excerpts from Ch 2
- Figures 12, 18, 19, 20

Chapter 2

Secondary strategies in the established phase

INTRODUCTION

The environments which, in Chapter 1, have been associated with the occurrence of competitors, stress-tolerators, and ruderals form only part of the spectrum of habitats available to plants. It seems reasonable to suppose, therefore, that in addition to the three extremes of evolutionary specialization there will be various secondary strategies which have evolved in habitats experiencing intermediate intensities of competition, stress, and disturbance.

The model drawn in Figure 12 illustrates the conditions in which various types of secondary strategies may be expected to occur. 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 indicated by three sets of contours. At their respective corners of the triangle, competitors, stress-tolerators, and ruderals become the exclusive constituents of the vegetation and the remaining areas of the triangle correspond to the various equilibria which are possible between competition, stress, and disturbance. Four main types of secondary strategy are proposed. 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;
2. *stress-tolerant ruderals* (S–R)—adapted to lightly-disturbed, unproductive habitats;
3. *stress-tolerant competitors* (C–S)—adapted to relatively undisturbed conditions experiencing moderate intensities of stress;
4. *'C–S–R strategists'*—adapted to habitats in which the level of competition is restricted by moderate intensities of both stress and disturbance.

From both field and laboratory investigations, there is evidence confirming the existence of these strategies and it would appear that the criteria which have

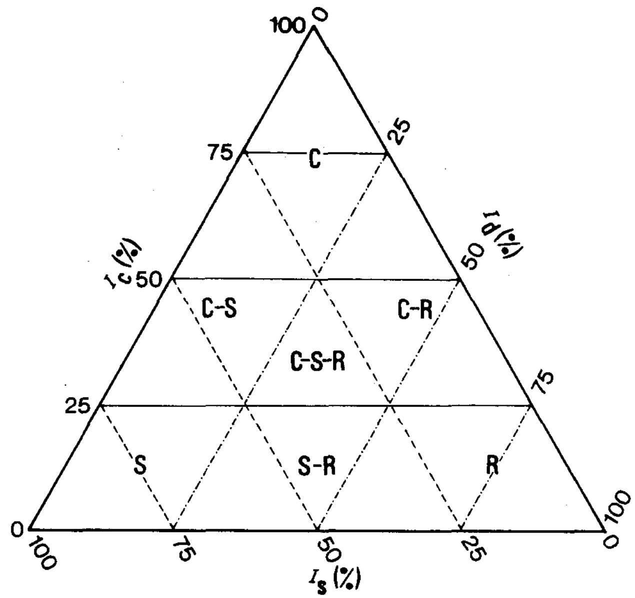

Figure 12 Model describing the various equilibria between competition, stress, and disturbance in vegetation and the location of primary and secondary strategies. I_c, relative importance of competition (——); I_s, relative importance of stress (– – –); I_d, relative importance of disturbance (–·–·–). A key to the symbols for the strategies is included in the text. (Reproduced from *American Naturalist*, **111**, by permission of the University of Chicago Press. ©1977. The University of Chicago Press.)

been used to define the primary strategies (Table 6) also provide a basis for recognition of the secondary strategies. Until comparative studies have been conducted on the ecology, life-histories, and physiology of a wider range of plants, a comprehensive account of the four secondary strategies cannot be attempted. However, mainly by reference to herbaceous plants of temperate environments, an attempt can be made to illustrate some of their key characteristics. Although, in the descriptions which follow, attention is confined to the established phase of the life-cycle, it is worth noting that certain of the secondary strategies usually occur in combination with particular regenerative strategies. An assessment of the significance of certain associations between secondary strategies and regenerative strategies is attempted at the end of Chapter 3.

COMPETITIVE-RUDERALS

The competitive-ruderals occur in habitats of high productivity in which dominance of the vegetation by competitors is prevented by disturbance. In *scorodonia*) the creeping shoots bear leaves and occasional adventitious roots along their entire length, whilst in others (e.g. *Fragaria vesca, Hieracium pilosella, Rubus saxatilis*) the shoots are in the form of stolons which are capable of producing daughter rosettes, which although often situated at considerable distance from the parent plant remain connected at least during the first year of their existence. It is tempting to interpret these growth-forms mainly in relation to the process of vegetative propagation. However, without denying this function, another possibility should be considered. A characteristic of the ecology of many, if not all, of these species is the association with habitats such as rock outcrops, screes, and quarry heaps, in which a high proportion of the ground surface is covered by stone. In this type of habitat opportunities for rooting are extremely localized and dense leaf canopies tend to develop above the areas where soil is accessible. In such circumstances it is apparent that a selective advantage may accrue to species which can absorb water and mineral nutrients from one part of the environmental mosaic, and photosynthesize in another, i.e. plants with growth forms which cause leaves to be subtended over areas of bare rock situated at a considerable distance from the roots. It seems reasonable to suggest that such growth forms may allow exploitation of gaps in herbaceous canopies which are inaccessible to the majority of neighbouring herbs.*

CONCLUSIONS

From the evidence reviewed in this chapter it would appear that plant strategies in the established phase of the life-cycle may be classified by reference to a defined range of equilibria between stress, disturbance, and competition. This classification introduces more subtlety in the recognition of strategies and allows some observations to be made concerning the strategic range of particular life-forms and taxonomic groups.

The relationship between strategy and life-form

In Figure 18 an attempt has been made to describe the approximate strategic range of selected life-forms. The widest range of strategies is that attributed to perennial herbs and ferns. Annual herbs are predominantly ruderal whilst biennial herbs become prominent in the areas of the triangular model 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 centre of the distribution in the stress-tolerant ruderals.

* In passing it is interesting to observe that the same explanation can be applied on a larger scale to the creeping growth-forms associated with the pools and bare mud in marshes (*Ranunculus repens, Agrostis stolonifera*), woodland hollows filled with persistent tree litter (*Rubus fruticosus, Galeobdolon luteum*), and walls, cliffs, and tree trunks (*Hedera helix, Clematis vitalba*).

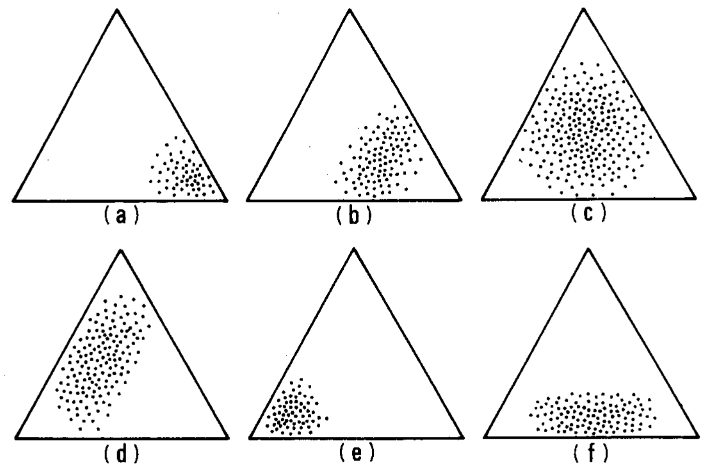

Figure 18 Diagrams describing the range of strategies encompassed by (a) annual herbs, (b) biennial herbs, (c) perennial herbs and ferns, (d) trees and shrubs, (e) lichens, and (f) bryophytes. For the distribution of strategies within the triangle, see Figure 12. (Reproduced from *American Naturalist*, **111**, by permission of the University of Chicago Press. ©1977. The University of Chicago Press.)

Triangular ordination

If the triangular model is an accurate general summary of the range of contingencies to which the established phase may be adapted then it should provide a basis upon which to classify both plants and vegetation types. In 1974 an attempt was made to explore this possibility using field survey data and growth analysis results based upon the herbaceous flora of the Sheffield region in Northern England. The method involved a triangular ordination in which species were classified with respect to two criteria. The first of these was the potential maximum rate of dry matter production (R_{max}) measured under a standardized productive environment, whilst the second was a morphology index* reflecting the maximum size attained by the plant under favourable conditions. This approach was based therefore upon the hypothesis that in herbaceous plants the primary strategies correspond to three permutations between R_{max} and morphology, i.e. rapidly-growing and large (competitors), rapidly-growing and small (ruderals), and slow-growing and small (stress-tolerators). Particularly in its use of provisional estimates of R_{max} based upon samples from single populations, this form of classification is extremely unsubtle. Despite these limitations, consistent patterns of distribution were obtained

*More recent studies suggest that, eventually, the morphology index (originally described inappropriately Grime, 1974 as a competitive index) may be replaced by a simpler index based upon the potential of the plant for lateral spread. On this basis, it would seem possible that a method of ordination may be devised which could be applied to woody species, herbs, and non-vascular plants.

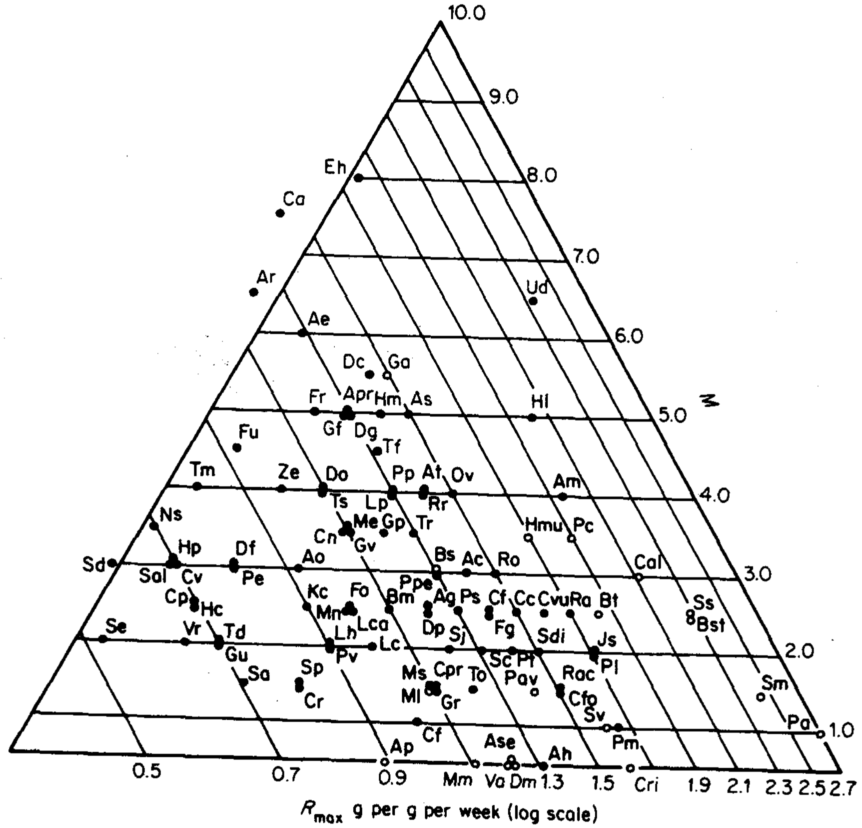

Figure 19 A triangular ordination of herbaceous species. o, annuals; •, perennials (including biennials). The morphology index (M) was calculated from the formula $M = (a + b + c)/2$ where a is the estimated maximum height of leaf canopy (1, <12 cm; 2, 12–25 cm; 3, 25–37 cm; 4, 37–50 cm; 5, 50–62 cm; 6, 62–75 cm; 7, 75–87 cm; 8, 87–100 cm; 9, 100–112 cm; 10, >112 cm); b is the lateral spread (0, small therophytes; 1, robust therophytes; 2, perennials with compact unbranched rhizome or forming small (<10 cm diameter) tussock; 3, perennials with rhizomatous system or tussock attaining diameter 10–25 cm; 4, perennials attaining diameter 26–100 cm; 5, perennials attaining diameter >100 cm); c is the estimated maximum accumulation of persistent litter (0, none; 1, thin discontinuous cover; 2, thin, continuous cover; 3, up to 1 cm depth; 4, up to 5 cm depth; 5, >5 cm depth) (Grime, 1974).

Key to species: Ac, *Agrostis canina*, ssp. *canina*; Ae, *Arrhenatherum elatius*; Ag, *Alopecurus geniculatus*; Ah, *Arabis hirsuta*; Am, *Achillea millefolium*; Ao, *Anthoxanthum ordoratum*; Ap, *Aira praecox*; Apr, *Alopecurus pratensis*; Ar, *Agropyron repens*; As, *Agrostis stolonifera*; Ase, *Arenaria serpyllifolia*; At, *Agrostis tenuis*, Bm, *Briza media*, Bs, *Brachypodium sylvaticum*; Bst, *Bromus sterilis*; Bt, *Bidens tripartita*; Ca, *Chamaenerion angustifolium*; Cal, *Chenopodium album*; Cc, *Cynosurus cristatus*; Cf, *Carex flacca*; Cfl, *Cardamine flexuosa*; Cfo, *Cerastium fontanum*, Cn, *Centaurea nigra*; Cp, *Carex panicea*; Cpr, *Cardamine pratensis*, Cr, *Campanula rotundifolia*; Cri, *Catapodium rigidum*; Cv, *Clinopodium vulgare*; Cvu, *Cirsium vulgare*; Dc, *Deschampsia cespitosa*; Df, *Deschampsia flexuosa*; Dg, *Dactylis glomerata*; Dm, *Draba muralis*; Do, *Dryas octopetala*; Dp, *Digitalis purpurea*; Eh, *Epilobium hirsutum*; Fg, *Festuca gigantea*; Fo, *Festuca ovina*; Fr, *Festuca rubra*; Fu, *Filipendula ulmaria*; Ga, *Galium aparine*; Gf, *Glyceria fluitans*; Gp, *Galium palustre*; Gr, *Geranium robertianum*; Gu, *Geum urbanum*; Gv, *Galium verum*; Hc, *Helianthemum chamaecistus*; Hl, *Holcus lanatus*; Hm, *Holcus mollis*; Hmu, *Hordeum murinum*; Hp, *Helictotrichon pratense*; Js, *Juncus squarrosus*; Kc, *Koeleria cristata*; Lc, *Lotus corniculatus*; Lca, *Luzula campestris*; Lh, *Leontodon hispidus*; Lp, *Lolium perenne*; Me, *Milium effusum*; Ml, *Medicago lupulina*; Mm, *Matricaria matricarioides*; Mn, *Melica nutans*; Ms, *Myosotis sylvatica*; Ns, *Nardus stricta*; Ov, *Origanum vulgare*, Pa, *Poa annua*, Pav, *Polygonum aviculare*; Pc, *Polygonum convolvulus*; Pe, *Potentilla erecta*; Pl, *Plantago lanceolata*; Pm, *Plantago major*; Pp, *Poa pratensis*; Ppe, *Polygonum persicaria*; Ps, *Poterium sanguisorba*; Pt, *Poa trivialis*; Pv, *Prunella vulgaris*; Ra, *Rumex acetosa*; Rac, *Rumex acetosella*; Ro, *Rumex obtusifolius*; Rr, *Ranunculus repens*; Sa, *Sedum acre*; Sal, *Sesleria albicans*; Sc, *Scabiosa columbaria*; Sd, *Sieglingia decumbens*; Sdi, *Silene dioica*; Sj, *Senecio jacobaea*; Sm, *Stellaria media*; Sp, *Succisa pratensis*; Ss, *Senecio squalidus*; Sv, *Senecio vulgaris*; Td, *Thymus drucei*; Tf, *Tussilago farfara*; Tm, *Trifolium medium*; To, *Taraxacum officinalis*; Tr, *Trifolium repens*; Ts, *Teucrium scorodonia*; Ud, *Urtica dioica*; Va, *Veronica arvensis*; Vr, *Viola riviniana*; Ze, *Bromus erectus*.

Estimates of R_{max} are based on measurements during the period 2–5 weeks after germination in a standardized productive controlled environment conducted on seedlings from seeds collected from a single population in Northern England (Grime, 1974). (Reproduced by permission of Macmillan (Journals) Ltd.)

(Figure 19) and, with few exceptions, species with strong ecological affinities were found to be located in close proximity to each other. The species which in Figure 19 are closest to the left-hand corner of the triangle include evergreens tolerant of desiccation (*Sedum acre, Thymus drucei, Helianthemum chamaecistus*), cold (*Dryas octopetala, Nardus stricta*), shade (*Viola riviniana, Sanicula europaea, Deschampsia flexuosa*), or frequent in mineral nutrient-deficient habitats (*Helictotrichon pratense, Sesleria albicans, Sieglingia decumbens*). As one might expect, annual plants of productive severely disturbed habitats such as arable land (*Poa annua, Stellaria media*) are located in the 'ruderal' corner and perennial herbs of fertile, derelict environments such as *Urtica dioica, Epilobium hirsutum, Chamaenerion angustifolium* occur towards the apex of the triangle.

Many of the species included in Figure 19 have been cited in earlier sections of this chapter as examples of particular secondary strategies, and it is interesting to observe that the majority of these plants also fall into the expected patterns of distribution. Typical examples here are the competitive-ruderals *Chenopodium album* and *Holcus lanatus*, and the stress-tolerant competitors *Festuca rubra* and *Bromus erectus*. The location of the small winter annuals *Aira praecox, Veronica arvensis, Arenaria serpyllifolia*, and *Draba muralis* coincides with that predicted for the stress-tolerant ruderals and is quite distinct from that of the C–S–R strategists such as *Festuca ovina* and *Koeleria cristata*, with which these annuals occur on limestone outcrops. This suggests that in such habitats the patches of bare soil occupied by the annuals constitute a distinct micro-environment (see page 167).

The second step in evaluating triangular ordination was to attempt to classify vegetation samples from a wide variety of habitats. The position of each square-metre sample in this ordination is derived from weighted means for R_{max}

and for the morphology index based upon all the species present in the vegetation sample.

A selection of the ordinations is presented in Figure 20a–o. The various types of vegetation occupy positions in close agreement with those which may be predicted from Figure 12. The distributions in Figure 20 illustrate the tendency of samples from stressed habitats (a, b, c), disturbed environments (j, k), and semi-derelict but productive sites (g, h, i) to extend into respective corners of the triangle. Rather unproductive vegetation types experiencing a moderate intensity of orderly disturbance (d, e, f) tend to occupy compact areas in the centre of the diagram. By contrast, samples from spoiled land (l–o) show an attenuated distribution which seems to represent the course of vegetation succession in these new habitats.

The consistent patterns evident in the results of this rudimentary 'classification by strategy' encourage the view, originating from the studies of Raunkiaer (1934), and sustained and expanded by Ellenberg (1963) and Ellenberg and Mueller-Dombois, (1967a, b), that future methods of vegetation analysis and description will rely increasingly upon criteria which are functional (i.e. concerned with characteristics of life-history and physiology) rather than taxonomic.

Intraspecific variation with respect to strategy

There is now a large quantity of published evidence of genetic variation within plant species, and it is clear that this variation may occur both between populations and within them. In our present state of knowledge it is not possible to draw a general perspective with regard to either the plant characteristics, which are most commonly subject to intraspecific variation, or to the circumstances in which the phenomenon exercises a major effect on the ecological amplitude of the species. It is already apparent, however, that in specific instances (e. g. Böcher, 1949) genetic variation is sufficient to enlarge substantially the strategic and ecological range of the species. From the investigations of Law *et al*. (1977) and Law (1978), for example, it is evident that within the common grass, *Poa annua*, there are populations which differ considerably in life-history. In severely disturbed habitats *P. annua* occurs as ephemeral plants which are typical representatives of the ruderal strategy. In marked contrast (Plate 13), populations of the same species in productive pastures contain a high proportion of biennial or possibly even perennial plants which may be described more accurately as competitive-ruderals.

A second example of intraspecific variation with respect to strategy is available from several studies conducted on the perennial grass *Agrostis tenuis*. From investigations such as those of Jowett (1964) it is apparent that whilst pasture populations are usually composed of potentially fast-growing plants of moderately high competitive ability, the species is represented on infertile mine-waste by stress-tolerant individuals of smaller stature and slower potential growth-rate.

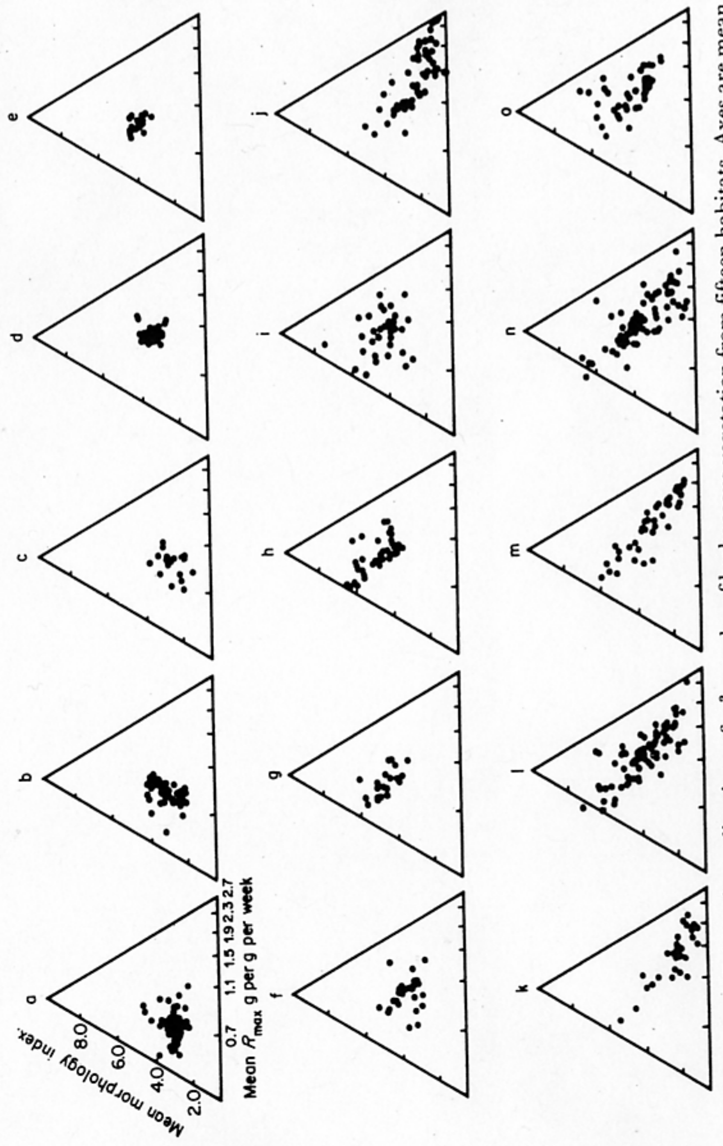

Figure 20 Triangular ordinations of m² samples of herbaceous vegetation from fifteen habitats. Axes are mean morphology index and mean R_{max} each derived as in Figure 19 and weighted according to the relative frequency of the species in the sample. (a) Unenclosed sheep pastures on acidic strata; (b) unenclosed sheep pastures on limestone; (c) limestone outcrops, (d) meadows; (e) road verges, mown frequently; (f) enclosed pastures; (g) road verges, mown infrequently; (h) hedge bottoms; (i) derelict banks of rivers, ponds, and ditches; (j) paths; (k) fallow arable; (l) heaps of mineral soil (such as building sites); (m) demolition sites (brick and mortar rubble); (n) cinders (tips and railway ballast); (o) manure heaps and sewage sludge (Grime, 1974). (Reproduced by permission of Macmillan (Journals) Ltd.)