THE MAINTENANCE OF SPECIES-RICHNESS IN PLANT COMMUNITIES: THE IMPORTANCE OF THE REGENERATION NICHE

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CONTENTS

I. Introduction .................................................. 107
II. Mechanisms not involving the process of regeneration ........ 108
   (a) Variation in life-form .................................. 108
   (b) Phenological spread .................................... 111
   (c) Fluctuations in the environment ....................... 111
   (d) Balanced mixtures ...................................... 113
   (e) Variation in competitive ability with physiological age . 114
III. Introduction to the involvement of regeneration .......... 116
IV. Definition of a plant's niche ................................ 119
V. Patterns of regeneration in different plant communities .... 119
VI. Examples of differentiation in the regeneration niche .... 121
   (a) Production of viable seed ............................ 121
   (b) Dispersal .............................................. 125
   (c) Germination ........................................... 126
   (d) Establishment of seedlings ............................ 128
   (e) Further development of the immature plant .......... 130
VII. Discussion .................................................. 131
VIII. Summary .................................................... 134
IX. References ................................................... 136

I. INTRODUCTION

According to 'Gause's hypothesis' a corollary of the process of evolution by natural selection is that in a community at equilibrium every species must occupy a different niche. This idea is generally accepted by zoologists (Krebs, 1972), but most botanists find difficulty in understanding how all the species in a species-rich plant community can possibly occupy different niches. Although many different factors are involved in the full definition of an animal's niche, one can fairly readily imagine sufficient niches for all the animal species known, using food-requirements alone; the million or so animal species can easily be 'explained' in terms of the 300000 species of plants (so many of which have markedly different parts such as leaves, bark, wood, roots, etc.) and the existence of three to four tiers of carnivores (Hutchinson, 1959). There is no comparable 'explanation' for autotrophic plants; they all need light, carbon dioxide, water and the same mineral nutrients.

Many ideas have been put forward to explain the indefinite co-existence of numerous species in particular communities, but it is the author's contention that most of these go
only a very little way toward explaining the persistence of numerous species in the more species-rich communities. One reason for the lack of understanding on the part of most botanists results from their failure to take into account the phenomenon of regeneration in plant communities, which was first discussed in general terms by A. S. Watt in 1947. Most communities that are not successional are longer-lived than their constituent individual plants. When any one plant individual dies, a gap is created and a new individual ultimately takes its place. It may or may not be of the same species and this is the crucial point. Heterogeneity of the environment (physico-chemical and biotic) does in fact ensure that the replacement plant (or plants) is sometimes of the same species as died and sometimes not. It is suggested in this review that this replacement stage is of great importance not only for understanding species-richness as such but also for understanding the basic processes of evolutionary divergence in plants and for the management of plant communities in conservation.

In order to view the problem as a whole, ideas not involving regeneration are considered briefly in the first part of the review (Section II), and ideas that do involve regeneration are covered in more detail in the second part (Sections III–VII). The nomenclature follows that used in the papers quoted except where otherwise indicated.

II. MECHANISMS NOT INVOLVING THE PROCESS OF REGENERATION

(a) Variation in life-form

It is useful to consider initially the various dominance-structures found in plant communities. The findings of many ecologists on the structures of natural communities are reflected in the dominance–diversity ideas of Whittaker (1965), who concluded that plant communities could be represented by a spectrum of curves relating the importance values of species and the number of species (Fig. 1). In the communities poorest in species, represented by type (a) curves, one species has a much greater productivity (or cover-abundance or standing crop) than any others and there is a short series of successively less productive species. At the other extreme (type (c) curves) there is no clear single dominant, but a group of most productive species followed by a larger group of moderately productive species and a final group of rare species contributing little to the productivity of the community. Many communities are intermediate in nature (type (b) curves).

The co-existence of species in type (a) communities can largely be explained in terms of complementarity of life-form. Very few, if any, dominant species are able to utilize the resources of an area totally or block off with complete success those they do not use themselves. Thus it is very likely that epiphytes (often cryptogamic) will be found on the mature dominant. Almost always one or a few species of shade-tolerant herbs or subshrubs can co-exist – their shoots receiving just enough light for persistence if not for flowering and their roots enough mineral nutrients and water. A tolerant species of climber may similarly co-exist with the dominant. The different productivities of the species in such systems are determined more by inherent differences in potential than by simple competition from the dominant. If the latter is
Maintenance of species-richness in plant communities

Fig. 1. The three major types of dominance-diversity curves presented by Whittaker (1965): (a) species-poor communities, (b, c) species-rich.

Fig. 2. A section of a model of a species-poor community with only one species in each major life-form; the resources are represented by a space of finite volume and the requirements of the three species by incompressible spheres. The larger spheres are seen to be unable to exclude the smaller ones. The arrangement of the spheres would be different if their sizes were kept constant and the space representing the resources were made bigger or smaller, e.g. if it were made the size of one of the four unit-spaces drawn in the figure.
removed, and no species is artificially introduced, none of the remaining species may be able to take over the role of dominant either in terms of standing crop or in dominating the others in a more general sense. The long-term co-existence of several species in these simple communities can largely be ‘explained’ in terms of a model in which they fit in the gaps between each other. Thus, if the available resources are represented by a cube of finite size and the plants by incompressible spheres, the size of which is proportional to the resources utilized or blocked off, then the larger spheres are not able to occupy all the space that encloses them (Fig. 2). Such a model represents only part of the truth because the plants in such a system do not grow independently and the spheres ought to be conceived of as capable of denting each other to some extent, just as the circles can overlap in the model of Putwain & Harper (1970). Thus the trees in forest systems of this type reduce the yield of the few species of herb beneath them (Watt & Fraser, 1933; Karpov, 1961) while the yield of the trees may be reduced by the herbs – after all, the grass sward in an orchard can reduce the fruit crop above it (Bedford & Pickering, 1919).

The model represented in Fig. 2 is also inadequate in that it fails to include the dependence-relationship which, together with competition and complementarity, characterizes the integrated plant community. Dependence is most clearly demonstrated by the epiphytes already mentioned, by the parasites and hemi-parasites and by
Maintenance of species-richness in plant communities

The epi-parasites ('saprophytes') often found growing in very dense shade where few autotrophic plants can persist. The dependence-relationship can be incorporated, as in Fig. 3, by conceiving the requirements of the host species as represented by large spheres with hollows of different shapes and sizes on their outsides and by representing the dependent species as cylinders or cones that fit these hollows exactly.

(b) Phenological spread

The second major way in which species are complementary to each other is in their seasonal development. A useful simple example comes from the persistence of certain weeds in crops. Quite often the crop, during its own active period of growth, very strongly suppresses a particular species of weed, as in the case of barley and white persicaria (Aspinall & Milthorpe, 1959; Aspinall, 1960), but the weed is not eliminated from the field because it combines an ability to persist in a suppressed state with an ability to develop rapidly to the stage of ripe seed production before harvest, starting as soon as the crop begins to divert its photosynthate into production of its own seed rather than into vegetative organs directly active in competition. At this time the crop may actually leak out nutrients of value to the weed, as potassium escapes from the grass Phalaris tuberosa (Richardson, Trumble & Shapter, 1932). Opportunism, coupled with persistence while suppressed, may be especially important for species at the bottom of the rank order in a particular natural community. Differences in seasonal development or phenology are one of the main findings of those who have developed the analytical approach with natural communities. The vernal flora of north temperate deciduous woodland is most often quoted but equally impressive are the successive flushes of activity in steppe (Walter, 1968) or semi-desert (Bykov, 1974) and the non-coincidence of flushing in trees of tropical rain-forest (Medway, 1972; Frankie, Baker & Opler, 1974).

(c) Fluctuations in the environment

In most, if not all, plant communities the processes by which certain species tend to oust others as a result of competition in the vegetative stage are greatly hindered by temporal fluctuations in the environment. The effects of short-term changes in the environment on species-balance can be very considerable. If a mature plant community is 'in equilibrium', then the equilibrium is highly dynamic. Thus, in certain semi-natural meadows in the U.S.S.R. the grasses Agropyron repens and Bromus inermis are particularly prominent in dry years while Alopecurus pratensis tends to dominate in wet years (Rabotnov, 1974). In the same general area temporary blockage of drainage, which can occur naturally, leads to an increase in Ranunculus repens and release of the blockage returns the balance in favour of Alopecurus pratensis (Rabotnov, 1974). Fluctuation in temperature is probably equally important, especially where species with a northern distribution and greater resistance to winter-killing are mixed naturally with those of southern distribution and lesser hardiness, e.g. Elymus canadensis and Sorghastrum (Andropogon) nutans in some North American prairies (Clements, Weaver & Hanson, 1929). Fluctuations with a period of 2–3 years grade into those
last lasting a decade, e.g. the long drought of the 1930s in the prairies of the U.S.A. and the wetter than average 1950s (Coupland, 1974). Since individuals of some grasses and plants of the woodland floor possibly persist for a thousand years or more (Harberd, 1961; Oinonen, 1967a, b), climatic fluctuations on the scale of centuries may be important in determining an inconstant balance between the vegetative plants of some species.

The biotic environment also fluctuates. Chilvers & Brittain (1972) have tried to explain co-existence of similar plant species in terms of a negative feed-back involving fluctuations in the numbers of host-specific parasites or herbivores. However, fluctuations in the severity of pests determined by climatic influences or by predators rather than by the abundance of the host will also play a role. So also will fluctuations in pests that are not host-specific but still selective, e.g. leatherjackets (Tipula spp.) eating roots of clover more than those of grass in a ley (White & French, 1968). Several observations suggest indirectly that pests may be important in limiting the abundance of plant species under natural conditions, e.g. the better growth of certain Eucalyptus spp. outside Australia but in climates very similar to those of their natural range (Gillett, 1962; Harper, 1969). The effectiveness of specific insects brought in to control particular weeds introduced by man is also impressive, e.g. in the control of St John’s Wort (Hypericum perforatum) by the beetle Chrysolina quadrigemina in California (Huffaker & Kennet, 1959). At one typical range-land site the cover of weed was reduced from ca. 75% to zero in four years. Similar effects in more nearly natural vegetation were found by Cantlon (1969), who studied the annual herb Melampyrum lineare in deciduous forest in Michigan. The plant is grazed by the katydid Atlanticus testaceus and in plots treated with a mixture of insecticides the number of seedlings was twice as great as in the control plots after 1 year, three times as great after 2 years and over three times as great after 4 years. Fluctuations in localized and roving populations of mammals, which are generally less selective than insects (Summerhayes 1941; Watt, 1957; Kydd, 1964; Stewart & Stewart, 1971), must also have been an important influence before man dominated the scene.

Temporal fluctuations in microbial pests may also be important for the control of the abundance of particular plants in the wild but little is known about this. The effects of spatial fluctuation – seen in the fairy rings of grasslands in the North Temperate Zone – are highly suggestive. These rings have been a great source of mythology but are still poorly understood in scientific terms (Shantz & Piemeisel, 1917; Ramsbottom 1953). Apparently a fungus spreads outwards slowly from its site of infection, suppressing the dominant grass to a variable degree (sometimes almost completely). Often, it seems, considerable quantities of major nutrients are liberated when the fungus dies and these stimulate the growth of the grass to a particularly high level at the margin of the infected area, thus forming the ‘ring’.

It has been suggested (Gillett, 1962; Janzen, 1970; Connell, 1971) that host-specific parasites and herbivores may have a rather special role to play in maintaining species-richness through their activities being concentrated on adult plants and inflicting especially heavy mortality on any offspring in the immediate neighbourhood of the parents. This idea will be further discussed on page 125.
Maintenance of species-richness in plant communities

Fig. 4. The two major kinds of result found when two species (x and y) are grown in mixture, starting with contrasted proportions of x (90% and 10%): (a) x always replaces y, (b) a balance between x and y is set up. The shape of the time course of the ratio may vary appreciably depending on the species tested, and there are likely to be fluctuations about the mean line of the time course depending on the season, as shown (discontinuous line) for one of the mixtures in (b).

(d) Balanced mixtures

Many experiments on competition have been made in recent years using even-aged mixtures of pairs of species, and with the two species sown in varying proportions as suggested by de Wit (1960, 1961). In most cases one species of the pair tends to oust the other, whatever the proportions at the start of the experiment (Fig. 4 a), but in a few cases there is evidence for a position of balance, which could persist indefinitely and toward which mixtures in all proportions tend to change (Fig. 4 b). In the first case there is eventually complete replacement of one species by the other. If the advantage of A over B is relatively small, as is often the case, replacement will take a very long time. However, such replacement can occur in quite short periods in annual species as is shown by the experiment of Harlan & Martini (1938). They sowed 11 varieties of barley in equal proportions at several different sites, harvested grain at random at the end of each season for sowing the next year, and found that less suitable varieties were completely eliminated within 4–11 years at any given site.

The maintenance of a balanced mixture, as in Fig. 4 b, is dependent on both the growing conditions (van der Bergh & de Wit, 1960) and the density of the plants (Marshall & Jain, 1969). It can be explained in general terms of either a balance of intraspecific versus interspecific competition (Harper, 1967) or limitation of the two species by different factors (Harper, Clatworthy, McNaughton & Sagar, 1961). The exact mechanisms involved in the first explanation are obscure, but may possibly involve the production of autotoxins, i.e. materials more toxic to the producer species than to the other species. Newman & Rovira (1975) have recently obtained evidence that production of materials that are more autotoxic than allotoxic may be characteristic of those species that occur as isolated individuals, whereas the reverse may be true of species that naturally form long-lasting and continuous swards. Limitation by different factors can be illustrated tentatively with respect to mineral requirements. For example, on some soils nitrogen is the primary limiting mineral for grasses, but phosphorus and potassium limit the growth of legumes (Thurston, 1969); on other soils phosphorus...
may be the primary limiting mineral for grasses and nitrogen for sedges (Willis, 1963). Similarly the root growth of one species may be best in soil pores of a certain size and that of another species best in adjacent pores of a different size (Sheikh & Rutter, 1969). It is often forgotten that the growth of most plants is limited by several or many factors simultaneously. In the cases just cited climatic and biotic factors limit as well as soil factors. It has to be emphasized that the persistence of mixtures of the species can only be accounted for in terms of different limiting minerals or pore sizes if these are of overwhelming importance in the limitation of growth.

The significance under natural conditions of the type of balance shown in Fig. 4b is not at all clear. The strong dependence on growing conditions and density must be emphasized. Thus two species of *Avena* were proven to have the appropriate combining ability in certain artificial experiments, but, in the field, more than half the populations within the geographical range of both species in California were found to contain only one of the species (Marshall & Jain, 1969). No experiments yielding evidence of stability in even-aged mixtures of three or more species have been reported. However, some highly relevant experiments on mixtures of four or more species have been made.

In two sets of experiments on mixtures of four species the different species were all sown in the same proportion (Bornkamm, 1961a, b). The results show that a fairly clear rank order ('pecking order') was established (Table I a). The same result emerged (Table I b) when five grass and four legume species were grown in all possible pairs (Caputa, 1948; Jacquard, 1968). Similar results were obtained when 11 different weeds were tested against two different crops (Welbank, 1963); experiments with only three species tested against each other are clearly much less likely to yield a definite rank order (Haizel & Harper, 1973). The rank order was certainly not completely constant in Caputa's experiment and one species, *Dactylis glomerata*, behaved very erratically (Table I b). It seems improbable that in mixtures involving three or more species many of the encounters between one species and its neighbours will lead to a self-balancing equilibrium. However, there may be very many occasions when a near-balance is struck (the equivalent of a small shift in Fig. 4 a) and this may be extremely important, as becomes clear later (see page 118).

(e) Variation in competitive ability with physiological age

The relevance of all the experiments mentioned in subsection II (d) is limited by the fact that most natural and semi-natural plant communities are of uneven age. The uneven age-structure is, in turn, important because success in competition depends on which developmental stage of one species is pitted against which stage of the other. A. S. Watt (1955) first illustrated this idea with an analysis of a semi-natural mixture of heather (*Calluna vulgaris*) and the bracken fern (*Pteridium aquilinum*) on acid, nutrient-poor sands in eastern England. He divided the life-history of each species into four successive phases on the basis of morphology alone though these phases plainly reflected physiological age (pioneer, building, mature, degenerate). He then observed which species succeeded when one invaded the other, and, in particular, how this depended on the growth phase of the species invaded. The pioneer phase of one
Table I. The results of two experiments in which all possible pairs of species within certain groups of species were grown together and a rank order established

(a) From Bornkamm (1961 a)

<table>
<thead>
<tr>
<th>Species affected</th>
<th>Decreasingly strong competitors</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>S A ≥ V ≥ T</td>
</tr>
<tr>
<td>A</td>
<td>S A T ≥ V</td>
</tr>
<tr>
<td>V</td>
<td>S A ≥ V T</td>
</tr>
<tr>
<td>T</td>
<td>S A V T</td>
</tr>
</tbody>
</table>

S = Sinapis alba, A = Avena sativa, V = Vicia sativa, T = Triticum aestivum.

(b) From Caputa (1948) – results of 1944

<table>
<thead>
<tr>
<th>Species affected</th>
<th>Species decreasingly aggressive to test species</th>
</tr>
</thead>
<tbody>
<tr>
<td>L</td>
<td>M L H X F P C A D</td>
</tr>
<tr>
<td>A</td>
<td>L M A X F P C H D</td>
</tr>
<tr>
<td>D</td>
<td>L M = X A F D P C H</td>
</tr>
<tr>
<td>F</td>
<td>L M = A P X F C H D</td>
</tr>
<tr>
<td>M</td>
<td>L X M C H A D F P</td>
</tr>
<tr>
<td>X</td>
<td>L D A X P F M C H</td>
</tr>
<tr>
<td>C</td>
<td>L M X A D F P C H</td>
</tr>
<tr>
<td>H</td>
<td>L M X A D P F H C</td>
</tr>
</tbody>
</table>

Strongly aggressive (in top two places for 7/9 species):
L = Lolium italicum
M = Medicago sativa

Moderately aggressive (in third, fourth or fifth places for 7/9 species):
A = Arrhenatherum elatius
X = Trifolium pratense

Slightly aggressive (in fifth, sixth or seventh places for 7/9 species):
P = Festuca pratensis
P = Phleum pratense

Not aggressive (in seventh, eighth or ninth places for 7/9 species):
C = Lotus corniculatus
H = Trifolium hybridum

Very variable (from second to ninth place):
D = Dactylis glomerata

species only succeeded if it invaded the pioneer or degenerate phase of the other. Such a relationship provides a possible basis for the indefinite persistence of two such species in mixture.

These various approaches to the analysis of plant communities that do not involve a consideration of regeneration – or only a minimal study of it – provide several distinct ways of explaining long-term co-existence of some plant species, but they do not convincingly ‘explain’ the long-term co-existence of the numerous species with essentially the same life-form, adult phenology and habitat-range, that are characteristic of so many species-rich communities.
III. INTRODUCTION TO THE INVOLVEMENT OF REGENERATION

The idea of two species with much the same life-form, phenology and habitat-range differing in requirements for regeneration is most easily grasped for tree species. Gaps arising in a forest are of different sizes. When a whole large tree is blown over, the gap produced is large; when an individual limb falls off a diseased tree, the gap formed is small. If the gap is large, an individual tree of some light-demanding species is most likely to be the next dominant on the spot. If the gap is small, a tree of some shade-tolerant species is likely to grow through and dominate the spot. Thus the light-demanding *Betula pendula* can persist with shade-tolerant *Fagus sylvatica* in semi-natural woodland on acid soils in Britain (Watt, 1934; 1947). One can easily envisage other factors that might swing the balance between colonizing species in the gap or in different parts of it. Such factors include the particular species which happen to be present at the right time as seed, seedlings, saplings or poles; the presence of the crown of the fallen tree (and its smothering effect) or just the tall bole; presence or absence of leaves on the fallen tree (and the green-manuring effect); the degree of disturbance to the litter and topsoil: the presence or absence of sunflecks in sunny weather depending on the side of the gap concerned (north or south) in a forest far away from the equator (Coombe, 1966); the adult trees left standing and the ground flora - both compete for light, water and mineral nutrients, and may exert allelopathic effects or harbour particular pests and diseases.

Table 2. Processes involved in the successful invasion of a gap by a given plant species and characters of the gap that may be important

<table>
<thead>
<tr>
<th>Processes</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Production of viable seed</td>
<td>Time of formation</td>
</tr>
<tr>
<td>Flowering</td>
<td>Size and shape</td>
</tr>
<tr>
<td>Pollination</td>
<td>Orientation</td>
</tr>
<tr>
<td>Setting of seed</td>
<td>Nature of soil surface</td>
</tr>
<tr>
<td>Dispersal of seed</td>
<td>Litter present</td>
</tr>
<tr>
<td>Through space</td>
<td>Other plants present</td>
</tr>
<tr>
<td>Through time</td>
<td>Animals present</td>
</tr>
<tr>
<td>Germination</td>
<td>Fungi, bacteria and viruses present</td>
</tr>
<tr>
<td>Establishment</td>
<td></td>
</tr>
<tr>
<td>Onward growth</td>
<td></td>
</tr>
</tbody>
</table>

The possibilities seem almost limitless. The processes involved in the successful invasion of a gap by a given plant species and characters of the gap that may be important are summarized in Table 2. Similar considerations apply when invasion of a gap is by vegetative means rather than by seed.

It becomes apparent that species-richness may be maintained by a heterogeneous environment acting on all of a series of stages in the reproduction of the plants present. The variable environment determines whether there is or is not at a particular place and time for a particular species an abundance of flower-formation, pollination, good seed-set, dispersal, germination, establishment of the juvenile plant and passage of the juvenile to the adult. The idea that all these stages are important in the maintenance of species-richness has been all too often ignored. It was not a matter of chance that the
example given above to illustrate the reality of differences in requirements for regeneration concerned trees. The examples that we now find easiest to comprehend and most convincing were also historically the first to be appreciated. It was the foresters who first realized the importance of differences in regeneration—requirements. Heyer (1852) seems to have been the first to publish an explicit account of differences in ‘tolerance’ of tree seedlings; as Tournay & Kostian (1937) pointed out, the original emphasis was on degrees of tolerance of shade, but in the present century differences in the ability to tolerate root competition have been increasingly emphasized. In the 1950s the importance of differences between species at all the stages in the regeneration cycle came to be appreciated particularly in relation to tropical rain-forest and tropical deciduous forest (Jones, 1955–6; Hewetson, 1956; Steenis, 1956). More recently the question has been discussed and illustrated for tropical rain-forest by Budowski (1965), Poore (1967, 1968), Ashton (1969), Richards (1969), Rollet (1969), Janzen (1970) and Whitmore (1974, 1975) and for a subtropical rain-forest by Webb, Tracey & Williams (1972). A particular idea that attracted much attention at the time was that of Aubreville (1938), who suggested that any one tree species never regenerated under itself; later workers, however, have shown that this generalization was not true (Jones, 1955–6; Foggie, 1960; Schulz, 1960; Rollet, 1969). Most recently emphasis among writers concerned with species-richness in tropical forests has been concentrated on differences in flowering phenology (Gentry, 1974, 1976; Stiles, 1975). There seems to have been much less explicit discussion of maintenance of species-richness in temperate forests, although more interest has been shown in the last two years — see, for example, the papers of Forcier (1975), Horn (1975), Pigott (1975) and Ash & Barkham (1976). Many earlier studies of regeneration showed implicitly that the same principles apply as in tropical forests, e.g. those of Watt (1934, 1947), Graham (1941), Jones (1945), Bray (1956), Curtis (1959), Franklyn & Dyrness (1969), Auclair & Cottam (1971), Williamson (1975), Sprugel (1976) and of various Continental authors as summarized by Ellenberg (1963). Whittaker (1969) mentioned the ‘successional niche’ and appeared to refer to the parts played by different species in the natural regeneration of eastern deciduous forest in the U.S.A. after sheet destruction by fire; in a later paper (Whittaker, 1972, pp. 239–40) he seemed to broaden his concept of the successional niche but he considered it only briefly. Loucks (1970), in a general treatment of diversity, also started from a forestry background; he emphasized the importance of species reacting differently to periodic perturbations, notably fires and cyclones. In treatments generally detached from the discussion of particular communities Skellam (1951) has shown the importance of differences in dispersability, and Harper and colleagues have repeatedly emphasized the potential importance of different requirements for germination and establishment, and the nature of ‘safe sites’ for particular species (Harper, 1961, 1965; Harper et al. 1961; Harper, Williams & Sagar, 1965; Cavers & Harper, 1967; Sheldon, 1974).

Most recent discussions on diversity in grasslands have been notable for a failure to appreciate the relevance of regeneration processes — see, for example, the articles of McNaughton (1967, 1968b), Grime (1937a, b) and Newman (1973). They have concentrated on the negative correlation often found between species-richness and
grassland productivity, i.e. the yield of new plant matter per unit area and time. This situation illustrates a point of great importance for the present discussion. Differences in requirements for regeneration can only be effective in maintaining species-richness if the adult plants of the many species are reasonably evenly balanced in competition. In some kinds of vegetation this is less likely to be the case if the growing conditions are generally very favourable to plant growth; under such conditions a few potentially vigorous and tall-growing species generally eliminate many species which could persist in the absence of competition. The grassland vegetation of N.W. Europe is a useful example; here there is a striking contrast between the species-richness of the grasslands on shallow calcareous soils (short of nitrogen, phosphorus and other mineral nutrients) and the species-paucity of much grassland on deeper soils at pH 5–6 (with a better supply of N and P). The potential for continued co-existence by differentiation in requirements for regeneration is very great in the calcareous grassland but much reduced in the grassland at pH 5–6. When species-rich, nutrient-poor grasslands are fertilized, the standing crop is increased and the species-richness sooner or later declines. This has been shown for calcareous fixed dunes by Willis (1963), for wet heaths by Sougnez (1966), and for montane calcareous pasture by Jeffrey & Pigott (1973). Whether there is a similar effect to be found generally in forests seems doubtful. Thus Watt (1934) recorded only 47 species in the herb-layer in 23 samples of escarpment beechwoods on calcareous soils in the Chiltern Hills compared with 64 species in 10 samples of plateau woods on clay-derived soils of pH 4.7–6.0 in the same area; ash, beech and oak all grow taller on the clay-soils than on the chalk soils (e.g. 25–32 m versus 20–23 m tall for beech) and the fertility for most plants is greater on the clay-soils. The data from Watt’s two samples are not strictly comparable because the list for the escarpment beechwoods is incomplete. However, this fact is counter-balanced by the inclusion in the lists of many species not typical of mature woods and suggesting a more recent origin for at least parts of the woodlands on the scarp. Watt’s data cannot be taken to prove that the field-layer is more species-rich on the more fertile soil, but they illustrate a general finding in central and northern Europe that beechwoods on deeper soils of pH 5–6 (Asperulo-Fagion) are generally more species-rich than those on shallow calcareous soils (Cephalanthero-Fagion), as documented by Ellenberg (1963). The contrast with grasslands in the same region in the trend in species-richness reflects the much smaller number of strictly calcicolous species found in woodlands, i.e. species strictly confined to calcareous soils (Fenner, 1975). The fact that many species able to grow on soils of pH < 5 can also grow at pH 5–6, but not on calcareous soils, is also important.

Despite the considerable history of discussion of regeneration processes, it is not only the students of grassland diversity who have ignored them. Several distinguished authors, who have written recently about co-existence of plant species in general, have failed even to mention the possibilities of differentiation in requirements for successful regeneration, e.g. Goodall (1970), Walter (1971) and Whittaker (1975).
IV. DEFINITION OF A PLANT'S NICHE

The niche of a plant is taken here to be the definition of its total relationship with its environment, both physico-chemical and biotic; such a definition necessarily includes a statement of the role played by the plant as well as a statement of its tolerance. The present author sees no advantage in replacing the term 'niche', used in this sense by 'ecotope', as suggested elsewhere (Whittaker, Levin & Root, 1973). My usage of 'niche' is essentially in agreement with that of Richards (1969) and Wuesscher (1969, 1974). Four component niches have to be recognized in a complete definition of a plant's niche.

(i) The habitat niche, i.e. the physical and chemical limits tolerated by the mature plant in nature. The definition should include an expression of the kinds of fluctuations from the mean climatic conditions which favour the plant's vegetative development.

(ii) The life-form niche, including an expression of size and annual productivity as well as three-dimensional pattern.

(iii) The phenological niche, i.e. the pattern of seasonal development.

(iv) The regeneration niche, i.e. an expression of the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation, concerning all the processes and characters indicated in Table 2.

The habitat niche is the plant's address. The life-form and phenological niches are the plant's profession. The regeneration niche includes elements of both address and profession.

Hutchinson's (1957) idea of recognizing a 'potential niche' (that effective in the absence of competitors and predators) and a 'realized niche' (that effective in the presence of competitors and predators) can be applied to all four aspects of the niche but is particularly important for the habitat niche.

Before considering examples of differentiation in the regeneration niche, it is necessary to recapitulate briefly what is known of the process of regeneration in the different major types of plant community.

V. PATTERNS OF REGENERATION IN DIFFERENT PLANT COMMUNITIES

Four major types of vegetation may be recognized in this context, determined by the dominant life-forms present: forests and woodlands, shrub-dominated communities, grasslands and associations of ephemeral herbs.

In most natural forests regeneration involves clearings of some kind, but the size of the clearings varies enormously. The two extremes are represented by forests suffering occasional sheet-destruction by fire and those with gaps created by the fall of single trees or branches. Intermediate types include those in which gaps of 0.1 to 1.0 ha are caused by cyclone damage (Webb, 1958; Whitmore, 1974) and those with strips of dead and dying trees somehow related to strong and constant winds (Oshima, Kimura, Iwaki & Kuroiwa, 1958; Iwaki & Totsuka, 1959; Sprugel, 1976). In many areas occasional regeneration in sheets after fire alternates with a patchwork regeneration...
pattern during fire-free periods, e.g. in the *Nothofagus* forests of Tasmania where *Eucalyptus regnans* colonizes after fire (Gilbert, 1959; Jackson, 1968), or in the *Picea-Tsuga* forests of western North America where *Pseudotsuga menziesii* invades after fire (Franklyn & Dyrness, 1969). In most forests some trees die 'on their feet' and new trees grow up in their place without the formation of an obvious gap in the canopy; this pattern is probably very widespread in low-stature forests (e.g. many subalpine and upper montane tropical forests), in which the individual trees rarely develop large trunks and appear to collapse after death without making gaps (Grubb & Stevens, 1976; Tanner, 1977). Regeneration of trees in all these forest-types is primarily by seed, but regeneration from burnt stumps may be important in mediterranean climates; a valuable summary of the relevant findings in California is given by Mooney & Dunn (1970) and some basic information for the European Mediterranean zone by Trabaud (1970). For shrubs and herbs, vegetative spread into clearings is relatively more important (Kujala, 1926; Whitford, 1949; Flower-Ellis, 1971; Korchagin & Karpov, 1974), but there are certainly many forest herbs for which regeneration is mainly by seed (Curtis, 1959; Wilson, 1959; Knight, 1964). Regeneration of climbers, epiphytes and parasites appears to occur most often by seed in a patchwork pattern, broadly analogous to that for most trees, though invasion of new gaps by vegetative spread is no doubt important for some climbers and scramblers, e.g. many bamboos.

In shrub-dominated communities regeneration is sometimes chiefly by seed as in the species-poor Callunetum of eastern England (Watt, 1947, 1955) and in semi-deserts (Bykov, 1974; Davies, 1976), but in many wetter communities with creeping Ericaceae or Epacridaceae (e.g. many subalpine heaths of both hemispheres) invasion of gaps by vegetative spread is more common (Burges, 1951; Chambers, 1959; Barrow, Costin & Lake, 1968; Keatinge, 1975).

In closed grassland, i.e. grassland with a continuous cover, the extent of regeneration by seed is not clear. Vegetative regeneration in a kaleidoscopic pattern is certainly important in a variety of grasslands, e.g. in meadows in Sweden (Tamm, 1956, 1972, a, b) and Russia (Rabotnov 1969b), in hill pasture in Scotland and Wales (Harberd, 1961; Chadwick, 1961), and in lowland grassland on chalk in England (Austin, 1968). The rates of vegetative spread vary greatly but have been estimated at 2–6 cm per year for certain dominant grasses (Harberd, 1961; Chadwick, 1961; Austin, 1968). However, the half-lives of adult plants of the perennial species commonly vary from 1–2 years up to more than 50 years (Harper, 1967; Tamm, 1972, a, b; Sarukhán & Harper, 1973), and for some species may be of the order of several hundred years (Harberd, 1961; Oinenen, 1967, a, b). The short-lived perennials as well as the annuals and biennials, found in continuous turf with gaps only 1–5 cm across must regenerate by seed (Sarukhán & Harper, 1973; Grubb, 1976), but for many grassland species creation of larger gaps by animals (e.g. soil-heaps of moles or gophers, or scratchings by rabbits or badgers) may be necessary for regeneration by seed (Watt, 1971, 1974; Miles, 1973; Platt, 1975). The pattern of regeneration is particularly obscure in closed grassland dominated by large tussocks such as those of *Molinia* in western Europe (Godwin, 1941; Rutter, 1955), *Danthonia* and *Poa* in New Zealand (Cockayne, 1928) or *Deyeuxia* (*Calamagrostis*) in the high Andes (Cuatrecasas, 1934; Diels, 1937).
In open grassland, developed in situations deficient in mineral nutrients and/or water and consisting of isolated plants, the latter may have quite short half-lives of 5–7 years (Sarukhán & Harper, 1973) and probably regenerate chiefly by seed. However, the huge tussocks of *Triodia* and *Plectrachne* ('spinifex') in the semi-deserts of central Australia (Winkworth, 1967; Beard, 1969) appear to be much longer-lived.

Natural associations of ephemeral herbs (plants represented only by bulbs, corms or seeds in the unfavourable season) usually exist as sub-systems of more extensive communities, e.g. in semi-deserts, on cliffs or in successional stages on dunes. Little is known about the regeneration of plants with bulbs and corms, but the others, by definition, regenerate only by seed.

In summary, it is apparent that very various patterns are involved in regeneration and that much remains to be discovered about the process. However, it is clear that regeneration involves both seed and vegetative organs and that the relative importance of these two depends on the community concerned.

It is necessary to comment here on the relation between regeneration and succession, two distinct processes which have often been confused, especially in the U.S.A., where much attention has been paid to the successions of species found after fire. Succession, as a term, is best reserved for non-cyclic series of vegetation types, either in primary seres (e.g. on moraines left by glaciers, in lakes or on sand dunes) or in secondary seres (e.g. on abandoned farm land). Confusion is bound to arise where man-made secondary successions merge with natural regeneration processes, as in the post-fire situation in much of the U.S.A. but it is still worth while to distinguish the processes in general. For most species the 'successional niche' is best treated as part of the definition of the habitat niche, but in the case of species in certain secondary seres (notably post-fire seres) it may be more useful to include it in the definition of the regeneration niche.

Regeneration in a gap of any kind usually involves a succession of species—the serule of Daubenmire (1968a). An obvious kind of differentiation in the regeneration niche concerns time of appearance in this serule (Gómez-Pompa, 1971). However, since several or many species are usually present at each stage, niche differentiation must concern gap quality as well.

VI. EXAMPLES OF DIFFERENTIATION IN THE REGENERATION NICHE

(a) Production of viable seed

It is a commonplace that in a particular region certain years are ‘good years’ for some crops and not for others and variation of this type for species cultivated in fields and orchards has been documented the world over. There is plenty of information too for forest trees in many parts of the world: Central Europe (Schwappach, 1895; Seeger, 1913), North America (Morris, 1951; Boe, 1954; Fowells & Schubert, 1956; Daubenmire, 1960; Baron, 1969; Clark, 1970), the U.S.S.R. (Molčanoñ, 1967), Japan (Tagawa, 1969, 1971) and New Zealand (Beveridge, 1964, 1973; Wardle, 1970). However, there is only a little information of this type for shrubs, e.g. that of Davies (1976) on Australian semi-desert species, or for perennial grassland herbs, e.g. that of Rabotnov (1950) and Golubeva (1968) for selected plants in meadows and pastures.
Fig. 5. Numbers of seed produced by three tree species in Prussia in the years 1874–93 (after Schwappach, 1895): (a) *Pinus sylvestris*, (b) *Quercus robur* (open columns) and *Fagus sylvatica* (filled columns).

Fig. 6. Numbers of sound seed per unit area produced in the years 1961–7 by marked trees of five species of Podocarpaceae in New Zealand: (a) *Dacrydium cupressinum*, (b) *Podocarpus ferrugineus*, (c) *P. spicatus*, (d) *P. totara* and (e) *P. dacrydioides* (after Beveridge, 1973).
Maintenance of species-richness in plant communities

Fig. 7. The crops of fruit produced by ten species of trees and shrubs over 10 years in an arid region of Western Australia (from Davies, 1976). The results are expressed as percentages of the best year’s production. Blanks indicate that no records were kept in those years. Reproduced from the *Journal of Ecology* with permission.

In the U.S.S.R. and of Sarukhán & Harper (1973) for plants in a Welsh pasture. There are also very few data for annuals, e.g. those of Newman (1964) for certain winter annuals in eastern England.

In each of the forest communities that have been studied, three main patterns of seed production have emerged: (a) moderate production in most years, (b) fruiting rather irregular, and (c) abundant fruiting strongly periodic (see Figs. 5 and 6). The same patterns have been found in a sample of species of semi-desert scrub (Fig. 7). Different species in group (b) are favoured by different years. It is important to realize that the variability in the supply of viable seed to different gaps will be greater than that suggested by the mean differences between species, not only because of differences in dispersal, etc., but also because of differences between individuals of each species – at least those in groups (a) and (b). In any one year some individuals fruit abundantly and others less so.

It is virtually certain that the three main patterns of seed production reflect three corresponding patterns of flowering, although there is little published evidence to prove the point. The three patterns have been shown clearly in herbs in Europe (Fig. 8) and trees in Malaya (Medway, 1972). However, no exact correspondence between the numbers of flowers and of viable seeds can be expected because of wide variations in the success of pollination and the ‘setting’ or ripening of the seed.
Unfortunately little is known about year-to-year variation in either of these processes. Circumstantial evidence exists for massive failure of pollination in some species in some years in communities as widely separated as the lowland tropics (Medway, 1972) and the Arctic (Kevan, 1972) and it seems virtually certain that less-dramatic fluctuations in the success of pollination also occur, e.g. in relation to the incidence of high winds or rain. As for the ripening of fruit the optimum conditions are known for only a very few wild species. Examples are the Douglas fir, *Pseudotsuga menziesii* (Lowry, 1966), the perennial thistle, *Cirsium acaulon* (Pigott, 1968), and the winter annual *Teesdalia nudicaulis* (Newman, 1964, 1965). For crop plants it is known that both optimum conditions and susceptibility to damaging conditions vary with the stage of development. For example, the yield of maize seeds was shown to suffer a 50% reduction as a result of a standardized drought treatment lasting 6–8 days at the stage when the primordia were growing most actively, but negligible reduction if the same stress was applied a little later in development (Robbins & Domingo, 1953). Similar results were obtained for barley by Aspinall, Nicholls & May (1964). Very high daytime temperatures (32–35 °C) cause flowers of the bean to abort if they occur on the day of opening or one day before or after that, but they cause much less damage if they occur at a later stage in development (Smith & Pryor, 1962). High night temperatures are especially damaging to seeds of peas about 5 days after flowering (Lambert & Linck, 1958; Karr, Linck & Swanson, 1959) and similar results have been obtained for cherries (Tukey, 1952), apples (Tukey, 1955) and grapes (Tukey, 1958). The incidence of short periods of drought and high temperatures in relation to the flowering periods of wild plants certainly varies from year to year and such periods must account for some of the year-to-year variation in seed-set. Much more investigation of this topic is needed. The losses due to seed-eating insects and birds, and to fungal and bacterial pathogens, also need to be quantified, for very little information is at present available (Rabotnov, 1969a; Janzen, 1971; Bohart & Koeber, 1972).

Great interest attaches to the physiological processes involved in the production
Maintenance of species-richness in plant communities

of viable seed and to the evolution of the variety of flowering and fruiting ‘strategies’ (not least the variation in phenology), but attention is concentrated here on the fact that in any one species-rich community the proportions of viable seeds of different species falling on any one area are certain to vary appreciably from year to year.

(b) Dispersal

First, we are concerned with dispersal in space. In every species-rich community that has been studied a great variety of dispersal mechanisms has been found (van der Pijl, 1971). There can be little doubt that seeds of some species are, in general, dispersed further afield than those of others and it has long been appreciated that wide dispersal is important in species less fit in a competitive struggle between vegetative plants (Skellam, 1951). In addition the relative effectiveness of different types of dispersal in space will vary from year to year in response to variations in wind speed, wind direction, abundance of particular animal vectors, incidence of flooding, etc.

The size of an individual gap in the community can also be important, e.g. in a large forest-clearing few seeds of a heavy-fruited tree like *Fagus* reach the centre of the gap, but large numbers of light seeds such as those of *Betula* may land there; so *Betula* is helped to persist in a forest dominated by *Fagus* (Watt, 1934).

Secondly, we are concerned with dispersal in time. It is well established that the seeds of the various species in particular communities vary in the length of time for which they remain viable and that this variability is reflected in the seed bank of the soil. Information on which species in particular communities are most abundant in the seed bank is available for temperate grasslands (Chippindale & Milton, 1934; Champness & Morris, 1948; Major & Pyott, 1966), and for temperate and tropical forests (Guyot, 1960; Guevara & Gómez-Pompa, 1972; Marks, 1974). It is probably extremely important for many subsidiary species that they can regenerate from seed that has been in the soil for decades, whenever and wherever a gap arises in the community. Examples are species of *Agrostis*, *Holcus* and *Poa* in grasslands in western Europe able to benefit from gaps made by animals, and species of *Hypericum*, *Juncus* and *Verbascum* in forests in the same area able to benefit from gaps made by tree-falls.

It is certain that seeds of different species vary inherently in longevity but differences in survival under natural conditions may be more closely related to palatability, digestibility and the incidence of predators (animals and microbes) than to inherent differences in longevity. Seeds certainly differ in palatability (Janzen, 1969) and the fact that the loss to predators is tremendous has been documented not only for forest trees with relatively large seeds (Watt, 1919, 1923; Curtis, 1959; Janzen, 1970; Medway, 1972) but also for herbs with quite small seeds (Tevis, 1958; Bohart & Koeber, 1972; Sarukhán, 1974). However, there are still very few data available on the absolute losses to microbes as opposed to animals (Sarukhán, 1974).

Variability in predation in time and space is bound to contribute to the variation in the numbers of viable seeds present at the time of formation of a particular gap. Janzen (1970) has placed great stress on losses to animals at this stage as critical to the maintenance of diversity in tropical rain-forests, arguing that more or less host-specific predators, accumulating on the parent tree, can destroy most seeds falling under it,
I 26

P. J. GRUBB

so that any one tree will rarely be replaced on that site by another of the same species. However, the observations of Connell (1971) suggest that the effects of animals with respect to the maintenance of species-richness are generally more important at a later (seedling) stage.

(c) Germination

There is a vast literature on this topic. The chief point to be made here is that very many of the differences between species are effective in ensuring that their seeds germinate in sites that differ in time and space. Some seeds germinate in shade but others only in the light (Koller, 1972; King, 1975). Most seeds germinate most rapidly in protected micro-sites, e.g. in small gaps, but some benefit from the alternating cycles of drying and rewetting suffered in more exposed sites, e.g. large gaps (Miles, 1974). Many seeds are destroyed by the high temperatures suffered in the litter and topsoil during a fire, but others are stimulated to germinate by such an event (Beadle, 1940; Gratkowski, 1961). Seed-form varies appreciably within most communities and it has been shown that the shape and size (Harper, Lovell & Moore, 1970) as well as the behaviour of hygroscopic pappus hairs (Sheldon, 1974) or awns (Kerner von Marilaun, 1902), are important in determining the degree of burial of a seed on a particular type of soil surface and the chance of its being able to take up enough water for enough time to germinate. Differences in soil chemistry also affect germination, for example the levels of nitrate (Williams & Harper, 1965; Williams, 1969), calcium (Parham, 1970), and ethylene (Olatoye & Hall, 1973). A special case is that of allelopathic inhibition, as seen in certain scrub communities (Deleuil, 1951; McPherson & Muller, 1969); particularly interesting for the maintenance of diversity is the inhibition of germination by the parents of the same species (Webb, Tracey & Haydock, 1967; McNaughton, 1968a; Friedman & Orshan, 1975). There can be little doubt that in most communities gaps of differing quality arise and that the proportions of the different species able to germinate differ from gap to gap.

Gaps differ not only in their quality at any one time but also in their timing. That this is important for maintenance of species mixtures can be shown by two examples. First, it is known that gaps on river-banks in eastern England caused by scour in autumn usually become occupied by Epilobium hirsutum and those formed in spring by Lythrum salicaria (Whitehead, 1971). The Epilobium excludes the Lythrum from autumn gaps by its earlier development. The Epilobium is unable to become established as late as the spring so that Lythrum succeeds at that time. The physiological basis of the distinction is fairly well understood (Shamsi & Whitehead, 1974). Secondly, it is known that Avena ludoviciana, which germinates in the winter, is a serious weed of winter cereals but it is almost totally destroyed by ploughing in early spring. A. fatua, which germinates in the spring, is a severe pest of spring-sown cereals (Thurston, 1951). In more general terms the periods of germination of different species in a particular community are spread throughout the year in such a way that species A has the maximum chance of success in a gap if it is formed by such-and-such a date and no catastrophe follows, but species B has the best chance if there is a catastrophe and it germinates afterward. Thus an autumn-germinating herb
Maintenance of species-richness in plant communities

in temperate grassland may succeed in regenerating an adult in a certain gap if there is no heavy frost-heaving (and subsequent drought risk) and plenty of rain in winter, but if there is plenty of frost-heaving and/or no rain, then a spring germinating species is at an advantage. An example was observed by Salisbury (1929, p. 222); all the seedlings of the autumn-germinating *Ranunculus parviflorus* were destroyed during severe and prolonged winter frosts whereas seedlings of ‘*Helianthemum breweri*’ (*Tuberaria guttata* (L.) Fourr.) germinating in spring escaped the hazard. In fact the year can be partitioned by the germination periods of different species into shorter spells than autumn or spring, as shown for weed species in Central Europe in Fig. 9. Some species spread the risk, germinating in autumn and spring or discontinuously throughout the year. Certain species with this ‘strategy’ show an obvious seed dimorphism related to the maintenance of at least two germination periods (Harper et al. 1970).

Much is known about the physiological control of the timing of germination in the kind of succession shown in Fig. 9, based on temperature-responses (Went, 1949; Lauer, 1953; Newman, 1963; Mott, 1972), breakdown of hard coats (Salisbury, 1929), leaching of inhibitors (Went, 1957; Koller, 1969), differences in the degree of hydration necessary for germination (McWilliam, Clements & Dowling, 1970; Mott, 1974) and the changes that occur during after-ripening (Newman, 1963; Villiers, 1972) or as a result of burial (Wesson & Wareing, 1969). It is particularly significant that appreciable differences in the temperature-responses of germination have been found in groups of species with very similar habitat-tolerances and reproductive ‘strategies’, e.g. among the winter annuals found on cliffs and sand-dunes in Europe and North America (Ratcliffe, 1961; Newman, 1963; Baskin & Baskin, 1971 a, b).

A further potentially important variable is the speed of germination under a given set of conditions. Species in chalk grassland in England, for example, vary greatly in this respect (J. B. Dickie, unpublished). Rapid germinators gain a competitive advantage if subsequent conditions remain favourable, but slow germinators, which may fail to germinate in short favourable periods, could benefit in the long run, provided they remain viable while the rapid germinators are killed in a subsequent catastrophe.

Whereas there is now available an impressive body of knowledge concerning seed behaviour in the laboratory, there is extremely little information available on germination as such in the field – nearly all the apparently relevant reports concern the establishment of seedlings and the optimum conditions for this stage of the life-cycle can be quite different from those for germination. Thus in temperate grasslands with distinct tussocks many seeds that come to rest beneath or within the tussocks germinate freely in the autumn and spring but their chances of establishment in the dense shade are negligible. Similarly those that germinate in more open microsites on deep litter are generally killed by desiccation before their roots reach the mineral soil below. Differences in requirements for germination and establishment have also been reported for plants in simple experimental systems (Harper et al. 1965; Sheldon, 1974).
Most of the information on the establishment of seedlings concerns the surface-types favoured by certain species, but some of it concerns variation from year to year at particular sites. Many species are known to have specific requirements for establishment, e.g. *Picea sitchensis* is found mainly on fallen trunks whereas the accompanying *Thuja plicata* and *Tsuga heterophylla* in the cool temperate rain-forest of the Olympic
Published records show that some years favour establishment of certain seedlings and other years other species (Daubenmire, 1968a; Bykov, 1974). Thus, in one part of the Turanian semi-desert, 1952 was good for *Artemisia pauciflora*, *Kochia prostrata* and *Agropyron pectiniforme*, 1956 for *Tanacetum achilleafoiium*, *Festuca sulcata* and *Medicago romanica*, 1958 for *Astragalus virgatus* and *Trinia hispida* (Bykov, 1974). Quantitative records for *Artemisia terrae-albae* and *Alyssum desertorum* in another area for the years 1965–69 are shown in Fig. 10. Large differences between years have been found for heathland in Scotland (Miles, 1974) and for forests and meadows in Finland (Pertulla, 1941).

The passage of the young seedling to the sapling or immature vegetative phase is only arbitrarily separated from the early seedling phase but most of the information concerning the effects of the physical environment concern the later stage. Experiments have shown that the effects of irradiance (Nicholson, 1960; Grime, 1966; Hutchinson, 1967) and water supply (Jarvis, 1963; Fenner, 1975) certainly differentiate species of the same community at this stage of the life-cycle. The ability to tolerate shade is often correlated with large seed-size, at any rate in species that do not depend on mycorrhiza for their organic nutrition as seedlings (Salisbury, 1941, 1974). However, there are many exceptions to the rule and the largest-seeded trees in European deciduous forests (*Castanea, Quercus*) are all light-demanding (Ellenberg, 1963). Possibly their large seeds evolved in relation to the occupation of dry sites and the advantage of...
rapidly developing a deep tap root; this seems to be the case in some other plants of open habitats, e.g. the strand-line species *Cakile maritima*. There is little doubt that differentiation in the regeneration niche has occurred through the function of seed size and its effects during establishment.

Not only physical environmental factors differentiate species at the establishment stage, but also biotic factors, notably grazing, even when the animals concerned are not monophagous e.g. snails (Grime, MacPherson-Stewart & Dearman, 1968) or deer (Knapp, 1974). Probably the selective effects of microbial pests and of allelopathic relations with plants of the same or other species are important in the field but there is very little proof (Webb et al., 1967). Particular interest arises from the idea that the risks of pests and allelopathic effects may be significantly greater near the parent plant so that invading species are at an advantage. Connell (1971) has provided evidence that seedlings of certain rain-forest trees in eastern Australia may suffer a greater mortality risk (at a given density) if under a tree of the parent species as opposed to another species and it is highly desirable that tests should be made on the applicability of this idea to other communities.

(e) Further development of the immature plant

Least of all, perhaps, is known about the conditions favouring the development of an established seedling or sapling of a given species into a mature adult. Although the process is only arbitrarily separable from the establishment of the seedling or sapling, it is well known that the optimum conditions for several forest trees are different in the two stages. Thus the Kauri, *Agathis australis*, needs a light cover (e.g. of *Leptospermum*) for survival as a seedling but requires a lack of overhead cover for development in the sapling and pole stages (Beveridge, 1973). Similar differences are recorded for certain species in the deciduous and coniferous forests of the U.S.A. (Curtis, 1959; Franklyn & Dyrness, 1969) and in the rain-forests of the Solomon Islands (Whitmore, 1974). Such considerations also apply to grasslands and heaths. It has been found that small clearings ($5 \times 5$ cm) in heathland are most favourable to the early establishment of most seedlings, but that after two years larger clearings ($50 \times 50$ cm, less overgrown than the smaller) have many more surviving plants per unit area (Miles, 1974).

In many studies on successions it has been found that certain species effectively make possible the invasion of species of a later stage, e.g. *Juniperus* spp. acting as nurses for *Taxus* (Watt, 1926) or *Fagus* (Watt, 1934) during invasion of ungrazed grassland in Britain or for *Quercus* spp. on sand dunes in the Lake States (Yarranton & Morrison, 1974). This sort of relationship is also found in the regeneration serule (Daubenmire, 1968a). The presence of certain gap-invaders can tip the balance between two species that might succeed on the site. One commercially important illustration of this point is the suppression of young *Picea sitchensis*, but not *Larix leptolepis*, by *Calluna vulgaris* (Weatherell, 1957). If the *Picea* and *Larix* are planted in mixture, the *Larix* may suppress the *Calluna* and, in due course, the *Picea* the *Larix*. Such relationships are often dependent on the weather at a particular time. Thus in most years a carpet of the herb *Mercurialis perennis* will inhibit growth of invading seedlings of the
Maintenance of species-richness in plant communities

tree *Fraxinus excelsior* in woodlands on boulder clay in eastern England (Wardle, 1959), but in an unusually wet spring the *Mercurialis* dies back on marginal sites (Martin, 1968) and *Fraxinus*, which is tolerant of waterlogging, can then grow through. The many relationships of this kind, which must contribute to the maintenance of diversity, have hardly begun to be explored.

VII. DISCUSSION

There can be no serious doubt that the kinds of differences between species in regeneration requirements considered in this review contribute a finite amount to the maintenance of species-richness in plant communities. The examples given all concern the regeneration of seed plants, but a parallel case could be made out for the pteridophytes, bryophytes, attached algae or fungi and indeed for corals and other attached animals. The really difficult problem is to establish that any two species may co-exist indefinitely on the basis of differences in the regeneration niche. If species A always tends to oust species B over a period of years in a particular part of the world, when individuals of the same physiological age are matched against each other, what are the conditions necessary for differentiation in the regeneration niche to be a basis of indefinite co-existence? There are two major conditions. The first is that B must be able to persist in the community as long as the mean time between those events which cause either the creation of a gap of a kind which favours the establishment of B more than A or the creation of a gap at a place where B has propagules and A has not. The second condition is that sufficient ‘B gaps’ must continue to arise as well as ‘A gaps’ in the area concerned; the exact proportion will be a major determinant of the relative abundance of species B and A in the community. Intuitively it seems reasonable that, in a temperate forest, large gaps should occur often enough to make possible the persistence of birch as well as beech. It is less clear that the hoof-marks of sheep or deer in a grassland should occur sufficiently often in places where species B has seed present and species A has not. Clearly the question can be settled for any one plant community only on the basis of detailed long-term studies of the gaps that arise, the differences there are between species in their responses to gaps of different kinds and of the differences there are in practice in terms of propagules of different species being present on the site. The results of any such study are bound to be so complex as to necessitate the building of a computer model of the situation, broadly speaking of the kind developed for temperate deciduous forest by Botkin, Janak & Wallis (1972).

Persistence of species B in the presence of species A between the times of gap formation may not necessarily be in the form of seed-producing adults; it may be as dormant seed in the soil or as plants in an adjacent community, e.g. on river gravels or rock outcrops next to the forest or grassland in question.

The idea that species-richness in plant communities is maintained in part as a result of recurrent perturbations by outside forces is shared with the theory of Loucks (1970). However, in the present account emphasis is also placed on the importance of gaps in the community that arise through the senescence and death of individuals more or less irrespective of outside forces and on the importance of a wide range of responses
to external factors in the plants of a species-rich community. Furthermore, external factors are seen as very important not only in creating some of the gaps in the community but also in determining which species are represented in any particular gap by propagules (a function of recent seed-set, dispersal, etc.).

If differences in the regeneration niche can account for the long-term co-existence of different species, just how different do species need to be? Particular interest attaches to those genera where the most obvious differences are in phenology, e.g. *Miconia* with nineteen species in Trinidad (Snow, 1965, 1968) or less remarkably *Guarea* with four species in the rain-forest of part of Costa Rica (Frankie et al., 1974) or *Neolitsea* with two species in the rain-forest of Japan (Ohwi, 1965). It is widely accepted that there is competition between plants for pollinators (Free, 1968; Hocking, 1968; Heinrich & Raven, 1972; Kevan, 1972; Gentry, 1974) and animal vectors of the seed (Snow, 1965, 1968) and the evolution of phenological spread is generally seen to be a result of this competition (Richards, 1969; Mosquin, 1971; Stiles, 1975).

It is less often pointed out that such spread is also seen in species pollinated and dispersed by wind, e.g. the annual grasses studied by Pemadasa & Lovell (1974). The groups of species concerned may well differ in their exact requirements for seed-set, as appears to be the case with six New Zealand species of *Podocarpus* (Fig. 6).

For most communities it seems unlikely that similar species will be found ultimately to differ in only a single characteristic in the regeneration niche but it is possible that this is the case in the astoundingly long series of species in certain genera in some rain-forests, e.g. *Eugenia* and *Shorea* in south-east Asia or *Diospyros* and *Rinorea* in Africa (Richards, 1969).

It is fashionable to emphasize the possible roles of predation by animals and intraspecific allelopathy in the context of the most species-rich communities and especially in the case of the long series of species in certain genera, but the general importance of these two mechanisms has yet to be proven. Critical evidence is needed to show that species are indeed unable to regenerate beneath their parents (though in a comparable degree of shade under other species) and that the lack of regeneration is specifically caused by predation or allelopathy.

The emphasis on differentiation in the regeneration niche is highly relevant to the contentious issue of continua in vegetation. Whittaker (1965, 1967, 1969, 1972) has repeatedly emphasized that gradient analysis leads to the conclusion that, while species are clumped in their habitat-tolerances, no two species are quite the same in this respect. He has suggested (Whittaker, 1969) that diversity in plant communities is made possible by a partitioning of the habitat, and indeed his emphasis is almost wholly on diversification in the habitat niche. In a popular text (Whittaker, 1975) he gives the student the impression that groups of species with strongly similar habitat
niches are not a general feature of vegetation. In fact most ecologists find that they are, whether they are working in the deciduous forests, grasslands or weed communities of Europe (Ellenberg, 1954, 1963; Ducaufour, 1960), the conifer forests and steppes of the western United States (Ducaufour, 1968b, 1970), the forests of eastern Australia (Webb, Tracey, Williams & Lance, 1970) or those on tropical mountains (Wade & McVean, 1969; Grubb & Stevens, 1976; Grubb & Tanner, 1976). This grouping of species in habitat niches is very often accompanied by a striking conformation in life-form, leaf-form, etc., and clearly many physiological characteristics in the vegetative adult are similar in all the species within each group. Just why the species involved should have ‘partitioned’ the physical environment into just so many sections and not more is a very deep question, e.g. why are there four main forest formations on most high tropical mountains and not two or six or twenty? Presumably patterns of vegetational history are partly involved here. Within most habitat-groups of species differentiation in the regeneration niche is almost certainly considerable.

Emphasis on the regeneration niche is also relevant to the many ordination studies made on vegetation in the last decade. Some of the axes of variation detected are bound to reflect regeneration characteristics rather than the features of the physical environment that those who ordinate usually seek to identify; in the case of the tropical rain-forest on one of the Solomon Islands some of the variation first found by an ordination analysis (Greig-Smith, Austin & Whitmore, 1967) is now known to reflect vegetation history (Whitmore, 1974).

The conclusion that species diversity has more to do with requirements for regeneration than with partitioning of the habitat niche of the adult fits well with the growing conviction of some evolutionists, e.g. Grant (1949), Stebbins (1951, 1970, 1971), Baker (1959, 1963, 1970) and van der Pijl (1960, 1961), that speciation and ultimately the differentiation of genera and families of plants have primarily to do with adaptive changes in reproductive characteristics, even though there are still many characters of taxonomic importance that are hard to explain functionally (Ehrendorfer, 1973). It seems that at all taxonomic levels evolutionary divergence may concern any aspect of the niche. Thus several families have evolved in certain narrow and well-defined habitat niches, while others have tremendously wide ranges. An inspection of any modern northern European flora will show that the ecological separation of species in most genera in that region is mainly through the habitat niche and the ecological picture is primarily one of each habitat niche being filled by a single species from several to many genera. Each genus is almost certain to be different from the next in several aspects of the regeneration niche. There are, of course, cases of species with virtually the same or very strongly overlapping habitat niches in certain genera, e.g. Carex, Cephalanthera, Orchis, Ophrys, Rosa, Trifolium. Such cases are particularly common in man-made communities and differences in the regeneration niche are presumably very important in the maintenance of co-existence there, e.g. of Plantago media and P. lanceolata in basic grassland (Sagar & Harper, 1964) or Ranunculus acris, R. bulbosus and R. repens in certain pastures (Sarukhân & Harper, 1973).

In regions of greater floristic richness than northern Europe differentiation in the regeneration niche separating species in a genus appears to be generally more impor-
tant. This is true not only of tropical regions but also of certain temperate regions, e.g. parts of northern China where the primary forests contained eight species of *Acer*, nine of *Betula*, five of *Tilia* and five of *Ulmus* (Wang, 1961).

The evolution of diversity is here envisaged as an inevitable process whereby the possible regeneration niches in the community are partitioned. There is no need to involve the idea that there are selective advantages in evolution arising from greater stability in systems of greater diversity, as suggested by MacArthur (1955) and Hutchinson (1959). This supposed increased stability is, in any case, very much questioned at the present time (May, 1975).

One of the central aims of much conservation is the preservation of diversity (Westhoff, 1971; van der Maarel, 1971) and the theme of this review is therefore highly relevant. It places an emphasis on the dynamic relations of plant communities, relations which have been repeatedly overlooked in an age when classical phytosociology, numerical analysis of vegetation and productivity studies have sapped the energies of those who might otherwise have provided a sounder basis for positive management in the conservation field. The need now is for proper attention to be paid to each stage in the regeneration cycle. The most sophisticated studies will require teams of research workers, long-term programmes and expertise in realistic modelling; however, in the recording of many of the processes involved, e.g. annual flowering and fruiting, amateur naturalists could play a vital role in the accumulation of valuable information.

VIII. SUMMARY

1. According to 'Gause's hypothesis' a corollary of the process of evolution by natural selection is that in a community at equilibrium every species must occupy a different niche. Many botanists have found this idea improbable because they have ignored the processes of regeneration in plant communities.

2. Most plant communities are longer-lived than their constituent individual plants. When an individual dies, it may or may not be replaced by an individual of the same species. It is this replacement stage which is all-important to the argument presented.

3. Several mechanisms not involving regeneration also contribute to the maintenance of species-richness:
   
   (a) differences in life-form coupled with the inability of larger plants to exhaust or cut off all resources, also the development of dependence-relationships,
   
   (b) differences in phenology coupled with tolerance of suppression,
   
   (c) fluctuations in the environment coupled with relatively small differences in competitive ability between many species,
   
   (d) the ability of certain species-pairs to form stable mixtures because of a balance of intraspecific competition against interspecific competition,
   
   (e) the production of substances more toxic to the producer-species than to the other species,
   
   (f) differences in the primary limiting mineral nutrients or pore-sizes in the soil for neighbouring plants of different species, and
(g) differences in the competitive abilities of species dependent on their physiological age coupled with the uneven-age structure of many populations.

4. The mechanisms listed above do not go far to explain the indefinite persistence in mixture of the many species in the most species-rich communities known.

5. In contrast there seem to be almost limitless possibilities for differences between species in their requirements for regeneration, i.e. the replacement of the individual plants of one generation by those of the next. This idea is illustrated for tree species and it is emphasized that foresters were the first by a wide margin to appreciate its importance.

6. The processes involved in the successful invasion of a gap by a given plant species and some characters of the gap that may be important are summarized in Table 2.

7. The definition of a plant's niche requires recognition of four components:
   (a) the habitat niche,
   (b) the life-form niche,
   (c) the phenological niche, and
   (d) the regeneration niche.

8. A brief account is given of the patterns of regeneration in different kinds of plant community to provide a background for studies of differentiation in the regeneration niche.

9. All stages in the regeneration-cycle are potentially important and examples of differentiation between species are given for each of the following stages:
   (a) Production of viable seed (including the sub-stages of flowering, pollination and seed-set),
   (b) dispersal, in space and time,
   (c) germination,
   (d) establishment, and
   (e) further development of the immature plant.

10. In the concluding discussion emphasis is placed on the following themes:
    (a) the kinds of work needed in future to prove or disprove that differentiation in the regeneration niche is the major explanation of the maintenance of species-richness in plant communities,
    (b) the relation of the present thesis to published ideas on the origin of phenological spread,
    (c) the relevance of the present thesis to the discussion on the presence of continua in vegetation,
    (d) the co-incidence of the present thesis and the emerging ideas of evolutionists about differentiation of angiosperm taxa, and
    (e) the importance of regeneration-studies for conservation.

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Maintenance of species-richness in plant communities


Maintenance of species-richness in plant communities 141


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Maintenance of species-richness in plant communities


