rung und Dominanz, dann hätten wir den Schlüssel gefunden zur Erklärung der auffälligen Erscheinung, dass in Mitteleuropa die Wälder aus so wenigen Arten, oft nur aus einer Art (Föhrenwald, Fichtenwald, Buchenwald) bestehen im Gegensatz zu den Wäldern anderer Länder (Karstwald, Tropischer Wald). Die pollenanalytischen Untersuchungen der Moore Mittel- und Nordeuropas lassen deutlich einen solchen Zusammenhang zwischen der Einwanderung der Waldelemente in das ehemals eisbedeckte Gebiet und dem Herrschendwerden der Einwanderer in ihrer zeitlichen Reihenfolge erkennen.

III.

The inter-relations of plants in vegetation, and the concept of "association"

By R. H. YAPP, Birmingham (England)

Eingegangen 1. März 1925

1. The concept of "association"

Ecological literature abounds with discussions regarding the concept of the plant association, its status as a unit of vegetation, and the criteria by which plant associations should be recognized and delimited in actual field practice. Yet the concept of "association" as such has been little debated, and the implications involved in this concept regarding the inter-relations of the associated plants, are not infrequently ignored. It may therefore be useful briefly to examine these implications.

One of the excellent features of CLEMENTS' well-known "Research Methods in Ecology" (1905) was his attempt, in the light of the knowledge of twenty years ago, to analyse the various concepts of ecology. This book contains (pp. 200 et seq.) the only examination of the concept of association I have seen. The following extracts give the essential points in CLEMENTS' analysis: —

"The principle of association is the fundamental law of vegetation . . . It is . . . the coming together and the staying together of individuals, and, ultimately of species . . . The term association has been used in both an active and a passive sense. In the former, it applies to the inevitable grouping together of plants, by means of reproduction and immobility. Passively, it refers to the actual groupings which result in this way, and in this sense it is practically synonymous with vegetation. . . . Since association contains two distinct, though related, ideas, it is of necessity ambiguous. It is very desirable that this be avoided, in order that each concept may be clearly delimited. For this reason, the act or process of grouping individuals is termed a g g r e g a t i o n, while the word association is restricted to the condition or state of being grouped together. In a word, aggregation is functional, association is structural; the one is the result of the other. This distinction makes clear the difference between association in the active and passive sense, and falls in with the need of keeping function and structure in the foreground".

CLEMENTS' statement that "aggregation is functional, association is structural," is open to objection. He appears to have missed the important point that while association results in structure, i. e. in plant associations, it is itself functional no less than aggregation. This is necessarily so, seeing that we are dealing with the association of living organisms, not inanimate objects. From the point of view of ecology, the really essential element in association, as distinct from aggregation, seems to me to lie in its functional significance, i. e. the inter-relations of the associated organisms; or in other words, the mutual influences they exert on one another. It is this that makes "the principle of association the fundamental law of vegetation". Apart from its functional implication there would be no real significance in the fact of the grouping of individuals; the problems would merely be those of the relations between individuals or species and the physical environment. The so-called biotic factors of a plant habitat are, for the most part, the direct outcome of association. CLEMENTS' definition of association as a passive "condition or state of being grouped together," excluding as it does the functional implications of this state, suggests a static rather than a dynamic view of vegetation. Yet elsewhere CLEMENTS himself emphasizes the importance of the inter-relations of plants in vegetation, and no one has done more than he to secure acceptance of the view that the nature of vegetation is essentially dynamic.

2. The meaning of the word "association"

By long and constant usage the word association has become an integral component of ecological terminology. Yet, according to the strict meaning of the word, the sense in which it is used in ecology is somewhat misleading. The essential idea underlying the English word association is that of community of interest, partnership, of combining or banding together for a common purpose.[1] In this sense it would be almost impossible to speak of the association of plants at all. It is true that in certain cases a limited degree of community of interest appears to exist (see "Mutuality" below), but a real state of "association" would, strictly speaking, exclude competition, a far more important relation in nature than that of partnership. Continental equivalents such as Verein, Genossenschaft, Gesellschaft (German), association (French), or samfund (Scandinavian), all convey a very similar meaning to that of the English word association. As an ecological term, however, association has come to stay, and no useful purpose would be served by an attempt to replace it. But it must be remembered that its ecological use involves an extension of the strictly literal meaning of the word. In all probability the earlier users of the term did not trouble themselves overmuch about either the precise meaning of the word association, or the real relations between the "associated" plants.

3. The phases of ecology

The history of plant ecology is curiously and yet naturally similar to that of the parent science of botany. In both cases systematic and morphological phases preceded the serious study

[1] Cf. MURRAY, A New English Dictionary, Vol. I, 1888.

of physiology. Ecology is still concerned mainly with systematic (i. e. descriptive and classificatory) and morphological (i. e. structural) work. Though useful physiological work has been done, ecology can scarcely be said as yet to have entered definitely on its inevitable physiological phase. It is, however, generally recognized that the ultimate problems of ecology are to a large extent physiological. A distinction must be drawn between extensive and intensive work in physiological ecology. The simpler problems are the extensive ones of synecology, many of which have already been attacked with a considerable measure of success. The broad, general relations between various types of vegetation on the one hand, and climatic and edaphic factors on the other, are now fairly well understood. Far less has been done towards the solution of the more ultimate problems, and as yet we have little really exact knowledge regarding the causal connexion between habitat factors and plant distribution. The following may be mentioned as examples of intensive problems the investigation of which falls within the scope of physiological ecology:

1. The physiological processes of plants or plant organs under natural or experimental conditions. Very often a careful investigation both of the physiological processes themselves and of "partial" [1] plant habitats is involved.[2]

---

[1] YAPP, The Concept of Habitat. Jour. Ecol., 10, 1922, p. 13. Habitats were classified as: — Successional, i. e. "The changing habitat occupied by an allied group of plant associations which, as a rule, comprise the stages of a normal succession or sere". Communal, "The general habitat of any recognizable plant community, such as an association or a society". Individual, "The habitat of an individual plant, whether solitary or forming part of a plant community". Partial, "The habitat of an individual plant during any given period or stage of existence".

[2] General measurements of the more important climatic and edaphic factors are of course often necessary in synecological work. But there seems little point in carrying out, as advocated by CLEMENTS (Research Methods in Ecology, Lincoln, Nebraska, 1905), the thorough quantitative investigation of habitats by means of instruments of precision, unless the data obtained can be directly correlated with definite physiological problems. In mixed vegetation this is comparatively rarely the case unless the problems are

2. The physiological inter-relations of the plants composing any given type of vegetation. Investigations of this kind often involve the analysis of complex "communal" [1] habitats into their component "individual" [1] and "partial" habitats.

3. The progressive reactions of plants on their habitats, which prepare the way for invasion by organisms with physiological equipments differing from those possessed by the inhabitants already in possession. Studies of progressive reactions deal with cumulative changes in "successional" [1] habitats (see below).

The object of this paper is to focus attention on the fundamental significance of the fact of "association", i. e. on the inter-relations of the associated plants. It is therefore mainly concerned with the second group of problems mentioned above.

4. The inter-relations of plants in vegetation

We have little really exact knowledge of these inter-relations, our current views being based largely on indirect evidence or a priori reasoning. That they are exceedingly complex there can be no doubt, and it is impossible to deal with them fully within the limits of a short paper. The discussion which follows will therefore be limited to a consideration of certain of the more important relations resulting from the proximity of associated plants to one another. Special relations, such as those between host on the one hand, and parasite, epiphyte or liane on the other, or between soil organisms and the roots of higher plants, as well as the relations involved in true symbiosis, helotism & c., are outside the scope of this paper.

carefully formulated beforehand. When Clements recommended (l. c. p. 17) that the accurate study of the habitat should come first, and the plant afterwards, he had apparently failed to realize the complex nature of most habitats. In intensive work, it is not until the physiological problem has been defined that the habitat factors can be studied intelligently and profitably (cf. Yapp, l. c. p. 14).

[1] see footnote 1 p. 687.

a) The Reactions of Plants on their Habitats.[1]

Apart from certain of the special relations mentioned above, there is no evidence that plants affect one another otherwise than indirectly, i. e. through some modification of, or reaction on, the physical factors of the habitat. The actual effects thus indirectly produced by the associated plants on one another depend of course partly on the nature of the reactions, and partly on the nature of the plants themselves. The reactions of plants on their habitats may be either transient or relatively permanent. The latter may be termed progressive, and the former temporary reactions.

1. Progressive reactions are those due to successive generations of plants; the effect produced is cumulative. Primarily they affect the soil, e. g. by the accumulation of humus, with all that that involves;[2] the trapping of silt or sand, and so on. In the course of time far-reaching modifications of habitats may be brought about. In consequence, within the limits imposed by general climatic and edaphic factors, progressive reactions play a very important part in controlling the course of plant successions.

2. Temporary reactions are those due to the presence of living plants as such. Either soil or air factors may be modified, but the effect produced is for the most part transient.

The soil is affected by the withdrawal by plants of raw food materials. This lessens the total amount available, and may therefore accentuate competition. Such reactions are temporary, as the substances are sooner or later returned to the soil.

Probably, however, the most important temporary reactions are those which affect the atmospheric factors of light, humidity and temperature. In many cases the resulting internal climate (or climates) i. e. that within the space occupied by the shoots of the plant community, differs considerably from the

[1] CLEMENTS (Plant Succession, Washington, 1916, p. 79), uses the term reaction for “the effect which a plant or a community exerts upon its habitat”.

[2] COWLES, The Causes of Vegetative Cycles, Bot. Gaz., 51, 1911, pp. 173—7.

general climate of the region.[1] In this way the complexity of communal habitats [2] is increased, and a greater variety of life-forms, each occupying its appropriate individual habitat,[2] can be accomodated in the community. This class of reactions is most marked in tall vegetation such as forest, and hence, as a rule, during the later stages of a sere. In these later stages, temporary reactions determine to a great extent (of course in conjunction with the general habitat factors) the subordinate members of the plant community. They may even in some cases determine the dominants, as, for instance, when the climax dominant is a tree the seedlings of which can endure deep shade.[3]

The coppicing of woodland will serve to illustrate the difference between temporary and progressive reactions. For the most part, temporary reactions cease automatically with the cutting of the trees, and this is followed by a change in the herbaceous vegetation. Owing to the increase of light and decrease of humidity, the resulting vegetation is of a more xerophytic character than that which grew under the shade of the trees. On the other hand, owing to the previous ameliorating effect on the soil of progressive reactions, the vegetation is less xerophytic than it would have been on a corresponding "primary bare area".

The following inter-relations of individuals or species in a state of association may be distinguished: competition, priority, dependence, independence and mutuality. These inter-relations of the constituent plants find their ultimate expression in vegetation in the establishment of various degrees of dominance and subordination.

b) Competition.

The familiar phrase "the struggle for existence" was used by Darwin in a comprehensive sense. In the "Origin of Species"

[1] Cf. Yapp, Stratification in the Vegetation of a Marsh, and its Relations to Evaporation and Temperature, Ann. Bot., 23, 1909. Also Salisbury, The Structure of Woodlands, This Volume.

[2] Yapp, The Concept of Habitat, p. 13.

[3] Clements, Plant Succession, p. 93.

(6th. edit. p. 47) he wrote, "As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life".

The term "competition" has a narrower meaning. It is, properly speaking, confined to those cases in the general struggle for existence in which living organisms compete or strive with one another for a limited supply of the necessaries of life — water, light, salts, insect visitors and so on.

There can be little doubt that of all the biotic inter-relations competition (together with priority) is the dominant one, and has the most profound and far-reaching effect.

The incidence of competition. The plans on which a higher plant and a higher animal respectively are constructed differ radically from one another. Individuality is less definite in the case of the plant, for there is no general control by a central nervous system. In consequence, the various organs of the plant are united, so to speak, by less definite bonds, and often exhibit a greater degree of independence than those of a higher animal. Hence whilst competition between organisms as a whole is probably the rule amongst higher animals, localized competition, that is, competition between certain organs only, is much more frequent amongst plants. Thus root-competition is generally quite independent of, though it may be accompanied by, shoot-competition. It is even true that portions of the shoot-system of an "individual" plant may actively compete with neighbouring plants whilst other portions are free from competition. Of course the organs themselves are not wholly independent, for severe competition experienced by one set of organs often reacts adversely on the plant as a whole, even though the competition itself is strictly localized.

Localized competition often results in a modification of the form of a plant. For instance, the branches of trees usually tend to develop most strongly in the direction of adequate illumination, whilst those compelled to compete for light with the branches of neighbouring trees are often either poorly developed or even entirely suppressed. Hence the one-sided forms of trees growing close together in a hedgerow or on the edge of a wood.

Again, in certain open plant communities for example, there is active root-competition for water, the shoots, which do not compete with each other, being directly influenced by the general climatic factors alone. EUGEN HESS [1] has shown that in open debris associations the available space in the soil (Wurzelraum) is entirely occupied by roots. In this case the openness of the community is determined by root-competition. It is not, however, always easy to decide when plants are or are not competing with one another. CLEMENTS says [2] "Competition occurs whenever two or more plants make demands in excess of the supply". And again, "Properly speaking, competition exists only when plants are more or less equal. . . . A dominant tree and a secondary herb of the forest floor" are in no sense competitors. Neither of these statements is entirely accurate. FRICKE,[3] for example, has shown that the roots of adults and seedlings of *Pinus sylvestris* may compete for water. If this is so, it would appear doubtful whether, during times of scarcity (e. g. of water), the roots even of plants of such different growth-forms as herbs and trees are ever wholly free from competition with one another. Again, the shoots of herbs and seedling trees may compete together for light (but see "priority" below"). But as soon as the tree overtops the herb, the competition for light ceases, even though, owing to the shade cast by the canopy above, the joint demands of the two for light are in excess of the supply. The tree now has "priority" of the herb, and the competitive relation is replaced by that of dominance and subordination. The roots of the two plants, however, may still continue to compete one with another.

[1] HESS, Ueber die Wuchsformen der alpinen Geröllpflanzen. Beihefte zum bot. Centralblatt, 37, Abt. II, 1910: quoted by FREY, Die Vegetationsverhältnisse der Grimselgegend. Bern, 1922, p. 155.

[2] Plant Succession, p. 72.

[3] FRICKE, Licht- und Schattenholzarten. Cent. Gesamt. Forstw. 30, 1904, quoted by CLEMENTS, l. c., p. 93.

D e g r e e s   o f   c o m p e t i t i o n. The degree as well as the results of competition depend, amongst other things, on (1) the numbers, distance from one another, age and growth-forms of the competing species; (2) the relative and seasonal demands made by the competitors on the available amounts of the various necessaries, and (3) in some cases on physical factors such as temperature, or the presence of some substance in the soil (e. g. NaCl or $CaCO_3$) which may hinder or promote the growth of particular species. The effect of such physical factors will in turn depend on the physiological constitutions of the plants concerned. Factors such as the above will decide in any given case how far the competition shall be on equal or unequal terms. But even so, the complex conditions of competition are unstable, for reactions of all kinds, both progressive and temporary, are more or less continually disturbing any equilibrium previously reached.

Speaking broadly, competition is usually most severe: —

1. During those stages of a sere when the population is most dense. Competition may be absent while the pioneers are still isolated, but "increases with the increase of population in successive stages until the climax or subclimax is reached, after which it decreases again with the population".[1]
2. Between individuals or species of the same or similar growth-form and requirements, and which therefore play similar rôles in the economy of nature.[2]
3. During the seedling stage and at the time of reproduction.[3]
4. During those periods of the year when growth activity is at its maximum.

W h a t   i s   m e a n t   b y   s e v e r i t y   o f   c o m p e t i t i o n? The rule mentioned above that competition is most severe between similar individuals or species is usually regarded as a fundamental law. DARWIN[4] stated it as follows: "The struggle

[1] CLEMENTS, Plant Succession, p. 72.

[2] Cf. DARWIN, Origin of Species, 6th. edit., p. 55; CLEMENTS, Research Methods, p. 287; WARMING, Oecology of Plants, Oxford, 1909, p. 93: but see discussion below.

[3] Cf. DARWIN, l. c., p. 49; CLEMENTS, Plant Succession, p. 73.

[4] DARWIN, l. c., p. 54.

will almost invariably be most severe between the individuals of the same species. . . . In the case of varieties of the same species the struggle will generally be almost equally severe, and we sometimes see the contest soon decided". According to CLEMENTS,[1] "The closeness of the competition between the individuals of different species varies directly with their similarity in vegetation or habitat form". In a general sense this law is no doubt true, yet it needs some further examination. By what standard are we to measure severity?

Theoretically, no doubt, the degree of severity could be expressed quantitatively as the ratio of the total collective needs of the competing organisms, to the total supply available of the particular necessity competed for. The higher the ratio the more severe the competition. Practically, however, it is impossible, with so many variables, to determine the value of this ratio, and we are driven to measure the severity of competition by results. Even then the problem is far from simple.

Imagine a case in which a very large number of seeds, belonging to species of different degrees of similarity or dissimilarity, germinate simultaneously on an unoccupied area of suitable soil. Competition would result in a considerable mortality amongst the seedlings or young plants. Some, however, would survive, and as many plants as conditions allowed would grow to maturity. The adults would continue to compete with one another, but on the whole competition would be less severe than with the crowded seedlings. The final composition of the vegetation would depend on the respective physiological equipments (including growth-forms) of the competing plants. Some one or more species would become dominant, others subordinate, while others again might be entirely exterminated. Which of these results would indicate the greatest severity of competition? It might well be urged that no result could be more severe than premature death. If this be adopted as the criterion, competition would appear to be most severe between the young (which is generally acknowledged to be the case), and more particularly between those of the exterminated species and their con-

[1] CLEMENTS, Research Methods, p. 287.

querors. As a rule the victors, whether belonging to the same or to different species, must have entered on the struggle with some advantage — either of age, position, suitability of the habitat, amount of leaf or root surface, growth-form or the like — over the individuals they are destined to vanquish. Provided then, that they come directly into competition, the contest will usually be decided most speedily, and in one sense may be most severe, when the competing species are to a certain extent unlike. But premature death is not the only possible criterion by which we may judge of the severity of competition. When plants compete more or less on terms of equality, as is often the case with individuals of the same species, the struggle will tend to be long drawn-out. It might be argued that a prolonged struggle, during which the mastery hangs in the balance, may be more severe than one which is quickly decided. *Ceteris paribus*, this view is certainly the correct one so far as the victors are concerned, whether victory ultimately results in the death or merely in the subordination of the vanquished. As for the vanquished themselves, it is a little more difficult to judge, for a struggle ending in premature death may well be regarded as more severe, at all events as long as it lasts, than one which results merely in subordination. So far as our knowledge goes at present, there seems no reason to doubt that the law that severity of competition is proportional to the degree of similarity between the competitors, holds for the victors. Probably it holds to a certain extent for the vanquished also, but here the matter is less clear. The reasons for failure are often obscure, though they must lie in a certain degree, it may be in some cases a considerable degree, of dissimilarity and inferiority.

Reasons for the exclusion of plants from certain habitats. It is a well-known fact that certain species are often partially or wholly excluded from habitats in which, so far as the general physical conditions are concerned, they might flourish. Such exclusion is often attributed to competition.[1] Undoubtedly competition is the deciding factor in many instances. Sometimes it is simple competition for one or

[1] WARMING, Oecology, p. 367.

more of the necessaries of life. In other cases exclusion may be due to some special condition which places some competitors at a disadvantage as compared with others. Examples are attacks by parasites, or the presence of an excess of NaCl or $CaCO_3$ in the soil.[1] A frequent reason for exclusion is partial unsuitability of the habitat, i. e. unsuitability at a particular stage of the life-history of a species. This is true both of exclusion due to the failure of an invader to enter a community, and of the driving out, during the course of succession, of certain previously established members of the community. An example will make this clear. CLEMENTS[2] has pointed out that the gradual replacement of pioneer forest trees by other species, is usually due to the failure of the seedlings of the former to establish themselves as the shade becomes denser. The pioneers are therefore replaced by trees the seedlings of which are more tolerant of shade. This is not, strictly speaking, due to competition between the two, but to a "temporary reaction" of the trees themselves. Increasing shade, in fact, changes the internal climate of the forest, so that it is no longer suitable for the seedlings of the pioneer trees, even though conditions may still be favourable for the adults.

The same may possibly apply, though perhaps to a less extent, to many cases of replacement of light-demanding by shade-tolerant herbs during a forest succession. But as yet we have little real knowledge of the actual causes, either of the total exclusion of particular species from given communities, or of the replacement of one species by another during succession. DARWIN[3] wrote in 1859: "Probably in no one case could we precisely say why one species has been victorious over another in the great battle of life". Half a century later, in 1909, WARMING[4], referring to the "nature of the weapons by which plants oust each other from habitats", said: "We are far from having exhaustively solved the problem even with regard to a single spe-

[1] WARMING, l. c., p. 71; TANSLEY, Competition between *Galium saxatile* and *G. sylvestre*, on different types of soil. Jour. Ecol. 5, 1917.

[2] Plant Succession, p. 93.

[3] DARWIN, l. c., p. 55.

[4] WARMING, Oecology, p. 366.

cies". We have not progressed very far even today.[1] Here is a wide and attractive field for exact observation and experiment. Few of the problems of physiological ecology referred to above would more richly repay intensive and critical investigation than the somewhat elusive ones of the competition between species, and allied phenomena.

In all probability, competition between two organisms is comparatively rarely on absolutely equal terms, but the degree of inequality varies greatly. The effects of competition on the individual vary both with the degree of inequality and with the degree of severity, and include — extermination, subordination, modification of form, and diminished luxuriance. From what has already been said, it seems clear that whatever the effect of competition may be on the maintenance of the standard of efficiency of the race, individual plants can hardly be said to benefit by it. For the vanquished, and often even for the victor, competition is, in varying degrees, an injurious relation resulting from association.

c) Priority.

True competition may be unequal, but it can never be entirely one-sided. An organism that has no chance of obtaining any share of the supply of a particular necessity, until another has taken all it can make use of, is not (in respect of this necessity) a competitor of the latter. The jackal does not compete with the lion for food, but contents himself with what is left after the lion has satisfied his hunger. We may say therefore that the lion has priority of the jackal with respect to the food supply. Similarly (though the analogy is not exact), a forest tree has priority of a subordinate herb for light; that is, it intercepts the light on its way to the herb, using all it can, the herb receiving as its share only a portion of what passes the taller plant. Priority then may be defined as a relation in which one

[1] The possibly toxic effect of plants on one another must be taken into account. See the interesting results recorded in Science and Fruit Growing (Chaps. 25 to 29), by the Duke of Bedford and Spencer Pickering. London, 1919.

organism is so situated that it can intercept and retain all it is capable of using of a particular necessity, before a second can procure any at all. Both priority and competition are inter-relations of organisms respecting the supply of the various necessaries of life. Priority is a relation in which one organism partially or even wholly deprives another of something it might otherwise obtain. Competition, on the other hand, involves mutual (though often unequal) deprivation.

Priority is closely bound up with the stratification of vegetation. The shoots of the taller, dominant plants invariably have priority of those of subordinate terrestrial herbs in respect of light. But it seems probable (though little is as yet known on this subject) that aerobic soil organisms, and the roots of subordinate, surface-rooted herbs, may have priority of the deeply placed roots of the dominants for oxygen, especially in poorly aerated soils.[1] Priority therefore is not synonymous with dominance.

In extreme cases priority may involve the extermination of an inferior species, as must frequently occur when a community of small plants is invaded in force by a larger species. In other cases less severe injury results. In yet others, as for instance pronounced shade plants, the inferior plant may benefit by conceding priority to the superior, the relation becoming one of dependence.

I am not aware of any previous suggestion to distinguish between competition and what is here termed priority. It may be that when the concept of "competition" is analysed in the light of fuller knowledge, other cases will be found really to be cases of priority. Undoubtedly competition is a complex phenomenon. In plants, for instance, we can distinguish between the passive interception and the active deflection of a necessity. Roots can deflect supplies of water and salts, and the most powerful competitor secure the largest share. Light, however, cannot be attracted or deflected by plants, its passive interception being a matter of the position of the receiving organs. Roots, then, in the strict sense of the word, may

[1] Cf. Salisbury. This Volume.

compete for water, but the so-called competition of shoots would appear to resolve itself into the priority of individual shoots or even leaves for light. Whether this and all other cases of passive interception should be regarded as distinct from, or merely as a special kind of, competition, it may be premature to judge. At all events it seems clear that priority may exist in the absence of competition.

d) Dependence.

The effect of association on the individual may be either injurious (e. g. competition, and often priority) or beneficial. The inter-relations from which individual plants derive benefit may be termed *dependence*, if the benefit is one-sided, or *mutuality*, if the resulting benefit is mutual. These relations, though entirely subordinate in importance to competition, must also be taken into account.

Dependence may be defined as *a relation between individuals, usually of different species and growth-forms, in which one form derives benefit from association with another, the benefit being one-sided, not reciprocal.* We are not concerned here with the dependence of parasites, lianes or epiphytes on their hosts, but merely with dependence arising from the proximity of one plant (usually the smaller) to another. Such dependence is found more particularly in complex communal habitats in which the internal climate is modified by the presence of the dominant species. Owing to this modification, species requiring greater shade or humidity than is afforded by the general climate of the region may be enabled to enter the community. Such forms are, at least in extreme cases, entirely dependent for their existence in the community on the presence of the larger plants. The element of dependence in vegetation steadily increases with the height of the dominant plants, the number of layers in the vegetation, and the diversity of growth-forms. It is therefore usually at its maximum in forest vegetation, and hence during the later stages of succession.

Under given climatic conditions, some species may be o b l i g a t e and others f a c u l t a t i v e d e p e n d a n t s. Examples of obligate dependants are pronounced shade plants, for which shade is an essential condition of existence. Such plants derive the maximum benefit from the relation of dependence. Facultative dependants, on the other hand, e. g. less pronounced shade plants such as *Pteridium aquilinum*, may attain a more luxuriant growth, or otherwise derive benefit from the presence of larger plants, but can live, or perhaps even flourish apart from them. Although many forest herbs, terrestrial algae & c., may pass their whole lives as dependants, obligate dependence is probably far more common amongst seedlings than adults. A striking case is given by Moore.[1] According to him, the park lands of the Tanganyika region of Central Africa originate on recent alluvial soils. The first colonists are grasses and succulent Euphorbias. Later on, seedlings of other species become established in the shade cast by the Euphorbias. Gradually the Euphorbias are overgrown and finally replaced by bushes and trees, the seedlings of which would have been unable to establish themselves but for the shelter afforded by the Euphorbias.

Apparently the nature of the benefits derived from dependence differs in different cases. In some, e. g. extreme shade plants, it may be that optimum conditions of light and humidity are secured by the association with larger plants. In other cases the physical conditions as modified by the presence of the dominants may be merely tolerated by the dependent species, the benefit resulting from association being freedom from excessive competition. The former are instances of d i r e c t, and the latter of i n d i r e c t d e p e n d e n c e. Indirect dependence may be looked upon as a special case of t o l e r a n c e.[2]

e) M u t u a l i t y.

According to Murray's dictionary (vol. 6), mutualism is "a c o n d i t i o n o f s y m b i o s i s i n w h i c h t w o a s s o c i a t e d

[1] MOORE, The Tanganyika Problem. London, 1903, pp. 114—117: quoted in New Phytologist, 2, 1903, p. 37.

[2] The term t o l e r a n c e may be applied to the endurance by plants of unfavourable physical conditions, which may be occasioned by the presence of some deleterious factor such as shade or NaCl.

organisms contribute mutually to the well-being of each other". Originally applied by VAN BENEDEN[1] to animal symbiosis, the term mutualism has also been used with reference to lichens. It would seem legitimate to extend its botanical use to cases in which plants derive mutual benefit from association of a less intimate character. In order to avoid possible confusion, however, it is proposed to apply the term mutuality, the meaning of which is similar to that of mutualism, to cases where mutual benefit (mutual dependence) arises from the proximity of plants to one another.

WARMING says[2] — "Only in a loose sense can we speak of certain individuals protecting others, as for example, when the outermost and most exposed individuals of scrub serve to shelter from the wind others, which consequently become taller and finer, for they do not afford protection from any special motive, such as is met with in some animal communities". Yet there can be no doubt that mutual protection, especially from the danger of excessive transpiration, is an important result of the gregarious habit of plants and of their shoots. It is, indeed, a far more general phenomenon than might be inferred from the passage quoted above. Well-defined contours, both of individual plants and also of vegetation, caused by the massing of shoots at about the same level, commonly occur, especially in wind-swept or other habitats in which transpiration tends to be excessive. In such cases individual plants (or their shoots) must benefit considerably by close association.[3] The absence of "motive" or "purpose" does not render this mutual protection less effective; any more than the severity of competition is reduced because it is unconscious.

The stabilization by plants of a mobile substratum, such as blown sand or estuarine silt, is an instance of another kind of mutual benefit due to association.

Mutuality is no doubt most frequent between individuals belonging either to the same species or to similar growth-forms,

[1] VAN BENEDEN, Animal Parasites and Messmates. London, 1876.

[2] WARMING, Oecology of Plants, p. 95.

[3] YAPP, l. c. (Stratification, 1909), pp. 303—5.

but it may exist between plants of very different habit. WARMING[1] points out that, "The carpet of moss in a pine-forest protects the soil from dessication, and is thus useful to the pine, yet, on the other hand, it profits from the shade cast by the latter".

Mutuality may be found during almost any stage of succession. Unlike dependence, which is usually at its maximum in the later stages, mutuality is often well-marked during the less mesophytic medial phases of a sere. When the subclimax or climax is reached, mutuality, if it exists at all, is mainly confined to the dominant species.

f) Independence.

When none of the foregoing relations exists, and a plant neither influences nor is influenced by its neighbours, it may be said to be independent. Mutual independence may be due to separation either in space or in time. Scattered pioneers on a bare area are an example of spatial independence, while seasonal independence is illustrated by certain woodland herbs which, though growing close together, both vegetate and reproduce at different seasons of the year. Complete independence may perhaps be rare, though practical independence is common. Independence merges on the one hand into competition and on the other into dependence: it is not always easy to determine where one relation begins and another leaves off.

5. The communal life of plants

Plant communities have often been compared with human or other animal societies. Perhaps the outstanding difference between the two is the absence in the plant community of any psychological element such as directive will, motive, common aim or purpose, instinct, or even (though egoism is the rule) conscious selfishness. The sedentary habit of plants, coupled with the absence of psychological processes, render the plant

[1] WARMING, l. c. p. 94.

community more completely under the control of the physical environment than is a community of at all events higher animals. Aggregation, in the first instance, is governed to a great extent by "chance", which is itself really subject to definite laws.[1] Whether the plants which arrive can establish themselves or not, as well as their inter-relations, when established, are determined by the interaction of the physical conditions of their "partial" or "individual" habitats, and the plants themselves, with their varying physiological constitutions. The result is that without any central control of a psychological nature, such as is found in a human community, vegetation tends to assume, in accordance with as yet imperfectly known laws, a definite organized structure. The physical conditions themselves, the only real control, are, as we have seen, determined partly by the general climatic and edaphic conditions of the communal habitat, and partly by reactions of the plants on that habitat.

It must be clearly recognized that the various inter-relations of plants, such as competition, priority, dependence and mutuality, are primarily relations governing the interchange of matter or energy with the physical environment. Further, the absence in plants of the single ingestive aperture characteristic of animals, together with other differences,[2] lead to more direct and independent relations between the various organs of a higher plant and the environment than is the case with animals. That being so, it is not surprising to find that though the whole organism may be, and usually is, affected, the inter-relations of plants are the inter-relations of particular organs to a far greater extent than with animals. This has been touched upon above, but is really of general application, the results being often of considerable complexity.

The oak trees in a forest, for example, may exhibit at one and the same time the following relations. Their roots may compete with one another for water, the conditions of competition possibly being modified by union owing to "natural grafting". Possibly also, the roots may to some extent yield prior-

[1] Cf. WELDON, Presidential Address to section D. British Association. Bristol, 1898.

[2] Cf. above, "The incidence of competition".

ity (e. g. for oxygen) to surface-rooted herbs. The leaf-bearing shoots on the other hand, by protecting one another from the drying effect of wind, may exhibit mutuality. The shoots (or some of them only) may "compete" for light with other shoots, of either the same or adjacent trees, at the same time having priority for light over subordinate herbs.

Again, a subordinate herb of the forest floor may yield priority for light to, and at the same time be directly or indirectly dependent on, the taller trees. Its roots may perhaps have priority over the more deeply-placed roots of the trees, and it may compete in various ways with other herbs or seedlings of the undergrowth.

The relative independence of the different organs of an "individual" plant frequently occasions relations between these organs similar to those which obtain between different plants. Competition, priority, mutuality, and at least partial independence between different shoots of the same plant certainly exist in very many cases. Similarly, competition and priority probably occur between the roots of an individual plant.

The inter-relations of plants or of their various organs, coupled with the relative independence of these organs, influence the form as well as the size of the individual plant.

6. Changes of relations during succession

Consider the probable course of events during a unit succession (sere) which begins on bare rock and ends with forest. The earlier initial stages of such a sere are characterized by open and relatively xerophytic vegetation, and by the dominating influence of the climatic and edaphic factors of the habitat, biotic factors being of subordinate importance.[1] During these earlier stages "association" is loose and ill-defined, indeed, in completely open pioneer stages association, so far as the influ-

[1] The so-called "biotic factors" are either (1) direct, e. g. those due to organisms such as parasites and herbivores, which utilize the bodies of other organisms as sources of food supply, or (2) indirect, i. e. those due to the reactions of organisms on their habitats. The phytobiotic factors considered in this paper belong to the second group; they are physical factors of the habitat as modified by the presence of plants.

ence of plants on one another is concerned, may hardly exist at all. The relations of competition, priority, dependence and mutuality are at their minimum, and that of independence at its maximum. In the sere under consideration, owing to the scarcity of soil in a rocky habitat, active root-competition may commence long before there is serious competition between the shoots (see above).

During the whole course of the sere there will no doubt be a more or less continual rain of seeds and spores of all kinds on the area. Which of the species represented by these seeds and spores can establish themselves, and at what stages of the sere, will be determined by the ever changing physical conditions of the successional habitat. As the sere progresses through the medial to the climax stages, the vegetation becomes more and more closed and mesophytic; the influence of indirect biotic factors more and more marked, and consequently (though climate still exercises general control) that of the primary climatic and edaphic factors relatively less. The successional habitat is gradually ameliorated, the soil conditions by progressive, and atmospheric conditions by temporary reactions. This amelioration of the habitat accounts for the increasing mesophytism of the vegetation.[1]

As the larger growth-forms assume dominance, the successive communal habitats, and with them the structure of the vegetation, become more complex. "Association" becomes more definite and precise as independence decreases, and the relations of competition, priority, dependence and mutuality increase. In the absence of any method of estimating the various relations quantitatively, it is difficult to speak, otherwise than vaguely, of maxima and minima. But it would seem that mutuality, often a somewhat indefinite relation, may attain its maximum during relatively early (e. g. medial) stages of the sere. Competition, priority and dependence, on the other hand, certainly increase towards the later stages. Provided that the shade cast by the dominant trees is not too great, priority and dependence probably attain their maximum in the climax stage, other-

[1] Cf. Cowles, l. c., Vegetative Cycles, p. 174.

wise they again decrease with the number of subordinate plants. On the whole it seems probable that competition may be at a maximum at a somewhat earlier stage, when the ground is thickly populated, and trees have not yet become completely dominant.[1]

During the course of a sere, then, the vegetation, and with it the inter-relations of the constituent plants, change with the physical conditions. But the rate of change must vary considerably. Periods when changes of all kinds are relatively rapid probably alternate with prolonged periods of relative stability, during which change is slow, the inter-relations of the plants remaining more or less constant. But there is no such thing as absolute stability, even in the most permanent of climax associations. Internal changes, locally affecting the inter-relations of the constituent elements of a community, are constantly occurring. Adult individuals die, seedlings become established, creeping plants alter their positions and so on. Such internal changes, which involve neither the appearance of new invading species, nor any radical alteration in the numerical proportions of those in occupation, have no far-reaching significance.

* * *

This provisional attempt to analyse and define the probable inter-relations of plants in vegetation is of necessity based on very incomplete evidence. But it may serve to draw attention to the fundamental significance of the association of plants. Even the few relations considered, some of which have not, I believe, previously attracted much attention, show great complexity. Other special relations, as well as the zoobiotic factors of the habitat, have been entirely omitted.

[1] Cf. CLEMENTS, Plant Succession, p. 72.