The University of Chicago

EVIDENCE FOR THE EXISTENCE OF THREE PRIMARY STRATEGIES IN PLANTS AND ITS RELEVANCE TO ECOLOGICAL AND EVOLUTIONARY THEORY

J. P. Grime

Unit of Comparative Plant Ecology (NERC), Department of Botany, The University, Sheffield S10 2TN, England

The external factors limiting plant biomass in any habitat may be classified into two categories. The first, which henceforth will be described as stress, consists of conditions that restrict production, e.g., shortages of light, water, or mineral nutrients and suboptimal temperatures. The second, referred to here as disturbance, is associated with the partial or total destruction of the plant biomass and arises from the activities of herbivores, pathogens, man (trampling, mowing, and plowing), and from phenomena such as wind damage, frosts, desiccation, soil erosion, and fire.

When the four permutations of high and low stress with high and low disturbance are examined (table 1), it is apparent that only three are viable as plant habitats. This is because, in highly disturbed habitats, severe stress prevents recovery or reestablishment of the vegetation. It is suggested that each of the three remaining contingencies has been associated with the evolution of a distinct type of strategy, i.e., low stress with low disturbance (competitive plants), high stress with low disturbance (stress-tolerant plants), and low stress with high disturbance (ruderal plants). These three strategies are, of course, extremes. The genotypes of the majority of plants appear to represent compromises between the conflicting selection pressures resulting from particular combinations of competition, stress, and disturbance.

In the first part of this paper, an attempt is made to define competition, stress, and disturbance more closely and to review some of the evidence, most of which refers to vascular plants, for the existence of three primary strategies.

The second part examines the implications of the three-strategy model with regard to (1) existing theories of natural selection, especially that of the r-K continuum (MacArthur and Wilson 1967; Pianka 1970); (2) secondary strategies; (3) vegetation succession; (4) dominance; and (5) strategies in fungi and in animals.

THE COMPETITIVE STRATEGY

A Definition of Competition between Plants

Wherever plants grow in close proximity, whether they are of the same or of different species, differences in vegetative growth, seed production, and plant

TABLE 1

SUGGESTED BASIS FOR THE EVOLUTION OF THREE STRATEGIES IN VASCULAR PLANTS

INTENSITY OF DISTURBANCE	INTENSITY OF STRESS	
	Low	High
Low	Competitive strategy	Stress-tolerant strategy
High.....................	Ruderal strategy	No viable strategy

mortality are observed. It would be a mistake, however, to attribute all such differences to competition, since disparities in the performance of neighboring plants may arise from differences in capacity to exploit (or in susceptibility to) features of the physical or biotic environment. If the term competition is to be useful to the analysis of vegetation mechanisms, a definition must be found which effectively distinguishes it from other processes which influence vegetation composition and species distribution.

In a most revealing paper, Milne (1961) has traced the history of biologists' attempts to define competition. He concludes that, far from achieving the necessary distinctions, a majority of authors have not sought to make them and have often used the word as a synonym for "the struggle for existence" (Darwin 1859). Perhaps because of the resulting confusion, Harper (1961) has proposed that, for the present at least, use of the term should be abandoned. However, it may be argued that competition as a process is too important and as a term is too useful to be allowed to suffer such a fate. An alternative is to apply a strict definition and to use the term as precisely as possible. Whatever the semantic difficulties, such an exercise will be justified if it facilitates the analysis of competition mechanisms.

Here, competition is defined as "the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space" (Grime 1973b, p. 311). This choice of words allows competition to be defined in relation to its mechanism rather than its effects, and the risk is avoided of confusion with mechanisms operating through the direct impact of the physiochemical environment or through biotic effects such as selective predation. The word "neighboring" is included to imply that a degree of physical intimacy is characteristic of competing plants.

Variation in the Competitive Ability of a Plant Species

A fundamental problem underlying any attempt to analyze the impact of competition in vegetation arises from the proposition, scarcely disputed among ecologists, that the competitive ability of a plant species varies according to the conditions in which it is growing. Variation in competitive ability may arise because environments differ in the extent to which they allow the competitive potential of a species to be realized. It is clear that competitive characteristics such as rapid growth in leaf area and root absorptive surface may be

inhibited by forms of stress and damage. Second, these same attributes may be subject to genetic variation. The literature provides numerous examples of intraspecific variation in competitive attributes (e.g., Clausen et al. 1940; Bradshaw 1959; Gadgil and Solbrig 1972; Mahmoud et al. 1975).

Phenotypic and genetic variation in competitive ability is not a severe impediment to the analysis of competition since it is clear that, with care, both may be recognized and taken into account. A more serious difficulty arises from the suggestion, implicit in many ecological writings, that the nature of competition itself may vary fundamentally from one field situation to another so that, relative to other species, a particular species or genotype may be a strong competitor in one site but a weak competitor in another. Inspection of the data which have been quoted in support of this view (e.g., Newman 1973; Ellenberg and Mueller-Dombois 1974) shows that often this concept has evolved in tandem with loose definitions of competition. That is, in certain cases, shifts in the fortunes of "competitors" coincident with changes in environment may be attributed more correctly to the incursion of noncompetitive effects (e.g., differential predation) rather than to any alteration in the relative abilities of the plants to compete for resources.

When noncompetitive effects have been discounted, the remaining objection to a unified concept of competitive ability arises because competition occurs with respect to several different resources including light, water, various mineral nutrients, and space. Hence it might be supposed that the ability to compete for a given resource varies independently from the ability to compete for each of the others. Moreover, the ability to compete for a given resource might be expected to change according to its availability.

There are grounds, both theoretical and empirical, for rejecting these possibilities as major sources of variation in competitive ability. A more logical interpretation is that the abilities to compete for light, water, mineral nutrients, and space are interdependent to the extent that natural selection has caused their development to a comparable extent in any particular genotype.

In circumstances which allow rapid development to a large standing crop, the most obvious competition is that occurring above ground for space and light, and it may not be immediately obvious why success should also depend upon the effective capture of water and mineral nutrients. However, as pointed out by Mahmoud and Grime (1976), it is clear that rapid buildup of a large biomass of shoot material, a prerequisite for effective above-ground competition, is dependent upon high rates of uptake of water and mineral nutrients. Consideration of the sequence of events in competition suggests that although in productive habitats the phenomenon culminates in above-ground competition for space and light, the outcome may be strongly influenced or even predetermined by earlier competition below ground.

The importance of below-ground interactions in competitions in productive environments is well illustrated by an experiment conducted by Donald (1958) involving competition between the perennial grasses *Lolium perenne* and *Phalaris tuberosa*. In this pot experiment, a system of partitions, above and below ground, was devised so that it was possible to compare the yield of each

of the two species under four treatments, i.e., competition above ground only, competition below ground only, competition above and below ground, and no competition (control). The experiment was carried out at high and low levels of nitrogen supply, but here it is only the former which is relevant to this point. The results showed that the clear advantage of *L. perenne* over *P. tuberosa* under productive conditions derived from the superior competitive ability of the species both above and below ground.

It is now necessary to turn to the vexed subject of competition in unproductive environments. The crucial problem here is to determine whether plants which occur naturally in dry, heavily shaded, or mineral deficient habitats are better able to compete for specific resources at low levels of supply than plants from productive habitats.

In searching for evidence, it is convenient first to return to Donald's (1958) experiment and in particular to consider the results obtained in the low-nitrogen treatments. These results show conclusively that the superior competitive ability exhibited by *L. perenne* under productive conditions was maintained when the two grasses competed on nitrogen-deficient soil. However, since both of the grasses in this experiment are characteristic of conditions of moderate to high fertility, it may be unwise to draw any general implication from this result.

In an experiment conducted by Mahmoud and Grime (1976), three perennial grasses of contrasted ecology were allowed to compete under productive and unproductive (low-nitrogen) conditions. One of the species, *Festuca ovina*, is restricted to unproductive sites; another, *Agrostis tenuis*, is associated with habitats of intermediate fertility; and the third, *Arrhenatherum elatius*, is a frequent dominant of productive meadows. Each species was grown in mono-culture and in separate 1 : 1 mixtures with each of the other two grasses. The results obtained in the productive treatment showed that the yield of *A. elatius* in monoculture was twice that of *A. tenuis* and approximately seven times that of *F. ovina*. In the mixtures grown under productive conditions, competition in each case was conclusive in that *F. ovina* was totally eliminated by both of the other grasses, and there were no survivors of *A. tenuis* when this species was grown with *A. elatius*. In the low-nitrogen treatment all three species showed a marked reduction in yield, and this was most pronounced in *A. elatius* and *A. tenuis*. However, there was no evidence to suggest that the competitive ability of *F. ovina* increased under conditions of nitrogen stress, and no competitive impact of *F. ovina* was detected on either of the other two species.

From this result, it would appear that the ability to compete for nitrogen plays little part in the mechanism whereby *F. ovina* is adapted to survive conditions of low soil fertility. A similar conclusion may be drawn not only with respect to nitrogen but also to other essential mineral nutrients from a number of laboratory experiments (e.g., Bradshaw et al. 1964; Hackett 1965; Clarkson 1967; Rorison 1968; Higgs and James 1969) in which plants of in-fertile habitats have been grown on nutrient-deficient soils and solution cultures. These studies provide no convincing evidence that plants indigenous to poor

soils are more efficient in the uptake of mineral nutrients when these are present at low concentrations.

An alternative explanation for the survival of plants under conditions of low soil fertility will be presented under the next heading. Essentially, this theory suggests that although competition, especially that for water and mineral nutrients, is not restricted to productive habitats, its importance in unproductive habitats is small relative to the direct impact upon the plants of those factors which cause the environment to be infertile. This argument may be extended to the full range of unproductive habitats, including those in which light and water supply are the main limiting factors. Further evidence of the decline in importance of competition in unproductive vegetation is available from a wide range of comparative studies (Ashton 1958; Pigott and Taylor 1964; Grime and Jeffrey 1965; Grime 1965, 1966; Clarkson 1967; Myerscough and Whitehead 1967; Hutchinson 1967; Loach 1970; Rorison 1968; Parsons 1968; Higgs and James 1969), from which there is accumulating evidence that, in both herbs and trees, characteristics such as rapid potential growth rate and high phenotypic plasticity with respect to the deployment of photosynthate (e.g., increase in leaf area in shade and increase in root : shoot ratio under mineral nutritional stress) become disadvantageous during extreme environmental stress.

It seems reasonable to conclude, therefore, that competition has been associated with the evolution of a distinct strategy, and that competitive ability is associated with characteristic and measurable genetic attributes (table 2) which, by maximizing the capture of resources, facilitate the exclusive occupation of fertile, relatively undisturbed environments.

As we shall see later, it is of considerable significance that no broad distinction may be drawn between herbaceous and woody species with respect to competitive ability. Perennial herbs, shrubs, and trees each appear to encompass a wide range of competitive abilities.

THE STRESS-TOLERANT STRATEGY

A Definition of Stress

Dry-matter production in vegetation is subject to a wide variety of environmetal constraints. These include not only shortages and excesses in the supply of solar energy, water, and mineral nutrients but also sub- and supraoptimal temperatures and growth-inhibiting toxins such as heavy metals from the soil or gaseous pollutants from the atmosphere. Plant species and even different genotypes may differ in susceptibility to particular forms of stress, and in consequence each stress may exercise a different effect on vegetation composition. Because many stresses may operate in the same habit over the course of a year, analyses of the impact of stress may become quite complex. Further complications arise when certain stresses either originate from or are intensified by the vegetation itself. Among the most important types of plant-induced

TABLE 2

SOME CHARACTERISTICS OF COMPETITIVE, STRESS-TOLERANT, AND RUDERAL PLANTS

	Competitive	Stress Tolerant	Ruderal
Morphology of shoot................	High dense canopy of leaves; extensive lateral spread above and below ground	Extremely wide range of growth forms	Small stature, limited lateral spread
Leaf form	Robust, often mesomorphic	Often small or leathery, or needle-like	Various, often mesomorphic
Litter	Copious, often persistent	Sparse, sometimes persistent	Sparse, not usually persistent
Maximum potential relative growth rate....	Rapid	Slow	Rapid
Life forms...................	Perennial herbs, shrubs, and trees	Lichens, perennial herbs, shrubs, and trees (often very long lived)	Annual herbs
Longevity of leaves	Relatively short	Long	Short
Phenology of leaf production	Well-defined peaks of leaf production coinciding with period(s) of maximum potential productivity	Evergreens with various patterns of leaf production	Short period of leaf production in period of high potential productivity
Phenology of flowering............	Flowers produced after (or, more rarely, before) periods of maximum potential productivity	No general relationship between time of flowering and season	Flowers produced at the end of temporarily favorable period
Proportion of annual production devoted to seeds	Small	Small	Large

stress are those arising from shading and reduction of the levels of mineral nutrients in the soil following their accumulation in the plant biomass.

In order to accommodate its diverse forms, stress will be defined simply as the external constraints which limit the rate of dry-matter production of all or part of the vegetation.

Adaptation to Severe Stress

Identification of the forms of stress characteristic of particular habitats is but one aspect of the analysis which is necessary to determine the influence of stress upon vegetation. Another requirement is to estimate the extent to which stress is limiting primary production in different types of vegetation. The need for such studies arises because the role of stress changes according to its severity. The low intensity of stress, characteristic of productive habitats, functions as a modifier of competition, whereas severe stress exercises a dominant and more immediate impact upon species composition and vegetation structure through its direct effects on survival and reproduction.

The most conspicuous effect of severe stress is to eliminate or to debilitate species of high competitive ability and to cause them to be replaced by stress-tolerant species. Although the identities of stress-tolerant species vary according to the type of stress, there is abundant evidence to suggest a basic similarity in the mechanisms whereby plants are adapted to survive different forms of severe stress. Some of this evidence will now be examined by briefly considering adaptation to severe stress in four contrasted types of habitat. In two of these (arctic-alpine and arid habitats) plant production is low and stress is mainly imposed by the environment. In the third (shaded habitats) stress is plant induced, while in the fourth (nutrient-deficient habitats) stress may be due to the low fertility of the habitat and/or to accumulation of the mineral nutrients in the vegetation.

a) Arctic and alpine habitats.—Without doubt, the dominant environmental stress in arctic and alpine habitats is low temperature. In these habitats, the opportunity for growth is limited to a short summer season. For the remainder of the year growth is prevented by low temperature, and the vegetation is either covered by snow or, where it remains exposed on ridges, is subjected to extreme cold coupled with the desiccating effect of dry winds. During the growing season, production is often severely restricted not only by low temperatures but also by desiccation and mineral nutrient stress, the latter largely a result of the low microbial activity of the soil. Alpine vegetation is subject to additional stresses peculiar to high altitudes, including strong winds and intense solar radiation.

The predominant life forms in arctic and alpine vegetation are very low-growing evergreen shrubs, small perennial herbs, bryophytes, and lichens (Billings and Mooney 1968). The adaptive significance of the small stature of all of these plants appears to be related in part to the observation that during the winter when the ground is frozen and no water is available to the roots, the aerial parts of low-growing plants tend to be insulated from desiccation

by a covering of snow. However, as suggested by Boysen-Jensen (1929), quite apart from the risk of winter kill of shoots projecting through the snow cover, the absence of larger plants and, in particular, erect shrubs and trees, is also related to the fact that the productivity of tundra and alpine habitats is so low that it is unlikely that there will be a sufficient surplus of photosynthate to sustain either wood production or the annual turnover of dry matter characteristic of deciduous trees and tall herbs.

A conspicuous feature of arctic and alpine floras is the preponderance of evergreen species. Annual plants are extremely rare, and the majority of bryophytes, lichens, herbs, and small shrubs remain green throughout the year. The advantage of the evergreen habit is particularly clear in long-lived prostrate shrubs. Here, Billings and Mooney (1968) suggest that the main advantage of the evergreen habit is that it obviates the necessity "to spend food resources on a wholly new photosynthetic apparatus each year" (p. 492).

It would appear, from the relatively small amount of information which is available, that both seed production and seedling establishment in arctic and alpine habitats are erratic and hazardous. However, as Billings and Mooney (1968) point out, this is compensated for first because the majority of species are long-lived perennials and second by the widespread occurrence of vegetative reproduction.

b) Arid habitats.—The comprehensive reviews by authors such as Walter (1973), Slatyer (1967), and Levitt (1975) make clear the pitfalls in attempting to generalize about the ways in which plants adapt to exploit conditions of low annual rainfall. However, if attention is confined to those species which in their natural habitats experience long periods of desiccating conditions without access to underground reservoirs of soil moisture, common adaptive features are apparent. These xerophytes are perennials in which the vegetative plant is adapted to survive for long periods during which little water is available. Several types of xerophytes may be distinguished according to the severity of moisture stress which they can survive.

In habitats which experience a short annual wet season, the most commonly occurring xerophytes are the sclerophylls. This group includes both small shrubs and trees, such as the evergreen oaks and the olive, all of which are distinguished by small hard leaves which are retained throughout the dry season. Walter (1973, p. 121) maintains that the ecological advantage of sclerophylly is related to the ability of sclerophyllous species "to conduct active gaseous exchange in the presence of an adequate water supply but to cut it down radically by shutting the stomata when water is scarce," a mechanism which enables these plants to "survive months of drought with neither alteration in plasma hydrature nor reduction in leaf area" and, when rains occur, to "immediately take up production again."

Under severely desiccating conditions, the most persistent of the xerophytes are the succulents, evergreens in which water is stored in swollen leaves, stems, or roots. During drought periods no water absorption occurs, but following rain, small, short-lived roots are produced extremely rapidly. Succulents are also distinguished by peculiarities in stomatal physiology and metabolism.

The stomata open at night and remain tightly closed during the day. Gaseous exchange occurs during the period of stomatal opening, at which time carbon dioxide is incorporated into organic acids. These are decarboxylated in the daylight to release carbon dioxide for photosynthesis. This mechanism, known as crassulacean acid metabolism, appears to represent a mechanism whereby low levels of photosynthesis may be maintained with minimal transpiration.

A well-known feature of many xerophytes and, in particular, the succulents is the rarity or erratic nature of flowing.

c) *Shaded habitats.*—The stresses associated with shade differ from those considered under the two previous headings in that they are not directly attributable to gross features of climate. However, although shade itself is not imposed by the physical environment, it becomes important only in climatic regimes which are conducive to the development of dense canopies. It may be important to bear in mind, therefore, that shade at its greatest intensities frequently coincides (1) with the high temperatures and humidities of tropical and subtropical climates or with the warm summer conditions of temperate regions and (2) with conditions of mineral nutrient depletion associated with the development of a large plant biomass. Hence, although the discussion which follows refers to adaptations to shade, there is a strong probability that some of the plant characteristics described are related to cotolerance of shade, warm temperatures, and mineral nutrient stress.

The effect of shading upon the growth rate and morphogenesis of shade-tolerant plants has been examined by growing various species, usually as seedlings, under screens of cotton, plastic, or metal (e.g., Burns 1923; Bordeau and Laverick 1958; Grime 1966; Loach 1970). The general conclusions which may be drawn from the results of these experiments is that the capacity to maximize dry-matter production in shade through modification of the phenotype (through increases in leaf area and reductions in root : shoot ratio) is most apparent in competitive species characteristic of unshaded or lightly shaded environments, while plants associated with deep shade tend to grow slowly and to show little morphogenetic response to shade treatment. The low rates of growth and the small extent of phenotypic response to shading in the shade-tolerant species suggest that adaptation to shade in these plants may be concerned more with the ability to survive for extended periods in deep shade than with the capacity to maximize light interception and dry-matter production. A similar conclusion is prompted by the observation that many of the more shade-tolerant plants, e.g., *Hedera helix* and *Deschampsia flexuosa*, have morphologies which allow considerable self-shading.

Among the shade-tolerant tree seedlings, climbing plants, and epiphytes of tropical rain forests are many which remain green throughout the year, and a similar phenology is evident in shade-tolerant herbs of temperate woodlands (Al-Mufti et al. 1977). An observation of considerable interest concerning the adaptive physiology of shade-tolerant plants is that of Woods and Turner (1971), who found in experimental studies with a range of North American trees that stomatal opening in response to increased light intensity was consistently more rapid in shade-tolerant species. The authors conclude that such rapid

stomatal response may allow shaded leaves to exploit brief periods of high illumination by sun flecks.

A characteristic of many shade-tolerant species is the paucity of flowering and seed production under heavily shaded conditions. This phenomenon is particularly obvious in British woodlands, where flowering in many common plants such as *H. helix*, *Lonicera periclymenum*, and *Rubus fruticosus* agg. is usually restricted to plants exposed to sunlight at the margins of woods or beneath gaps in the tree canopy.

d) Nutrient-deficient habitats.—Under this heading attention will be confined to habitats in which mineral nutrient stress arises from the impoverished nature of the habitat. It is in these habitats that mechanisms of adaptation to mineral nutrient stress have been most closely studied. However, it is vital to the arguments developed later in this paper to recognize that severe stress may also arise under conditions in which mineral nutrients are sequestered in the living or nonliving parts of the biomass.

When the range of vegetation types characteristic of severely nutrient deficient soils is examined, certain common features are immediately apparent. Although the identity of the species involved varies in different parts of the world and according to local factors such as soil type and vegetation management, similar plant morphologies may be recognized. The herbaceous component shows a marked reduction in growth form. Among the grasses, narrow-leaved creeping or rosette species predominate. Under management conditions which allow the development of woody vegetation, nutrient-deficient soils are usually colonized by small (often coniferous) trees or sclerophyllous shrubs. In Europe and North America members of the Ericaceae such as *Calluna vulgaris*, *Vaccinium myrtillus*, and *Erica cinerea* are particularly common on highly acidic soils, while on shallow nutrient-deficient calcareous soils species such as *Helianthemum chamaecistus* and *Thymus drucei* occur. The xeromorphy evident in all these shrubs could be conceived to be an adaptation to winter or summer desiccation. However, this explanation cannot be applied in the case of the xerophytic shrubs which are known to occur on infertile soils in tropical and subtropical regions. In New Caledonia, for example, Birrel and Wright (1945) described xerophyllous shrub vegetation varying between 1–2 m in height on serpentine soil and commented upon its "unusual appearance in this region of high rainfall in which tropical forest is the ordinary plant cover" (p. 72).

Another feature which is characteristic of the vegetation of nutrient-deficient soils is the high frequency of species of inherently slow growth rate. Among the first to recognize this was Kruckeberg (1954), who noted that even when growing on fertile soils certain ecotypes of herbaceous plants adapted to survive on serpentine soils in North America grew slowly in comparison with species and ecotypes from fertile habitats. Another important early contribution was that of Beadle (1954, 1962), who recognized that slow growth rates were characteristic of species of *Eucalyptus* growing on Australian soils with low phosphorus availability. Slow rates of growth were also found to occur in *Festuca ovina* and *Nardus stricta*, two grasses of widespread occurrence on infertile soils in the British Isles (Bradshaw et al. 1964). Jowett (1964) con-

cluded from his investigation with the grass *Agrostis tenuis* that the effect of natural selection under conditions of severe mineral nutrient deficiency had been to reduce the potential growth rate of local populations established on mine waste in Wales. Subsequent investigations (e.g., Hackett 1965; Clarkson 1967; Higgs and James 1969; Grime and Hunt 1975) have confirmed that there is a strong correlation between low potential growth rate and tolerance of mineral nutrient deficiencies.

It would appear, therefore, that adaptation for survival in infertile soils has involved in both woody and herbaceous species reductions in stature, in leaf form, and in potential growth rate. The explanation which has been put forward with varying degrees of elaboration by a number of authors (e.g., Kruckeberg 1954; Loveless 1961; Jowett 1964) to account for this phenomenon is that it is primarily an adaptation for survival under conditions of low mineral nutrient supply. This suggests that under conditions in which elements such as phosphorus and nitrogen are scarcely available, natural selection has led to the evolution of plant species and ecotypes which make low demands upon the mineral nutrient reserves of the soil and are therefore less likely to exhaust the supply in their immediate root environment. Consistent with this hypothesis are the results of a number of experiments in which species from infertile habitats have been grown under various levels of supply of major mineral nutrients (Bradshaw et al. 1964; Hackett 1965; Clarkson 1967). From these studies there is no convincing evidence that species normally restricted to infertile soils are better adapted than species from fertile habitats to maintain dry-matter production under conditions in which mineral nutrients are provided at low rates of supply. The results of an experiment by Bradshaw et al. (1964), for example, illustrate clearly that under low levels of nitrate nitrogen supply *F. ovina* and *N. stricta*, both grasses of infertile pastures, are outyielded by *Lolium perenne* and *Cynosurus cristatus*, species which are normally restricted to fertile soils.

An advantage which a low rate of dry-matter production appears to confer on a plant growing on an infertile soil is that during periods of the year when mineral nutrients are more readily available, uptake is likely to exceed the rate of utilization in growth allowing the accumulation of reserves which may be drawn upon during subsequent periods of stress (Clarkson 1967).

An additional feature of many of the slow-growing species characteristic of infertile soils is the lack of a sharply defined seasonal pattern of growth. The majority of woody and herbaceous species from infertile habitats are evergreen plants in which the leaves have a comparatively long life span. Measurements by Williamson (1976), for example, on grasses of derelict calcareous pastures in southern England have shown that in two evergreen species of nutrient-deficient soils, *Helictotrichon pratense* and *H. pubescens*, the functional life of the leaf is considerably longer than in *Arrhenatherum elatius* and *Dactylis glomerata* species which are associated with more fertile soil conditions and show a well-defined summer peak in leaf production. The most likely explanation for the greater longevity and slower replacement of leaves in plants of infertile habitats is that it represents an adaptation slowing the rate of nutrient

cycling between plant and soil and hence reduces the risk of nutrient loss. It would appear, therefore, that species of infertile habitats are adapted to conserve absorbed mineral nutrients rather than to maximize the quantity captured.

General Features of Stress Tolerance

From this brief survey it is apparent that vascular plants adapted to contrasted forms of severe stress exhibit a range of features which, although varying in detailed mechanisms, represent basically similar adaptations for endurance of conditions of limited productivity. These features, listed in table 2, include inherently slow rates of growth, the evergreen habit, long-lived organs, sequestration and slow turnover of carbon, mineral nutrients and water, low phenotypic plasticity, shy flowering, and the presence of mechanisms which allow the vegetative plant an opportunistic exploitation of temporarily favorable conditions. The latter consist not only of the presence throughout the year of functional leaves (and, presumably, roots also) but, in addition, special mechanisms such as the rapid activating of stomata in sclerophylls and shade plants and the rapid sprouting of roots by succulents.

As in the case of the competitive strategy, no simple generalization can be made with regard to the stature and life form of stress-tolerant plants. Although in extremely unproductive environments stress tolerance is associated with trees, shrubs, and herbs of reduced stature, account must be taken of the fact that many of the shade-tolerant trees in temperate and tropical habitats are long lived and attain a very large size at maturity. An explanation for the wide morphological variety among stress-tolerant plants is advanced later in this paper.

An additional characteristic which may be predicted for stress-tolerant plants is that of low palatability. Because of their slow growth rates, stress-tolerant plants are likely to exhibit slow rates of recovery from defoliation, and during the protracted phase of establishment, seedlings will be particularly vulnerable to damage. It would not be surprising, therefore, to find that many stress-tolerant plants had experienced intensive natural selection for resistance to predation.

Stress Tolerance and Symbiosis

(a) *Lichens*.—Three features which under the last heading have been associated with stress tolerance in flowering plants (slow growth rate, longevity, and opportunism) are expressed in a most extreme form in lichens. This is hardly surprising in view of their ecology. Lichens are able to survive in extremely harsh environments under conditions in which vascular plants are totally excluded and in which they experience extremes of temperature and moisture supply and are subject to low availability of mineral nutrients. Although there is some diversity of opinion with regard to the longevity of lichens

(see, for example, the review by Billings and Mooney [1968]), there is general agreement that many are exceedingly long lived. From experimental studies, such as those of Farrar (1976*a*, 1976*b*, 1976*c*), there is abundant evidence of the tendency of lichens to sequester a high proportion of the photosynthate rather than to expend it in growth. Much of the assimilate appears to be stored as sugar alcohols (polyols) in the fungal component. Lichens are able to remain alive during prolonged periods of desiccation and, on rewetting, to resume nutrient uptake and photosynthesis extremely rapidly.

(*b*) *Ectotrophic mycorrhizas.*—An interesting parallel may be explored between the lichens and another type of symbiosis involving fungi. In many trees and shrubs the roots develop a thick investment of fungal hyphae (ectotrophic mycorrhizas) which are connected on the inside with living cells of the root and on the outside with hyphae which are in contact with the soil and leaf litter.

A considerable amount of physiological work has been carried out to assess the ecological significance of ectotrophic mycorrhizal associations and has been reviewed extensively (Harley 1969, 1970, 1971). It has been clearly established that the uptake of mineral nutrients such as phosphorus and nitrogen may be facilitated and the yield of the host plant increased by the presence of mycorrhizal infections. Ectotrophic mycorrhizas are abundant near the soil surface, and it seems likely that they enable nutrient elements mineralized during the decay of litter to be efficiently reabsorbed into the plants.

Review of the distribution of ectotrophic mycorrhizas shows that they are strongly associated with conditions of mineral nutrient stress. These include not only vegetation types such as heathland and sclerophyllous scrub, in which the vegetation density is severely limited by the low mineral nutrient content of the habitat, but also mature temperate and tropical forests in which mineral nutrient scarcity in the soil arises from the scale of nutrient accumulation within the plant biomass.

In comparison with the roots of crop plants and species restricted to fertile soils, ectotrophic mycorrhizas appear to be long lived, and the possibility should be considered that this attribute is itself a considerable advantage to a host plant growing under conditions of severe mineral nutrient stress. In competitive herbs adapted to exploit soils with a large reservoir of available mineral nutrients, high rates of uptake are attained first through the production of a very large absorptive surface of fine roots and root hairs and second through continuous and rapid morphogenetic responses in root : shoot ratio and in the extension growth of individual parts of the root system. There is, however, continuous decay and replacement of roots, a process analogous to the rapid turnover of leaves occurring simultaneously above ground in these species. It is clear that this system of nutrient absorption, while effective in absorbing mineral nutrients, even from infertile soils, is achieved through a high expenditure of photosynthate. The main benefit of a mycorrhizal association to a host plant growing under conditions of mineral nutrient stress may be an absorptive system which, because it remains functional over a long time, allows exploitation of temporary periods of mineral nutrient availability at lower cost to the synthetic resources of the plant.

A Definition of Disturbance

Reference has been made under the preceding heading to a variety of habitats in which the density of living and dead plant material is low because production is severely restricted by environmental stress. It is quite clear, however, that low vegetation densities are not confined to unproductive habitats. Some of the world's most productive terrestrial environments, including many arable fields, are characterized by a rather sparce vegetation cover. Here the low densities arise because the vegetation is subject to partial or total destruction.

Although more obvious in habitats such as arable land, the effects of damage upon vegetation are ubiquitous. The amount of vegetation and the ratio of living to dead plant material in any habitat at any point in time depend upon the balance between the processes of production and destruction.

Even within one environment there may be considerable variety in the mechanisms which bring about the destruction of living or dead vegetation components. In addition to natural catastrophies (e.g., floods and windstorms) and the more drastic forms of human impact (e.g., plowing, mowing, trampling, and burning), account must be taken of more subtle effects, i.e., seasonal, fluctuations in climate or the activities of herbivores, decomposing organisms, and pathogens.

Forms of disturbance differ with respect to their selectivity. While the effects of herbivores and decomposing organisms tend to be restricted to the living and the dead material, respectively, certain phenomena, e.g., fire, may affect both components of the vegetation. In general, there is an inverse correlation between degree of selectivity and intensity of disturbance, a relationship which may be exemplified at one extreme by molecular discrimination between litter constituents by microbial decomposing organisms and at the other by the total vegetation destruction associated with phenomena such as severe soil erosion.

Among the forms of disturbance which affect living components, a distinction may be drawn between mechanisms which involve the immediate removal of plant structures from the habitat (e.g., grazing, mowing) and those in which plant material is killed but remains in situ (e.g., frost, drought, applications of herbicides). In the latter, destruction usually proceeds in two stages. An initial rapid loss of solutes is followed by a rather longer phase in which the residue of plant structures is attacked by decomposing organisms.

To analyze the primary mechanism of vegetation, a term is required which encompasses this wide range of phenomena yet can be simply defined. The term used here is *disturbance*, which may be said to consist of the mechanisms which limit the plant biomass by causing its destruction.

Adaptation to Severe Disturbance

Just as the impact of stress upon vegetation changes according to its intensity, so also does that of disturbance. Whereas in potentially productive environments a low intensity of disturbance modifies the balance between competitive

species, severe disturbance selects species with phenologies adapted to exploit temporarily favorable conditions.

Flowering plants adapted to persistent and severe disturbance (henceforth described as ruderals) have several features in common (table 2). The most consistent among these is the tendency for the life cycle to be that of the annual or short-lived perennial, a specialization clearly adapted to exploit environments intermittently favorable for rapid plant growth. A related characteristic of many ruderals is the capacity for high rates of dry-matter production (Baker 1965; Grime and Hunt 1975), a feature which appears to facilitate rapid completion of the life cycle and maximizes seed production. In ruderal plants a large proportion of the photosynthate is directed into seeds, and under conditions of stress seed production is usually maintained at the expense of a curtailment of vegetative development (Salisbury 1942; Harper 1961; Harper and Ogden 1970).

A feature of the reproductive biology of many ruderals, especially the weeds of arable fields (Barton 1961), is the ability of buried seeds to survive in the soil for long periods and, if the climate is favorable, to germinate rapidly when disturbance either exposes the seeds to light or, through removal of the insulating effect of foliage and litter, causes buried seeds of certain species to experience large diurnal fluctuations of temperature (Thompson et al. 1977).

THEORETICAL IMPLICATIONS

C-, S-, and R-Selection

The information reviewed here suggests that, during the evolution of plants, three fundamentally different forms of natural selection have occurred. The first of these (C-selection) has involved selection for highly competitive ability which depends upon plant characteristics that maximize vegetative growth in productive, relatively undisturbed conditions. The second (S-selection) has brought about reductions in both vegetative and reproductive vigor, adaptations which allow endurance of continuously unproductive conditions arising from environmental stress, severe resource depletion by the vegetation, or the combined effect of the two. The third (R-selection) is associated with a short life span and with high seed production and has evolved in severely disturbed but potentially productive environments.

It is concluded that R-selected (ruderal), S-selected (stress-tolerant), and C-selected (competitive) plants each possess a distinct family of genetic characteristics, and an attempt has been made in table 2 to list some of these.

A crucial genetic difference between competitive, stress-tolerant, and ruderal plants concerns the form and extent of phenotypic response to stress. Many of the stresses which are a persistent feature of the environments of stress-tolerant plants are experienced, although less frequently and in different contexts, by competitive and ruderal plants. From the evidence reviewed here, competitive, stress-tolerant, and ruderal plants seem to exhibit three quite distinct types of response to stress. It is concluded that such differences constitute one of the more fundamental criteria whereby the three strategies may be distinguished.

In table 3, an attempt has been made (1) to compare the circumstances in which competitive, stress-tolerant, and ruderal plants are normally exposed to major forms of stress; (2) to describe the stress response characteristic of each strategy; and (3) to predict the different consequences attending each type of response in different ecological situations.

It is concluded that the small degree of phenotypic response which is associated with endurance of protracted and severe stress in stress-tolerant plants is of low survival value in situations where stress is a prelude to either competitive exclusion or to disturbance by phenomena such as drought. Similarly, the rapid and highly plastic stress responses of competitive plants (tending to maximize vegetative growth) and of ruderals (tending to curtail vegetative growth and maximize seed production) are highly advantageous only in the specific circumstances associated, respectively, with competition and disturbance.

r- and K-Selection

It is interesting to compare the concept of C-, S-, and R-selection with those derived from previous attempts to identify strategies in plants (e.g., Harper and Ogden 1970; Gadgil and Solbrig 1972). These authors have been mainly concerned to extend to plants concepts originally applied to animals (Cody 1966; MacArthur and Wilson 1967).

The most generally accepted theory to emerge from earlier studies with both animals and plants is the concept of r- and K-selection, originally proposed by MacArthur and Wilson (1967) and expanded by Pianka (1970). This theory recognizes two types of organisms as opposite poles in the evolutionary spectrum. The first, said to be K-selected, consists of organisms in which the life expectancy of the individual is long and the proportion of the energy and other captured resources devoted to reproduction is small. The second, or r-selected type, is made up of organisms with a short life expectancy and large reproductive effort. It is now widely accepted that the majority of organisms fall between the extremes of r- and K-selection. More recent evidence (e.g., Gadgil and Solbrig 1972) suggests that genetic variation may cause populations of the same species to occupy different positions along an r-K continuum.

The diagram in figure 1 attempts to reconcile the concept of the three primary plant strategies with that of r- and K-selection. It is suggested that the ruderal and stress-tolerant strategies correspond, respectively, to the extremes of r- and K-selection, and that highly competitive species occupy an intermediate position. This relationship is consistent with the model proposed later to explain the involvement of the three strategies in the process of vegetation succession.

The most substantial way in which the three-strategy model differs from that of the r-K continuum lies in recognition of stress tolerance as a distinct strategy evolved in intrinsically unproductive habitats or under conditions of extreme resource depletion induced by the vegetation itself. Inspection of figure 1 suggests that there are two critical points along the r-K continuum. At (1), the intensity of disturbance becomes insufficient to prevent the exclusion of ruderals by competitors, while at (2) the level of supply of resources is depleted

TABLE 3

MORPHOGENETIC RESPONSES TO DESICCATION, SHADING, OR MINERAL NUTRIENT STRESS OF COMPETITIVE, STRESS-TOLERANT, AND RUDERAL PLANTS AND THEIR ECOLOGICAL CONSEQUENCES IN THREE TYPES OF HABITAT

STRATEGY	RESPONSE TO STRESS	CONSEQUENCES		
		Habitat 1*	Habitat 2†	Habitat 3‡
Competitive	Large and rapid changes in root: shoot ratio, leaf area, and root surface area	Tendency to sustain high rates of uptake of water and mineral nutrients to maintain dry-matter production under stress and to succeed in competition	Tendency to exhaust reserves of water and/or mineral nutrients both in rhizosphere and within the plant; etiolation in response to shade increases susceptibility to fungal attack	Failure rapidly to produce seeds reduces chance of rehabilitation after disturbance
Stress tolerant ...	Changes in morphology slow and often small in magnitude	Overgrown by competitors	Conservative utilization of water, mineral nutrients, and photosynthate allows survival over long periods in which little dry-matter production is possible	
Ruderal..........	Rapid curtailment of vegetative growth and diversion of resources into seed production		Chronically low seed production fails to compensate for high rate of mortality	Rapid production of seeds ensures rehabilitation after disturbance

* In the early successional stages of productive, undisturbed habitats (stresses mainly plant induced and coinciding with competition).
† In either continuously unproductive habitats (stresses more or less constant and due to unfavorable climate and/or soil) or in the late stages of succession in productive habitats.
‡ In severely disturbed, potentially productive habitats (stresses either a prelude to disturbance, e.g., moisture stress preceding drought fatalities, or plant induced, between periods of disturbance).
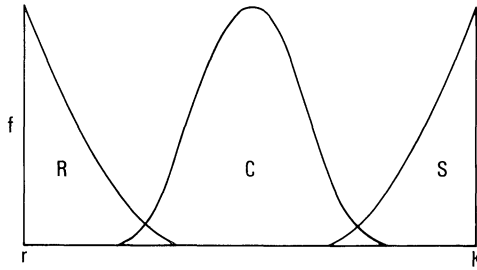
FIG. 1.—Diagram describing the frequency (f) of ruderal (R), competitive (C), and stress-tolerant (S) strategies along the r-K continuum. An explanation of the significance of critical points (1) and (2) is included in the text.

below the level required to sustain the high rates of growth characteristic of competitors, and selection begins to favor the more conservative physiologies of the stress tolerators.

The scheme represented in figure 1 is, however, both incomplete and misleading. This is because the linear arrangement of the three primary strategies does not provide for the existence of the wide range of equilibria which may exist between stress, disturbance, and competition and which has provided conditions for the evolution of the various types of "secondary" strategy described under the next heading.

Secondary Strategies

So far, it has been convenient to concentrate on plants which belong to one or another of the three primary strategies. However, it is clear that between the three extremes there are plants which are adapted to intermediate intensities of competition, stress, and disturbance.

The triangular model (Grime 1974) reproduced in figure 2 describes the various equilibria which are possible between competition, stress, and disturbance and recognizes four main types of secondary strategies which appear to have evolved in relation to particular equilibria. These consist of: (1) competitive ruderals (C-R)—adapted to circumstances in which there is a low impact of stress and competition is restricted to a moderate intensity by disturbance (e.g., fertile cattle pastures and meadows); (2) stress-tolerant competitors (C-S) —adapted to undisturbed conditions experiencing moderate intensities of stress (e.g., open forest or scrub on infertile soils); (3) stress-tolerant ruderals (S-R)—adapted to lightly disturbed unproductive habitats (e.g., droughted rock outcrops and crevices in cliffs and walls); (4) "C-S-R plants"—confined to habitats in which competition is restricted to moderate intensities by the combined effects of stress and disturbance (e.g., unfertilized pastures and meadows).

A detailed analysis of the secondary strategies is beyond the scope of this paper. However, it is possible to draw a general perspective with regard to the range of strategies encompassed by certain life forms or taxonomic groups. It
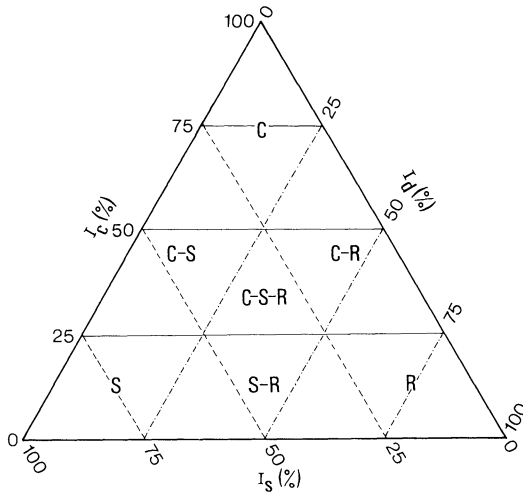
FIG. 2.—Model describing the various equilibria between competition, stress, and disturbance in vegetation and the location of primary and secondary strategies. I_c—relative importance of competition (———), I_s—relative importance of stress (– – –), I_d—relative importance of disturbance (·—·—·). A key to the symbols for the strategies is included in the text.

has been noted already that quite distinct life forms occur among the competitors and stress tolerators. In figure 3 this observation has been extended to include the secondary strategies by attempting to map the approximate distribution of selected life forms and taxa within the triangular model. This figure suggests that perennial herbs and ferns include the widest range of strategies. Annual herbs are mainly restricted to severely disturbed habitats, while biennials become prominent in the areas of the triangle corresponding to the competitive ruderals and the stress-tolerant ruderals. Trees and shrubs comprise competitors, stress-tolerant competitors, and stress tolerators. Although lichens are confined to the stress-tolerant corner of the model, bryophytes are more wide ranging with the center of the distribution in the stress-tolerant ruderals.

Vegetation Succession

Whereas the ruderal strategy comprises a fairly homogeneous group of ephemeral plants with many similarities in life history and ecology, the competitors consist of a wide range of plant forms including perennial herbs, shrubs, and trees. However, the most remarkable conjunctions in plant form and ecology occur within the stress tolerators, where we find such apparently diverse organisms as lichens and some forest trees.

In order to explain the adaptive significance of the morphological variety among the ranks of the competitors and stress tolerators, it is necessary to refer to the process of secondary (Horn 1974) vegetation succession.
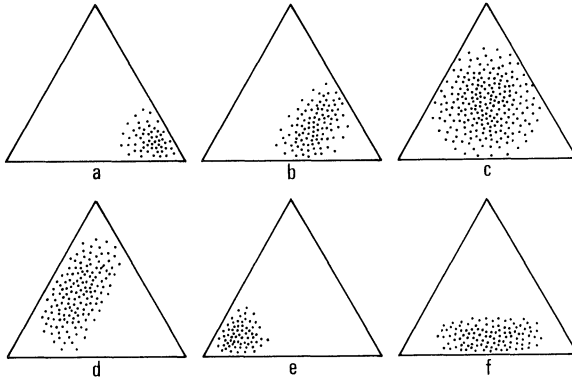
FIG. 3.—Diagrams describing the range of strategies encompassed by (*a*) annual herbs, (*b*) biennial herbs, (*c*) perennial herbs and ferns, (*d*) trees and shrubs, (*e*) lichens, and (*f*) bryophytes. For the distribution of strategies within the triangle, see figure 2.

A major factor determining the relative importance of the three primary strategies in vegetation succession is the potential productivity of the habitat. The model in figure 4 summarizes the influence of potential productivity on vegetation succession.

The model consists of an equilateral triangle in which variation in the relative importance of competition, stress, and disturbance as determinants of the vegetation is the same as that indicated by the three sets of contours in figure 2. At their respective corners of the triangle, competitors, stress tolerators, and ruderals become the exclusive constituents of the vegetation. The curves S_1, S_2, and S_3 describe, respectively, the path of succession in conditions of high, moderate, and low potential productivity, while the circles superimposed on the curves represent the relative size of the plant biomass at each stage of the succession. By comparing the course of these curves with the distributions illustrated in figure 3, it is possible to recognize the probable sequence of life forms in each succession. In the most productive habitat, the course of succession (S_1) is characterized by a middle phase of intense competition in which first competitive herbs then competitive, shade-intolerant shrubs and trees (e.g., *Rhus glabra, Ailanthus altissima*) dominate the vegetation. This is followed by a terminal phase in which stress tolerance becomes progressively more important as shading and nutrient stress coincide with the development of a large plant biomass dominated by large, long-lived forest trees. Where succession occurs in less productive habitats (S_2), the appearance of highly competitive species is prevented by the earlier onset of resource depletion; the stress-tolerant phase is associated with dominance by smaller slow-growing trees and shrubs in various vegetation types of lower biomass than those obtained at a comparable stage in S_1. In an unproductive habitat, the plant biomass remains low; the dominant life forms include lichens, bryophytes, small herbs, and dwarf shrubs; and the path of succession (S_3) moves almost
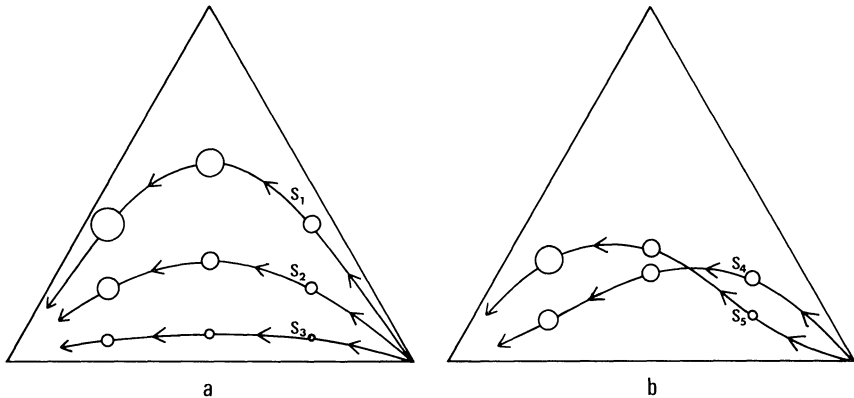
FIG. 4.—Diagrams representing the path of vegetation succession (a) under conditions of high (S_1), moderate (S_2), and low (S_3) potential productivity and (b) under conditions of increasing (S_4) and decreasing (S_5) potential productivity. The size of the plant biomass at each stage of succession is indicated by the circles. For the distribution of strategies and life forms within the triangle, see figures 2 and 3, respectively.

directly from the ruderal to the stress-tolerant phase. Under extremely un-productive conditions it seems likely that the ruderal phase may disappear altogether, and that vegetation succession will simply involve a slow progression from small to larger stress-tolerant life forms.

The curves S_1–S_3 refer to successions under conditions of fixed potential productivity, a situation which is unlikely to occur in nature. In most habitats, the process is associated with a progressive gain or loss in potential productivity. Increase in productivity, for example, may arise from nitrogen fixation or input of agricultural fertilizer. Conversely, losses of mineral nutrients may result from the harvesting of crops or from leaching of the soil. In figure 4 curves have been drawn to describe courses of succession theoretically possible under conditions of increasing (S_4) and decreasing (S_5) potential productivity.

Dominance

For both plants and animals, there is abundant evidence of the advantage of larger size in many of the interactions which occur either between species or between individuals of the same species (e.g., Black 1958; Bronson 1964; Miller 1968; Grant 1970; Grime 1973a). In natural vegetation, examples of the impact of plant size are widespread. A consistent feature of vegetation succession is the incursion of plants of greater stature, and at each stage of succession the major components of the plant biomass are usually the species with the largest life forms. It is necessary, therefore, to acknowledge the existence of another dimension—that of dominance—in the mechanism controlling the composition of plant communities and the differentiation of vegetation types.

In attempting to analyze the nature of dominance it is helpful to recognize two components: (*a*) the mechanism whereby the dominant plant achieves a size larger than that of its associates (this mechanism will vary according to which strategy is favored by the habitat conditions); (*b*) the deleterious effects which large plants may exert upon the fitness of smaller neighbors (the form of these effects does not vary substantially according to habitat or strategy, and they consist principally of the forms of stress which arise from shading, deposition of leaf litter, and depletion of mineral nutrients and water in the soil).

It is suggested, first, that dominance depends upon a positive feedback between (*a*) and (*b*), and second, that because of the variable nature of (*a*), different types of dominance may be recognized. In particular, a distinction can be drawn between "competitive" and "stress-tolerant" dominants. In the former, large stature depends upon a high rate of uptake of resources from the environment, while in the latter it is related to the ability to sustain slow rates of growth under limiting conditions over a very long period.

Strategies in Fungi and in Animals

The evidence reviewed here suggests that autotrophic plants conform to three basic strategies and to various compromises between them. It is therefore interesting to consider whether the same pattern obtains in heterotrophic organisms.

In fungi, there is strong evidence of the existence of strategies corresponding to those recognized in green plants. "Ruderal" life-styles are particularly characteristic of the *Mucorales*, in which most species are ephemeral colonists of organic substrates. These fungi grow exceedingly rapidly and exploit the initial abundance of sugars, but as the supply of soluble carbohydrate declines, they cease mycelial growth and sporulate profusely. "Competitive" characteristics are evident in fungi such as *Merculius lacrymans* and *Armillaria mellea*, which are responsible for long-term infections of timber and produce a consolidated mycelium which may extend rapidly through the production of rhizomorphs. Examples of "stress-tolerant" fungi appear to include the slow-growing basidiomycetes, which form the terminal stages of fungal succession on decaying matter, and the various fungi that occur in lichens and ectotrophic mycorrhizas. All of the "stress-tolerant" fungi are characterized by slow-growing, relatively persistent mycelia and low reproductive effort.

In the animal kingdom, "ruderal" life histories occur in both herbivores and carnivores. They are particularly common in insects (e.g., aphids, blowflies) where, as in ruderal plants, populations expand and contract rapidly in response to conditions of temporary abundance in food supply.

Earlier in this paper it was pointed out that the outstanding characteristic of competitive plants is the possession of mechanisms of phenotypic response which maximize the capture of resources. It was argued that these mechanisms are advantageous only in environments in which high rates of absorption of light, water, and mineral nutrients can be sustained. The same principle may apply in many animals, and a direct analogy may be drawn between the pheno-

typic responses of competitive plants and the activities associated with food gathering and defense of feeding and reproductive territory which are characteristic of the majority of mammals and birds in stable productive environments. Support for this hypothesis is contained in a recent review by Horn (1974), who describes as "competitively superior" the birds which characterize the second phase of avian succession and "reduce the equilibrial level of resources" during the recolonization of defaunated islands.

Consideration of the basic principles of feeding behavior (Emlen 1966; MacArthur and Pianka 1966; Schoener 1969) suggests that in extreme habitats where food is scarce, the level and frequency of food capture may be too low and the risks of environmental stress (e.g., desiccation, hypothermia) too great to permit domination of the fauna by species which indulge in very active methods of food gathering. Studies of the animals which occur in habitats such as deserts (Pianka 1966; Tinkle 1969) and coral reefs (Odum and Odum 1955; Muscatine and Cernichiari 1969; Goreau and Yonge 1971) indicate that, in the most unproductive environments, strategies of active food gathering give way to feeding mechanisms which are more conservative and appear to be analogous to the assimilatory specializations observed in stress-tolerant plants.

SUMMARY

It is suggested that evolution in plants may be associated with the emergence of three primary strategies, each of which may be identified by reference to a number of characteristics including morphological features, resource allocation, phenology, and response to stress. The competitive strategy prevails in productive, relatively undisturbed vegetation, the stress-tolerant strategy is associated with continuously unproductive conditions, and the ruderal strategy is characteristic of severely disturbed but potentially productive habitats.

A triangular model based upon the three strategies may be reconciled with the theory of r- and K-selection, provides an insight into the processes of vegetation succession and dominance, and appears to be capable of extension to fungi and to animals.

LITERATURE CITED

Al-Mufti, M. M., C. L. Wall, S. B. Furness, J. P. Grime, and S. R. Band. 1977. A quantitative analysis of plant phenology and dominance in herbaceous vegetation. J. Ecol. 65 (in press).

Ashton, D. H. 1958. The ecology of *Eucalyptus regnans* F. Muell: the species and its frost resistance. Australian J. Bot. 6:154–176.

Baker, H. G. 1965. Characteristics and modes of orgin of weeds. Pages 147–168 *in* H. G.

Baker and G. L. Stebbins, eds. The genetics of colonizing species. Academic Press, New York. 588 pp.

Barton, L. V. 1961. Seed preservation and longevity. Hill, London. 216 pp.

Beadle, N. C. W. 1954. Soil phosphate and the delimitation of plant communities in eastern Australia. I. Ecology 35:370–375.

———. 1962. Soil phosphate and the delimitation of plant communities in eastern Australia. II. Ecology 43:281–288.

Billings, W. D., and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biol. Rev. 43:481–529.

Birrel, K. S., and A. C. S. Wright. 1945. A serpentine soil in New Caledonia. New Zeal. J. Sci. Technol. 27A:72–76.

Black, J. M. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light micro climate. Australian J. Agr. Res. 9:299–312.

Bordeau, P. F., and M. L. Laverick. 1958. Tolerance and photosynthetic adaptability to light intensity in white pine, red pine, hemlock and ailanthus seedlings. Forest Sci. 4:196–207.

Boysen-Jensen, P. 1929. Studier over Skovtracerres Forhold til Lyset. Dansk Skovforeningens Tidsskrift 14:5–31.

Bradshaw, A. D. 1959. Population differentiation in *Agrostis tenuis* Sibth. I. Morphological differentiation. New Phytol. 58:208–227.

Bradshaw, A. D., M. J. Chadwick, D. Jowett, and R. W. Snaydon. 1964. Experimental investigations into the mineral nutrition of several grass species. IV. Nitrogen level. J. Ecol. 52:665–676.

Bronson, F. W. 1964. Agonistic behavior in woodchucks. Anim. Behav. 12:270–278.

Burns, G. P. 1923. Studies in tolerance of New England forest trees. IV. Minimum light requirement referred to a definite standard. Bull. Vermont. Agr. Exp. Sta. 235.

Clarkson, D. T. 1967. Phosphorus supply and growth rate in species of *Agrostis* L. J. Ecol. 55:111–118.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Washington Pub. 520.

Cody, M. 1966. A general theory of clutch size. Evolution 20:174–184.

Darwin, C. 1859. The origin of species by means of natural selection or the preservation of favored races in the struggle for life. Murray, London. 251 pp.

Donald, C. M. 1958. The interaction of competition for light and for nutrients. Australian J. Agr. Res. 9:421–432.

Ellenberg, J., and D. Mueller-Dombois. 1974. Aims and methods of vegetation ecology. Wiley, New York. 547 pp.

Emlen, J. M. 1966. The role of time and energy in food preference. Amer. Natur. 100:611–617.

Farrar, J. F. 1976a. Ecological physiology of the lichen *Hypogymnia physodes*. II. Effects of wetting and drying cycles and the concept of physiological buffering. New Phytol. 77:105–113.

———. 1976b. Ecological physiology of the lichen *Hypogymnia physodes*. III. The importance of the rewetting phase. New Phytol. 77:115–125.

———. 1976c. The uptake and metabolism of phosphate by the lichen *Hypogymnia physodes*. New Phytol. 77:127–134.

Gadgil, M., and O. T. Solbrig. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. Amer. Natur. 106:14–31.

Goreau, N. I., and C. M. Yonge. 1971. Reef corals: autotrophs or heterotrophs? Biol. Bull. Marine Biol. Lab., Woods Hole 141:247–260.

Grant, P. R. 1970. Experimental studies of competitive interactions in a two-species system. II. The behavior of *Microtus*, *Peromyscus* and *Clethrionomys* species. Anim. Behav. 18:411–426.

Grime, J. P. 1965. Comparative experiments as a key to the ecology of flowering plants. Ecology 45:513–515.

———. 1966. Shade avoidance and tolerance in flowering plants. Pages 281–301 *in* R. Bainbridge, G. C. Evans, and O. Rackham, eds. Light as an ecological factor. Blackwell, Oxford.

———. 1973*a*. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

———. 1973*b*. Competition and diversity in herbaceous vegetation—a reply. Nature 244: 310–311.

———. 1974. Vegetation classification by reference to strategies. Nature 250:26–31.

Grime, J. P., and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. J. Ecol. 63:393–422.

Grime, J. P., and D. W. Jeffrey. 1965. Seedling establishment in vertical gradients of sunlight. J. Ecol. 53:621–642.

Hackett, C. 1965. Ecological aspects of the nutrition of *Deschampsia flexuosa* (L.) Trin. II. The effects of Al, Ca, Fe, K, Mn, N, P and pH on the growth of seedlings and established plants. J. Ecol. 53:315.

Harley, J. L. 1969. The biology of Mycorrhiza. 2d ed. Hill, London. 334 pp.

———. 1970. Mycorrhiza and nutrient uptake in forest trees. Pages 163–178 *in* L. Luckwill and C. Cutting, eds. Physiology of tree crops. Academic Press, New York.

———. 1971. Fungi in ecosystems. J. Ecol. 59:653–686.

Harper, J. L. 1961. Approaches to the study of plant competition. Symp. Soc. Exp. Biol. 15:1–39.

Harper, J. L., and J. Ogden. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. J. Ecol. 58:681–698.

Higgs, D. E. B., and D. B. James. 1969. Comparative studies on the biology of upland grasses. I. Rate of dry matter production and its control in four grass species. J. Ecol 57:553–563.

Horn, H. S. 1974. The ecology of secondary succession. Annu. Rev. Ecol. Syst. 5:25–37.

Hutchinson, T. C. 1967. Comparative studies of the ability of species to withstand prolonged periods of darkness. J. Ecol. 55:291–299.

Jowett, D. 1964. Population studies on lead-tolerant *Agrostis tenuis*. Evolution 18:70–80.

Kruckeberg, A. R. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. Ecology 35:267–274.

Levitt, J. 1975. Responses of plants to environmental stresses. Academic Press, New York. 697 pp.

Loach, K. 1970. Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. New Phytol. 69:273–286.

Loveless, A. R. 1961. A nutritional interpretation of sclerophylly based on differences in chemical composition of sclerophyllous and mesophytic leaves. Ann. Bot., N.S., 25:168–176.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. Amer. Natur. 100:603–609.

MacArthur, R. H., and E. D. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J. 203 pp.

Mahmoud, A., and J. P. Grime. 1976. An analysis of competitive ability in three perennial grasses. New Phytol. 77:431–435.

Mahmoud, A., J. P. Grime, and S. B. Furness. 1975. Polymorphism in *Arrhenatherum elatius* (L.) Beauv. ex. J. & C. Presl. New Phytol. 75:269–276.

Miller, R. S. 1968. Conditions of competition between redwings and yellow-headed blackbirds. J. Anim. Ecol. 37:43–62.

Milne, A. 1961. Definition of competition among animals. Pages 40–61 *in* F. L. Milnthorpe, ed. Mechanisms in biological competition. Cambridge University Press, London.

Muscatine, L., and E. Cernichiari. 1969. Assimilation of photosynthetic products of zooxanthellae by a reef coral. Biol. Bull. 137:506–523.

Myerscough, P. J., and F. H. Whitehead. 1967. Comparative biology of *Tussilago farfara* L.

and *Epilobium adenocaulon* Hausskn. II. Growth and ecology. New Phytol. 66: 785–823.

Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. Nature 244:310.

Odum, H. T., and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25:291–320.

Parsons, R. F. 1968. The significance of growth rate comparisons for plant ecology. Amer. Natur. 102:595–597.

Pianka, E. R. 1966. Convexity, desert lizards and spatial heterogeneity. Ecology 47:1055–1059.

———. 1970. On *r*- and *K*-selection. Amer. Natur. 104:592–597.

Pigott, C. D., and K. Taylor. 1964. The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. J. Ecol. 52:175–185.

Rorison, I. H. 1968. The response to phosphorus of some ecologically distinct plant species. I. Growth rates and phosphorus absorption. New Phytol. 67:913–923.

Salisbury, E. J. 1942. The reproductive capacity of plants. Bell, London. 244 pp.

Schoener, T. W. 1969. Models of optimal size for solitary predators. Amer. Natur. 103:277–313.

Slatyer, R. O. 1967. Plant-water relationships. Academic Press, London. 366 pp.

Thompson, K., J. P. Grime, and G. Mason. 1977. Seed germination in response to diurnal fluctuations of temperature. Nature 67:147–149.

Tinkle, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. Amer. Natur. 103:501–515.

Walter, H. 1973. Vegetation of the Earth in relation to climate and the ecophysiological conditions. English Universities Press, London. 237 pp.

Williamson, P. 1976. Above-ground primary production of chalk grassland allowing for leaf death. J. Ecol. 64:1059–1075.

Woods, D. B., and N. C. Turner. 1971. Stomatal response to changing light by four tree species of varying shade tolerance. New Phytol. 70:77–84.