region, their tall stature is probably not as closely correlated with rapid transpiration as are the hard woods. The present gymnosperms are the remaining members of an earlier dominant type of vegetation in the long term evolutionary succession. Their general wood structure without ray cells and with tracheids instead of vessels very likely corresponds to a slower translocation of water. The sclerophyll nature of their leaves and normal lack of deciduousness go together logically with a slower movement of water.

Also their general monopodial type of growth conforms most closely with a structure evolved to move water upwards to considerable height without much possibility of permitting lateral movements of water from the stem into branches. Many of the broadleaf trees with an apparently more efficient movement of water upwards through vessels can develop very broad crowns at the expense of height when grown in the open.

Cordia alliodora of the Boraginaceae appears to be an example of a broad-leaf species with little possibilities for lateral movement of water in the stem. Its height growth and development are rapid. Even when grown in the open in full sunlight the lower side branches develop very little, soon dying and dropping off. They obviously die, not because of lack of light but rather inability to draw enough water from the main stem to maintain growth.

Under the canopy in a several storey tropical forest, light may well be limiting and kill off lower lateral branches even though lateral water movement is possible. There is a possibility that cauliflory may be correlated with generally understory species which permit easy lateral water movements in the stem but which cannot maintain branches due to the low light intensity. Those species which by chance evolution hit on cauliflory found an abundant supply of moisture and nutrients for the development of flowers and fruits which need little light for their development.

Potential Evapotranspiration

Potential evapotranspiration, being a hypothetical quantity and seemingly not amenable to direct measurement, merits more consideration than that given in a simple definition. Moreover, if potential evapotranspiration is to be used as a bench mark, to which other water movements may be compared, its definition must be specific enough to give only one value for each site.

Although there is still discussion as to whether calculations should be made from air temperature or net radiant energy data, most workers appear to agree that potential evapotranspiration is a function of solar energy on the earth’s surface. There is fairly general agreement also that soil moisture and vegetation must be ideal or optimal, but usually no mention of the character of the soil or climate is made in the definitions.

Thornthwaite (1948), who published the first lengthy discussion of potential evapotranspiration, defined it as the transfer of water to the atmosphere that would be possible under ideal conditions of soil moisture and vegetation. Van Wijk and De Vries (1-54) distinguished it similarly as the amount of water evaporated under optimal conditions of soil moisture and vegetation. Penman (1956) who prefers to shorten the term to potential transpiration, defined it as the amount of water transpired in unit time by a short green crop, completely shading the ground, of uniform height and never short of water.

Although Pelton et al, (1960) wrote: "Potential evapotranspiration has been defined in several ways, all of which have essentially the same meaning”, it is difficult to understand how the short green crop of uniform height of Penman’s definition can be essentially the same as an ideal or optimum vegetation for an area. Evolution over the ages should have evolved such an optimum vegetation for each environment. Over a large portion of the land surface of our planet, the supposedly optimum, natural vegetation is a high forest rather than a short green crop.

Technicians frequently use an irrigated agricultural crop to determine actual water use and then compare the findings favorably or unfavorably with the calculated values of potential evapotranspiration from a nomogram or formula based on temperature or the energy balance. Such research usually leaves It to the reader to decide whether or not such a crop represents the optimum vegetative cover and gives little heed to possible differences in water needs Of distinct crops.

Penman (1956) Implied that there might be some difference in water use by stating in a broad, hypothetical generalization: "For complete crop covers of different plants having about the same colour, i.e. the same reflexion coefficient, the potential evapotranspiration rate is the same, irrespective of plant or soil type". Essentially, Penman has been more scientific or precise in specifying a short green crop of uniform height, but has evaded by such a definition the difficult problem of determining the effect on potential water use of different vegetative covers.

Fundamentally, however, there is a more serious error in such comparison research. If potential evapotranspiration depends only on temperature or energy balance, how can the investigators correct for or disregard differences in soils and local atmospheric conditions between the separate areas where tests are carried out? It is very doubtful that water use would be the same in an extremely shallow, sandy soil as compared with a deep, fertile loam or that exceptionally strong, steady winds could be disregarded, even though the same crop were to be utilized in each case. Even though researchers might avoid such adverse sites purposely, it still cannot be denied that such variations might occur in separate areas where temperatures or energy balances are equal. Thus, rather than pretend to be a search for broad principles of atmospheric water movements, most of such investigation should be designated as local studies to determine the actual water use of specific crops.

On the other hand, if the specifications of a zonal soil and a zonal climate are included in the definition of potential evapotranspiration, the utilization of a nomogram or formula based on temperature alone for obtaining a precise value becomes possible.

This is true because, if optimum soil moisture derived from evenly distributed precipitation were available at a given temperature mean in the same elevational belt, there would be no range of climatic conditions from desert to rain forest, but rather a uniform climate, a single zonal soil and a single, optimal vegetation type, all characteristic of the temperature, moisture and elevational belt. Thus, if only one value of potential evapotranspiration is possible for a given temperature mean, obviously, that quantity may be obtained by multi-plying the temperature mean by a numerical factor.

If potential evapotranspiration is determined in that manner for a series of different temperatures, each result must coincide with the mean annual precipitation at a potential evapotranspiration ratio value of 1. Holdridge (1947) (1959) (1960) found that the unity ratio crossed his life zone chart as a straight line and that the factor 58.93, previously mentioned, multiplied by any mean annual biotem-perature gave a plotted position on the unity potential evapotranspiration ratio line which coincided with a value of mean annual precipitation equal to potential evapotranspiration. The same procedure of plotting on the other ratio lines gave a correspondingly correct value of mean annual precipitation across the chart relative to any given biotemperature mean.

Since the potential evapotranspiration ratio lines on the formation chart serve equally well in moving both from low to high latitudes and from sea-level to upper elevations, the general determination of potential evapotranspiration by the simple formula, $PE = 58.93 \times t^{(bio)}$, appeared feasible and in accordance with natural vegetation distribution as previously plotted with the employment of precipitation and temperature values only.

Thus, it appears that Thornthwaite (1948) was on the correct track in deriving potential evapotranspiration from temperature data, even though his use of standard mean temperatures resulted in a rather cumbersome procedure for obtaining values. However, Van Wijk and De Vries (1954) and Pelton et al, (1960) have presented evidence to show that standard mean temperatures are not satisfactory for calculations of potential evapotranspiration for short periods within a year's cycle. They believe that net radiation measurements are much more satisfactory than temperature means for evapotranspiration studies.

There still remains the possibility that mean biotemperatures may eliminate the apparent seasonal lag in air temperatures related with thermal storage by the earth and, at least, merits trial. Since the present paper is concerned with annual water movements only, considerations of short-period analyses are not explored further here than the above brief mention.

Up to this point, consideration has been given to only the definition and derivation of potential evapotranspiration values. However, all such discussion of a hypothetical quantity of water has no significance, unless there exists some physical basis which could have served as a guiding limit for the evolution of natural vegetation. Necessarily, such a physical basis should have been operative on earth even before the appearance of vegetation.

Implications from the distribution of natural vegetation and careful perusal of the subject led the author to believe that such a physical basis should be the speed of evaporation from open, fresh water. If this were true, then potential evapotranspiration might be defined also as the average quantity of water evaporated annually from a fresh-water lake in a zonal climate where the mean annual precipitation is equal to evaporation.

Nomogram of Water Movements in Climatic Associations

Based on the hypotheses that potential evapotranspiration has only a single value on any isotherm on the earth's surface and that atmospheric water movements follow a regular pattern in areas of zonal climates and soils, the nomogram in Figure

6 was constructed to permit extrapolation of the quantities of such water movements for any station located within any climatic association.

Potential evapotranspiration is plotted as a horizontal line running across the center of the nomogram. The annual value of this in mm. for any given station may be determined from the formula: $PE = 58.93 \times t^{(bio)}$. This quantity is taken as 100%. Values of other water movements may then be determined through comparison with the quantity of potential evapotranspiration by means of the vertical series of percentage value at the right- and left-hand margins.

Potential evapotranspiration ratio lines with their values are placed vertically above the potential evapotranspiration line. The names of the humidity provinces which they separate are inserted. Still drier humidity provinces may actually exist on earth, but such a possibility is disregarded in order not to extend the nomogram unduly. Corresponding to the respective potential evapotranspiration ratio lines above, ratios of the effectively dry to the effectively wet portions of the temperature growing season are placed along the bottom of the nomogram.

On the basis of the definite relation between precipitation and potential evapotranspiration ratios, a curve of mean annual precipitation is plotted on the diagram passing through the points equal to 200% of potential evapotranspiration at the ratio line of. 5, 100 at 1, 50 at 2, 25 at 4, 12.5 at 8, 6.25 at 16, 3.125 at 32 and 1.562% at the border potential evapotranspiration ratio value of 64. For lack of space, the upper end of the precipitation curve is not plotted, but would continue regularly by the same projection to 400% at the ratio line of .25, 800 at .125, 1600 at .0625, 3200 at .03125 and 6400% at the border value of .015625. There is no implication that the last, heavy precipitation means may actually be found on earth.

Up to this point, all of the bases for the framework of the nomogram, with the exception of the expanded number of humidity provinces, have been taken from the life zone chart of Holdridge (1947). For the location of the remaining lines, the dearth of relevant basic data has made obligatory a high dependence on observations of climatic association vegetations, the physiognomy of which can be related directly with climate and which also must reflect the character and magnitude of water movements.

Admittedly, the location of the water movement lines is hypothetical, but due to the mathematical regularity of the formation chart and the apparent mathematical relations between physiognomic characters of climatic associations, the location of those lines is expected to be not often appreciably distant from their true positions. At any rate, whether confirmed or corrected in the future, they do indicate where and what basic research is needed in order to develop a final, correct nomogram of atmospheric water movements in the climatic associations.

The straight line for open-water evaporation from fresh-water lakes extends from zero per cent of potential evapotranspiration at the lower right corner through 100% at the unity ratio line and on to 200% at the upper left corner. The assumed bases for this line were the theoretical equality to potential evapotranspiration at the unity ratio line and the supposition that effective evaporation would cease at about the .015625 ratio line. In the lowland tropics, open water evaporation is thus assumed to reach zero per cent at a hypothetical average precipitation of over 250 mm. per day, under which conditions a supposed saturation of the atmosphere with a cessation of net evaporation does not seem improbable.

In order to start plotting actual water movements from vegetated areas, some guide lines were needed. Also, because transpiration and evaporation do not lend themselves to direct measurements of differentiation, a method of separation by the use of two equations was sought for, just as the same system is used in algebra to solve for two unknowns. In this case, evapotranspiration could serve as x +y and evaporation as y.

To set up something comparable to an equation for x + y or evapotranspiration, the following question was formulated: What percentage of a quantity of water equal to 100% of potential evapotranspiration would be evapotranspired across the range of humidity provinces at a given biotemperature by a hypothetical vegetation without any special storage organs and which could exist for any portion of the temperature growing season, if the precipitation minus runoff were just sufficient to maintain a soil moisture at an optimum condition in accordance with the ratios of effectively dry to effectively wet periods as presented at the lower margin of the nomogram?

The equation or answer to the above question is placed on the nomogram as the straight, theoretical guide line for evapotranspiration, starting at 0% at the ratio line of 16, where no effectively wet period would exist, and rising to 100% at the ratio line of .25, where the entire growing season would be effectively wet.

To devise an equation for a y or evaporation alone, a second question was proposed, as follows: If evaporation took place strictly in accordance with the ratio of dry to wet periods, if it utilized only water not used in transpiration by the hypothetical vegetation of the first question and if precipitation were equal to potential evapotranspiration all across the range of humidity provinces, what would be the percentage of evaporation across the same range?

The equation or answer to the above is placed on the nomogram as the straight guide line for evaporation, starting at 100% at the ratio line of 16 and dropping down to 0% at the ratio line of .25.

Because of the stipulation in the second question of a mean precipitation equal to potential evapotranspiration, the only situation where actual conditions occur on earth which do satisfy the requirements of both equations is on the vertical line of unity ratio where mean precipitation does equal potential evapotranspiration. At that line, the values of evapotranspiration and evaporation have values of 66-2/3 and 33-1/3% respectively of potential evapotranspiration. The remaining 33-1/3% would be runoff. Transpiration being evapotranspiration minus evaporation would have a value of 33-1/3% and be equal to evaporation at the unity ratio line.

Natural vegetation indicates that this equality of transpiration and evaporation may hold true throughout almost the entire range of vegetational distribution. As one moves from the unity ratio line towards drier districts one would expect the proportion of evaporation to increase relative to transpiration, but apparently vegetation maintains the equality by an increase in the percentage of plant species which by means of relatively more extensive root-systems or water storage tissues can continue to transpire throughout the temperature growing season.

In the opposite direction or towards more humid conditions, apparently transpiration also is increased to maintain equality with evaporation through the development of greater leaf areas, more complex vegetation and increasing epiphytism.

In the second question, an assumption had to be made that evaporation at the ratio line of 16 could transfer to the atmosphere during a year's time a quantity of water equal to potential evapotranspiration. Effectively, this means that such a quantity of water would be evaporated from a zonal soil kept at optimum moisture throughout the temperature growing season.

This appears probable because in that case a hypothetical line of evaporation from bare zonal soils at optimum moisture across the range of humidity provinces would extend from 100% at the ratio line of 16 through 66-2/3% at the unity ratio line and 50% at the ratio line of .25 and continue on, at first, in the direction of 13% at the ratio line of .015625. Very likely, with the increasingly high humidity beyond the ratio line of .25, the bare-soil evaporation line would turn downwards to join and subsequently coincide with the line of open water evaporation on to zero per cent at the border ratio line.

The crossing of such a bare-soil evaporation line with the guide line for evapotranspiration at a point on the unity ratio line is considered indirect evidence of the validity of the bare-soil evaporation line since both lines would concur at that point as to a value for runoff equal to 33-1/3% of potential evapotranspiration.

In the humidity provinces where precipitation is less than potential evapotranspiration, actual evapotranspiration and actual evaporation are affected most directly by the differences in mean annual precipitation. Since the line for precipitation is a logarithmic curve, they also must be represented by similar curves through this portion of the nomogram.

From the unity ratio line to the ratio line of 16, the curves for actual evapotranspiration and actual evaporation are drawn so that their percentage value are reduced by one-half at each succeeding humidity province boundary to match the equivalent decrease in precipitation with which they are directly correlated.

The same relation is utilized to prolong the actual evaporation curve to the left side of the nomogram, but in crossing the superarid humidity province, the actual evapotranspiration curve is dropped so that it Joins the evaporation curve at the ratio line of 32. Although, admittedly, there is a lack of information on such areas, the lowering of the actual evapotranspiration curve is done on the assumption that there is no significant vegetation in the climatic association beyond the superarid humidity province.

To the right of the unity potential evapotranspiration ratio line, both curves must change direction due to the continually increasing excess of precipitation over potential evapotranspiration. The curve for actual evapotranspiration is first extended as if it were to reach 100% of potential evapotranspiration at the ratio line of .25. However, from the discussion of potential evapotranspiration, this cannot be attained by natural vegetation in a climatic association, because when conditions for optimum moisture throughout the year are attained, the zonal climate at such a station is already too rainy and too cloudy for optimum rates of transpiration and evaporation. On the contrary, potential evapotranspiration may be equalled or surpassed in drier climates where soils with a raised water-table exist to provide water during what would be the effectively dry period in a zonal climate.

The direction of the actual evapotranspiration curve is changed again when it crosses the line of evaporation from open water, because the high humidity of the air would be a strong, influential factor beyond that point. The curve is then extended to meet the open water evaporation line at zero per cent.

The actual evaporation curve is drawn similarly, heading first for 50% at the ratio line of .25 and subsequently changed in direction to meet zero percent with the other lines. At all points to the right of the semiarid humidity province, the percentage value of actual evaporation is assumed to be one half of the percentage of actual evapotranspiration.

Use of the Nomogram

For easy use, the nomogram should be plotted in large size on quadriculate paper with the potential evapotranspiration line placed at 100 units from the bottom line of the diagram. Because any calculated, intermediate, potential evapotranspiration ratio lines must be located logarithmically, the diagram may be plotted on logarithmic paper to facilitate their location or it may be drawn on regular, quadriculate paper with the numbered potential evapotranspiration ratio lines spaced to correspond to the distances between the same numbers on a slide rule.

The steps in the use of the nomogram for a given site are as follows:

1. Calculate the value of potential evapotranspiration in millimeters.

2. Calculate the potential evapotranspiration ratio.

3. Locate the vertical line corresponding to that ratio logarithmically, either with a slide rule or directly on logarithmic paper.

4. Read off the percentage value where this vertical ratio line intersects the curve or the line of the item to be determined.

5. Multiply this percentage by the value of potential evapotranspiration to obtain the value of the item in millimeters.

Examples of the calculations of 2 distinct atmospheric water movements at 2 sites with very different climatic conditions are shown in the following paragraphs. These two examples provided satisfactory samples because of complete natural vegetation coverage in the first and certainty of a lack of bottom seepage in the second.

Watershed 21 of the Coweeta Hydrologic Laboratory, U.S. Forest Service, in North Carolina, showed from 17 yrs. of records a mean annual temperature of 12. 78°C, which was not considered essentially different from the mean annual biotemperature at that location, and a mean annual precipitation of 2080 mm. Potential evapotranspiration for N° 21= 12.78 x 58.93 = 753 mm. The potential evapotranspiration ratio = 753:2080 = .366. A short section of the ratio line of .366 is drawn on Figure 6 and labeled as A. The percentage reading for actual evapotranspiration at the intersection with the ratio line of .366 = 92. The mean annual evapotranspiration at Watershed 21 = .92 x 753 = 693 mm/yr. This figure agrees within 2% with the difference between the mean annual precipitation calculated from the records of pluviometers in the watershed and the mean annual runoff as recorded from stream flow out of the watershed.

Silver Lake, Cal. was studied from May, 1938 through April, 1939. The data presented by Blaney (1947) show a mean air temperature of 70^0F (21.1°C) and rainfall of 3.90 in. (99.06 mm). Potential evapotranspiration = 21.1 x 58.93 = 1243 mm. The potential evapotranspiration ratio derived from this data = 1243: 99.06 = 12.55. A section of the ratio line of 12.55 is drawn on Figure 6 and labelled as B. The percentage reading for evaporation from open water for the ratio line of 12.55 = 160.5. Thus, the calculated open water evaporation for that period at silver lake = 1.605 x 1243 = 1995 mm. This is a close fit, as the measured evaporation for the period is given as 79.46 inches or 2018 mm. The calculated evaporation is 1.1% less than the measured evaporation for the 12 month period.

Runnoff may be derived from the nomogram by subtracting the calculated amount of actual evapotranspiration from the value for precipitation. In a like manner, actual transpiration is the difference between actual evapotranspiration and actual evaporation.

Calculations of Water Movements from Other kinds of Associations

The nomogram of Figure 6 is designed for application to climatic associations only. Variations from the depicted patterns of atmospheric water movements are to be expected in the edaphic, atmospheric and hydric associations. Such variations are one of the major problems when any attempt is made to correlate and compare research results on water movements at widely separated stations.

The variations within other associations are of such a nature that it would be impractical to attempt to design a nomogram to depict general patterns of water movements, as is possible for the climatic associations. A more sound approach appears to be that of going directly to an interpretation of the distinct physiognomies of natural vegetation associations. A start has been made in that direction by the author, but admittedly more investigation is needed for refinement of the formulas.

After the nomogram in Figure 6 had been developed, a similarity of the relations between the percentages of actual transpiration from climatic associations along a series of plant formations to that of the relations between the heights of the dominant trees of the same climatic associations was noticed. The lead was studied and the following formula developed:

Ht. in meters of dominant trees in climatic associations

$$= 2\ t^{(bio)} \times \%\ \text{actual evapotranspiration}$$

The formula may be transposed to read:

$$\%\ \text{Actual evapotranspiration} = \frac{\text{Height in m}}{2\ t^{(bio)}}$$

Because actual evapotranspiration = % actual evapotranspiration x potential evapotranspiration, an interesting result is obtained if the formula based on height is utilized instead of % actual evapotranspiration in the latter equation. Such a formula then reads and may be simplified as follows:

$$\text{Actual evapotranspiration} = \frac{\text{Ht. in m.} \times 58.93 \times t^{(bio)}}{2\ t^{(bio)}}$$

$$= \frac{\text{Ht. in m.} \times 58.93}{2}$$

$$= 29.47 \times \text{Ht. in m.}$$

Such a formula makes it possible to derive a value for actual evapotranspiration from any climatic association which contains arboreal vegetation as the dominants.

To make such a formula more generalized so that it would include bush or herbaceous climatic association vegetations which lack trees, a correction factor for the difference in actual evapotranspiration from bush or herbaceous vegetation, as compared with an arboreal association was needed. To satisfy that need an assumption was made of a 4 and 8 times greater evapotranspiration rate for bush and herbaceous vegetation as compared with trees. This relation needs study, but for the present, a general formula for actual evapotranspiration from physiognomic characters of climatic association vegetation is proposed, as follows:

$$\begin{array}{l} \text{Actual evapotranspiration} \\ \text{from climatic associations} \end{array} = 29.47 \times \text{Ht. in m. of dominant vegetation} \begin{array}{l} \times 4 \text{ if hush or} \\ \times 8 \text{ if herbaceous} \end{array}$$

The above formula not only offered an alternative method, apart from the use of the nomogram with climatic data, for obtaining a value for actual evapotranspiration from climatic associations, but also offered promise of a means for determining the same water movement in edaphic and atmospheric associations from physiognomic characters. Study of this possibility in the latter associations let to the conclusion that after height of the dominant vegetation the physiognomic character most indicative of water use relations is that of the number of stories or strata of the dominant type of plant in the association.

On the basis of observations of vegetation associations and considerations of the availability of water in the environments of many different associations, the following general formula was made up:

$$\begin{array}{l} \text{Actual evapotranspiration from} \\ \text{any land-vegetation association} \end{array} = 29.47 \times \text{Ht. in m.} \times \frac{\text{No. actual stories}}{\text{No. stories in clim.assoc.}} \begin{array}{l} \times 4 \text{ if bush} \\ \times 8 \text{ if herbaceous} \end{array}$$

The number of stories of dominant vegetation in the climatic associations of the various plant formations needs further study. In addition, unfortunately, stories or strata are frequently not clearly demarcated, especially in tropical lowlands where the vegetation is so complex. However, there is a clear indication from the investigations of the author that this physiognomic character of vegetation must be given more attention.

Perhaps the ratio of actual evapotranspiration in an edaphic or atmospheric association to that of a climatic association with the same mean biotemperature and precipitation for a station may be used as a correctional factor for open fresh water evaporation at the same station, but this possibility has not been explored. The greater relative heights of vegetation in mist or fog condensation areas indicate also that comparison with climatic association vegetation heights may permit calculations of the extra precipitation received as condensation. As yet, no consideration has been given to water movements from hydric associations.

Finally, to round out the picture of water movements from natural vegetation, consideration was given to successional phases of vegetation associations. Evaporation appears to remain constant regardless of the nature of the vegetation cover. Successional vegetation and transpiration appear to increase in relation to time intervals, i.e. if the first stage of redevelopment of vegetation take x months or years, a second equivalent stage will require 2x, a third stage 4x and so on up to full transpiration. Because height growth is most rapid in young trees, the relative heights of successional growth relative to a mature stand may well serve as a measure of transpiration.

Based on the above considerations the following formula is proposed for actual evapotranspiration from successional vegetation:

$$\begin{array}{l}\text{Actual evapotranspiration}\\ \text{from successional vegetation}\end{array} = 1 + \frac{\text{Actual Ht. of second growth}}{\text{Ht. of mature vegetation}} \quad \text{X} \quad \frac{\text{Actual evapotranspiration from mature vegetation}}{2}$$

CHAPTER IX
HUMAN ECOLOGY

Man's Original Niche in Warm Climates

In general, as with plants, the niches for animals comprise food and space. For the simpler animals space primarily signifies an area of a very small radius within which it can find sufficient food. In proportion to the increasing mobility of animals, the area from which an individual procures food becomes correspondingly larger. Most animals have few other necessities beyond food and space, the latter including cover. Salt is the one mineral sought by larger mammals which may or may not be considered as food. Birds, especially, use a few, predominantly plant materials for nest building. A few animals like the squirrel and muskrat also construct nests or homes. Perhaps the beaver utilizes the greatest amount of material from the environment other than food, for the construction of dams and house.

The ancestors of primitive man like the great apes of the present were concerned only with a niche providing food and space. like the jaguar and the present apes, they must have migrated as hunters and harvesters of wild plant product over an area of fairly large radius. Because of their traveling in family or social units of several individuals, the space for an individual corresponded to the space for the group and was relatively extensive.

The earlier ancestors were very likely limited by climates to the tropical and subtropical life zones with their amenable temperatures. We can also hypothesize fairly safely that they primarily inhabited climates of medium rainfall and humidity in part due to the greater abundance of food in those life zones and partly for comfort. Within these life zones of the tropics and sub-tropics, they competed with the larger carnivores for meat and with many other forms of life for plant fruits.

Extension of Man’s Area

Very likely at the borders of those benevolent climates, they made warm-season forays into the colder regions of the temperate zone or the higher mountains. Extended forays into colder regions may have stimulated or amplified the use of clothing and fire, which, when well mastered, opened up a great many more life zones to permanent occupancy. At any rate, archaeological findings in the caves of Europe show clearly that men were well established in that area very close to the edge of the ice during the later glacial periods.

Thus, the manipulation of microclimates through the use of fire and clothing would have permitted men to penetrate and occupy colder climates than those of the life zones where they originated even when still only hunters and foragers.

Archaeological findings up to the present indicate that the great cultural advance of the development of agriculture took place in the Middle East. The development of wild grains and fruit as crops and the domestication of animals were apparently the first significant manipulations of natural ecological systems by man as this meant specific husbandry of other organisms. The only comparable developments in nature are those of fungus culture and husbandry of other insects by the ants. In both cases, considerable refinement of social structure was probably an essential base for the attainment to such a stage.

Although hunting and foraging activities had led man into a wide range of humidity provinces, the initiation of agriculture appears to have developed first near the unity line of potential evapotranspiration (Fig. 1) or on alluvial plains with a raised water table in the adjacent drier life zones. At any rate, it appears logical to assume that early crop cultivation was confined to soils of high fertility and to climates where any land clearing and the fight against weeds or natural succession was not too difficult.

Whereas the initiation of control of his microenvironments with fire and clothing had permitted man to compete successfully with other carnivores for the niches of the latter in new life zones for man, the step forward to agriculture comprised the amplification of or the development of essentially new niches for man. This meant an increased carrying capacity of the land in numbers of people, less time involved in moving about and consequently more time available for the development' of tools and systems associated with social progress.

The resultant local concentrations of population allowed man to better his agriculture which soon led to considerable progress in crop and animal selection for improvement as well as refined agricultural techniques such as irrigation. simultaneously, the importance of territory must have increased, necessitating the specialization of portions of the communities for protection of the area controlled. The same had earlier taken place in the social insects with the development of a soldier cast.

But this device for protection automatically added another check and balance to population increase. The same warriors who attempted to protect a given community could serve as the spearhead of an aggressive force. Thus, while man's early control of the environment and other organisms permitted his increase in numbers with less deaths from hunting accidents or climatic extremes, the initiation of effective warfare between communities or tribes placed another check on rapid expansions in numbers. With concentration in larger and larger communities, the possibilities of disease epidemics and widespread famine caused by climatic extremes or concentrations of crop insects also became more effective as a population check.

Development of a Separate Human Ecological System

However, through the centuries and millennia, man continued to refine his social organizations, his culture, his tools and techniques so that his numbers slowly increased while his enlarged partially controlled niche or set of niches was extended farther and farther through the world. The development of communications, transport and hence trade made more specialization possible. Gradually, after first extending his own particular niche on earth, man had converted this into a wide collection of niches. One could work as a sailor, a merchant, a mason, a miner or at a hundred other specialties which were not even food-producing tasks. In a sense, man had created with his cultural specializations a completely new ecological system.

Nevertheless, human ecology which had been superimposed on the earth^1 5 natural ecological system was still connected or joined to the latter at a great many points. Agriculturally, man was closely tied to nature He was substituting artificially tended associations for natural successions but still largely subject to the natural variations of climate, as well as the natural disposition of landscape and soil fertility and unable to cope satisfactorily with the natural fluxes of insect predators or plant and animal diseases.

Although he had gained better control of microclimatic conditions in his better engineered homes and clothing, he was still subject to the law of survival of the fittest as a natural organism. Plagues and other diseases were just as serious as under natural ecological conditions and possibly more disastrous because of the increased crowding of humans into settlements. He was still only a partial master of his fate, even in good health, when he ventured forth on the seas or into less favorable climatic conditions.

since those past historical days, the situation has changed very greatly. The development of nations, the sweeps of conquest through vast areas of the world and the long successions of rulers are all part of man' 5 vivid history$_1$ Those movements are probably most significant ecologically as a beginning of a rapid break down of the natural biological racial area segregations which presumably had taken shape in prehistoric times.

The biological races of the zoologist are sub-specific variations usually found to correspond with separate geographical subdivisions of the total range of a species. Because human racial differences apparently arose within the general confines of the connected or approximate land masses of the Old World~ comprising Eurasia, Africa and the chains of islands extending down to Australia or out into the Pacific$_1$ geographical Isolation appears to be an Inefficient hypothesis for original racial differentiation.

Anthropologists claim that a number of factors affected variations, including that of isolation. Considering the wide range of climates of the Old World land masses$_1$ the climatic differences appear to have been the prime factor in fostering the physiological variations which resulted In early racial groupings.

A careful analysis of possible climatic subdivisions In relation to the findings of the physical anthropologists suggests as an hypothesis a correlation of only four natural climatic divisions with original, distinct racial groupings. Such a climatic division would separate first the land environment Into two major divisions of moist and dry along the unity line of potential evapotranspiration ratio and further subdivide both these humidity divisions into temperature regions of cold and hot.

Within the Old World region. a correlation of the moist-cold region with the Caucasoid races is not too strained. likewise an original development of the Negroid race in the hot-moist region appears tenable. The common subdivisions of the Negroid race by the physical anthropologists could be considered as subsequent sub-racial differentiation which came about due to geographical isolation caused by the Indian Ocean and the present general aridity of the African- Asian connection between the eastern and western portions of the Old World hot-moist environment.

The climatic division hypothesis would vary most from present anthropological views in indicating an original Mid-Eastern group separate from the Caucasoid corresponding to the hot-dry division. This would have occupied the dry Middle East, extended southeast with India and westward into the Mediterranean with Its greatest br9adth there on the African continent.

Although, admittedly, color may be a character of no great significant weight as compared with less obvious physiological characteristics, skin pigmentation is firmly fixed in our minds as one of the most obvious racial designations and provides a handy reference guide for setting up the four ecological groupings.

Koons, who has delved deeply into the subject of human races, suggests five divisions, namely, the Caucasold, the Mongoloid, the Capoid, the Congoid and the Australoid. His work appears excellent *per se* and is derived from a wide range of evidence. However, if one attempts to correlate his divisions with a climatic or other factorial basis as a cause for racial differences, the correlation is only partial. Nevertheless, his careful work offers one racial framework with which a climatic division concept may be compared.

The cool wet portion of Eurasia and Africa comprised most of Europe, with northern and northeastern Asia. Northern Europe still represents the heartland of the Caucasoid or white race on the old continental masse There is complete agreement there on race with climate. The major area of cool dry climate lies in the central part of Asia, which could be considered the original center of development of the Mongoloid race. That they were numerous and expanding has been indicated by their early invasion into the Western Hemisphere and their sweeps down through Southeastern Asia and into the East Indies in prehistoric times as evidenced by remaining populations. Also in early historic times they swept westward into contact with the Caucasoids. Their influence on the probably original Caucasoid peoples of northeastern and eastern Asia has been profound.

The black or negroid race which is suggested here as correlated originally with hot wet climates is separated by Coons into the Congoid, Australoid and Capoid races. The first two are considered here as sub-racial groups corresponding to the separate geographic divisions of hot-wet climates in Africa and the Indian-Pacific Ocean general area.

This leaves in a rather central position the hot-dry climatic region of Southern Europe, Northern Africa, and the Near East to India region. The hypothesis here is that this region originally was the home of the brown race. Coons has placed the peoples of this general climatic region with the Caucasoid race. Because of their central location, they were in a position for the greatest mutual interaction with other races.

Around the Mediterranean and apparently to a more limited extent through the Near East there has occurred a strong interaction with the white or Caucasoid race. Interaction appears to have occurred in both directions. Eastward into Southeastern Asia and southwards into the islands, the brown race has moved to interact strongly with the yellow or Mongoloid southern movements, both largely at the expense of the original black racial peoples of the region. However, the negroids have persisted in isolated areas such as the Andaman Islands group and the Dravidian peoples of South India.

With a continuation of the same line of reasoning, the Capoids of Coons appear to be a result of early interaction of the brown and negroid race, but with dominance of the negroid side.

The resultant picture sketched out in extreme brevity has been offered in an attempt to interpret the general present distribution of peoples in the Old World, utilizing an hypothesis of climate-race correlation and recognizing the geographical relationships of these areas to point out where interactions were bound to occur.

One of the interesting results of this mental exercise is to indicate that the Near East would be approximately the place for the strongest conquest and cultural interactions between the white, yellow and brown races. Whether or not this is significant, it does provoke thought as to a possible correlation of such a probable meeting place and the generally conceded notion that this also was one of the most important if not the only area where early civilizations prospered.

The greatest changes in the human ecological system have been brought about with rapidly increasing tempo during the last two centuries This epoch has seen the rapid development of science which not only has given man the power and machinery to tremendously augment his force, but more importantly a basic understanding of his environment and other organisms.

Genetics, selection and refinement of favorable qualities in crops and domestic animals made possible significant advances in food production. With improved breeding stock, use of fertilizers, insecticides, funglcides and weed killers combined with mechanical power for their application as well as for planting, cultivation and harvesting, agriculture could be raised to a high productive level with low demands upon man' s own energy.

Advances in engineering have created highly effective means of manufacturing, working of other resources than the soil, building construction and means of transportation. Man can now travel safely on land and water, over snow and ice, under the seas or through the atmosphere and has just recently learned to traverse nearby space beyond the atmosphere.

Most profound in its ecological effect on man has been the progress in human medical knowledge. Whereas formerly shelter, fuel and clothing only provided microclimatic control of temperature and humidity, medical knowledge has made po8sible a much more profound micro-environmental control so that sanitation measures, sterilization of food and water supplies, controlled immunization and air conditioning combined with wide- spread control of disease vectors provide an artificial environmental barrier to factors which formerly took a heavy toll of human life. Even when cases of breakthrough of disease occur, advances in medical care of the individual and chemotherapy provide means of arresting or eliminating most disease attacks on the individual.

Further, progress in surgical techniques and equipment have allowed the correction or adjustment of accidental injuries and genetic malformations which has resulted in the possibility of maintaining or prolonging the life of individuals who would have died rapidly without the intervention of medical assistance. When such interventions affect hereditable factors, the individuals reproduce and build up significant numbers of the human population which are kept alive only by continued medical support.

Gradually, the replacement of the natural by the human ecological system progresses. This progress is not at all uniform but depends on sectional technological and intellectual advancement which usually is directly correlated with accumulated wealth in terms of those exchange values which can purchase food, resources and services. Nevertheless, medical assistance is so avidly desired by all, that much of the medical knowledge and readily applied techniques or pharmaceuticals have become available throughout large extensions of the planet. Well-to-do nations have also extended programs of sanitation and vector control to nations which could not by themselves have afforded such refinements.

The Population Explosion

All of this has had an extremely profound effect) namely, that of a tremendous rapidity in human population growth, in recent decades. Populations of some nations can double in from only 20 to 25 years while the average for the world is still around 40 years. Since part of the growth is due to an increasing average length of life at the present time, the current increase may be disproportionately large and will not be maintained in most nations as a higher percent of older people is attained. However, only a few decades will be necessary to bring about an unsupportable concentration of human beings on the earth.

This is primarily because of the elimination of the checks and balances of the natural ecological system during the progress towards a synthetic human ecological system. At least, exchange and transportation have allowed a fair dominance to date of the specter of famine. Disease and epidemic controls are of international concern and have fairly well eliminated widespread ravages of human diseases as a control of population expansion.

As culture advances there is an increasing desire to eliminate warfare of which certain aspects have been effective in decreasing populations, at least temporarily. However, most efforts have been directed towards a control of the decisions for war making and armaments rather than attacking the basic causes of war. Unlimited warfare or conflicts continue in many spots of the world, but these as a whole have little effect on the inexorable growth of the total human population. Thus, the present period finds man still able to avoid the major checks on population increase; namely, of famine, pestilence and warfare. The dire predictions of Malthus made in 1796 have been effectively thwarted up to the present. In fact) there are many leaders and even scientists so imbued with optimism as to man' s ability to conquer indefinitely those potential natural population checks as to think that they can be ignored completely.

However, geometric increases are always deceptive. Doubling of small numbers appears to be not too different from an arithmetic increase, but sooner or later one of the doublings suddenly becomes overwhelming. Up to the present the multiplications of human numbers has been absorbed at the expense of the natural ecological system. High percentages of the individuals of the flora and fauna are being eliminated to make way for the expansion of only one species. Several animal species have completely vanished or are at a point close to extermination due to human pressure during the last two centuries.

Before many years pass, there will remain few unoccupied or sparsely populated regions on this planet where conditions for human life are not too uncomfortable. When that time arrives, coupled with an immense geometrical increase of an already large population, the overwhelming point will have arrived. No possible advances in food production could then keep up with the geometrical increase, even if the crowding of mankind had not already given rise to holocausts of terror from warfare or disease. At that time, the whole painfully constructed human ecological system will break down with a fast return to a natural ecological system which, after all the material and cultural advances, will then be very distasteful to man. Also, man would be forced to return to a natural ecological system within greatly impoverished environmental conditions, so that the adjustments would be not only unpleasant but extremely difficult.

Every advance in culture or in the development of the synthetic human ecological system takes man farther away from and further blinds him to the workings of the natural ecological system from which he arose. With his essential needs for food and space obviously fulfilled by an ever stocked supermarket, a working desk or bench and an apartment or home on a few-meters-square lot, the average human being of an affluent society has little direct contact with nature. Whenever he does Intentionally set forth to sample nature "in the raw" during a vacation period, most traverse farmlands of artificial associations to shore or park areas already controlled and welded into the human ecological system.

Therefore, whenever individuals do something personally about population increase rates, very likely such action has little or no connection in their minds with thoughts of the need for balance in the human ecological system. If done, it is probably for the purpose of avoiding social repercussions on the individual or in order to obtain more material benefits and higher social status for him and his children. This is a long cry from the previous practice of infanticide on Polynesian islands where humans were still so intensely aware of the balance in natural ecological systems that the idea of survival of the group could outweigh the innate strength of mother love.

Undoubtedly, such infanticide to hold population in balance with resources was a community cultural directive rather than an individual decision. But, at any rate, it was a directive which the individual could readily comprehend. In modern society fortunately, population control can be effected with less pressure on emotions than the system of infanticide. However, it must come soon to save the advances made in human culture and only awaits effective instigation by the leaders of our culture.

The Approaching Crisis of Overpopulation

There is a growing uneasiness among leaders who recognize the increasing problem, but who do not as yet realize the urgency of the situation Most efforts are applied as indirectly and as obscurely as possible to avoid conflicts with those who openly oppose direct interference with human reproductive processes.

At the forefront of such opposition are the conservative philosophies and religious which were founded in the distant past when mankind was largely still subject to the controls and balances of a natural ecological system. Such leaders along with economic and political leaders are also influenced by the power which numbers of followers give them. Thus, the major blocks to divulging information and materials for effective planned parenthood are simply ignorance or selfishness.

At any rate, the advent of effective checks on human population increase is bound to take place within the next few decades. Whether this can be done in a cultured way with international cooperation and wide spread education or whether it is left to be taken care of by the natural ecological system with the inhumane methods of famine, pestilence or warfare will depend largely on whether the national and world political and religious leaders attack the problem in time.

In the meantime, the stage is being prepared for rapid diminution of human population. The very development of the complexity of social organization which permits a high level of living for the advanced nations and which is pointed out by the optimists as the reason to scoff at worries about overpopulation becomes more vulnerable to disintegration every year. High level food production occupying only a small percentage of the workers in an advanced society is dependent on a complex cultural system providing them with machinery, fuels, fertilizers and water for irrigation. No longer would it be possible for the high percentage of tile population who are not food producers to live off the land ii' a period of cultural disruption. With steadily increasing numbers of humans, the entire food system must obviously become ever more complex and continually more vulnerable to disruption.

However, food is only one of the great ecological needs of an organism. Space Is the other. Crowding of humankind is not so much a physical problem as it is psychological. We know too little of the significance of such a psychological problem to discuss it clearly. However, there appears to be a point where the swing of the emotional pendulum from loneliness to gregariousness encounters too much crowding and desires to swing back towards freer spatial limitations.

Territoriality

Under the natural ecological system, the point of crowding is recognized In the phenomenon of territorially This works with either a group comprising a mated pair with offspring or a larger social group. Under the human ecological *system,* the very complex socio-economic groupings have not even worked out satisfactory or convincing units of homogeneity. Perhaps the largest satisfactory homogeneous ecological group attained by mankind was that of the tribe which corresponds to a still low cultural stage.

Beyond that point, the groupings set up become more and more complex with overlapping and schisms. There are ethnic groups, language groups, religious followings, social and economic classes, political cliques, races and nations. Of all these groupings, in spite of the fact that racial, ethnic and language units are seemingly more natural, national groupings have been the most strongly addicted to the idea of territoriality. The latter is such a strong concept that all other differences are usually subjugated during any threat of invasion or change in national boundaries.

However, national territories have been established more or less at random by historical accidents or incidents. Except also by chance accidents of history, they are not normally sound ecological groupings. As long as there was little crowding within a nation or where emigration could take place without restrictions, national boundaries served satisfactorily as territorial symbols.

In recent times, with the build-up of population pressure and the gradual curtailment of emigration possibilities, the artificial concept of national boundaries as ecological territorial limits is becoming more and more strained. As long as abundant space for expansion within a nation is available, there is a general lack of competition between minority groups. But when population pressure develops, the sub-groupings such as of racial, ethnic and common language stocks develop strong unities which may even outweigh national cohesion. Further, neighboring nations which have much in common are beginning to form blocks based on mutual economic and protective interests, thus, also indicating a search for the replacement of national boundaries by other stronger grouping bases for territoriality.

This clearly indicates that major readjustments in the human ecological system must be made within the very near future in order to avoid disastrous territorial wars based on other groupings than those of individual national boundaries, which have served for a short historical period as a symbol of territoriality.

Such questions fall more within the realm of social and political sciences, but must be weighed satisfactorily from the ecological point of view. Man cannot only be considered as a social organism. Other societies, such as the social insects, have been able to adapt to a natural ecological balance by the evolution of a society in which the reproduction of the population is confined to one or a very few specialized individuals. This made the social and territorial units essentially one family, a unit very easy to control. Other social insect adaptations are a fixed caste system which can be controlled by differential feeding of the young.

For man$_1$ there Is still no possibility of such simple solutions for the development of satisfactory ecological or territorial units, although political evolution with increasing population pressure is tending somewhat to follow the social insects Evolution of governments proceeds towards an even greater breadth of control of the life and activities of the individual human. Obviously, if unrestricted population growth continues, a nation wishing to survive as a social unit must inflict more discipline on and lessen the freedom of action of the individual. This is clearly the road of the socialistic governments, a route already essentially mapped out by the social insects which with their very short generations reached a situation similar to that of humans long ages ago. Even then, in addition to reducing the individual insect to a low value and rigidly controlled by the group, it was necessary to find a system for controlling the reproduction of the social unit in order to maintain a balance within the territorial unit.

The other major social experiment of today is to try to raise the cultural, intellectual and productive capacity of all the individuals in a nation or social unit to a level where the group differences within the nation are kept subordinate by cultural tolerance or are eliminated by intermixing. This is the road of the advanced democratic nations. Both are human social evolutionary trials to find a solution to population pressure and the establishment of satisfactory territorial units and control of numbers within the social unit.

The Future

The preceding sections in this chapter have attempted to sketch out the long-developing replacement of the natural by a human ecological system. The latter is now threatened by its very success in favoring humans, because the rapidly increasing human population will soon make highly questionable the probability of maintaining our present highly developed human ecological system in the advanced nations.

Supposedly, man will meet this challenge in large part by rapidly accepting the need for planned control of his own reproductive capacity within the next few decades. However, the lethargy and opposition on the part of political, religious and other leaders are likely to delay this step regionally long enough to create not only widespread human suffering, but also to effectively wipe out much of the rich natural heritage of this planet.

An early attainment of an ecological balance in numbers of the human species with the natural environment of the earth would have permitted a richer life and greater freedom for individual humans as well as the possibility of completely subordinating the reasons for political and racial differences. Since we did not choose that road soon enough we must face more difficult periods ahead and hope eventually to reduce our populations voluntarily so that the possibility of a rich life for all will again be feasible.

CHAPTER X

LAND USE PLANNING

Land Use Methods of Little Significance in Man's Early History

In the natural ecological system, evolution gradually expanded one or a few simple forms of life into an extremely wide array of species, races and forms of plants and animals. Those in existence in recent times along with man represent the surviving species whose adaptations have permitted them to fit satisfactorily and maintain themselves in given niches within one or more ecosystems. In other words, the best adapted species always filled the niches and in the natural ecological system continued to occupy those niches until evolutionary changes made new readjustments necessary within any ecosystem.

With the cultural rise of man, with his development of a relatively separate ecological system, with man's assistance to certain species of interest to him and with his ability to greatly alter or disrupt natural ecosystems, an entirely new force separate from evolution began to be exerted on the natural ecological system.

As long as man existed in relatively small numbers, these effects on nature were not significant. Succession was a natural process which could cure any injury or replace any damaged portion of an ecosystem. The clearing of an area by man was essentially no different from or even less severe than the damage caused by fires, hurricanes, volcanic eruptions or geological erosion.

For thousands of years, culturally-emerged man gave little attention to his own effects on the natural ecosystems. There were certain items such as air, water, land, fish and game which were always available for the taking and seemed inexhaustible. If they ever became short in any given area for the number of people present, it was only necessary to move the people or some of them to new places on earth.

However, even in relatively early agricultural times certain localities possessed such a favorable combination of climatic, edaphic and other factors, that the concept of ownership of land was developed. When such valuable lands could be made more productive with irrigation and a stable culture permitted the laborious installation and maintenance of water catchment and conduction systems, the concept of water rights evolved. Man then found that his permanence in such an area, apart from intrusions by other people, depended on his success in maintaining the soils and on operating irrigation systems.

Also, because he worked with both crops and domestic animals he must have found out early that different topographies and distinct classes of soils responded differently to his uses. Thus, he must have early developed some concepts concerning what is now known as land use planning. Nevertheless, a concept which is necessarily almost as old as agriculture had until very recently scarcely progressed beyond the obviously logical farm pattern of matching up the correct crop or rotation of crops to particular types of soils.

Factors which affect Land Use

Wherever economically profitable crops can be grown and the ecological factors of climate, soil and others permit permanent use of the land for those crops, what is obviously good land use follows. The resultant human ecological system landscape with productive, well-tended cultivated fields, pastures and sometimes with or sometimes without patches of woodland along with soundly constructed and well-maintained homes and farm buildings produce a picturesque or aesthetically satisfying landscape. Rational land use is economically productive on a long term basis. When land use is economically productive there is not only greater satisfaction and pride in ownership, but also time and means are available for the proper tending and maintenance of all the elements comprising the landscape. In effect, even though the natural ecological system has been replaced by a human ecological system, the latter is obviously in balance or equilibrium. Thus, good land use is basically the result of the attainment of an ecological equilibrium.

Even though time and growing experience would appear to favor the development of good land use, there are many factors working against its attainment. Even in the best environments, population pressure tends to cause parcelization to such a degree that there is not space for adequate rotation of crops. Technology is constantly changing, so that not only is long term planning almost impossible, but maintenance of good land use may depend primarily on cultural flexibility rather than efforts or specific environments.

However, with the complexities of trade and transportation, economics, in the form of markets, exerts probably the greatest single effect on land use. Nations which because of their technical and industrial advantages are major purchasers exert a profound effect on land use far beyond their own territories. Whereas such a nation may favor its own land resource producers, it purchases outside products only in accordance with its own needs and prosperity. Competition for such markets between and within producer nations necessarily favors not only the cheapest producers or those willing to accept lowest prices which usually are synonymous with the lowest level of living, but also those nations or individuals willing to sacrifice good land use principles for the questionable benefit of temporary high productivity.

This defines actual land use as the actual result of a combination of many forces namely, the different economic levels between nations, effective population pressure, the chance coincidence of natural resources with national territories, all further complicated by the short life span of man which gives rise to a short term concept of values of land use and conservation and finally the internal complications of intranational social structure affecting land ownership, patterns of production and many other aspects of culture.

Thus, effective long-term land use which is absolutely essential to the establishment and maintenance of a sound, permanent human ecological system is only widespread in the highly advanced nations. In most all nations there are local sections which display the attributes of good land use, but in most cases these correspond to a small percentage of the total land area. Such areas of satisfactory land use have usually been developed in long stable communities so that neighboring farmers have developed a cultural concordance as to how a farm should be operated. Thus, the result is one of long-term development rather than the result of land use planning.

Effects of Overpopulation

Under the natural ecological system, each ecosystem was evolved to attain the highest possible production from its specific environment. Even though production varies widely through the range of ecosystems, at least, total production may be directly compared because the measure is the same in all, namely, the weight of dry matter per unit area per unit time. Under the human ecological system with trade and commerce, production is of very diverse materials which are reduced to the common unit of exchange value. Thus, the major influence affecting actual land use under the human ecological system is the money value of the crops which may be produced. That this factor predominates over food production per se may be noted by the growing tendency for subsistence agriculture to be eliminated from the more productive environments and pushed farther and farther onto less desirable sites.

This process in advanced nations results in good land use because an opulent society can absorb the subsistence agriculturalist or less competitive farmers within the fields of industry and service. The expanded market for agricultural products promotes technification and increased efficiency of agriculture on favorable sites, which can be aided and abetted by research financed by the whole nation.

On the contrary, in poor nations, subsistence farmers displaced from good cannot be absorbed in industry and service as fast as their numbers increase. when subsistence agriculture is pushed onto poorer sites, increasing numbers subsistence farmers can only result in lower standards of living. This gives rise to poor land use with more rapid deterioration of the sites. At the same time, the subsistence agriculturalists produce enough local market crops on a low level economy to slow up capital inversions on good sites for local market production.

Thus, agriculture on the better sites tends more and more to produce export crops only for the advanced nations. As this takes place in many under-developed nations, cycles of over-production for the international market are automatic, so that even the best agricultural lands of the less affluent nations do not tend to develop permanent, high level land use. Incomes wax and wane. The degree of care and maintenance given to the crop area varies accordingly.

Given the close ties of land use with economics and population pressure, it is obvious that good land use can be established either when a high national level of prosperity exists or when a national population is stable. Formerly, when extensive areas of undeveloped land resources were still available, population pressure was not important as new population growth could expand into such areas. Such conditions are almost non-existent today. Even though several nations have extensive areas of lands with low population density, most of these are of such a character that they offer little possibilities of successful colonization except with a high degree of technical knowledge.

Until man learns to restrict his population growth, good land use will remain only a theoretical consideration. The attainment of such use in prosperous nations which still have a rapid population growth is still essentially due to a stabilization or even a reduction of rural population. Industry and service are able to lower or eliminate any population pressure on the land. As an example the United States of America during the past few decades has actually continued to reduce the cultivated farm acreage as well as the number of people engaged in agriculture and grazing. This means that land areas where cultivation would not be conducive to good land use may be left for grazing or forests.

It is extremely important for man to understand this relation of numbers of people engaged in agriculture with the state of land use. One should not compare densities based on total population but rather densities based on populations engaged in agricultural pursuits. Further, these latter figures must be correlated with topography, fertility of soils and climate to obtain satisfactory relative comparisons.

The term of land use planning must be given a completely reverse application to that of the present. We now try to work out good land use plans with existing populations and existing population growth potentials. In most cases, this cannot possibly permit good land use planning. Exactly the opposite concept is needed. We should evaluate an area as to how many people could be supported at a satisfactory level of living with good land use. This is a concept which is applied by man to effective pasture and wild life management. The same must be applied to people. Only, in that manner, will it be possible to attain to widespread good land use management and to a satisfactory equilibrium in the human ecological system.

Major Divisions of Land Use

There are only three major basic land uses; agriculture, grazing and forestry. Other uses such as for factories, cities and transportation right of ways occupy land, but do not utilize the soil resources in the sense of the three major uses. Even the three are not always precisely divisible because of combinations of agriculture and grazing in rotations or the partial use of forests as extensive range or grazing lands.

However, it is still possible to separate all lands Into the three categories by their major use.

Cultivation or agriculture because of its generally intense nature and usual movement of the soil is the form of land use which is the most difficult to carry on perpetually without deterioration of the site. Since land use should be planned for extremely long periods the definition of agricultural lands is crucial to the entire subject of land use planning. If such lands cannot be defined by actual land use as well as theoretically on maps, then there is little or no possibility of land use planning.

This is the major land use problem at present in the underdeveloped nations. Although, obviously many of these nations have only a relatively small percentage of true agricultural lands, cultivation as a result of population pressure has been extended to both grazing and forest land categories. The net result is an extremely low level of living of those farmers and their families who try to carry on agriculture on lands not suitable for such uses. Further, cultivation of lands not appropriate for permanent agriculture leads on to deterioration of the sites bringing about either a still lower level of living or abandonment. The latter event forces the families to move to still less desirable sites and increases the total pressure on the lands of a nation.

Without any limits to agricultural use, the land categories which would be suitable for grazing or forestry use become steadily reduced and pushed back farther and farther on to the less choice sites for those activities. The forests are the first to go. Without forests for fuel, animal dung is substituted, reducing still more the fertility that can be returned to the soil. Then, when there is no pasture left for grazing animals, only cultivation is possible, with the utilization of dry plant matter for fuels. Such heavy use can be continued for a relatively long time on highly fertile soils or on alluvial lands, but tropical slopes will not long support the pressure.

Disregard of the boundary lines between agricultural, grazing and forest lands, at first, seems not especially important and even desirable to avert the suffering of a few families. However, once the lines are breached the process of misadjustment continues until the whole nation suffers the consequences. Not only do the grazing and forest lands eventually become unfit for further agriculture use, but also they will have been so deteriorated by the time of abandonment that they are not even suitable for the uses which could have maintained them in perma-nent production.

Even in the face of evidence In a great many countries of the disastrous results of such inappropriate land use, the leaders in various fields of the nations apparently fail to recognize that a generally careless land use policy is the cause of their widespread poverty. Not a single one of those leaders would probably fail to understand the fact that a pasture has a certain definite productive limit and that it is Impossible to continue to double the number of cattle in the same pasture with-out their suffering. Yet no one appears to be willing to apply the same logical reasoning to land occupation by people.

At the present time, even where the true agricultural land category has been completely occupied with considerable invasion of the grazing land and forest categories, government leaders consider sponsored colonization in unoccupied areas as the best solution to population pressure. Often the areas selected for colonization are not permanent agricultural lands, so that an expensive short term solution can only lead to still more serious socio-economic problems in the future.

Where grazing and forest lands are already being utilized for cultivation, the only practical solution is to arrest or even reverse population growth until the population is in equilibrium with the land use classes. Although, at present, this is still a very difficult problem, it will have to be faced eventually anyway. The earlier the basic problem is faced and solved, the less land will have been seriously deteriorated and the easier will it be to get all lands into utilization according to their permanent land use potential.

Agricultural land comprises those areas of terrain which because of favorable topography, soil fertility, depth, drainage and rainfall pattern may be cultivated in crops permanently on a reasonably profitable basis without deterioration under the typical cultivation systems of the locality. To such natural areas may be added lands with lower soil fertility, poor drainage and a low rainfall, if sound economics permit fertilizer application, artificial drainage or irrigation practices.

The limits of the agricultural land category will vary from nation to nation and from life zone to life zone within a nation in accordance with the skill of the farmers in maintaining soil productivity as well as the type of crops grown.

Grazing lands comprise those areas of terrain with somewhat steeper topography than agricultural lands along with terrain of topography suitable for agricultural use, but lacking some other favorable characteristic for the latter, which can be maintained permanently without deterioration and which can provide a satisfactory level of living for the land owners and workers. Normally, the topographic limits for grazing lands are considered to range from the upper slope limits of agricultural use to 40 per cent slopes. In grasslands too arid for agriculture where irrigation is not feasible, grazing may be the only suitable land use for plains or flat lands.

Forest lands include all of the remaining areas which produce tree growth. Forest use does not necessarily imply timber production because watershed protection, stream regulation, wild life management and recreation are recognized economic forms of utilization of areas within the forest land category.

After these three classes of land are mapped as defined, some non-productive areas such as deserts, salt flats, recent lava flows or ice-covered terrain remain. These areas still cannot be utilized within the usual consensus of land use, thus falling outside of the three main categories.

Actual vs. potential use

The inappropriate use of forest or grazing lands for agriculture is common in the less advanced nations. Leaving that point aside, there is also a wide variation in the effectiveness of use or productivity within the correct category, i.e. of agricultural use of agricultural lands, grazing use of grazing lands or forestry use of forest lands. Such differentials depend on many factors such as skill of the users, availability of capital for improvements of the site or for production artifacts, market conditions, availability of research findings and a great many others.

When all or most of such factors are favorable, production per unit area can be very high. Also, equal crop production can be obtained with a great reduction in time and effort on the part of the farmers, effectively reducing the number who are necessary to provide food for the nation.

Again, it is obvious that good land use requires fewer people which in itself reduces pressure on the land. The remainder of the population are freed from the assignment of food production and are available for industrialization and services. Obviously, the total population desirable for a nation is basically dependent on its food production potential. This may be increased to the extent that other than soil or marine resource productivity, such as mining, manufacturing and export of services provide a net exchange surplus available for food import.

Even if the underdeveloped nations established a satisfactory land classification and stabilized their populations at a level which could be well fed from non- destructive land use, they would still find that a large percentage of the population would be existing at a low level of living. However, from such an established base, continual gains could be made by improvements in land use techniques. Without any such stabilization of population numbers as a base for raising levels of living, all improvements tend only to increase the numbers of inhabitants on a low level of existence.

In fact, every improvement which raises the level of land productivity before population is stabilized will only make any improvement plan subsequent to population regulation more difficult and slower of realization. Most foreign aid programs of the advanced nations have failed to understand that their well intentioned assistance to raise productivity has actually hindered more than helped the eventual solution of the problem of obtaining an ecological balance in the underdeveloped nations. Increased productivity should be utilized to raise living levels rather than to facilitate population increases.

In summary, land use planning should first map the extensions of the three major categories in each nation. Calculations should then be made of the approximate number of people that a nation can support permanently on the basis of actual systems of land use. Population planning should then aim at arresting population growth if actual population has already passed such totals. Once the mechanics of arresting population growth are put into operation, the general educational and living level of the masses can then be elevated rapidly with improved techniques, research and capital investment.

CHAPTER XI

PRODUCTIVITY

With a constantly augmenting number of human inhabitants on the earth relative to its fixed surface area, the subject of productivity becomes increasingly important. Indications of this concern are the growing number of scientific articles relative to the topic and the present planning to emphasize productivity as a very important aspect of the proposed International Biological Program.

Malthus long ago clearly pointed out that the relationships between unlimited population growth and limited food production possibilities would lead directly to food shortages and starvation. However, Malthus underestimated the rapid technical developments, which through mechanization of agriculture together with improved techniques of genetic selection, fertilization, weed and pest control, food storage and better distribution systems would delay his dire predictions for a great many decades.

In fact, up until recently many scientists paid little attention to the geometric increase of human population and felt assured that science could easily maintain its pace of rapidly stepping up productivity. In addition, man appeared to have scarcely begun to draw on the tremendous potential food resources of the seas which cover about two thirds of the surface of the globe.

Within the last few years, experts have looked more critically at the relations of population and productivity figures. Their findings indicate a growing unfavorable balance with dim prospects in the very near future of meeting adequately the total needs of food for the projected world population. Thus, the reasoning of Malthus appears to have been sound even though his predictions were erroneous as to the timing.

Definitions

Productivity may be studied in various lights. First, one may consider the productivity of specific environments which, on land surfaces, corresponds to an evaluation of the climate and soils. In this strictly ecological sense, productivity can be defined as the production of dry matter in kilograms per unit surface area per year. Dry matter, the weight of organic matter without its water content is utilized to eliminate the excessive variability in percentages of water content in different species and different tissues.

Dry matter productivity alone may be the best measure of environmental productivity, but it is far from synonymous with economic productivity, which is based on the value of the product to man, or with food productivity which constitutes only a portion of those products of economic value to man.

Economic productivity may also be expressed in standard units per hectare per year, in this case, by converting the production to its monetary value. There are, however, two main problems which complicate the results. First, market prices fluctuate from year to year so that often the actual potential of the area for production may be of less importance in determining economic productivity than the astuteness of the grower in selecting the right crop at the correct time. Second, the economic values of the produce may be strongly affected by location and means of transportation to the market.

Thus, although the economics of productivity are one of the most important impetuses for any given crop production, a competitive free market gives rise to many anomalies and complexities in scientific correlations. Because production tends often to be directed towards specific money markets it may lead to conflicts between those who wish to produce money and those who need to produce food, thus becoming involved in social values and conflicts. Economic productivity evaluations become even more complex when the relations extend across cultural and technological boundaries.

Third, the quantity in weight or measure units of a specific crop per hectare per year is another possible measure of productivity. With such a system one utilizes or converts to a standard unit, for each commodity, the measures of the product which are normally harvested by the grower. Also, a great deal of information on such production per unit area is already available. Measurement is facilitated due to the fact that only that portion of the crop which is of use to man is measure.

Although this latter method can provide one of the most satisfactory measures of production for comparison between different environments the method can not utilize any specific crop beyond the limits of its own environmental conditions.

Discussion of the Three Methods of Measuring Productivity

The three fundamental methods of measuring productivity may then be stated as 1) a measure of the dry matter produced in kilograms per hectare per year, whether of value to man or not. 2) A monetary value of the crop or product produced per hectare per year and 3), a measure of the weight or volume of the crop or products useful to man produced per hectare per year.

Of the three possibilities the monetary value method appears the least satisfactory as an ecological measure. Often, a crop may be produced not in the most suitable environment, but rather in those areas where poverty and the resultant cheap labor make it economically more profitable for the grower. Instead of involving productivity with social complications, ecology should derive productivity-environment measures which will assist in pointing out anomalies and thus tend to stimulate correction of socio- economic land-use problems.

The dry matter productivity measure would appear offhand to be the most accurate and scientific evaluation for environmental comparisons. Still the method offers many difficulties. Not least of these is the problem of actual measurements. This system is primarily being applied in the temperate regions where natural vegetation is not as luxuriant or as complex as that in the tropics. (Odum). The physical task in the latter region appears to be staggering.

Then too, with dry matter production the question arises as to when productivity should be measured. Apparently, mature natural stands have only to replace dead or fallen trees as well as falling leaves, dead branches and sloughed off bark. This must vary from year to year because the replacement of individuals in the stand appears to vary considerably over a period of years. This is especially true as applied to any plot or portion of the stand which could feasibly be measured.

Probably growth or annual production of dry matter is considerably greater during the successional stages. The highest production per year should take place in a late stage of succession when there is a considerable mass upon which to add growth, but before the slowing down of growth due to full stocking of the stand has been reached.

While good results have been obtained in simple conifer stands in the north, such as from the research carried out by Ovington in Great Britain, the problems involved in handling a mixed hardwood stand of many species with their varied forms and different wood densities would be serious. Although satisfactory techniques may be developed, given sufficient time, there also exists the problem that many natural associations which occupied favorable climates and fertile soils have already been eliminated or only considerably altered remnants remain. Without appreciable adjacent natural forests, succession is less apt to follow the same pattern of development as that which is natural in less disturbed areas.

Basic research on methods for determining total dry matter production should be continued, but it is unlikely that this approach will give quick enough results on any appreciable number of associations to serve human needs for satisfactory productivity measures as a useful guide in the critical years of scarcity which are rapidly approaching.

The most logical approach appears to be the third system, that of measuring production of harvest units per crop or product per hectare per year. This is the simplest method, for which there is already much accumulated data. This type of productivity information is of the greatest interest and could provide us with the basic data for careful land use planning which will be very necessary in the future.

The major problem involved is that specific crops or products generally involve only a relatively limited range of climatic and other environmental factors where conditions are favorable for their production. Thus, to utilize commodity production figures for evaluating environmental productivity will require that equivalent comparisons be developed between such products as orange fruits, coffee beans, raw sugar, wheat grains and beef.

Although this may appear off-hand to be quite difficult, the overlapping of environmental ranges should make it possible to compare productivity between the ends of wide environmental ranges through a series of intermediate comparisons.

Commodity productivity comparisons would not be feasible, without at the same time, locating such productivity within a precise environmental classification system. The life zone system with the subdivision of each life zone into associations provides such a basis for complete environmental classification.

Given the possibility of matching up commodity production precisely with environmental conditions, it is then possible to draw upon the experience of the peoples of the entire earth. Once one studies a specific crop within its satisfactory environmental range, one can then point out the genetic selections, the cultural practices and other technological innovations which can best be employed to raise production. Also, economic studies can then be carried out more effectively, as relevant within environmental and technological level controls.

Method of Rating Commodity Productivity

The first step should be the determination of those life zones which offer the suitable, major climatic conditions for good to excellent production of a given crop. This will require the establishment of ranges of productivity in units classified as Poor, Fair, Good, Excellent and Superior for that particular crop. The life zones considered suitable for a crop should give at least Good production. In general, the ranges of Excellent and Superior production would only be obtained with considerable technological advances through advanced genetic selection, fertilizer applications or other improved techniques.

Once the life zone range is determined, comparisons by associations or groups of associations should be made to determine what specific environmental conditions are desirable for satisfactory production of the commodity within such life zones. These are primarily suitable or unsuitable due to topography and drainage conditions, soil fertility, soil depth, precipitation distribution or the like.

It should be easier to divide a life zone area into commodity productivity association groupings than into the natural associations which support or previously supported different plant communities. This is because some differences which are significant enough to produce separate natural plant communities can be handled technologically to produce equal crop production results. Thus, a certain range in fertility can be handled by distinctive fertilization programs so that an area of alluvium with four or five original associations can provide equally satisfactory productivity over the total area.

Usually within the natural climatic life zone range for a commodity, several associations or association groupings will be found satisfactory for good or better productivity of a commodity. The wide-spread use of paddy rice on a wide range of alluviums in Thailand is an example. In addition to this optimum life zone range, a crop may also do well in special environmental conditions in one or more adjacent life zones.

As an example, certain deep rooted crops of the moist forest life zone may be produced with good results on alluviums with a raised water table within the dry forest life zone. Again a moist life zone crop may be extended satisfactorily into the wet life zone either in monsoonal associations with their extended dry season or on recent volcanic ash soils where the porous structure and high fertility of the latter provide compensating factors for the adverse climate of heavy precipitation. Such ilfe zone extensions of a commodity range constitute, in effect, special natural condition life zone ranges.

Again with technology, a commodity may be extended into life zones beyond both the optimum and the special condition life zone ranges. An example is the growing of crops with irrigation in semi-arid or drier life zones outside of the natural climatic range of the commodity. Because the soils of arid climates are generally fertile and the use of irrigation implies technologically oriented farmers, production of commodities or crops in the technologically extended life zone range may be even better than within the natural range. This is not so much indicative of a higher potential productivity of the technologically extended life zone range but rather that commodity production could be raised much more within the natural range if adequate technology were applied.

Following the determination of the life zone ranges for a commodity one can then set up a complete comparative table comprising life zone ranges, technological level and productivity level. The first category comprises 1. the natural life zone range, 2. the special natural condition life zone range and 3, the technologically extended life zone range.

Under technological level, there should be several divisions, more or less as follows: L low level, i.e. with simple practices and without any technological advances. 2. Moderate level, with irrigation, some fertilization or crop rotation, or other crudely managed technological advances, 3. High level, with some genetic selection, high fertilization, technological weed and pest control and some other technological advances in harvesting and crop handling and finally, 4. the highly advanced level when all or practically all of the technological advances indicated by high quality research are put into practice. Finally, specific areas under the divisions of the above two categories are to be rated within the established productivity ranges of the given commodity as poor, fair, good, excellent and superior.

In evaluating the level of technology, some technical aspects such as tractor plows for preparing land, harvesting machines, or the like, which have been developed to offset the economic disadvantages of high labor costs must not be confused with technological advances which increase production. Although it is often true that labor saving devices accompany or are directly correlated with high production technology, this is not always the case. For example, certain grain production is higher in parts of Europe than in Mid-western U.S.A. Although grain may be produced just as cheaply with more advanced labor saving devices in the latter region, the former region, even with generally poorer soils, has attained to a higher level of technological production.

Once such a classification of productivity based on environment and technological level for a specific commodity were worked out, economists and other social scientists could carry out their research or analyses of the human-controlled factors much more effectively. At that stage it would be possible to effectively analyze and compare costs, as well as attitudes, and prepare plans and programs for needed research, extension, improved transportation systems and the like.

Use of Productivity Information

The advantages which can arise from such a rating of commodity productivity within environmental and technological classifications are numerous. Within any given nation, the environmental classification can clearly Indicate just what commodities should be produced and specifically where within the nation. Based on the technological classification, planning officers not only would have the specific data as to how much productivity might be increased by improvement of the technology, but also could determine from international studies just where they could best obtain the technological information and genetic material most suitable for the specific environmental conditions of the country. Such information can also provide the most accurate guides for extension and credit programs, while at the same time could indicate to research planners where and how their efforts would be most productive.

On a broader international level, the same productivity-environmental technological level data would provide a sound basis for international planning, commodity control and technical assistance programming. On a world wide basis with a rapidly approaching need for raising productivity rapidly, national production programs can not be scheduled according to long term custom alone, but must be based almost entirely on what can be produced most effectively in accordance with the environmental situations. This is primarily due to the fact that environmental conditions are largely fixed, whereas feasibility for improvement.

The Three Major Land Use Systems

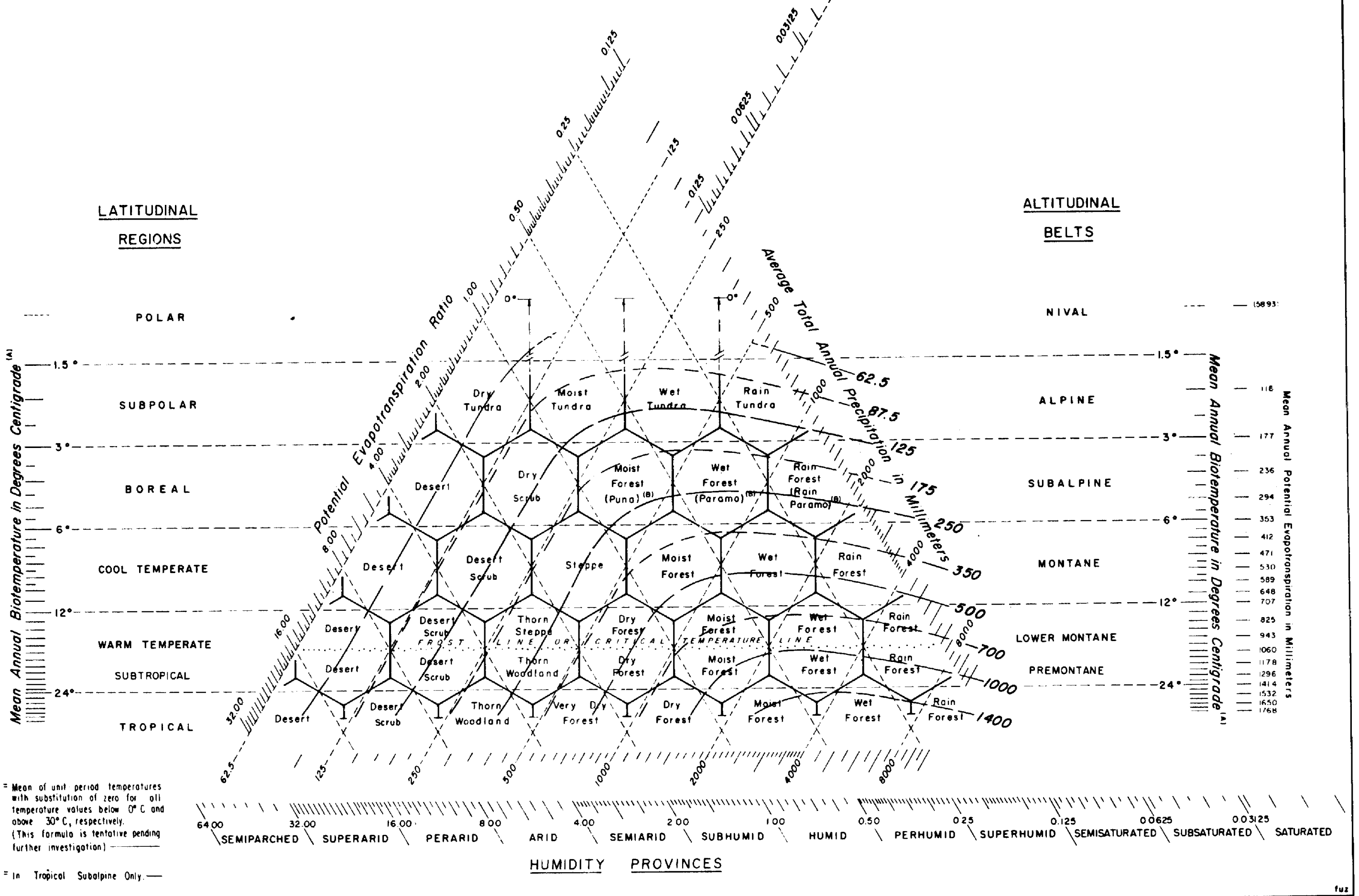
Although the outlined productivity evaluation system appears offhand to be most suitable for agricultural crop commodities, the productivity system must include also the two other major land uses of grazing and forestry.

At the present time, general productivity is low in the underdeveloped nations not only because of wrong environmental location or undue extension of many crops, together with low technological levels, but also to a major degree because of misadjustments between the three major land uses.

Extensive grazing is still being carried out on large areas of alluvium or soils of gentle topography where cultivated crops would be more productive for mankind. This is primarily due to preferences and long established customs which are erroneously allowed to persist due to social and power imbalances.

This is not as serious as the second misadjustment of land use which has resulted and continues to expand even more strongly today under population pressure. This second more serious land use error is the extension of both cultivation and grazing utilization onto lands which would be most highly productive for the nation and the world if kept in forestry use.

FIGURE 7 ISOPLETHS OF MEAN ANNUAL ACTUAL EVAPOTRANSPIRATION IN MILLIMETERS FOR THE CLIMATIC ASSOCIATIONS SUPERIMPOSED ON THE LIFE ZONE CHART.——



(A) t_{bio} = Mean of unit period temperatures with substitution of zero for all temperature values below 0° C and above 30° C, respectively. (This formula is tentative pending further investigation) ——

(B) = In Tropical Subalpine Only. ——

Fotos\Figure7.bmp

Such over-extended agricultural and grazing land use is usually carried out on a low productivity, low technology level and continues to foster and expand low levels of living and education in general rural slums.

In the tropics, especially, where the potentialities for wood production are so great, it is a serious commentary on our civilization that so little thought and attention is being given to this latter form of land use in the tropics, namely, forestry.

Primarily, this is due to the fact that the wood using industries have not learned how to handle the tremendously mixed assortment of broad-leaf timber trees which grow in the Subtropical regions. Sustained yield wood production is still primarily linked with the coniferous stands of Boreal, Cool Temperate and Warm Temperate regions with minor extensions into the corresponding higher altitudinal belts in the Subtropical Region.

Although the coniferous forests of the three latitudinal regions are all being brought into productive forest management, experience is demonstrating that the highest forest productivity is being obtained in the warmest of these, the Warm Temperate region. Hence, the great recent expansion of forest management in the Southeast and Pacific Coastal regions of the U.S.A., Chile, South America, Australia and New Zealand.

This all appears to demonstrate that higher forest productivity is attained with higher temperatures and adequate moisture. Forest production should logically move into still warmer regions as time progresses and will make this jump rapidly to the benefit of many underdeveloped countries as soon as the forest product industry learns how to adequately handle the mixed broadleaf forest products of the tropics.

Comparisons of Commodity Productivity with Basic Natural Productivity

Although the evaluation of commodity productivity appears to offer the best methods to obtain scientific guidance in land use, this will undoubtedly not be entirely consistent with the basic natural productivity of different environments. This is primarily because the major portion of the agricultural commodities produced by man will be found to coincide with natural life zones ranges centering on the life zones of the dry and moist humidity provinces. This is due to the fact that man’s greatest agricultural development has been concentrated within those favorable humidity provinces.

Furthermore agricultural commodities have always been, on a global basis, relatively more scarce and higher priced than forest products. As more and more natural forests are cleared for agriculture and grazing use, this economic adjustment will tend to disappear and land use for wood production will become more competitive with the other uses.

Although such economic readjustments will eventually tend to stabilize and fix more precisely the correct divisions of land use there is a danger of a severe global economic loss if agriculture and grazing are mistakenly allowed to not only remove the forest cover from areas potentially more productive in forest, but, by so doing, to degrade the soil to an extent that several generations will be needed to return the areas to high productivity.

Thus, a potential productivity evaluation is also needed as a guide for planning future land use. As previously pointed out the difficulties of obtaining figures on dry matter production per unit area per year will long delay the availability of such data. Until such are available, some other relative evaluation of productivity is need.

In work with the theory of potential and actual evapotranspiration the conclusion is reached that actual transpiration may well be closely correlated with potential productivity. In Chapter VIII, a theoretical method is offered for the calculation of actual transpiration values for the climatic associations.

Utilizing this theoretical method, Dr. J. A. Tosi has plotted the location of iso-value lines of actual evapotranspiration in millimeters on the life zone chart. Although these lines do not pretend to offer any specific values of productivity, nevertheless, if one accepts the possibility that the latter may be directly correlated with actual evapotranspiration, then the same isopleths would indicate the relative productivity potential of the climatic associations anywhere in the world. The chart showing lines and theoretical values of actual transpiration for the climatic associations is shown as Figure 7.

A relative comparison of the position of these isopleths of actual evapotranspiration with the data from dry matter production studies will be extremely interesting, because if a simple factorial correlation is possible, this would automatically obviate the need for any extensive carrying out of the cumbersome dry matter production determinations. Unfortunately, as yet, to my knowledge, the latter type of studies has only been carried out in a small sector on the chart within the Cool Temperate region so that it is still not possible to discover or check out a possible correlation with actual evapotranspiration.

In such comparisons, care must be taken to either obtain dry matter production from climatic associations or to calculate a corrected actual evapotranspiration value if a non-climatic association is utilized. Formulas for such calculations outside of the climatic association are given in Chapter VIII, but these are still theoretical and have not been tested out. At least, productivity data on dry matter should by all means be accompanied with available climatic data plus stand data sufficient at least for the derivation of the complexity index. An idealized profile diagram would also be helpful for clarifying the number of stories or strata which are considered necessary for the derivation of the values of actual evapotranspiration.

Actual complexity indices may be higher or lower than the one value of the complexity index for the climatic association of a given life zone. Field observations indicate a strong possibility that edaphic and local climatic factors are more favorable or less favorable in direct ratio with the difference in the actual complexity index from that of the index of the climatic association. Thus if some figures of productivity can be correlated directly with the actual evapotranspiration isopleths, there exists the strong possibility that the theoretical climatic association productivity figure can be related to actual conditions through multiplication by the ratio of the actual complexity index over the climatic association complexity index.

Balance Between Population Growth and Productivity

Although increase in productivity must be a fundamental goal of science in the coming years, it must not be considered as a solution to the problem of the rapidly growing world population. In fact, more eventual suffering would be caused by such a policy because there would exist a much greater total population when human needs finally surpassed productivity. Furthermore, an early drive to step up productivity, much of it at the expense of wasted resources and a resulting largely despoiled planet will find mankind in a “cul-de-sac" predicament with no way to go except to starve, or make war or reduce living levels of the masses to unsatisfactory levels.

As a matter of fact, our world population has already outstripped productivity. Too high a percentage of mankind lives daily on a level of malnutrition or relatively close to starvation. But man needs much more than his daily sustenance. A satisfactory level of living involves much more than having an adequate diet. If he is to be given dignity and security, education and a happier life, the human population growth must be stopped or even reversed.

The world’s leaders, as a group, have moved very slowly in speaking out clearly for population control and in helping make information on methods of birth control available to the impoverished and suffering masses of mankind. Instead, the leaders often take the easy way out by requesting greater productivity. This is not only a temporary short-term measure which can not long be successful, but at the same time will lead to the despoilation of much of the rich heritage of beauty and natural life of our planet.

We should be studying the subject of productivity during the coming years and preparing the bases for correct land use and high biological commodity production. But we should not use that knowledge of how to increase productivity foolishly in permitting it to allow a continual increase in human numbers.

Productivity increases must be utilized wisely to raise levels of living. As long as we refuse to accept that more satisfactory use of augmented productivity and go on attempting to pack more under-nourished and hopeless humans on the globe, the more we lessen the future chances of raising all peoples up to a satisfactory level of living. Only a relatively few more years of stability remain for the human population on earth within which we can find the correct solution without major catastrophies. Such a solution must involve the proper attitude towards increased productivity and its utilization, once our population is stabilized, for rapidly raising the general level of living. We know that it is possible to raise productivity a few percent per year so that this would be extremely successful in doing away with poverty in a world of a steady or even declining population.

APPENDIX A

EVAPOTRANSPIRATION EQUILIBRIUM IN A CLOUD CHAPPARAL ASSOCIATION OF COASTAL PERU

Between the lofty ramparts of the western wall of the Andes and the Pacific Ocean$_1$ where the cold, Humboldt ocean-current courses northward just off-shore, lowland western Peru presents the stark, impressive aspect of a desert. Masses of air moving shore-wards are cooled and form mist over the Humboldt current. During the warm months of the year, such clouds are dissipated when they encounter the warm air rising from the heated land surface, but during the cold season they form an abundant cloud-cover over the desert,

At Lima, close by the coast$_1$ airplanes very frequently land with the use of radio beams during the cloudy season, while the city itself may pass several days at a time without the casting of a single shadow. Although this period of year is known as the rainy season, very little precipitation falls. At Lima, mean annual precipitation has averaged only 46 mm. over 18 years. we may feel almost uncomfortably cool at Lima during the cold season. Even though the area is only a few degrees south of the equator, the adjacent Humboldt current and the cloud cover lower the temperature sufficiently to make this a Subtropical Desert rather than a Tropical Desert life zone.

Away from the alluvial plains or river-valley bottoms, which are occupied largely by irrigated agriculture, the Subtropical Desert life zone of Peru supports very little vegetation. Small or large clusters of rootless Tillandsia are encountered on the areas of wind-blown sand, while an occasional, low, upright cactus, probably Cereus sp., may be observed in the areas not covered by sand. Other vegetation present, is not apparent to the traveler riding on the highways.

Wherever the hills of the coast rise to sufficient heights to intercept the cold-season clouds, the greater precipitation, increased moisture condensation and the lower temperature due to elevation produce considerably more humid conditions, so that a continuous natural vegetation is possible. Such areas are called "lomas" locally. Ecologically, the “lomas” may be considered as belonging to the Tropical Lower Montane altitudinal belt.

Today only scattered individuals of the woody vegetation from 5 to 9 meters in height remain and the low vegetation ~as been reduced largely to ephemeral annuals by heavy seasonal pasturing of flocks of goats. Imagination must be employed to picture beautiful areas of continuous forest, with an occasional spring cropping out, as the lomas well may have appeared in the distant past.

Possible indirect evidence for the former beauty of such an area is suggested by the location of a cemetery of upper-class Incas near the Lomas de Lachay. These hills are situated close to the coast, two or three hours by automobile north from Llma on the coastal highway. The rich findings in the graves, so far from any known archeological settlement site, may be interpreted as an indication that the area had some special significance for the ruling class. One seemingly logical inference is that the natural vegetation on the surrounding hills were sufficiently striking in contrast to most of coastal Peru to have been given that special significance, whether from a religious or some other view point.

The Lomas of Lachay are of additional interest because the Forestry Department of the Ministry of Agriculture of Peru has taken some meteorological data there continuously since 1931. The gathering of this information and the forest plantation experimental work in the area have been carried out under the supervision of Hans Rossi, Chief Forester, who kindly furnished the data utilized in this paper.

Temperature and precipitation readings were taken at an approximate elevation of 500 meters above sea-level. The mean annual temperature is 14.9 ^{0}C. The mean annual precipitation based on 29 years records, from 1931 to 1959 inclusive, in a rain-gauge placed in the open is 201 mm, The maximum annual precipitation was 309 mm, in 1941 and the minimum 100 mm, in 1959.

The 14. 9^{0}C. and 201 mm, plotted logarithmically on the world formation chart place this site in the Tropical Lower Montane Desert Scrub Life Zone. The potential evapotranspiration at this point equals 14.9 X 58.93 or 878 mm. per year. The potential evapotranspiration ratio, the potential evapotranspiration in millimeters divided by the mean annual precipitation in millimeters equals $\underline{878/201}$=4.37. Plotted on the diagram of atmospheric water movements, the ratio falls in the *Arid* Humidity province well to one side toward the *Semi-arid* Humidity province.

If this were a climatic association, then the reading on the atmospheric water movement diagram at the point where the potential evapotranspiration ratio line of 4.37 crosses the actual evapotranspiration curve would be 15.5 per cent of the potential evapotranspiration, Actual evapotranspiration would be indicated as 1.55 x 878 = 136 mm. per year.

The height of the mature dominant natural vegetation in a climatic bush association with the meteorological data of this area would equal

$\frac{2t^{(bio)} \text{ x \% actual evapotranspiration}}{4}$ or ($\frac{2 \text{ x } 14.9) \text{ x } 15.5}{4}$, which solves out to 1.15 m. If the vegetation were arboreal, height would equal $2t^{(bio)}$ x % actual evapotranspiration = (2 x 14.9 x 15.5: 4,6 m). The latter result is a bit lower than the 5 meters usually considered as the minimum height in the definition of a tree.

Since calculations for both bush or arboreal vegetation give results lower than the heights of the vegetation remnants, there is mathematical corroboration that the natural vegetation at Lomas de Lachay does not belong to a climatic association.

The natural climatic association for such meteorological data should be desert bush. The height of 4.6 meters is probably about what could be expected of chapparal with the given values of temperature and precipitation in a Mediterranean climate. The precipitation on the lomas of Peru falls in the cold season of the year as in a Mediterranean climate so that the vegetation may be considered an atmospheric association due to an abnormal pattern of precipitation as compared with that of the climatic association of such a formation or life zone.

However, there is a further climatic complication here due to the fog or mist of the sea-clouds which press against the hills, a condition similar to that of the cloud forests found in many tropical areas of higher rainfall. Thus, even without the Mediterranean climate, the lomas vegetation would be classed as an atmospheric association due to the mist or higher relative humidity of the air as compared with that of the climatic association in a normal climate of the same temperature and precipitation. Considering both climatic abnormalities, perhaps the vegetation could be named most aptly as a Cloud Chapparal Association of the Subtropical Desert Scrub Life Zone.

In the particular case of Lomas de Lachay, thanks to the curiosity and perspicacity of Ing. Rossl, additional data of considerable interest have been assembled. Having noticed the remnant trees from the original vegetation, he induced the Ministry of Agriculture to try out forest plantations in the area. Over the years$_3$ several hectares of tree plantations were set out, using various species, but mostly Eucalyptus and Casuarina equisetifolia. Impressed by the evidence of increased condensation on the planted trees, Rossl established a second rain-gauge under the crown of a eucalyptus tree. The data obtained from both the rain-gauge in the open and under the tree crown are shown in Figure 8. The precipitation recorded under the tree-crown is consistently higher than that recorded in the open.

The average annual precipitation recorded under the tree-crown over the 18 year period is 491 mm. This is 290 mm. or 144 per cent more than the average precipitation in the open of 201 mm. for 29 years including the 18. Also it is 310 mm. or 171 per cent more than the average annual precipitation in the open of 181 mm. for the 18 year period. The remarkable increase can be ascribed to condensation of moisture or deposition of cloud-droplets on the aerial portion of the tree.

The accuracy of the precipitation data is open to some question. Since only one rain-gauge was placed under one tree- crown, there is no definite assurance that branch arrangements above did not concentrate or reduce the drip into the rain-gauge. However, observations under several trees during late June of 1960 showed a marked uniformity of grass cover from the trunks out to a clearly defined border of termination of grass growth which corresponded very closely to the projection of the tree crowns on the ground. Thus$_3$ although the recorded data may be higher or lower than the actual average drip beneath the tree-crown, the difference in either direction is probably not of any very appreciable magnitude.

As shown in Figure 8, the variation from high to low values of the annual precipitation recorded under the tree crown is several times greater than the corresponding variations in precipitation values recorded in the open. This difference is especially interesting as it indicates a lack of equilibrium between the eucalyptus tree and the conditions of the environment. Apparently, there is an interplay between the two factors, amount of mist condensation and quantity of foliage, which mutually affect each other.

Following a period of over- average precipitation with the probable accumulation of some moisture in the soil, new growth of branches and leaves would be stimulated• All increase in foliage surface-area would augment moisture interception proportionately. This would lead on to ever increasing vegetative growth until the volume of transpired water plus moisture evaporated would exceed the moisture available to the tree or vegetation. As indicated by the aspect of the plantation, the lack of available moisture to continue growth is followed by a reduction of foliage and the die-back of branches. Apparently, this frequently follows a drop-off in annual precipitation, which, at the same time may coincide with a lesser density of cloud cover. Figure 8, indicates that moisture interception by foliage in the following years Is influenced most, either by a reduction in precipitation when foliage is great in area or by an increase in precipitation after the foliage has been reduced considerably.

The date and observations would lead one to believe that tall-growing, exotic trees such as <u>Casuarina equisetifolia</u> and the species of Eucalyptus utilized at Lomas de Lachay in the past might never be able to attain a 5 a e 0 equilibrium with the climatic conditions of the site. Normal variations of precipitation over the years would continue to cause pronounced changes in the condition of the trees or plantation, with foliage increasing in area or being reduced following the trends of the precipitation and evapotranspiration. The trend towards lesser fluctuations in intercepted moisture during the later years as shown in Figure 8 is not due to an approach towards a status of equilibrium, but rather reflects a lesser variation in the annual precipitation pattern.

The scattered remnant trees in the area vary from about 5 to 9 meters in height. They are somewhat spreading in form, which in part, could have resulted from their growth in the open for many years. Their branches are rather densely covered with epiphytic plants. Apparently, only one story of arboreal vegetation was present in the original forest. Although based largely on the criteria of personal judgement, the large remnant trees do appear to be characteristic individuals of the original forest. On that basis, the original forest was estimated as not surpassing 9 meters in height.

Applying the formula for determining the actual evapotranspiration as eucalyptus to the height of the mature arboreal vegetation divided by 2 times the bio temperature in degrees Centigrade =$\underline{\qquad 9 \qquad}$ a value of 30.2 per cent is

2 x14.9

obtained. This percentage multiplied by the potential evapotranspiration, .302 x 849 gives an actual evapotranspiration of 256 mm per year. Since actual evapotranspiration to the left or dry side of the unity potential evapotranspiration rate line should equal two thirds of the precipitation, then 256 x 3/2 would give 384 mm. as a value for mean annual precipitation at this site with cover conditions of mature natural vegetation.

Utilizing the calculated data for precipitation with forest cover of 384 mm. and 201 mm. the recorded mean annual precipitation in the open, 384-201 6r 183 mm. should represent the amount of precipitation received in the form of condensation or deposition of the mist on the foliage. This is 107 mm. less than the difference of 290 mm. per year between the 18 year average of recorded precipitation of 491 mm. per year under a tree crown and the 20 year average of precipitation recorded in the open. The considerable difference might be due to the exceptional responses of a young fast growing Eucalyptus tree.

The natural forest which evolved at Lomas de Lachay should have attained a state of equilibrium with the existing climatic conditions. Surely, the natural vegetation was better adapted than the eucalyptus or Casuarina due to deciduousness, however, the same possibilities of overgrowth and des-equilibrium would exist, as new branch growth and food storage in a moister than average year would result in a denser foliage the following year.

Apparently, in this association, the epiphytic flora evolved to fill a definite niche and the filling of that niche helped to bring equilibrium to the forest, Any increase ii, condensation or precipitation would stimulate new growth of the epiphytes which then would capture more of the drip from reaching the soil where it subsequently would produce excessive tree branch growth. By the same token, during the drier periods, reduction in the absorbing surface of the epiphytes would let a higher percentage of the precipitation fall down to the soil.

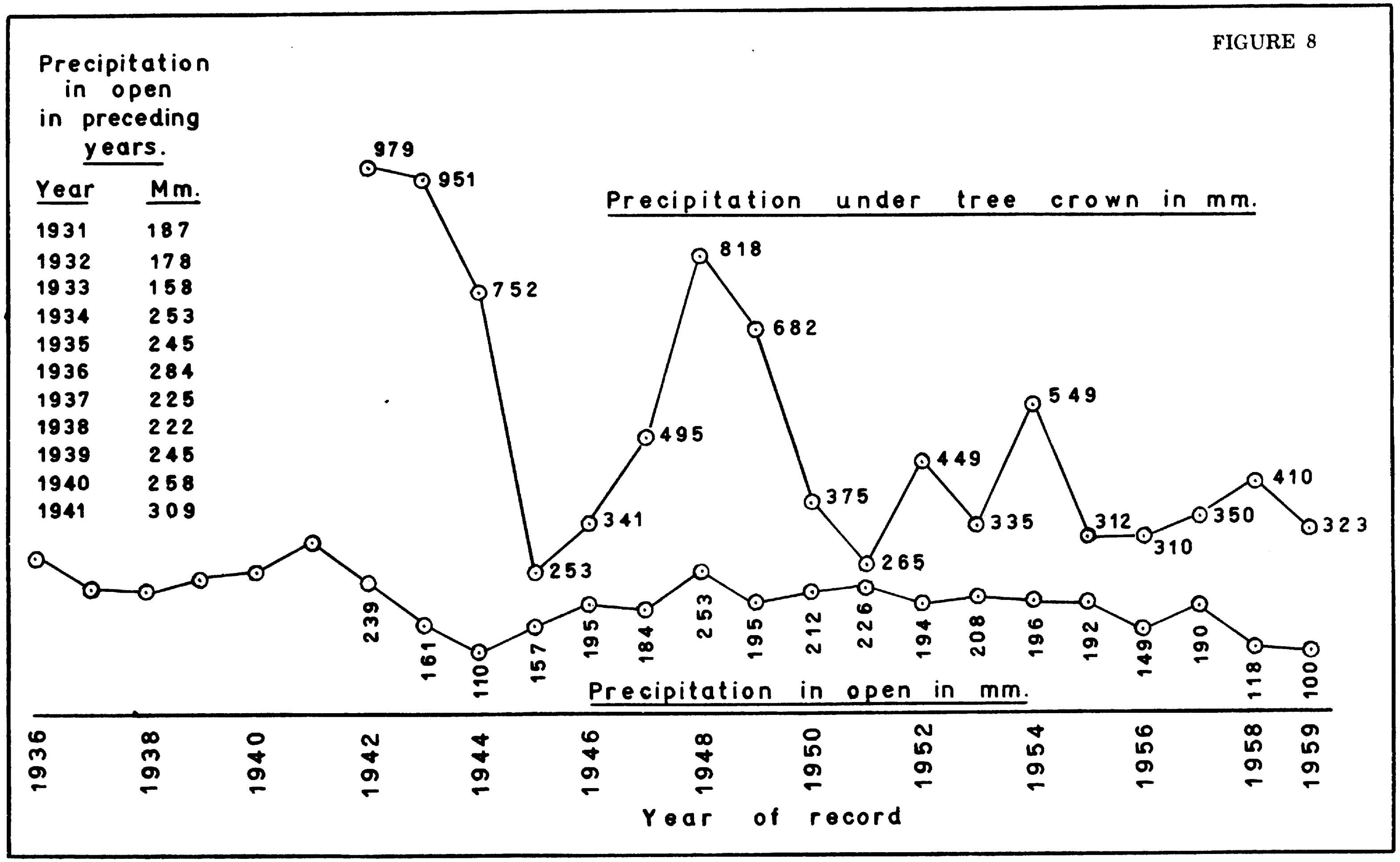
Since the epiphytes are relatively small individual plants, they should react sooner to the effects of seasonal weather than the arboreal vegetation. The hypothesis is presented that the epiphytic flora of this association operates as a governor on a motor, indirectly throttling down the growth of the tree foliage relative to the precipitation when the latter becomes abundant and indirectly increasing tree branch growth relative to the amount of precipitation when the latter is below normal.

A similar influence toward equilibrium of tree growth might be exerted also by the shallow-rooted short-season grasses and other herbaceous plants on the ground. However, one cannot be certain from observations under individual trees growing in the open that a similar ground flora would have been present under a presumably closed canopy.

The above hypothesis is based on only a few hours of observation of a greatly altered natural community plus some simple meteorological data. However, the interpretation appears to fit well if one believes that evolution affected not only individual species, but also in a broader sense, plant communities, developing them to a state of equilibrium with climatic and other local conditions. The latter would be accomplished by the evolution of species to occupy the niches essential for attaining equilibrium between the community and the environment.

if the epiphytes do fill such an equilibrating niche in the *cloud chapparal* association of the lomas of Peru, then there is a likely possibility that the abundant epiphytes in other similar atmospheric associations, such as cloud forest, are filling a niche also which helps to give stability or equilibrium to the plant communities.

FIGURE 8



Precipitation in open in preceding years.

Year	Mm.
1931	187
1932	178
1933	158
1934	253
1935	245
1936	284
1937	225
1938	222
1939	245
1940	258
1941	309

Annual precipitation in millimeters under a tree-crown and in the open at Lomas de Lachay, Peru.

Fotos\Figure8.bmp

APPENDIX B

SOME ASPECTS OF NATURAL VEGETATION AND ACTUAL LAND UTILIZATION IN SOME LIFE ZONES OF THE AMERICAN TROPICAL AND SUBTROPICAL REGIONS:

A COMPARATIVE PHOTOGRAPHIC STUDY

by Joseph A. Tosi, Jr.

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