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PATTERN AND PROCESS IN THE PLANT COMMUNITY*

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(*With eleven Figures in the Text*)

CONTENTS

THE PLANT COMMUNITY AS A WORKING MECHANISM

The plant community may be described from two points of view, for diagnosis and classification, and as a working mechanism. My primary concern is with the second of these. But inasmuch as the two aspects are not mutually exclusive, a contribution to our understanding of how a community is put together, and how it works, may contain something of value in description for diagnosis.

It is now half a century since the study of ecology was injected with the dynamic concept, yet in the vast output of literature stimulated by it there is no record of an attempt to apply dynamic principles to the elucidation of the plant community itself and to formulate laws according to which it maintains and regenerates itself. Pavillard's assessment of the dynamic behaviour of species comes very near it, but is essentially concerned with the 'influence (direct or indirect) of the species on the natural evolution of plant communities' (Braun-Blanquet & Pavillard, 1930). As things are, the current descriptions of plant communities provide information of some, but not critical, value to an understanding of them; how the individuals and the species are put together, what determines their relative proportions and their spatial and temporal relations to each other, are for the most part unknown. It is true that certain recent statistical work is stretching out towards that end, but the application of statistical technique, the formulation of laws and their expression in mathematical terms, will be facilitated if an acceptable qualitative statement of the nature of the relations between the components of the community is first presented. Such a statement is now made based on the study of seven communities in greater or less detail, for data of the kind required are seldom recorded.

The ultimate parts of the community are the individual plants, but a description of it in terms of the characters of these units and their spatial relations to each other is impracticable at the individual level. It is, however, feasible in terms of the aggregates of

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individuals and of species which form different kinds of patches; these patches form a mosaic and together constitute the community. Recognition of the patch is fundamental to an understanding of structure as analysed here.

In the subsequent analysis evidence is adduced to show that the patches (or phases, as I am calling them) are dynamically related to each other. Out of this arises that orderly change which accounts for the persistence of the pattern in the plant community. But there are also departures from this inherent tendency to orderliness caused by fortuitous obstacles to the normal time sequence. At any given time, therefore, structure is the resultant of causes which make for order and those that tend to upset it. Both sets of causes must be appreciated.

In describing the seven communities I propose in the first examples to emphasize those features which make for orderliness, in the later to content myself with little more than passing reference to these and to dwell specifically upon departures from it; in all examples to bring out special points for the illustration of which particular communities are well suited or for which data happen to be available.

For the present the field of inquiry is limited to the plant community, divorced from its context in the sere; all reference to relics from its antecedents and to invaders from the next state is omitted. I am assuming essential uniformity in the fundamental factors of the habitat and essential stability of the community over a reasonable period of time.

THE EVIDENCE FROM SEVEN COMMUNITIES

The regeneration complex

Regarded by some as an aggregate of communities, by others as one community, the regeneration complex fittingly serves as an introduction because its study emphasizes the underlying uniformity of the nature of vegetational processes. It consists of a mosaic of patches forming an intergrading series the members of which are readily enough assignable to a few types or phases. The samples of these phases are repeated again and again over the area; each is surrounded by samples of other, but not always the same phases.

As the work of Osvald (1923) and of Godwin & Conway (1939) shows, these phases are dynamically related to each other. For Tregaron Bog the sequence is briefly as follows. The open water of the pool is invaded by *Sphagnum cuspidatum* which in turn is invaded and then replaced first by *S. pulchrum*, then by *S. papillosum*, by whose peculiar growth a hummock is formed. This hummock is first crowned by *Calluna vulgaris, Erica tetralix, Eriophorum vaginatum* and *Scirpus caespitosus*, later by *Calluna vulgaris* with *Cladonia silvatica* forming a subsidiary layer. The proof of the time sequence lies in the vertical sequence of plant remains in the peat itself.

Each of the phases of the regeneration complex was at one time regarded as a community, and the whole as an aggregate of communities dynamically related to each other. Tansley (1939), for example, still calls them seral. The resemblance to a sere is close; each phase from the open water to the hummock with *Calluna* depends on its antecedents and is the forerunner of the next, the sequence depending on plant reaction.

The resemblance, however, is partial only, for a cycle of change is completed by the replacement of the hummock by the pool, a topographical change brought about by differential rates of rise in the different patches. That is, the immediate cause does not reside exclusively in the patch itself but in the spatial relation between patches and their relative changes in level. Thus the *Calluna* of the hummock dies or is killed and is followed in the place vacated by it by other species which have had no direct or indirect hand in its death. Thus in the full cycle we may distinguish an upgrade series and a downgrade.

Each patch in this space-time mosaic is dependent on its neighbours and develops under conditions partly imposed by them. The samples of a phase will in general develop under similar conditions but not necessarily the same, for the juxtaposition of phases will vary. This may be expected to affect the rate of development of the patches of a phase and their duration. But on the duration of the full cycle of change and its component phases there is inadequate information, although the *impression* is gained that in the upgrade series the net rate of production per annum is at first slow, then fast in the *Sphagnum papillosum* phase, then slow again in the final phases.

This brief summary presents the regeneration complex as a community of diverse phases forming a space-time pattern. Although there is change in time at a given place, the whole community remains essentially the same; the thing that persists unchanged is the process and its manifestation in the sequence of phases.

Dwarf Callunetum

It may well be argued that the regeneration complex is a special case. It is one of my objects to show that these dynamic phenomena are paralleled in a wide range of communities, all of which can hardly be set aside as special cases.

Occasionally in the regeneration complex there occur partial sequences in space which correspond with the time sequence. Complete correspondence between the space and time sequence is found, however, in certain communities under highly specialized conditions. Such conditions are found in the Arctic (Walton, 1922), where the prevailing winds determine the alinement of the plants in the community and their unidirectional vegetative spread. Similar phenomena are shown by the dwarf Callunetum of highly exposed places on the slopes of the Cairngorms.

The Callunetum consists of strips of *Calluna* separated by strips of bare wind-swept soil; all the *Calluna* plants lie side by side and in line, their apices spreading into the shelter created by the plant itself and their old parts dying away behind. In other places the strip of vegetation is double, consisting mainly of *Calluna* and *Arctostaphylos uva-ursi*; under the prevailing conditions both species have the same habit, but they differ so far in their specific make-up that *Arctostaphylos* is generally found to leeward of *Calluna* (Fig. 1). The spatial relation between these two species and their unidirectional growth suggest that as *Arctostaphylos* grows forward over the eroded soil, *Calluna* grows over the older parts of *Arctostaphylos*, suppressing the leaf-bearing shoots though not killing the old stems. This is, indeed, the case, and proof of the dynamic relation is found in the dead remains of *Arctostaphylos* below the *Calluna*.

The community just described is a three-phase (or more-phase depending on the refinement of the analysis) system with the phases arranged in linear series. In the dwarf Callunetum of more sheltered places unidirectional spread is replaced by centrifugal; each *Calluna* plant is free to spread until checked by other plants in its neighbourhood. The static pattern of the mature community is a background of *Calluna* with scattered patches of *Arctostaphylos, Cladonia silvatica* and bare soil in it. But the time sequence remains essentially the same, with four phases in the full cycle, which may be shortened to three or even to two phases.

Briefly summarized from details obtained by Dr G. Metcalfe (to whom I am also indebted for Fig. 1) during the Cambridge Botanical Expedition to the Cairngorms and kindly placed by him at my disposal, the history of the relations between the phases is as follows, the kind of evidence being the same (except for the positional relation) as that obtained from the linear series. The young vigorous shoots of *Calluna* are usually dense enough to exclude lichens; the older, fewer and less vigorous shoots are unable to do so and *Cladonia silvatica* is often abundant on the old parts of the plant. On its death *Cladonia* becomes dominant, anchored on the dead stems. (The counterpart of this phase in the linear series is the strip of dead *Calluna* stems behind the live; owing to the violence of the wind, *Cladonia*, although present, is unable to dominate.) In time the *Cladonia* mat disintegrates (in much the same way as it does in Breckland (Watt, 1937)) and bare soil is exposed, often with some remains of *Calluna* stems on it. If *Arctostaphylos* happens to be near such a gap (and a much ramified system of non-leaf bearing stems occurs under the *Calluna* mat) invasion is followed by complete occupation. In time by

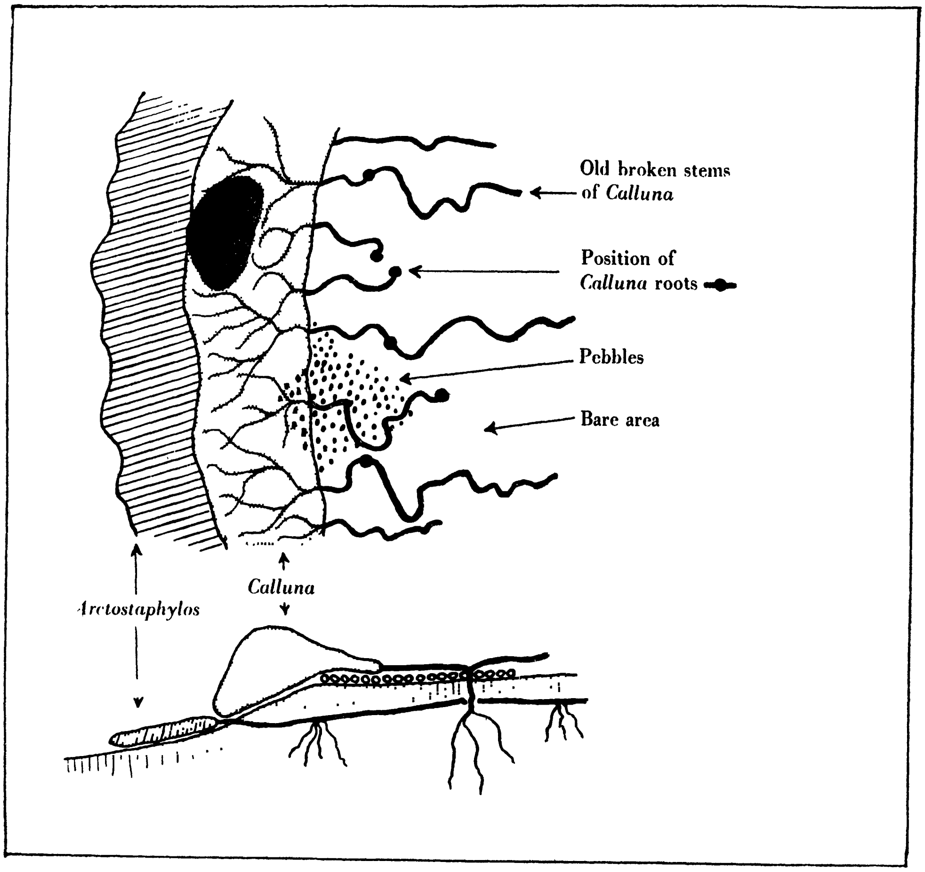

Fig. 1. Diagrammatic representation in plan and elevation to show the spatial relation between *Calluna* and *Arctostaphylos* in the 'double strips' separated by wind-swept bare soil in the Dwarf Callunetum of highly exposed places at approx. 2500 ft. on the northern slopes of the Cairngorms. The double strip moves forward in time; *Arctostaphylos* invades bare soil, and *Calluna* moves on and suppresses the adjacent *Arctostaphylos*.

vegetative spread from the margin *Calluna* replaces the *Arctostaphylos*. The relations between the phases are indicated diagrammatically in Fig. 2, which also shows the short-circuiting in the absence of *Arctostaphylos*.

Clearly *Calluna* is the dominant plant; the locally dominant *Arctostaphylos* and *Cladonia* are allowed to occupy the ground which *Calluna* must temporarily vacate, *Arctostaphylos* as a phase in the upgrade series and *Cladonia* in the downgrade. Although no data are available it may be pointed out that from the annual rings of the woody stems of *Calluna* and *Arctostaphylos* some estimate of the duration of the phases is made possible.

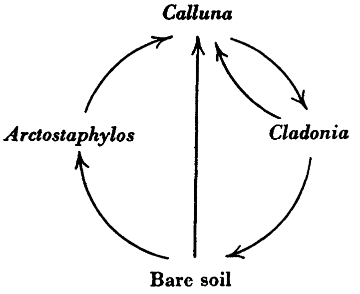

Fig. 2. Diagram illustrating the dynamic relations between the chief species in Dwarf Callunetum in less exposed places than those mentioned in Fig. 1. The arrows indicate the direction of change.

Eroded Rhacomitrietum

At somewhat higher altitudes on the Cairngorms an eroded community dominated by *Rhacomitrium lanuginosum* shows phenomena similar to those of the *Calluna* strips. For here, too, the direction of the prevailing wind, by determining the direction of spread of the plants, imposes on the patches of vegetation a space sequence which is also a time sequence.

The following very short account is based on details kindly supplied by Dr N. A. Burges, to whom I am also indebted for Fig. 3.

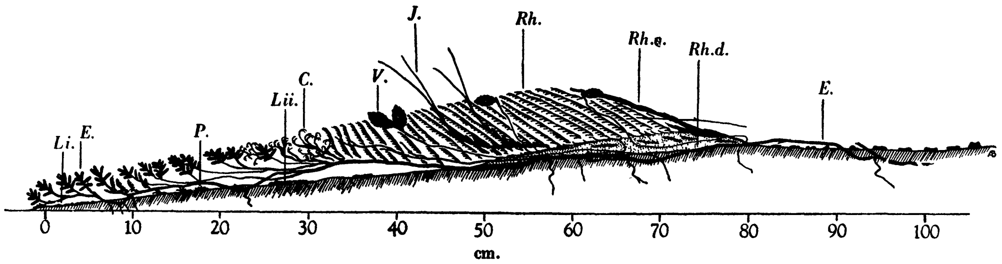

Fig. 3. Profile downwind or across a patch of vegetation in eroded Rhacomitrietum at approx. 3500 ft. on the northern slopes of Cairngorm. The spatial sequence is also a time sequence. *Li.*, *Lii.* and *P.* = bryophytes, *E.* = *Empetrum hermaphroditum*, *C.* = *Cladonia rangiferina*, *V.* = *Vaccinium myrtillus*, *J.* = *Juncus trifidus*, *Rh.* = *Rhacomitrium lanuginosum*, *Rh.e.* = *R. lanuginosum*, eroded face, *Rh.d.* = *R. lanuginosum*, dead.

The community consists of a network of patches of bare soil and of vegetation; each of the latter shows from the lee side to the exposed and eroded western side (Fig. 3) a series of phases characterized respectively by bryophytes, *Empetrum hermaphroditum*, a mixture of *Vaccinium myrtillus*, *V. uliginosum* and *Rhacomitrium lanuginosum*, and finally *Rhacomitrium* itself. Proof of the temporal sequence is found in the vertical layering of peaty remains found under the last phase. The *Rhacomitrium* phase is eroded by the wind, the exposed accumulated humus dispersed and mineral soil once again laid bare. Since the stems of *Empetrum* stretch from end to end of the patch the number of rings enables an estimate to be made of the duration of the whole and of its phases. The rate of advance is approximately 1 m. in 50 years.

Bracken

The relation of *Arctostaphylos* to *Calluna* in the dwarf Callunetum of the less exposed places is deduced from internal evidence and supported by evidence provided by the study of their spatial and temporal relations in the specialized double strips. The Pteridietum (Fig. 4) which has been studied (Watt, 1947) provides a close parallel, for the area in which it occurs consists of a hinterland (comparable with the continuous Callunetum) in which the fronds are patchily distributed and the axes of the bracken plants form a loose network; marginal to the hinterland is a belt of bracken invading grass-heath in which the individual plants lie side by side, with their main axes parallel to each other and their apices in line (cf. the strip of *Calluna*).

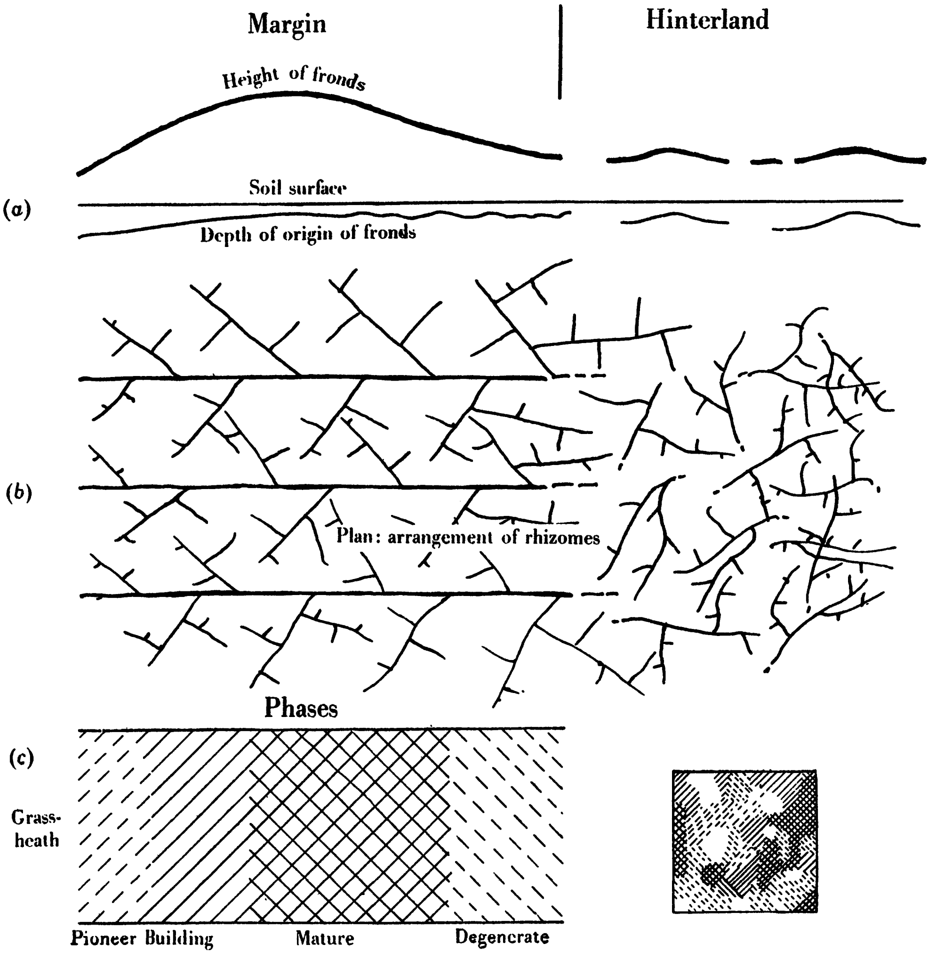

Fig. 4. Diagram to illustrate the spatial and temporal relations between the phases in the marginal belt and in the hinterland of a bracken community on Lakenheath Warren (Breckland). In (*a*) the change in height and in continuity of cover of the fronds are indicated: also the change in depth of origin of the fronds. In (*b*) the relative size and direction of growth of the main axes of the bracken plants are shown. In the marginal belt the axes are parallel, in the hinterland they form a network. In (*c*) the phases in the margin are in linear series: in the hinterland they are irregularly arranged.

Such a marginal belt with unidirectional spread can be divided into a series of zones or phases by lines running parallel with the invading front. These phases can be distinguished by data from the frond and rhizome. The inherent circumstances make it clear that, from back to front, the space sequence of phases represents a sequence in time. Among the overdispersed fronds of the hinterland there are patches without fronds (the grass-heath phase) and patches with fronds which vary among themselves in features of frond and rhizome in much the same way as the sequence in the marginal belt; these are distinguished as the pioneer, building, mature and degenerate phases. These phases, together with the grass-heath phase, form a cycle of change in time at one place. Comparison of the two sets of data (Watt, 1945, 1947)—from the zones of the marginal belt and the patches of the hinterland—shows close agreement between the relations between the values within each set, an agreement all the more striking when allowance is made for the different circumstances. For in the marginal belt the phases are in linear series and bracken invades grass-heath free from bracken; in the hinterland the grass-heath phase is vacated by bracken but seldom completely before reinvasion takes place. There is thus some overlap between the beginning and end phases of the cyclic series.

The evidence for cyclic change derived from the specialized marginal belt is supported by the internal evidence from the hinterland itself. For in the grass-heath phase without fronds there are abundant remains of decaying rhizome, and under the litter in the later phases with bracken are the recognizable remains of *Festuca* and *Agrostis* of the grass-heath phase. Phases with, and a phase without, fronds alternate in time.

The processes involved in the marginal belt and the hinterland are the same. In the marginal belt the natural tendency of the bracken to spread centrifugally is checked by lateral competition; spread is thus directed by ecological opportunity into the grass-heath which is free from bracken. Once established the sequence of phases depends on the development of the bracken itself and development as affected by its own reaction. In the hinterland, where the axes form a loose network, rejuvenation is similarly directed by ecological opportunity and essentially restricted to areas vacated by the death of the bracken. The phases which follow are a biological consequence of established invasion and are limited to the area of that invasion.

Running parallel with the change in the vegetation of the cycle, there is change in the factors of the habitat and in total habitat potential. The variable factors of microclimate and soil, e.g. shelter, light intensity, temperature, the amount of litter, the state of the humus and its distribution in the soil, are differentiae of the phases superposed on the original foundation of a uniform habitat. They are closely linked with the phases because they are the effects of the plants themselves; the effects of one phase become part cause of the next. Thus the spatial variation in the habitat is primarily caused by the variable vegetational cover. Further, taking a broad view, we may note that in the upgrade series there is an accumulation of plant material and an increase in habitat potential; in the downgrade both are dissipated.

The significance of the differential action of the phases on microclimate may be illustrated by the effect of frost during the winter 1939–40. In the grass-heath or pioneer phase rhizome apices were killed at a maximum depth of 20 cm.; in the mature phase, protected by a blanket of litter, the maximum depth of lethal damage was 6 cm. Action of this kind retards development and prolongs the duration of a phase, upsetting the smooth course of the time sequence.

Grassland A (*Breckland*)

The vegetation of Grassland A (Watt, 1940) is obviously patchy. In its hollows and hummocks the habitat presents a striking resemblance to the regeneration complex, and here, too, vegetational variation is linked with variation in microtopography and soil habitat.

In a reinvestigation of the community upon dynamic lines four phases are recognized: the hollow, building, mature, degenerate. There are intermediates, but little difficulty is experienced in assigning all parts of the typical community to one or other of these four phases.

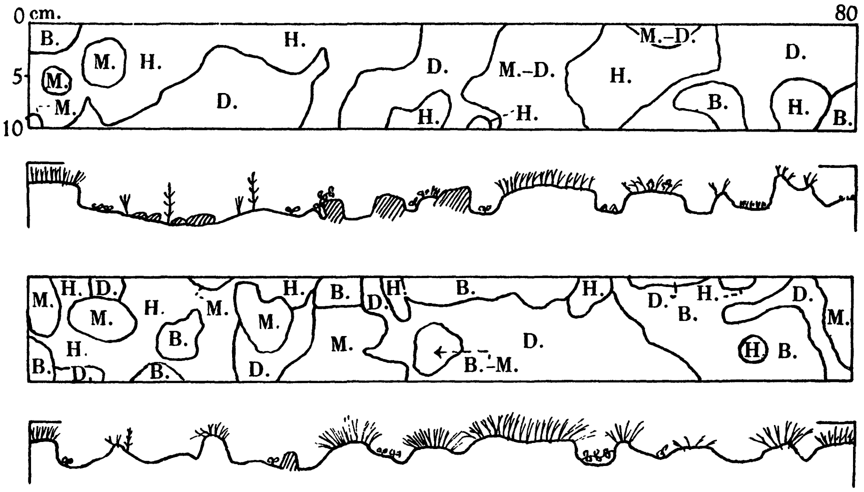

Fig. 5. The relative size and spatial relations of the phases in a plot of 160 × 10 cm. in Grassland A. The relation between the phases and the microtopography is seen in the profile taken along the upper edge of the plot.

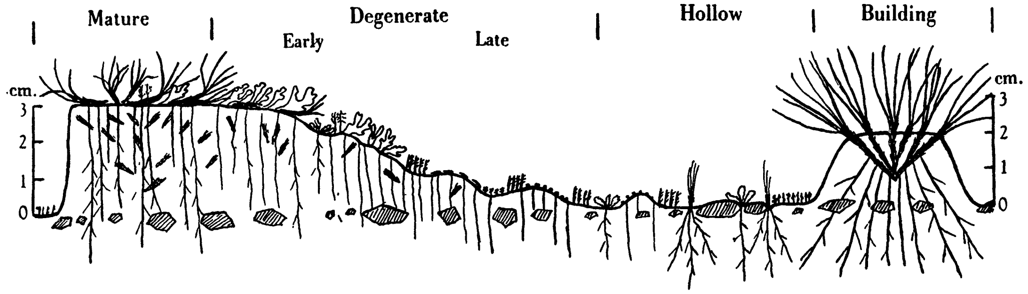

Fig. 6. Diagrammatic representation of the phases showing change in flora and habitat and indicating the 'fossil' shoot bases and detached roots of *Festuca ovina* in the soil.

Their spatial distribution is shown in Fig. 5; the patches are irregular in size and shape and their juxtaposition varies. These four phases form a time sequence, the evidence for which is emphasized in the following reconstruction (Fig. 6). The whole 'life' of the community centres round the reactions and life history of *Festuca ovina*, its growth and reproduction; it has every right to be called the dominant plant even although it occupies less than one-half of the total area (approximately 45%). The seedling becomes established among the stones which floor the hollow phase; as the plant grows and spreads the level of the mineral soil inside the tussock rises. This soil is free from stones and its accumulation is due to the activities of ants and earthworms, very probably also to wind-borne particles and particles water-borne in the splash of heavy rain. The young vigorous fescue with relatively long leaves and many inflorescences on relatively long stalks constitutes the building phase; in it the shoots of the plants are still attached to the parent stock. By further accumulation of soil the hummock increases in height, attaining a maximum of about 4 cm., and then carrying much less vigorous fescue, with shorter leaves and fewer inflorescences with shorter stalks. The original many-branched tussock is replaced by numerous small plants each lying horizontally and consisting of one or two shoots with vertically descending roots; they have arisen from the larger plant by the separation of branches through the death and decay of the parent stock, the evidence for this being the presence throughout the soil profile of the hummock of the bases of lateral branches which are resistant to decay and thus persist.

In the spaces between the individual plants in the mature phase, the fruticose lichens *Cladonia alcicornis* and *C. rangiformis* become established. They spread and ultimately form a mat below which the remains of fescue are found. This is the early degenerate phase. 'Fossil' shoots and unattached roots are found in the soil. In the late degenerate phase, characterized by the crustaceous lichens *Psora decipiens* and *Biatorina coeruleonigricans*, 'fossil' shoots and unattached roots are again found. In places these roots project above the soil surface and bear witness to the erosion (already suggested by the pitted surface) which gradually wears down the hummock. Some vestiges of the hummock survive into the hollow phase, but eventually these disappear and the erosion pavement of flint and chalk stones is once again exposed.

Every part of the surface of the typical community can be assigned to one or other of these four phases. A single set of them is fully representative of the whole and summarizes in itself the processes at work and their manifestations. The understanding of the community as a working mechanism is based on the elucidation of the relations of the phases to each other. They are its minimum representative (minimum area), its very core.

Now the contributions which the phases make to the community as a whole may vary among themselves and also from year to year. To eliminate one source of variability, and at the same time to take account of it as an ecological phenomenon of great importance, I propose to base the description of the community upon areas of equal size in the several phases (and to call the whole the unit pattern) and to make a separate assessment of the relative areas occupied by the phases.

Some of the data for the unit pattern of Grassland A are presented graphically in Fig. 7; the diversity as well as the unifying continuity of the phenomena are clearly shown. The cover percentage of fescue and 'bare soil and stones' are inversely related. The holophytic bryophytes are virtually excluded from the building and mature phases and increase to a maximum in the hollow, where competition from fescue is least. For the lichens, on the other hand, the maximum appropriately lies in the phase where the fungal partners can utilize the organic remains accumulated during previous phases.

The selective effect of the phasic microenvironments on the distribution of seedlings and their subsequent fate is shown in Table 1. The total number of seedlings varies directly with the 'bare soil and stones'. The distribution of the adults suggests failure of the seedlings to reach maturity in the mature and degenerate phases and shows restriction to the building and hollow phase and virtually to the hollow phase because the great bulk of

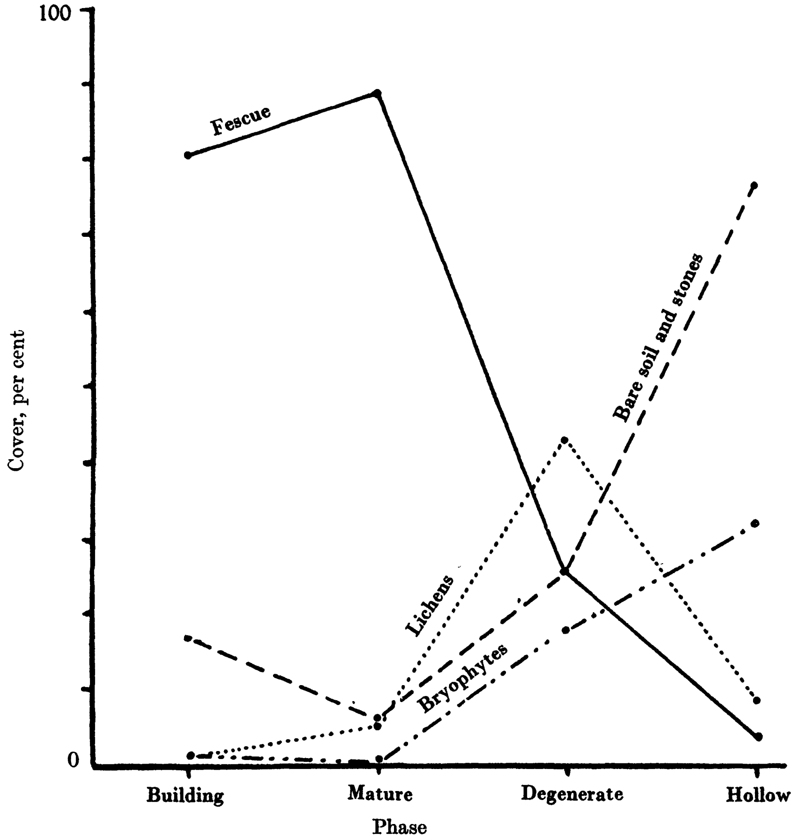

Fig. 7. Graphical presentation of some data for Grassland A. Note that most of the data for the building phase are from late stages.

Table 1. *Grassland A*

Species	Phases			
	Building	Mature	Degenerate	Hollow
	Total no. in 40 plots, each 5 × 5 cm.			
	Seedlings			
Arenaria serpyllifolia	0	0	0	1
Avena pratensis	0	0	0	2
Calamintha acinos	3	3	8	6
Cirsium lanceolatum	0	0	1	0
Crepis virens	24	7	10	21
Erigeron acre	25	17	31	68
Festuca ovina	2	0	10	66
Hieracium pilosella	9	5	6	7
Koeleria gracilis	0	0	1	0
Senecio jacobaea	0	0	0	1
Total	63	32	67	172
	Adults			
Arenaria serpyllifolia	0	0	0	1
Calamintha acinos	0	0	0	3
Cerastium semidecandrum	1	0	0	8
Crepis virens	1	0	0	0
Erigeron acre	3	0	1	3
Galium anglicum	11	0	0	7
Hieracium pilosella	2	0	0	4
Saxifraga tridactylites	1	0	0	0
Total	19	0	1	26

the adults recorded from the building phase are in the immediate surround of the fescue tussock and not in it. This restriction to the hollow phase in all probability holds for the surviving fescue seedlings as well. Thus at any given time the initiation of the cycle of change is restricted in space, and at any given place to the hollow phase in the time sequence.

Estimated by two different methods the relative areas of the phases hollow, building, mature, degenerate are, respectively, 25·7, 15·1, 16·3 and 42·9. As far as I can judge from the annual charting of two plots since 1936, but without actually noting the spatial limits of the phases, Grassland A is remarkably stable both in its unit pattern and the areal extent of its phases.

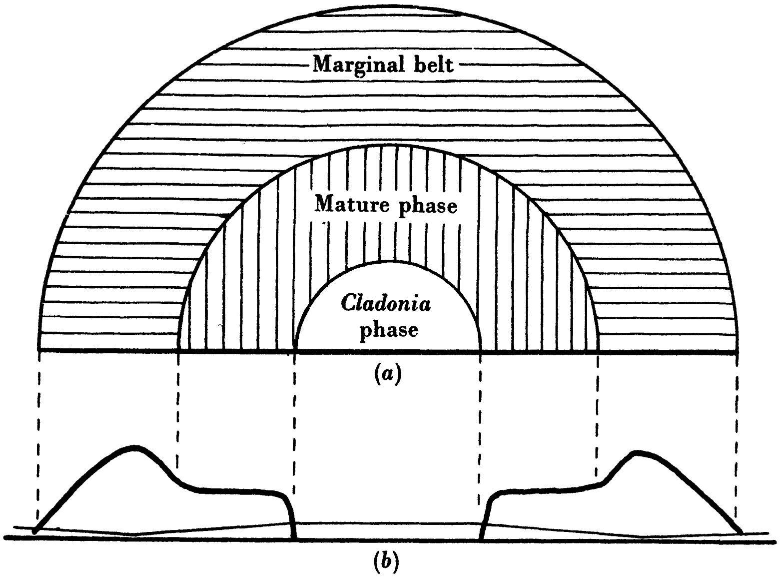

Fig. 8. Diagrammatic representation in plan (*a*) and profile (*b*) of an *Agrostis* ring set in a background of *Cladonia silvatica*. In (*b*) the darker line indicates the change in height (and/or number) of *Agrostis* shoots, the thinner line the change in thickness of the *Cladonia* mat.

Grass-heath on acid sands (*Breckland*)

The grass-heath on acid sands in Breckland has been sufficiently investigated to provide supporting evidence for the dynamic interpretation of the plant community and also to demonstrate the usefulness in description of separating the estimate of the relative areas of the phases from the unit pattern.

Fundamentally the community consists of rings (both solid and hollow) of *Agrostis tenuis* and *A. canina*, and occasional tussocks of *Festuca ovina* set in a background of *Cladonia silvatica*. (Further reference to *Festuca* is omitted because its relations to other species in the community are not fully elucidated.) Each ring is derived by vegetative spread from one plant and epitomizes in itself the spatial and temporal changes within the community. A typical ring (Fig. 8) of medium size consists of a peripheral zone of numerous, vigorous, vegetative and flowering shoots arising from large plants with rhizomes radiating outwards, an inner zone (mature phase) with fewer and shorter vegetative and flowering shoots, or no flowering shoots at all, on smaller plants whose rhizomes form a loose open network (cf. Bracken, p. 6). In the centre of the ring *Agrostis* as a live plant is absent, but its abundant dead remains are found below the mat of dominant *Cladonia silvatica* which is from 3 to 4 cm. thick; to this thickness it has gradually risen from a thickness of 1 cm. only in the middle of the peripheral zone.

Fuller investigation of the dynamic behaviour of the rings justifies the recognition of phases within the marginal belt and in a full cycle additional phases of degeneration and rebuilding following disruption of the lichen mat (Watt, 1938). But to keep the issue simple no more than the three phases need be further considered since they may complete a short cycle; samples from unit areas in each constitute the unit pattern.

The mutual relations between *Agrostis* and *Cladonia* have not been investigated to the degree necessary to decide whether the death of *Agrostis* is due to age, or in some measure to the influence of *Cladonia* or to both acting together. Similar problems arise at this stage of the cycle of change in all the communities examined; the problems are universal because they concern death and its causes. Their solution, although important, is not necessary to establish the fact of replacement.

The extension of the *Cladonia* phase at the expense of the mature phase (inner zone with *Agrostis*) is not, however, merely a question of time; it is primarily due to drought, which differentiates between the *Agrostis* plant of the peripheral zone (which survives) and that of the mature phase (which dies). As the result of a severe drought the mature phase passes wholesale and abruptly to the *Cladonia* phase, and the extent of the change will depend on the area of the phase capable of being affected by it. An area occupied by a large number of small patches of *Agrostis* will be relatively little affected by drought, while one which is almost entirely in the mature phase, through the spread and fusion of rings, will be almost wholly affected by it (Fig. 9). This explains the violent fluctuations met with in the populations of *Agrostis* in this community; in certain areas fluctuations have been so wide that estimates of abundance for one year are of no value as a diagnostic character. They do, however, reflect the vagaries in meteorological factors. On the other hand, data from the unit pattern would be much less affected.

Beechwood

The effect on the structure of a community of drought or other efficient cause may persist long after the cause has ceased to operate. In fact, at any given time, there may be no correspondence between structure and the current meteorological factors. The point is best illustrated by reference to communities with long-lived dominants. But first a brief note on phasic change in beechwoods.

The patchiness in some all-aged beechwoods on the Chilterns, reputedly managed on a selection system, is interpretable in terms of the temporal sequence of phases as revealed by the study of the life history of pure even-aged beechwoods of the same ecological type on the South Downs (Fig. 10) (Watt, 1925). To the three phases recognized—Bare, *Oxalis*, *Rubus*—there should be added a fourth, the gap phase, to which regeneration is confined because it is excluded from other phases. At any given place there is a cycle of change consisting of an upgrade series of phases in which there is a continual change in ecological structure, associated with changing age, rate of growth and density of the dominant trees and correlated with changes in the field layer, and a downgrade of the dying, dead and rotting stems and the vegetation of the gap.

For the time-productivity curve for the upgrade series we have the foresters' yield tables for managed woods. Although the data take no account of the yield from the subsidiary vegetation, we may assume this to be small in relation to the yield of the trees and without appreciable effect on the course of the curve. This is of the familiar growth type, rising slowly at first, then fast, then slowly again.

The phasic phenomena of woodland are on a scale to be immediately obvious. Again because of the scale, but also because we have the data, woodlands afford an excellent illustration of the cyclic relation between tree species and of causes having long-continued effects in structure. Both points have been dealt with recently by Jones (1945); brief reference is all that is necessary here.

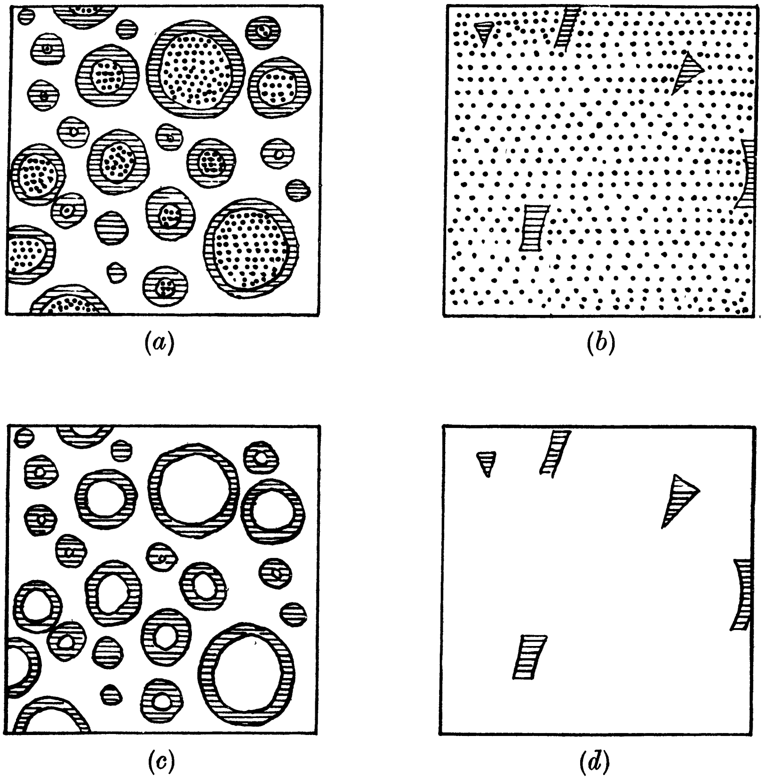

Fig. 9. Diagram to show the effect of drought on *Agrostis* in two areas of Festuco-Agrostidetum at different stages of development. In (*a*) there are many small (young) patches of *Agrostis*; in (*b*) the patches have grown and fused so that the bulk of the area is in the mature phase. In (*c*) and (*d*) drought has killed the *Agrostis* in the mature phase only of (*a*) and (*b*).

Viewed against the ideal of sustained yield, aimed at most simply among foresters by allocating equal areas to each age class or group of age classes, the primeval wood by all accounts more often than not shows an unequal distribution of the areas occupied by its age classes. Aside from minor fluctuations over periods of time in, say, the number of deaths among old trees, there are exceptional factors of rare or sporadic occurrence, such as storms, fire, drought, epidemics, which create a gap phase of exceptional dimensions. If the whole gap phase is regenerated about the same time—and various circumstances, both inherent and external, like periodicity in seed years and suitable meteorological factors for seedling survival may help in that direction—then there is initiated an age class of abnormal area. This will persist like a tidal wave moving along the age classes until at least the death of the trees; it may even influence the structure of the next generation. In other words, the relative areas under the age classes (as a super refinement of phasic subdivision) need bear no relation to current meteorological factors but be explicable in terms of some past event which happened, it may be, 200 or 300 years ago.

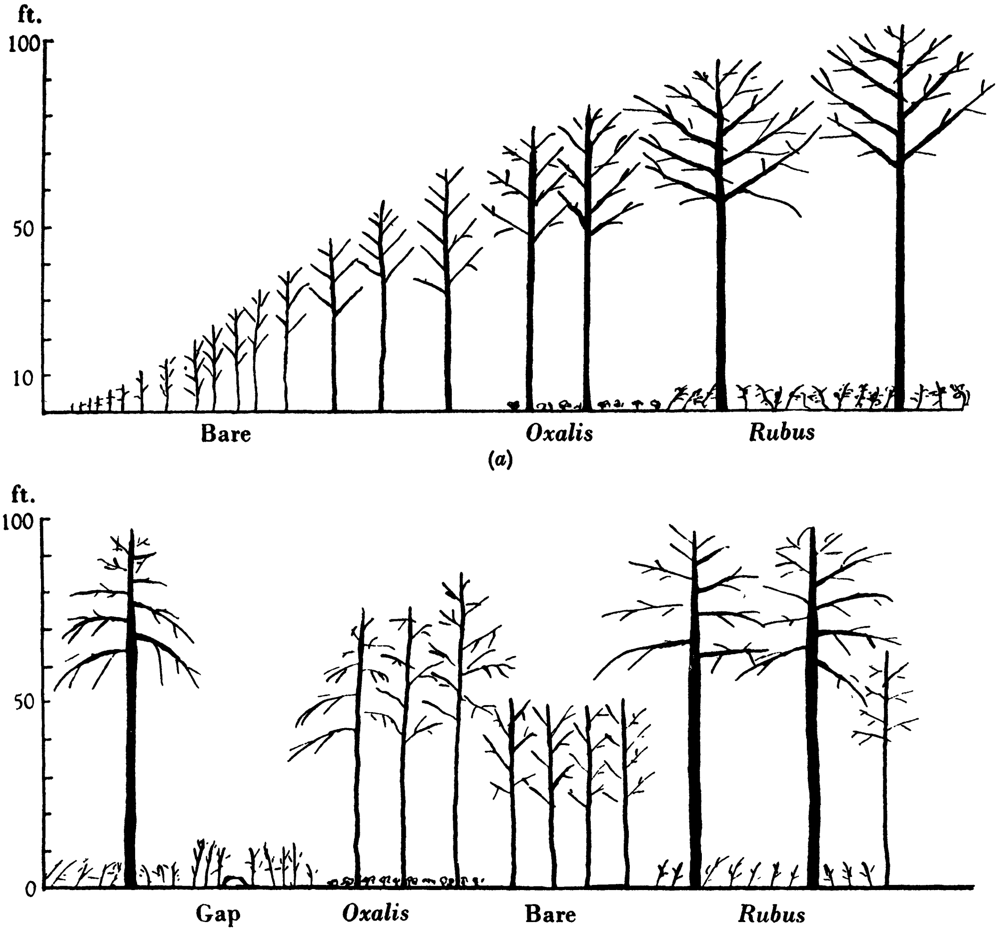

Fig. 10. Diagram to illustrate (*a*) the phasic change during the life history of an even-aged pure beechwood and (*b*) the distribution in space of the phases when the old wood is left to itself.

A series of sporadic exceptional events will obviously increase the difficulties of 'explaining' current relative areas, as also will the selective destruction of phases their juxtaposition in space. Fortuitous fluctuations of climate and other causes may thus bring about major departures from the normal or ideal wood.

The second point refers to the normal inclusion in the cycle of change of a phase dominated by another species of tree, in different kinds of beechwoods, for example, by ash, oak or birch. Such a phase (e.g. birch) may occupy small or large areas, but irrespective of the area it occupies, if the relation is cyclic and not seral (that is, one of alternating equilibrium in which successful regeneration of the beech is inhibited by itself but promoted by the conditions brought about by the other species of tree), then such a phase is part and parcel of the system. To recognize the birchwood and beechwood as separate entities may be convenient in classification, but successful practical management of such woods depends on their recognition as integral parts of a coordinated whole.

SUPPLEMENTARY EVIDENCE

Doubtless because of its universality, its familiarity and its apparent lack of significance the fact of the impermanence of the individual or group of individuals has seldom evoked comment. Butcher (1933) has, however, called attention to the changing pattern of river vegetation over a short period and suggests progressive impoverishment of the soil of the river bed as the cause of the disappearance of *Sium erectum* from a given place in it. Tutin (1938) has attributed the marked reduction in area occupied by *Zostera marina* primarily to deficiency in light intensity; this predisposed the plants to disease, which is a symptom of weakness rather than a cause of its virtual disappearance. Without contesting the accuracy of the immediate diagnosis, I would suggest that both phenomena may be more fully and satisfactorily explained against the background of cyclic change.

Phenomena similar to those described have been seen but not investigated in communities dominated respectively by *Polytrichum piliferum* (in Breckland), *Ammophila arenaria* and *Carex rigida-Rhacomitrium lanuginosum* of mountain tops. Poole (1937), from a study of mixed temperate rain forest in New Zealand, concludes that *Dacrydium cupressinum* on the one hand, and *Quintinia acutifolia* and *Weinmannia racemosa* on the other, alternate in time at one place.

The phenomena are not confined to temperate regions. In the high arctic the few species are represented by scattered individuals, and communities are distinguished by the quantitative relations of their chief components and/or by habitat factors (Griggs, 1934). Where there are few individuals competition is negligible or absent; factors of soil and climate are the primary selective agents. Griggs says there is not only change from place to place, but change in time at a given place (he refers to unpublished data from permanent quadrats as the basis for this latter statement). This distribution in place and in time, is, according to Griggs, erratic, but no details are given.

At the first remove in the low arctic a two-stage succession from open initial communities to the closed association of heath and bog shows the emergence of the organic environment into importance. Competition now is a factor limiting the distribution of species.

At the other extreme is tropical forest, the most complex of plant communities in which the biotic environment plays an outstanding part. It is not to be expected that such a complex community will be amenable to a simple dynamic interpretation. Yet presumptive evidence is given by Aubréville (1938) who has expressed views on the structure of the forest closely akin to those advocated here for a selection of communities. He finds that although there are in tropical forests very many species of tree the dominant or most abundant species are relatively few in number (about a score) their relative proportions varying from place to place, some dominating in one place, some in another.

But also at a given place there is a change in the dominant species with time, for, in the subsidiary layers the young trees (the dominants of the future) are often specifically different from the dominants of the uppermost layer. Aubréville, however, does not mention a regular cycle of change at a given place; in fact, as far as can be judged from his account the assemblage of species in a newly formed gap depends on the fortuitous occurrence of a number of factors, including distance of parents, mobility and abundance of seed, frequency of seed production, dispersal agents and their habits, and various factors like animals eating the seed, duration of life of the seed, light intensity, root competition and the kind of undergrowth, affecting the survival of the seed and the establishment of the seedling. Although the earlier stages of gap colonization may show diversity in floristic composition the later ones, according to Dr P. W. Richards (oral communication), are much more uniform.

If we assume with Aubréville that the general climatic and soil conditions are uniform over a large area then the differentiating biological characters of the many species assume primary importance, and variation in floristic composition from place to place is the resultant of the impact of these biological characters and environmental factors, largely, but not exclusively, residing in the plant community itself; that is, the community itself largely determines the distribution, density and gregariousness of its component parts.

COMPARISON AND SYNTHESIS

The analysis of the seven communities, documented by observations over a period of time, by comparative studies and by appeal to the registration of the time change either in the plants themselves or in their subfossil remains, shows that there is an orderly sequence of phases in time at a given place and that the spatial relation between the phases can be interpreted in terms of their temporal relations. I now propose to correlate the observed phenomena and to offer a simple generalization and explanation.

The cycle of change in all the communities is divisible into two parts, an upgrade and a downgrade. The upgrade series is essentially a process or set of processes resulting in a building up of plant material and of habitat potential and the downgrade a dispersion of these mainly by fungi, bacteria, insects, etc., but also by inorganic agents. At each stage, of course, there is both a building up and a breaking down, but in the upgrade series the balance is positive, in the downgrade negative.

When bracken was being investigated the field phenomena evoked the spontaneous application of the names for the phases, pioneer, building, mature, degenerate. They undoubtedly conveyed impressions which later study hardened, for they are obviously applicable to several of the communities. The quantitative graphical expression of the change for the upgrade series for woodland and the qualitative description for other communities lead me to suggest that a curve of the growth or logistic type expresses the general course of change in total production in the upgrade series of each of the communities (Fig. 11 and appended correlation table). This is doubtless an oversimplification of the whole concrete situation. But there are data enough to show that we are dealing with something fundamental, with in fact, some biological law which operates in the plant community.

For the downgrade series a curve of similar form is tentatively suggested. There are many partial assessments of the course of the changes, but none to my knowledge dealing with the whole series in a comprehensive way.

The basis of these regular phenomena of change may be sought in the behaviour of populations and in the sequence of a plant succession on the restricted area of a patch. The community as we have seen consists of patches, each of limited area, and differentiated by floristic composition, age of dominant species and by habitat.

Patchiness can be readily enough detected in all the communities investigated and in the others referred to. In forest, the community about whose structural types more is known than about any other kind of community, patchiness is widespread. There is a form of 'irregular forest' that would appear to be an exception, although it is not known how far it is local or temporary, and until it has been examined by the use of criteria in addition to the distribution of crown classes, judgement must be suspended. A comparable structure may be found in other communities and at the moment no claim can be made that patchiness, as understood here, is universal. It certainly is widespread.

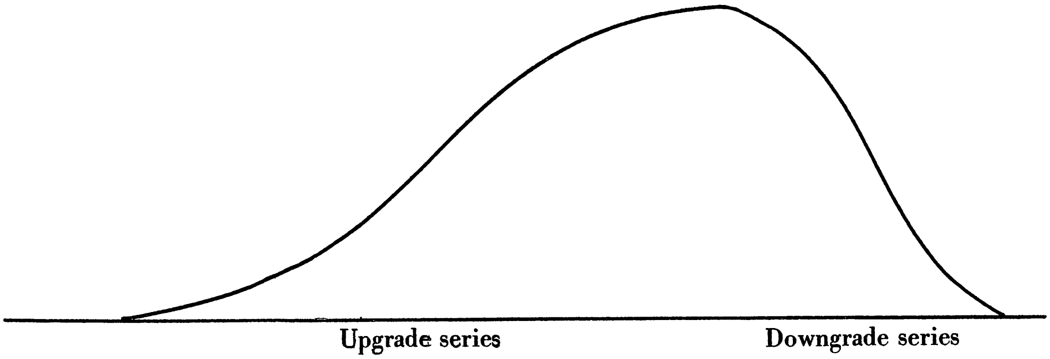

Fig. 11. The graphs illustrate in a general way the assumed course of change in the total productivity of the sequence of phases in the upgrade and downgrade portions of the cycle of change. The appended table correlates the phase sequences of the different communities.

Plant community				Phase	Hummock with:		
Regeneration complex	Pool	*Sphagnum cuspidatum*	*Sphagnum pulchrum*	*Sphagnum papillosum*	*Erica* *Scirpus*	*Calluna* *Cladonia*	Degenerate
Dwarf Callunetum	Bare soil	*Arctostaphylos*		*Calluna*	*Calluna*		*Cladonia*
Eroded Rhacomitrietum	Bare soil	Bryophytes *Empetrum*		*Rhacomitrium-Vaccinium*	*Rhacomitrium*		Eroding face
Pteridietum		Grass-heath	Pioneer	Building	Mature		Degenerate
Grassland A		Hollow		Building	Mature		Degenerate
Acid grass-heath		*Cladonia*	Pioneer	Building	Mature		*Cladonia*
Beechwood (sere 2)		Gap (late)	Bare stage	*Oxalis* stage	*Rubus* stage		Gap (early)

The widespread occurrence of patchiness is of interest in itself, but the persistence of the patch in time under continuing normal conditions is fundamental. Why, for example, starting with a set of patches, do we not get a general blending of the whole with the vegetation of every square foot a replica of every other?

May I first remind you that we are assuming uniformity in the fundamental soil and climatic factors of the community. Over and above this foundation we get, as we have seen, modifications of the soil and climate which are closely linked with the phases; these floating differentiae are in the first instance reactions of the phases and in the second, causes. We have, in fact, habitat variation in space as in time. (Also it should be noted that the habitat factors inherent in a phase modify and are themselves modified by the habitats of surrounding phases.) Seeds and propagules falling on a plant community therefore fall on a diversified environment (varying habitat and competitive power in the phases), and establishment is restricted to the phase where the plants survive; for many species this phase is the gap phase, or phase corresponding to it, formed by the death of the dominant in the mature phase or end-phase of the upgrade series. For plants spreading by rhizome the same holds good; in bracken, effective invasion is limited to the grass-heath phase, although it may begin in the mature phase and continue into the pioneer phase.

But not only is establishment of many species thus restricted in space, it is also restricted in time, to the period during which the gap phase is receptive. Checks to further colonization may be made by the invaders themselves, thus setting a time limit to the period within which establishment takes place. In this way, there is a tendency towards the production of even-aged or near-aged populations.. Besides this restricted period during which colonization may take place, there are many other factors which tend to produce even-aged populations, some of which have already been alluded to and will not be further discussed.

Mainly because of competition, the plants established in the gap or corresponding phase are unable to invade and suppress surrounding phases. Thus prevented from spreading laterally, the patch becomes a microcosm of limited area with continuous but restricted food supply. Hence the population of that area behaves like a population of flies or human beings under similar restrictions of space and food. It is unable to spread, but it may develop.

This development in the upgrade series may take one of two forms, either as an even-aged population of a dominant species or as a series of dominants as in a plant succession. In the former the successive phases are distinguished by the species accompanying the dominant but primarily by the age and density of the dominant itself. The justification of the recognition of age in individuals or shoots as a basis for subdivision lies in the changing needs of the individual with age, its changing form (height, spread, root distribution, area of absorptive and anchoring surface, etc.) and its changing competitive power. The need for such recognition is obvious in a plant, whose gametophyte and sporophyte are separate and have different requirements, or in an insect with complete metamorphosis, in which the structure and habits of the larva differ so widely from those of the adult; but it holds also for higher plants because their requirements change during their life history.

The second type of change is found in communities where the successive phases (or some of them) have distinct dominants, that is, the phenomena are strictly comparable with those in a sere, where new dominants come in when the environment becomes suitable for them.

Now in both these, the even-aged population and the plant succession, the course of temporal change in total production per unit area is represented by a curve of the growth type (Pearl, 1926; Braun-Blanquet & Jenny, 1926). The reason for the general equation of corresponding phases now becomes obvious. In both, the phenomena of orderly change have their basis in the universal rhythmic phenomena of population development and of plant succession. It would thus appear that certain phenomena of the plant community can be brought within the scope of mathematical inquiry. This opens up an entirely new field in the study of natural communities with the possibility of putting the practical management of communities, as the forester has done the forest, upon a sound basis of natural law.

The description of the plant community is based on the unit pattern, which is the present expression of the continuous process of development and decline in a population broadly interpreted. The qualitative and quantitative assessment, therefore, of the plant community may be expressed in terms of the temporal changes in such a population.

Now it has been shown mathematically and confirmed experimentally that certain species with different ecological requirements live together and maintain stability only in a definite proportion (Gause, 1935). In like manner we may assume (although independent confirmation is necessary) that the plant community in a constant environment will show a steady state or a definite proportion between the constituent phases. This steady state we may call the phasic equilibrium, that is, the community is in harmony with itself and with its environment. Departures from this phasic equilibrium either in space or in time could then be measured and correlated with the changed factors of the environment.

The difficulties confronting this procedure are obvious. There are doubtless some communities (e.g. Grassland A) of which it would be possible to say with some assurance that they are in phasic equilibrium. But there are others like grass-heath on acid soil, and woodland, where, on account of the lag in response or repeated and fortuitous checks to normal orderliness, or the long delay between the incidence of the disturbing factor and return to a possible normal, anything like phasic equilibrium may rarely be achieved even although the tendency is always in that direction. In such circumstances we may copy the forester whose normal forest may be defined in terms of areas as one in which equal areas are occupied by a regular gradation of age classes. If we think in terms of natural groupings (phases) of unequal duration, then the areas would be proportional to the duration of the phases, the total equalling the duration of the cycle of change. The standard of comparison or normal would then be based on the unit pattern and duration of the phases. With such a standard, departures from it could then be assessed and comparisons made, but attempts to correlate such deviations with changes in the causal environmental factors would be confronted with great if not insurmountable difficulties. But once again there is brought into prominence the need for data on the duration of life of the plant in a variety of habitats and as affected by competition.

Relative areas of the phases is only one aspect of the general problem of the texture of the pattern or of the way in which the community is put together. The other two aspects are the size of the individual sample of the phase and the arrangement of the phases. Both these are important because the conditions of establishment and growth of plants vary with the size of the sample of the phase and with its surroundings.

SOME IMPLICATIONS

Animals and micro-organisms

I have thus far alluded almost solely to the higher plants and described the communities in terms of them, but it should be clear from the insistence on process that organisms other than higher plants play an important and sometimes a fundamental role, and that in the system of which the plant community is a part they ought to be investigated. On reading *Bioecology* (Clements & Shelford, 1939) I confess to a feeling of disappointment, because the data given to support the concept of the biome fall short of demonstrating that intimacy and integration between plants and animals which we are led to expect. Perhaps this is due to the lack of data for the communities described. The degree of intimacy varies, but all organisms whether loosely attached or occupying key positions in the system should be considered part of it.

Tragardh (1923) has given a good illustration of the interactions between plants and insects in pinewoods in northern Sweden where the nun moth is a normal inhabitant, which never becomes epidemic as it does in pure pine or spruce woods in central Europe. This he attributes to the presence in the open pinewoods of *Calluna*, *Cynoglossum*, etc., which are the food plants of species of caterpillars which provide a constant supply of hosts for the polyphagous parasitic species of *Pimpla* which also attack the nun moth and so keep it in check. In the dense conifer forest of central Europe from which *Calluna* is excluded the population of *Pimpla* rises and falls with that of the nun moth but with a distinct lag; it also dies out with the extermination of its food supply. The reappearance of the nun moth is followed by rapid multiplication, and much damage is done before *Pimpla* arrives and increases in numbers to be an effective check to it. In the Swedish forest, on the other hand, a continuity of the population of the parasite is assured here because of the presence of alternative hosts feeding on *Calluna*, etc. Here we have interrelations between components of the tree layer and the field layer and the insects peculiar to each forming a complex web which makes for stability. This stability may be assured only so long as the food supply of the alternative hosts is present in sufficient amount. Further excellent examples of the intimacy and complexity of the relations between insects and plants are given by Beeson (1941).

This address would be too long if adequate reference were made to the variety of relationship between organisms associative, co-operative, antagonistic, symbiotic, etc.—and to the change in the nature of the food supply during the period covering the death of the plants in the mature phase and the complete disintegration of the accumulated organic matter. But that the change is regular is shown by the work of Blackman & Stage (1924) on the sequence of insects on living, dying, dead and decaying walnuts, of Graham (1925) on the earlier stages in the rotting of a log, of Saveley (1939) for insects and other invertebrates on dead pine and oak logs, and of Mohr (1943) on the changes in the species population during ageing and disintegration of cow droppings.

Comparable sequences are known among fungi. Parasites, facultative parasites and saprophytes succeed each other on dying and dead stems, and Garrett (1944) writes of the succession of micro-organisms on dead and decomposing roots. Generally on organic remains the sugar fungi develop first and are succeeded later by the cellulose fungi.

The part these organisms play is essential to the maintenance of the community; no assessment of the communal life can be complete without adequate appreciation of what is taking place.

The suggestion may be made that the life histories and food habits of micro-organisms in general, and insects and fungi, in particular those with complicated life histories, may be more profitably studied against the background of phasic change and that the parallelism between the change of food and habitat requirements during the life history of an organism (e.g. some insects with soil larvae) and the spatial change in the condition and floristic composition, or in age of dominant, of juxtaposed phases may be more than fanciful speculation about origins and survival.

The nature of the plant community

Tansley (1935) has coined the term ecosystem for the basic units in nature—units in which plants, animals and habitat factors of soil and climate interact in one system. The term is primarily used in reference to the larger geographical units. The words steppe, prairie, moor, bog apply to such systems and not to the plants alone. But the use of the term ecosystem is elastic; it may be applied to the smaller units like the 'plant community'.

The first step in the shattering of this unified system is the separation of the living plants and animals (the biome) from the non-living habitat, the components of the latter being regarded as factors affecting the former. The next step, which Tansley justifies partly on the ground of practical convenience, is to associate the animals with climate and soil as factors affecting plants. Further subdivision refers to the plants alone. According to Lippmaa (1933) the plant community is composed of synusiae or strata which he regards as the fundamental units of vegetation. The final step is Gleason's; to him the plant association is 'merely a fortuitous juxtaposition of plant individuals' (1936*b*).

In support of his view Gleason cites the randomicity of the component species of the association. This is by no means universal (Clapham, 1936; Blackman, 1935). The restriction of establishment in space and in time to certain phases in a diversified pattern tends towards the grouping of age classes (that is, there is overdispersed distribution in time), even although the species as a whole may be at random. Further, two species characteristic of a phase may be randomly distributed but show a high degree of association between them.

This assumed randomicity also enables Gleason to cut the community into small pieces, each of which he regards as representative of the whole. Such a proceeding ignores the significance of the diversity manifested in pattern; this pattern sets a lower limit to the representative minimum.

It is, however, important to realize that Gleason uses the word individual in the sense of an ecosystem of which the plant is the centre, that is, in which the plant and its environment form one interacting system. The individual plant (in the ordinary sense) is a part product of its environment and itself modifies the environment. Position therefore must be important.

Gleason himself cogently argues that by splitting an association into its synusiae, Lippmaa is separating synusiae which are 'united by relatively strong genetic and dynamic bonds' (1936*a*). The same argument is valid if it can be shown that in lateral spacing as well as in vertical there is dependence of one part on another, as is held to be shown by the evidence adduced here. His skeleton picture of a two-layered community consisting of a tree and a herb below it is divorced from its spatial moulding context and set in a moment in time. In time, both will change and their successors be influenced by their collective surroundings. In short Gleason has minimized the significance of the relations between the components of the community in horizontal space and in time. These relations constitute a primary bond in the maintenance of the integrity of the plant community; they give to it the unity of a co-ordinated system.

This co-ordinated unit may be studied as a plant community, the central object of study of plant sociology; round this unit knowledge is accumulated for use and classification. The functional relations of the community may be systematized in laws and hypotheses.

To draw a dividing line between the approach to the study of natural units through the plant community and through the ecosystem is difficult, if not impossible. But clearly it is one thing to study the plant community and assess the effect of factors which obviously and directly influence it, and another to study the interrelations of all the components of the ecosystem with an equal equipment in all branches of knowledge concerned. With a limited objective, whether it be climate, soil, animals or plants which are elevated into the central prejudiced position, much of interest and importance to the subordinate studies and perhaps even to the central study itself is set aside. To have the ultimate even if idealistic objective of fusing the shattered fragments into the original unity is of great scientific and practical importance; practical because so many problems in nature are problems of the ecosystem rather than of soil, animals or plants, and scientific because it is our primary business to understand.

What I want to say is what T. S. Eliot said of Shakespeare's work: we must know all of it in order to know any of it.

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