

### INTRODUCTION

# THE UNITS OF VEGETATION—THEIR RELATIONSHIPS AND CLASSIFICATION

It has been well said by the distinguished plant-geographer Professor Drude of Dresden that plants may be studied in pure science from three points of view, and from three only:—the physiological, the phylogenetic and the geographical. Geographical Botany or Plant-geography may be defined as the study of the facts and causes of the distribution of plant-life over the surface of the earth.

When we consider the distribution of the plant-life of any given region or country, whether large or small, we find that it may be regarded from two distinct points of view. In the first place we may study the distribution of the species, and, in the case of the larger areas of the earth, the distribution of the genera and families of plants. The list of species, arranged taxonomically, is called the flora of the region or country, and the study of their distribution is floristic plant-geography.

But there is another way of regarding the distribution of plant-life. If we consider the general plant-covering or vegetation of any geographical region we find that it is naturally divided into units, each of which has a characteristic appearance or physiognomy and consists

Vegetationunits or plantcommunities. of characteristic species. These vegetationunits have been recognised from the earliest times, since not only do they form outstanding features of all landscapes, but man absolutely

**T.** 1



# 2 Introduction

depends upon them in his primitive relations to nature. In their more obvious forms, therefore, the units of vegetation have common names in all languages, and these are everywhere preserved in the names of places. Wood, moor, heath, marsh, are some of the commonest and most obvious examples. Now it is to be observed that most of these names refer to something more than the vegetation alone. A moor is an area supporting certain kinds of plants, but it also implies the presence of a peat-soil on which those plants flourish. Heathland nearly always involves a relatively poor and dry soil. A marsh is an area where the soil is always wet. In other words a vegetation-unit is always developed in a habitat of definite characteristics.

To look at the matter from the opposite standpoint, synthetically instead of analytically, certain kinds of plants are always found associated together under definite conditions of life, and such groupings may be called plant-communities. A plant-community is simply a vegetation-unit regarded as an aggregation of species and individuals instead of as a division of the whole vegetation of the region. Whichever standpoint we adopt, the connexion with habitat is a fundamental part of the conception. This way of considering the distribution of plant-life is called ecological plant-geography, from the Greek olkos, a house (habitat), in contradistinction to the floristic plant-geography, referred to above, which is concerned primarily with the distribution of species.

Ecology includes more than the study of vegetationunits or plant-communities; it deals with the whole of the relations of individual plants to their habitats. This latter branch evidently cannot be sharply separated from physiology; and may in fact be justly considered as a part of that subject. It has been aptly called by Professor Schröter of Zurich autecology, to distinguish it from synecology or the study of plant-communities.



# Synecology and Autecology

3

The present book attempts to describe the principal kinds of plant-communities or units of vegetation met with in the British Isles. During the last twelve years a great deal of work has been done in observing and describing these vegetation-units, and their relationships. The work is far from complete even in the matter of mere description, and this book necessarily carries many evidences of the incompleteness. Yet enough is known to justify the attempt at a preliminary sketch of the subject, which it is believed will interest botanists and lovers of nature, as well as students of scientific geography.

It may be said that we ought not to occupy ourselves with synecology till we have a complete or an approximately complete knowledge of autecology, but this is a mistaken notion. It might as reasonably be contended that we ought not to study the phenomena presented by the nations and races of men before we know all about the physiology and psychology of the individual man. As a matter of fact the study of synecology is considerably in advance of autecology (which is indeed still in a very backward state of development), and the progress made has amply justified the attention devoted to the wider though less fundamental branch of the subject. The plant-community, in fact, offers a convenient mode of approach to the study of plant-life in relation to habitat. The systematic description and classification of vegetation affords a natural framework in which autecological studies will find their proper place.

There has recently been a great deal of discussion as to the nomenclature of ecological phytogeography or synecology, and nothing like geography or synecology, and nothing like general agreement yet exists as to the proper naming and classification of the different categories of vegetation-units or plant-communities. One of the main subjects of contention is the use of the term plant-formation, which we

1-2



#### Introduction

originally owe to Grisebach'. It is not intended to enter here into a discussion of this question, for which the

The plantformation, the plantassociation, and the plant-society.

4

literature must be consulted<sup>2</sup>. The uses of the terms plant-formation, plant-association and plant-society in this book are those adopted by the Central Committee for the Survey and Study of British Vegetation. Whatever may be the ultimate fate of these

terms it will be generally conceded that their consistent use in the description of the types of vegetation of a given region will afford a useful test of their appropriateness.

#### THE PLANT-FORMATION

A plant-formation is the natural vegetation occupying a habitat with constant general characters which determine the communities of plants occurring in that habitat<sup>3</sup>.

Ecological factors.

The characters, or as they are often called the ecological factors, of the habitat, which influence vegetation, are often classed as climatic and edaphic.

Climatic factors are those primarily dependent on the climate of the region in which the plant-formation is developed, such as temperature, precipitation (i.e. rainfall, snowfall, dew, etc.), humidity of the air and wind.

<sup>1</sup> Grisebach, H. R. A., "Ueber den Einfluss des Climas auf die Begränzung der natürlichen Floren." *Linnæa*, xii. 1838.

<sup>2</sup> See especially Schimper, A. F. W., Pflanzengeographie auf physiologischer Grundlage, Berlin, 1898 (English translation, Plant Geography upon a Physiological Basis, Oxford, 1903-4); Clements, F. E., Research Methods in Ecology, Lincoln, Neb., U.S.A., 1905; Warming, E., The Œcology of Plants, Oxford, 1909; Moss, C. E., "The Fundamental Units of Vegetation," New Phytologist, ix. 1910 (issued separately by the New Phytologist, Botany School, Cambridge); Ch. Flahault and C. Schröber, Phytogeographical Nomenclature, Zurich, 1910.

<sup>3</sup> This of course is not a logical definition but only a preliminary description. The conception of a plant-formation, as understood in this book, can only be made fully clear by reference to the examples dealt with in Part II.



# **Ecological factors**

5

Edaphic factors, on the other hand, depend upon the features of the soil in which the plants grow, such as water-content, food-content, aeration, the presence and amount of humus and of certain minerals, acidity, and so on.

Not all the features of a habitat can be reckoned as effective ecological factors. Thus two soils, alike in many respects, may differ in others, such as the presence or amount of certain salts. But unless the differences have an actual effect on the vegetation they cannot be considered as ecological factors. Similarly one locality may have twice the rainfall of another, and yet the same type of soil may bear the same plant-formation in both.

The effective ecological factors which separate one formation from another we shall call the determining, differentiating or master-factors.

In the British Islands the most striking effect of climate is seen on the higher mountains. The various climatic factors involved in differences of altitude determine for instance a limit above which woodland does not extend; and the rock-vegetation near mountain summits is another effect, though partly an indirect effect, of increased altitude (see Chapter XIV). There is also a considerable difference in the climate of the eastern and western portions of Great Britain, and this is probably related to the prevalence of moors in the west as opposed to heaths in the east.

Characteristic but subordinate features of other plantformations also depend on climate, for instance the abundance of ferns in the woods of the west and north as contrasted with their paucity in the east and south-east. Certain species of plants are confined to parts of the country characterised by a definite climate, and their absence elsewhere may often be due to climatic factors,

<sup>1</sup> It must be understood that nothing approaching a detailed treatment of ecological factors, and of their relations to one another, is possible in the present work.



#### 6 Introduction

though a strict determination of the various cases is lacking. But these phenomena, interesting as they are, do not count in the determination of the fundamental units of vegetation, the plant-formations, and we may fairly say that, on the whole, the plant-formations of the British Isles are mainly determined by edaphic factors, i.e. by soil.

Many plant-formations are easy to determine, because they are limited by quite obvious habitats to which very definite and characteristic plant-communities correspond. Such are for instance the two chief "maritime" formations, those of the sand dunes and of the salt marshes.

The moor-formations are also well characterised, if we take the word "moor" in its current German sense to apply to types of vegetation developed on deep peat. Two principal formations with essentially different plant-communities may be distinguished, that on peat relatively rich in mineral salts and neutral or alkaline in reaction—"fen" as it is called in this country (Niedermoor of Weber, Flachmoor of various authors)—contrasting strongly with the formation on peat poor in mineral salts and acid in reaction—the moor proper (Hochmoor of German writers). Whether we should distinguish a third formation—the "transition-moor" (Uebergangsmoor)—is open to question.

The vegetation of chalk and limestone, of the non-calcareous clays and loams, of the sands relatively rich in plant-foods, and of the sands and gravels relatively poor in plant-foods and developing an acid humus, fall into different plant-formations. Each of these types of soil bears vegetation with characteristic features and characteristic species of plants, though many of the species are common to several. There are however certain

 $^{\rm 1}$  This use is not, however, in accord with the current use of the common English word "moor." For a discussion of the subject see Chapter IX.



## Retrogression of Plant-formations

7

superficial difficulties in determining the nature and limits of these formations, difficulties mainly due to human interference with natural vegetation.

In the days before the face of the country was changed by the activity of man woodland prevailed over practically the whole area of the types of soil mentioned, with the exception, probably, of parts of the first and last, *i.e.* of the chalk and limestone and of the poorer sands. At the

Retrogressive changes in formations. present day, cultivated crops, "permanent pasture" which has been "laid down" and plantations, occupy, of course, the greater portion of the country, but apart altogether

from these the natural vegetation of each type of soil is actually varied. Besides woodland each type has a characteristic "scrub" or bushland, and a corresponding grassland or, in the case of many sands, a heathland.

These different types of plant-community on the same soil have no doubt originated mainly from the clearing of the original woodland and the pasturing of sheep and cattle. This prevents the regeneration of the woodland, and of most of the shrubs also, if the pasturing is sufficiently heavy and continuous, while it encourages the growth of grasses. Thus the plant-formation determined by the particular soil, and once represented by woodland, shows a series of phases of degeneration or retrogression from the original woodland, brought about by the activity of The intimate relationship of the various phases are clearly seen in the associated plants. The woodland proper has of course a ground vegetation consisting of characteristic shade plants, but the open places, and the "drives" or "rides" of the wood, are occupied by many of the species found among the scrub and in the grassland, while those true woodland plants which can endure exposure to bright light and the drier air outside the shelter of the trees often persist among the grasses of the open. In some cases where grassland is



8

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#### Introduction

not pastured the shrubs and trees of the formation recolonise the open land, and woodland is regenerated.

Besides these degenerative processes, due to human interference, there are others due to "natural" causes, which are for the most part little understood.

The natural process of the development of formations on new soils has also to be taken into con-Primary sideration. The formation which is to occupy a new soil rarely springs into being fully development or primary succession in constituted. It normally passes through a a formation. series of phases of development (primary succession), each phase exhibiting a definite plant-association (see below). Clements has given a very interesting account of this primary succession of associations (called by him "formations") in the case of several American formations; while the primary successions met with on sand-dunes, on salt-marshes, and on the borders of inland lakes where peat accumulates, have long been familiar to European plant-geographers. Clements<sup>2</sup> has shown that primary succession follows definite laws, and has pointed out that the pioneer species generally form an association in which but few species occur and which does not completely cover the soil (open association), while the succeeding associations are mixed in character and the final association is closed and often dominated by a single species, or by a few similar species.

Primary succession must take place universally where new land habitable by plants is formed, but in a country like our own, where geological changes are slow and insignificant, there is little opportunity for observing it

<sup>&</sup>lt;sup>1</sup> This very brief summary of the relation of woodland, scrub and grassland or heathland omits all reference to complicating factors. Some of these are discussed under the different formations in Part 11.

<sup>&</sup>lt;sup>2</sup> The Development and Structure of Vegetation, Lincoln, Neb., U.S.A., 1904; Research Methods in Ecology, Lincoln, Neb., 1905. See also Moss, op. cit.



# Determination of Formations

9

except on the sea-coast where new land is constantly being formed in certain places, on the edges of certain lakes where the land is gaining on the water, and to some extent on the talus of cliffs, and on the detritus of mountains.

The colonisation of waste ground, such as derelict building sites, of ballast heaps, etc., furnish, it is true, very interesting and instructive studies in the succession of plant-communities; but owing to the peculiar nature of the substratum in many of these cases, and also owing to the supply of seed available, these successions do not often lead to the establishment of communities belonging to the normal plant-formations of the country, and such land forms a battle-ground for aliens and casuals.

In the normal primary development of a formation, as in the retrogressive processes before mentioned, the associations involved show intimate relations and transitions one to another, and the whole set of associations has a definite flora dependent on the type of soil. It is for these reasons that we consider the entire set of plant-communities on a given type of soil, in the same geographical region, and under given climatic conditions, as belonging to one formation, in spite of the diversity of the dominant plant-forms in the different associations.

The plant-formation thus appears as the whole of the natural and semi-natural plant-covering occupying a certain type of soil, characterised by definite plant-communities and a definite flora. The "wilder" formations, those less modified by man, for instance sand-dunes, salt-marshes, heaths and moors, are quite easily determined, but where human agency has been extensively at work, a careful study of the flora and vegetation and of their relations to the soil is needed before the formation can be accurately determined. In some cases we cannot as yet

1 i.e. owing its present form to human activity though not planted by man.



#### 10 Introduction

decide with certainty, in others we may never be able to decide, where to draw the limits of the original formations. For instance, much of our heathland is undoubtedly degenerate forest, but in other cases it is probably primitive, existing on soil which does not naturally bear woodland at all. Let us suppose that a tract of primitive heathland (which must be counted as a separate formation) adjoined a tract of woodland on a light sandy soil. If the woodland is extensively cleared the heath community will undoubtedly invade its area, and the original limits of the two formations will be obliterated. The same is true of chalk pasture. There is evidence that some of our chalk downs are primitive grassland, that is, were never covered by forest; but there are many tracts of chalk pasture which certainly occupy the sites of old beech and ash woods that have disappeared under the axe or from other causes. It is difficult or impossible in the present state of our knowledge to draw the limit between the two cases, which may be represented by identical associations.

When habitats and their corresponding plant-communities are separated by characters less important than the master-factors determining formations, the term *sub-formation* is employed to designate a division of a formation, based on these less important factors. A sub-formation however exhibits the same features (of succession etc.) as a formation and is to be distinguished carefully from an association.

#### THE PLANT-ASSOCIATION

The plant-association is the vegetation-unit next below the plant-formation. Plant-associations are in general the most obvious plant-communities that we recognise in the field. Thus each of the types of vegetation, woodland, scrub and grassland, within a given formation, is a plantassociation, and so is each definite phase in the primary development of a formation.