A related form is the "phrygana" in the Balkans. Other uncultivated lands are found in the tropics, as savannah, campos, llanos, and in the Arctic as tundra, but these I shall omit as I have not yet seen them myself.

CONCLUSION

All the vernacular terms here treated—Heath, Heide, Hede, Lande, Steppe, Desert, Wüste, Puszta, Pusstynia, Pusstosch, Prairie, Plains, Pampas, Macchia, Garigue, Tomillares, Phrygana—have in their original countries the same original meaning of *uncultivated land.* The sense is purely economic. But according to different ecological conditions the vegetation is very different. On being brought into scientific use the terms vary largely in their application from the broadest to the strictest sense, from one meaning to a totally different meaning, according to the different language-groups as well as according to the varying views of individual observers. By too variable an application terms become used up or worn out—they become unfit for a precise phytogeographical use. I have abandoned the attempt to use "steppe" without a prefix or suffix for any particular community. In the case of heath (Heide, lande) I would tentatively suggest the restriction of the term to ericoid-leaved bushland such as British heaths, the Heiden of north-western Germany, the landes of south-western France, the Canary heaths, and the Cape heaths.

THE INTERNATIONAL PHYTOGEOGRAPHIC EXCURSION OF 1913 AND ITS SIGNIFICANCE TO ECOLOGY IN AMERICA

BY ALFRED DACHNOWSKI

To Professors Cowles and Clements belongs the distinction of having recognized the absolute necessity for organized excursions into various parts of the United States, and the value of such excursions and conferences to students and investigators alike for the problems of American ecology. The botanists of America are under many obligations to these two leaders in ecology.

Convinced of the important outcome of the excursions held in recent years by Swiss and British ecologists, these two leaders arranged for 1913 the International excursion in America. The remarkable success of the American expedition in every detail is a worthy testimony to the great organizing ability of Professor Cowles, upon whom rested the work of perfecting the itinerary and of supplying the foreign visitors with the information and assistance needed for the greatest possible result from such a tour.

The foreign members of the International party were Dr H. Brockmann-Jerosch and Frau Dr Marie Brockmann-Jerosch, Zürich; Geheimrat Prof. Dr Engler,

Berlin; Dr Ove Paulsen, Copenhagen; Dr Edward Rübel, Zürich; Prof. Dr C. Schröter, Zürich; Dr T. J. Stomps, Amsterdam; Mr A. G. Tansley and Mrs Tansley, Cambridge; Prof. Dr C. von Tubeuf, Munich.

Besides Prof. Cowles, Prof. Clements, Mrs Dr E. S. Clements, Prof. Cowles' two able and invaluable assistants Mr George E. Fuller and Dr George E. Nichols, and the present writer and his wife, many botanists participated in the excursion for shorter periods. Indeed, one of the pleasantest features lay in the opportunities of becoming acquainted with and experiencing instances of the extraordinary hospitality of scientific institutions and citizens as well. It would be impossible in the course of a brief review to give a full and adequate record of this magnificent tour; it would require a book of no small magnitude to give a bare summary of the nine weeks journey[1]. The following account is restricted to (1) reflections upon the significance of the I. P. E. to ecology in America, and to (2) the impressions of social vegetation types in the United States, especially the structure, relationships, and development of plant populations, from observations which the writer obtained.

I. The International Phytogeographic Conference and Excursion in the United States and its Significance to Ecology in America

The importance of the International Phytogeographic Conference and Excursion to ourselves individually is not due primarily, or in a large measure, to the observation of certain kinds of species of plants or the knowledge of certain kinds of facts. Achievements in so many ways and on so many different lines for the advancement of knowledge come through the stimulating influence engendered by the presence of men of research, their companionship, their kindly appreciation and keen criticism, and the better understanding of the terms used. It is due to the way and the manner of looking at problems and dealing with them. The individual habit of observation and deduction, the method of hypothesis and verification, the point of view—this elusive "personal equation"—is after all a master factor in scientific research.

We still fall short of the advantages to be gained if we fail to recognize more clearly and generally the practical service which the conference and excursion renders, and the beneficent effect it must have upon the movement for the progressive organization of ecology as a science. No other field of scientific inquiry has more manifold interrelations than ecology, and as yet there has been no permanent attempt made among American and European botanists to connect adequately the work of foreign and local investigators in allied fields of knowledge. There has been nowhere a due correlation between the work of different specialists and the more important methods of ecological activity. The organization for an interchange of views as well as for collective action is still in need to be effected.

It has seemed to the writer that the time is ripe to secure the desired co-operation. The American phytogeographic conference and excursion offers the most

[1] A general account by A. G. Tansley of the American tour has been published in the *New Phytologist* (**12**, 1913; **13**, 1914).

desirable psychological moment to utilize to a greater extent the influence of foreign visitors and to inaugurate and secure an organization of wide scope and high standard which would furnish both an effective guide to the complex currents and the co-operation so essential in all problems of a wider and more productive range. The International Phytogeographic Excursion and Conference would be really furthering the interests of ecologists throughout the world as well as those of this country, and would go far to justify itself, if the defects now so obvious could be minimized by the development of a permanent organization of broader, indeed of international scope, serving to counteract provincial tendencies. The endeavour of specifically national societies to foster and promote an international organization with the aims and the common interests of related problems and co-operative branches of science would unquestionably play an important part in the growth and the advance of ecology and its application to human welfare.

It is scarcely necessary to indicate the advantages to be gained by such an organization. Some of the purposes, and they have without doubt impressed themselves upon the several members of this conference and excursion as of the greatest importance, may be estimated by considering the following. (1) The investigation of problems which cannot be solved unless observations and experiments are made under standard conditions accepted by common agreement, and with appropriate methods of ecological study, instruments and units of vegetation (nomenclature, specification, etc.), yielding comparative data and records. (2) The distribution of the larger problems between different institutions and nations for the purpose of economizing time, expenditure and effort. (3) The unification of problems which are intimately associated and blend with research in various other sciences, and which until recently have been either neglected or pursued independently of each other. (4) The organization and support of international stations, laboratories and courses of instruction in which foreign scholars are invited to take part. (5) The representation by a central authority of sufficient eminence and responsibility to act in an advisory capacity or as a centre of general scientific activity, and to facilitate the study of questions requiring international co-operation. (6) The effective organization for an interchange of views, promoting a more definite and comprehensive discussion of the fundamental problems of ecology, and for collective action on investigations of more than local significance.

It is needless to force into discussion the general merits of any one of these aims of co-operation in research. No one interested in scientific research which is of the highest type and is internationally organized underestimates the task involved in the problems and aims enumerated above. The demands of ecology in America will, sooner or later, call into existence such an organization as an indispensable instrument for efficiency in research, for the solution of the problems of variation, of heredity and environment, and for the results which are pre-requisite to practical and economic aspects. Very frequently the degree of specialization proves inadequate to meet all the requirements for the solution of a problem, and the remedial action needed in science, as in any other field of thought and activity, against the factors that limit progress, must be found in the new spirit of international co-operation.

II. Impressions of the Nature of Social Types of Vegetation in the United States

The personal experiences of the writer with the International Phytogeographic Excursion began at Chicago among the magnificent series of sand-dunes on the southern and eastern shore of Lake Michigan. They are well known from Cowles' work and that of his students. There can be no question that the commanding influence that has justly been exercised by the Chicago school of ecology lies in the interesting and significant facts and problems of the physiography of the Chicago area. It is a region of great interest, representing in part the northern coniferous, the eastern deciduous, and the prairie vegetation provinces, each of the two latter especially showing several distinct stages of development of social vegetation groups, and transitional as well as retrogression features.

The sand-dune series of vegetation successions is well marked, leading from a beach association through the fore-dune associations and through all stages of fixation with cottonwood, willow, pine and oak to old or fossil dunes covered with the beech-maple forest. The proportion of the members which have gained predominance in addition to the beech and sugar-maple is augmented by *Tsuga*, *Liriodendron* and various species from other portions of the country. The forest is much the same throughout the region which it controls; it is a geographical phase of the typical climax association that once covered on all kinds of soil and topography nearly the whole of the eastern United States. One of the few remaining fragments of this splendid deciduous forest was seen on clay soil at Three Oaks, Michigan.

The list of characteristic species in this series of successions includes evergreens and many plants of evident boreal affinities in varying proportions, others which are largely confined to the Appalachians and more southern latitudes or have a wide distribution westward. One is left wondering why such a vegetation group composed of numerous social units and synecological associates of diverse ranges of distribution does not enable some definite agreement as to the nature of vegetation units or as to the method of classifying them. Each association is large enough to form in some measure a complete entity with a relative permanence of relations among the component parts throughout the area. Clearer conceptions of these relations are absolutely essential to the progress of ecology, and the demand for studies of this nature is surely more urgent than for floristic or distributional observations.

A vegetation unit is not a mere aggregate, a collective name for a number of individuals, but a product ascribable in part to the conditions under which the plants exist, and in part to the character of the plants, their functional limits, and the degree of the reciprocal influence between the group and its units. Moreover, plant associations have a life history. In their earlier stages all plant populations begin their development in like ways; they are "open," lack density and occupy large spaces; they spread over wide areas relatively to their small numbers; they depend largely on a favourable combination of soil conditions. With advancing development, where there are formed more definite social aggregates of groups, the plants are differently related to conditions, assume different positions of

dependence. This is at first vague, but increasingly definite in such integrated groups as the higher plant associations. There is an increasing vegetative competition and a greater dependence upon the character of the climate rather than that of the soil. Vegetation types over large areas in the United States and elsewhere have an astonishing fundamental similarity in regard to structure, differentiation and relation to habitat. This is due partly to the fact that plants affect one another through intervening space relations modifying conditions of humidity, light, etc., and through time relations of growth, maturity and seeding, partly because climatic provinces are usually geographic regions as well. But the simple growth of populations causes transformations that become more important as the social vegetation groups evolve. The changes give rise to secondary, derived conditions which are at once a consequence and a cause of further complexity. The potency of this set of derived factors can scarcely be overestimated, for they cause migrations, a wave of diffusion, replacement and temporary concentration and successions within the area occupied. Habitat distinctions, whether based on clay, sand, lime or peat or upon different lengths of physiographic history, are of small consequence for the delimitation of social vegetation units of an advanced type. The widely different vegetation in the same region of Chicago suggests not so much environmental relations as features of a kind contributing to the evolution of plant associations. The floristic method and the habitat method of classification should and will continue, since the one is equally as important as the other in the early stages of the life history of social vegetation units. But the view regarding them more from the developmental standpoint than from that of the flora in composition or growth-form or that of the habitat, whether edaphic, climatic or regional, must appear to be the more appropriate and indeed the more fundamental for areal instances where plant associations are found to compete and evolve under conditions which are unlike or which have little in common with so-called typical localities. Their movement and increasing range of distribution is not a dispersal like that of more or less nomadic species, but a migration and invasion, dependent upon a time element and certain channels. The degree of reciprocal influence between a vegetation group and its incorporate units, in coherence of parts and development of stability, in predominance resulting from successful competition with other associations of plants around them, seems to be the more exact test which can be had as to the nature of a vegetation unit. A vegetation unit must be recognizable not only by its members but must be distinctive from other populations similarly held together by relations of coherence, whether developed in one climatic region or in another. Between social vegetation units widely unlike in kind no "progeny" can arise; the ecological forms contributed by them respectively cannot merge so as to produce a new or a more advantageously related social group, just as imperfectly organized and early stages of successions cannot form a stable group leading, for example, to a forest.

Verification as to the nature of a social vegetation unit is gained by observing the very interesting example of retrogression stages at Dune Park, Indiana, and at Sawyer, Michigan. Gigantic masses of sand are advancing and overwhelming the deciduous forests of fixed dunes. The capacity to form adventitious roots in

the layer of damp soil a few inches from the surface of the sand enables *Populus* and *Salix* to survive in the less rapidly moving dunes, while *Tilia*, *Ulmus*, *Prunus*, *Cornus*, *Vitis* and a few other swamp plants and mesophytes maintain themselves above the rising sand by stem elongation. The few leafy shoots flower and fruit vigorously. Such populations of plants, retrogressive from forests and surviving partial burial by dunes, are not, of course, a distinctive social entity, and hence cannot be given the rank of a society or of an association.

Examples showing the nature of the process by which social vegetation units are evolved may be seen in the alterations of plant associations which are, for instance, characteristic stages in the north, leading to forests of the north-eastern conifer province, and such leading to forests that follow river bottoms into the Prairie region. The small sand-dune area observed north of Chicago at Lake Bluff has beach associations ecologically in marked correspondence with the vegetation of maritime areas in general; developmentally, however, they closely resemble those found more distinctive in northern Michigan. The belt of *Populus deltoides* is replaced by *P. balsamifera* and is succeeded by *Juniperus horizontalis*, *Arctostaphylos uva-ursi*, and others, but here leading to an oak-hickory forest. The sporadic development of oak-hickory groves on the clay cliffs and on the prairies of central Illinois gives the impression of a much interrupted path of migration, and of leading to the development of the maple-basswood type of forest. At Northport Point, Michigan, the succession from the heaths just mentioned is through *Thuja occidentalis* covering the present beach, with *Abies balsamea*, *Betula papyrifera*, and occasionally *Picea canadensis* on the Telleston beach, to a maple-beech forest occupying the Calumet and a remnant of the Glenwood beach, the first of the ancient series of postglacial beaches when receding Lake Chicago was 60 feet above the present lake level. In shrubs and in herbaceous undergrowth the deciduous forest now includes some of the characteristic plants of the southern type, while the conifer forest, covering the slopes, shows in the undergrowth typical to it, local variations due to a gradual elimination and substitutions of its dependent species. The northward advance of vegetation, conifers as pioneers closely followed by deciduous social units, is still going on. The dominance of the latter upon the oldest ridges and their ability to supersede the conifers and birch indicate that climatic limits of areal distribution have not yet been reached, and that essentially stable vegetation types have not yet been evolved. Obviously developmental and historical considerations rather than soil or atmospheric factors must be taken into account for this example of geographic distribution of social vegetation units. These conditions may possibly account for the differences in polar tree limit in the northern hemisphere and for the number of instances which various recent writers have attributed to the influence of climate character.

Equally interesting is the forest type which follows river bottoms and extends westward into the region of climatic prairie and up to the foothills of the Rocky Mountains. In the Chicago area and eastward a mature flood plain forest is a definite type of deciduous forests with several stages in its development. The vegetation is well marked structurally, quite rich in species common also to the maple-beech forest, but characterized by the predominance of *Ulmus*, *Fraxinus*, *Celtis*, and *Platanus*. The rapidly growing undergrowth has an abundance of

climbing and twining plants. This type shows considerable variation in specific composition from east to west which can be explained only by the gradual and continuous migration of the plants, chiefly along the highway of a river system.

A striking example illustrating the continuity of this type of forest associations and its steady advance on the prairie was observed fringing the streams near Lincoln, Nebraska. Even in the case of artificially planted woodlots of elm, ash and others, the trees not only reproduce themselves freely but give rise to secondary conditions which enable a great majority of the typical dependent species to appear. The list, supplied by Prof. Bessey, of species now present but not planted by man includes a number of trees and various shrubs, lianas and herbaceous species. The areal range of some of them is thus considerably enlarged. The planted woodlot is now a definite social entity of co-ordinate parts, not in any way the product of soil conditions or climate alone, but a result of development under the modifying influence of environment. Undoubtedly any peculiarities in floristic composition that belong to this type of forest on account of geographical position, immature development, and the conflict with native vegetation forms able to endure competition will tend to become intensified and to differentiate further under conditions of physiographic isolation. The valley woodland of Bear Creek Canyon, near Colorado Springs, with an undergrowth of plants from the east and the west might serve as an illustration. How far that process of differentiation has gone in giving rise to distinctive associations, time did not permit to observe. Since the cessation of prairie fires, the flood plain forest is steadily encroaching on the prairie, greatly impoverished floristically, but replacing components and presenting various transitional stages which negative sharp division. The mutual dependence of parts and the increasing complexity of a plant population which constitutes a social entity cannot arise without some development of lines of migration and succession. In this order the evolution of vegetation types has gone on and only in this order does the evolution of further social types appear to be possible.

A real distribution and the development of vegetation types cannot continue without exercising a modifying influence upon the biotic environment existing around it as well as upon the physical habitat conditions. Only recently (*Science*, **38,** 1913) many facts have come up which point strongly to the possibility of forests contributing by transpiration to an increased humidity of the air carried into the prairie region. It is known that during the close of the Tertiary period a forest of great denseness extended over the territory west of the Mississippi. The flora was fairly uniform and consisted of a great variety of trees, shrubs, and herbaceous plants, some of which have become extinct, while others are at present extremely local in distribution. The differentiation and isolation of vegetation regions probably began before the glacial period. Extensive migration and development is again taking place, but it is beyond the province of this paper to deal with the speculation respecting the possible future type of vegetation. The inevitable economic development of the country necessarily involves checking and the use of much of the forest and grassland for the needs of commerce and industry.

For want of space it is necessary to pass over a discussion of the extremely interesting vegetation types of the prairies, the great plains, the open character of forests in arid and in alpine regions, and the striking differences in vegetation

which are reflected in the climate between the western coastal region of high rainfall and the arid region of the east. Whatever the part of the United States visited the phenomenon most frequently observed is the existence of distinct synecological units differentiated by soil and co-ordinated by climate and the successive changes implying correspondence between environment and the development of a vegetation to its full floristic character. There are few vegetation types which could be more advantageously compared with each other as to the relation between extent of distribution and ecologically induced variations than the chaparral of the Pacific coast. The chaparral of the Californian Sierra and its generic and specific modifications up the mountains and along the coast through Oregon, colonizing different associations with different ecologically equivalent species and forming a transitional phase in the history of the forest types within the Cascade Mountains, is an evidence in support of no particular present theory of plant geography. Such modifications are responsible for the production of geographic variations in species and in associations of plants, and hence of specific types and distinct forms with no hybrids in evidence as intervening sub-units.

The study of geographic ecology touches plant physiology at many points, especially if it is viewed from the standpoint of the development of vegetation units and of morphogenesis under different environmental conditions. Especially the correspondence of the effects on plant growth with the factors of soil and climate, in terms of physical and chemical reactions, needs further inquiry before "ratios," etc., can be satisfactorily applied to any general correlation of vegetation types with environment or with geographic distribution. The origin of new species and of new vegetation units, however conditioned, postulates the necessity of identifying congenital factors with the biochemical activity of organisms. This is the most difficult task that confronts the physiologist and the phytogeographer, for experiment alone can decide how to regard critical, representative and endemic units. It is difficult to conceive of any one set of delimiting factors affecting any vegetation unit alike. In regions where water is the critical factor, it is a well-known physiological fact that high yield of crops and dry material produced are not related to mere water consumption[1]. The absorption-transpiration ratio alone cannot, therefore, be of great importance in the water cost of irrigation as well as in questions relative to the distribution of plants or their morphological structure. The forces which are active in the process of the retention of water during development or the evolution of succulency (of fruits, etc.) in the higher plants are largely hydrolytic in nature. The explanation is perhaps more to be sought in temperature exposure (as an expression of the resultant action of insolation and soil radiation), mainly because it is only within a certain range of temperature that the water retained within the plants can act in the metabolism of materials and the energy transformations leading to survival and greater areal distribution. There is an indication that higher plants during the various stages of growth may exert an influence on the character of the active colonizing period and hence on the life history of an association through changes in the mineral constituents of the soil. In itself, the acid or alkaline

[1] **Dachnowski, A.** "Transpiration in relation to growth and to the successional and geographic distribution of plants." *Ohio Naturalist*, **14**, 1914, pp. 241—251.

character of a soil is not always a disturbing factor[1]. There is a variety of evidence that a salt may act as a catalyzer, altering specifically the quantity of water retained by certain plants during growth and development. The action may be the effect of the presence of some salt which is in large measure the reaction of the solution after synecological associates have been growing in the soil for some time. To ascertain what physiological processes are involved in this phase of the association-factor necessitates more experimental work. The demands of science have now called into existence stations and laboratories for environmental studies. The future will undoubtedly witness an increase in their number, and in their scope, and secure among investigators the active and intelligent co-operation that is needed to develop ecology in America.

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[1] **Dachnowski, A.** "The effects of acid and alkaline solutions upon the water relation and the metabolism of plants." *American Journal of Botany*, **1**, 1914, pp. 412—439.

THE NATURE AND METHODS OF EXTRACTION OF THE SOIL SOLUTION

BY WALTER STILES AND INGVAR JØRGENSEN

Introduction

As the study of ecology from a physiological standpoint becomes more developed, so will the investigation of problems of root absorption assume greater importance. It is obvious that in such ecological studies a knowledge of the medium in contact with the roots, the actual nutrient medium of the plant, is all-important. It is for this reason that considerable attention has been devoted during recent years to questions connected with the water contained in the soil—the soil solution. In this paper we propose to give a brief account of the various methods which have been used to obtain knowledge of the soil water, and of the results obtained by their means.

It is a matter of common knowledge that the soil consists of a complex system of solid particles of various sizes and different composition in the spaces between which gases (the soil atmosphere) and a liquid (the soil solution) are contained. Earlier investigations of the soil, which had for their object the determination of the nutritive value of the soils of different areas, took the form of mechanical and chemical analysis of the solid particles of the soil. Analyses of this kind give valuable information in regard to the water-content of soils, but it does not follow that the results of chemical analysis necessarily give at all an exact idea of the composition, or even of the relative compositions in different soils, of the medium from which plant roots directly absorb. It was really the recognition of this that led to the distinction between available and non-available plant-nutrients among