Yuval Travertine contains late Acheulian implements and corresponds stratigraphically to the Rissian Benot Ya'akov Formation of the Hula Valley[10]. The Dan Travertine overlies the Hasbani Basalt and can be correlated with the Würmian Ashmura Formation of the Hula Valley which contains implements of Mousterian to Epipalaeolithic age, and with the Roqqad (or Naharayim) Basalt[16] of the central Jordan Valley with which it is stratigraphically analogous[10]. The Hasbani Basalt thus constitutes a precise marker for the calibration of the Riss–Würm interpluvial. The age of 73×10^3 yr indicated for this phase agrees with estimates of sedimentation rates and radiocarbon age determinations of the Würmian sequence in Israel[8,10,17]. The sampled flows from the Golan Plateau do not interdigitate with any sediments and are not subject to direct stratigraphic control, but their radiometric ages clearly show that they correlate with the Hasbani Basalt.

Discussion

The maximum development of the Miocene marine transgression in the Mediterranean region, allocated a Middle Miocene age by Gignoux[18], has been shown by our dating of the Lower Basalt to have occurred between 12.2 and 14.6 Myr ago, which is in good agreement with evidence from other regions[19]. The Tabianian marine transgression, represented in Israel by sediments of the Pliocene Bira Formation, which are about 4.8 Myr old, is thought to have been very rapid, and to have reached its maximum extent within about 0.5 to 0.75 Myr (ref. 20).

The age of the Cover Basalt is relevant to the dating of the preglacial and the beginning of the Pleistocene glacial stages. The dated specimens were collected from the upper flows of this volcanic sequence and represent the end of the preglacial Pleistocene, about 1.7–2.0 Myr ago. The reversed magnetic polarity of the upper section of the Cover Basalt, and the consistently normal polarity of its lowermost flows[21,22], strongly suggests that its eruption straddled the transition from the Gauss Normal to the Matuyama Reversed epochs, estimated at 2.4 Myr (ref. 23). The beginning of the preglacial Pleistocene therefore predates the polarity transition and we propose, provisionally, to allocate it an age in the range 2.6 to 3.0 Myr—a date which also corresponds to the close of the Pliocene.

The radiometric dating of the Yarda and Yarmuk Basalts, stratigraphically of late or post-Mindel age, indicates a minimum age of 0.66 Myr for the Mindel. This age limit provides an important link between the early Acheulian cultures of Europe and Africa and has been discussed in detail[24]. Radiometric dates from Pleistocene deposits in Africa are fairly numerous, but in Europe there is almost no dateable Pleistocene material. Furthermore, climatic correlation between the European and African Pleistocene is poor, whereas the correlation between the European and Israeli Pleistocene seems well established[17]. Dating of the Israeli Pleistocene thus provides a sound basis for Pleistocene geochronology in Europe.

We thank Professor E. Jaeger and Dr J. C. Hunziker of the Mineralogisch-Petrographisch Institut, University of Bern, for facilities and assistance in the Ar-isotope determinations. We are grateful to I. Brenner, Geological Survey of Israel, for the specimens and unpublished field data, and to Dr J. A. Miller for reading the manuscript.

Received December 4, 1973; revised January 23, 1974.

1 Bender, F., *Geologie von Jordanien* (Gebrüder Borntraeger, Berlin, 1968).
2 Van den Boom, G., *Geol. Jb.*, **85**, 489 (1968).
3 Oppenheim, M. J., *Bull. Res. Coun. Israel*, **11G**, 58 (1962).
4 McDougall, I., Polach, H. A., and Stipp, J. J., *Geochim. cosmochim. Acta*, **33**, 1485 (1969).
5 Dubertret, L., *Notes Mém. Moyen-Orient*, **VIII**, 250 (1966).
6 Brown, G. F., *Phil. Trans. R. Soc.*, **A267**, 75 (1970).
7 Schulman, N., *Bull. Res. Coun. Israel*, **8**, 63 (1959).
8 Gvirtzman, G., *Geol. Surv. Israel Rep.*, **OD/5/67** (1970).
9 Derin, B., and Reiss, Z., *Israel Inst. Petrol., Rep.* 4/71 (1971).
10 Horowitz, A., *Israel J. Earth Sci.*, **22**, 107 (1973).
11 Picard, L., *Hebrew Univ. geol. Dep. Bull.*, **1B**, (1943).
12 Moshkowitz, S., *Israel J. Earth Sci.*, **12**, 97 (1964).
13 Colalongo, E. A., *Boll. Soc. geol. Etal.*, **91**, 489 (1972).
14 deVries, H. L., and Barendsen, G. W., *Nature*, **174**, 1138 (1954).
15 Picard, L., *Geol. Soc. Am. Spec. Paper*, **84**, 337 (1965).
16 Michelson, H., *Water Planning for Israel, Rep. HR*/72/037 (1972).
17 Horowitz, A., *Pollen Spores*, **XII**, 2,255 (1971).
18 Gignoux, M., *Stratigraphic Geology* (Freeman, New York, 1955).
19 Eicher, D. L., *Geologic Time* (Prentice-Hall, New Jersey, 1968).
20 Hsü, K. J., *Scient. Am.*, **227**, 6,27 (1972).
21 Freund, R., Oppenheim, M. J., and Schulman, N., *Israel J. Earth Sci.*, **14**, 37 (1965).
22 Nur, A., and Helsley, C. E., *Earth planet. Sci. Lett.*, **10**, 375 (1971).
23 Cox, A., Doell, R. R., and Dalrymple, C. B., *Q. Jl geol. Soc. Lond.*, **124**, 53 (1968).
24 Horowitz, A., Siedner, G., and Bar Josef, O., *Nature*, **262**, 186 (1973).
25 Horowitz, A., *Israel J. Earth Sci.* (in the press).

Vegetation classification by reference to strategies

J. P. Grime

Unit of Comparative Plant Ecology, Department of Botany, The University, Sheffield S10 2TN, UK

It is suggested that there are three major determinants of vegetation—competition, stress and disturbance—and that each has invoked a distinct strategy on the part of the flowering plant. A method is described whereby it is possible to distinguish types of herbaceous vegetation by reference to the relative importance of the three strategies in the genotypes of the component species.

THE electronic computer has been a mixed blessing to vegetation classification. On the one hand, it has facilitated the development of methods of numerical and multivariate analysis. On the other, it has contributed to the decline in confidence in established methods but has yet to replace them with a new *lingua franca*. The resultant confusion in the field of vegetation classification is unfortunate in that it coincides with an unprecedented demand for standardised botanical information which can be readily interpreted and assimilated into plans to reclaim or manage the landscape.

This is not to argue for a return to the older methods of phytosociology which apart from their subjectivity are often difficult to apply in a world landscape experiencing increasingly diverse and disruptive interference by man. The current requirement is for methods of classification which can include recent or unstable vegetation, avoid unnecessary abstraction and provide data intelligible to nonspecialists. An approach to the classification of herbaceous vegetation has been made with these considerations in mind.

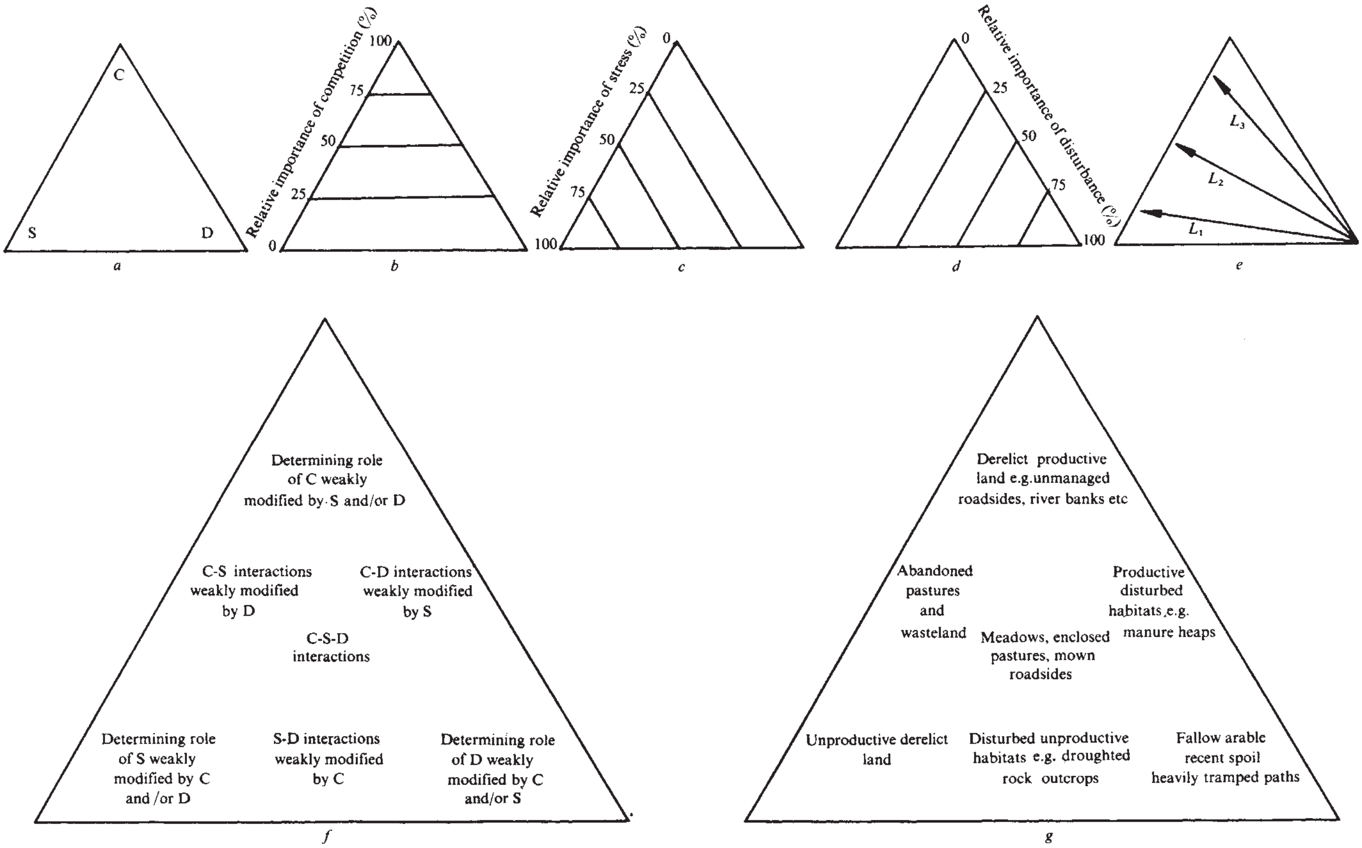

Fig. 1 A triangular model of herbaceous vegetation. *a*, Identification of the corners at which competition (C), stress (S) and disturbance (D) are exclusive determinants. *b–d*, Contours in percentage contribution of competition, stress and disturbance, respectively. *e*, Course of vegetation succession. The arrows correspond to lines of succession of low (L_1), moderate (L_2) and high (L_3) productivity. *f*, Interaction of competition, stress and disturbance. *g*, Location of selected habitat types.

Triangular ordination

The method depends upon the assertion that, basically, there are three determinants of herbaceous vegetation—competition, stress and disturbance—and that each has invoked a distinct strategy on the part of the flowering plant. The possibility arises therefore that an ordination of vegetation types can be based on measurements of the relative importance of the three strategies among the component species. More specifically, it is suggested that the spectrum of herbaceous vegetation types may be accommodated in a model (Fig. 1*a*) consisting of an equilateral triangle in the corners of which the relative importance of competition (C), stress (S) and disturbance (D) reach their respective maxima. In Fig. 1*b–d*, the gradients in relative importance of each of the three determinants are indicated by means of contours and in Fig. 1*f* the interactions between competition, stress and disturbance are summarised. Figure 1*g* illustrates the predicted location of selected habitat types within the triangle. The triangular model also appears to incorporate some of the dynamic features of herbaceous vegetation. The course of succession (Fig. 1*e*) is from the right-hand corner of the triangle towards the opposite side which constitutes the interface with woody vegetation. Increase in the angle of elevation of the line of succession (L_1–L_3) above the horizontal is associated with a progressive increase in productivity. Species density (number of species per unit area) would be expected to show a progressive decline towards the apex as a result of competitive exclusion.

To derive from this model a practical method of ordination, the minimum requirement is to find measurable attributes of the flowering plant which vary in accordance with any two of the three sets of contours in Fig. 1*b–d*. To explore the possible means by which this requirement may be fulfilled it is necessary to consider the essential nature of competition, stress and disturbance and the strategies which they seem to have invoked.

Competition, stress and disturbance

Competition may be defined as the attempt by neighbouring plants to utilise the same units of light, water, mineral nutrients or space[1]. By definition, therefore, competition exerts its maximum impact as a determinant of vegetation in circumstances where the competition is resolved perhaps even to the extent that the habitat is occupied by one species, possibly one individual plant. Stress and disturbance together comprise those phenomena which prevent the resolution of competition. At moderate intensities this intervention has the effect of creating spatial or temporal niches; at their most severe both stress and disturbance may so suppress plant development that individual plants scarcely impinge on each other and competition is occluded. The difference between stress and disturbance lies in the fact that whilst both inhibit the development of a large standing crop the former does so by restricting primary production, the latter by damage to the vegetation. Whereas stress is usually imposed by the physical environment (shortages of light, water, mineral nutrients, suboptimal temperatures, soil and toxins), disturbance arises from the activities of grazing animals, pathogens, man (trampling, mowing and ploughing) and from physical phenomena such as soil erosion. The same environmental factor, drought for example, may cause both stress and disturbance. In certain situations it is difficult to distinguish between competition and stress. In particular, problems of definition arise where herbaceous vegetation derives shade or phytotoxins from a remote tree canopy.

Three strategies

Many plant attributes have been implicated in adaptations to particular forms of competition, stress or disturbance. Here attention is focused on general characteristics of the competitive, stress-tolerant and ruderal strategies.

The competitive strategy. From both field and laboratory investigations of competition[2–15], it seems that a number of plant attributes are conducive to the efficient capture and utilisation of light, water, mineral nutrients and space. These include an elevated leaf canopy, the capacity for extensive lateral spread both above and below ground and the tendency to accumulate a thick layer of litter on the ground surface, all characteristics which are especially prominent in herbaceous species such as *Pteridium aquilinum* and *Epilobium hirsutum*, which frequently occupy extensive areas of vegetation to the virtual exclusion of other species. The ability of these three attributes to distinguish the competitive strategy is suggested by their very low incidence in environments subjected either to severe stress or to continuous disturbance[16].

The stress tolerant strategy. In addition to small stature, a general characteristic of herbaceous plants in environments experiencing continuous and severe stress is a low potential relative growth rate[17]. This generalisation appears to hold for a wide variety of stresses including those associated with nutrient deficiencies on basic and acidic soils[18–23], shading[24,25] and

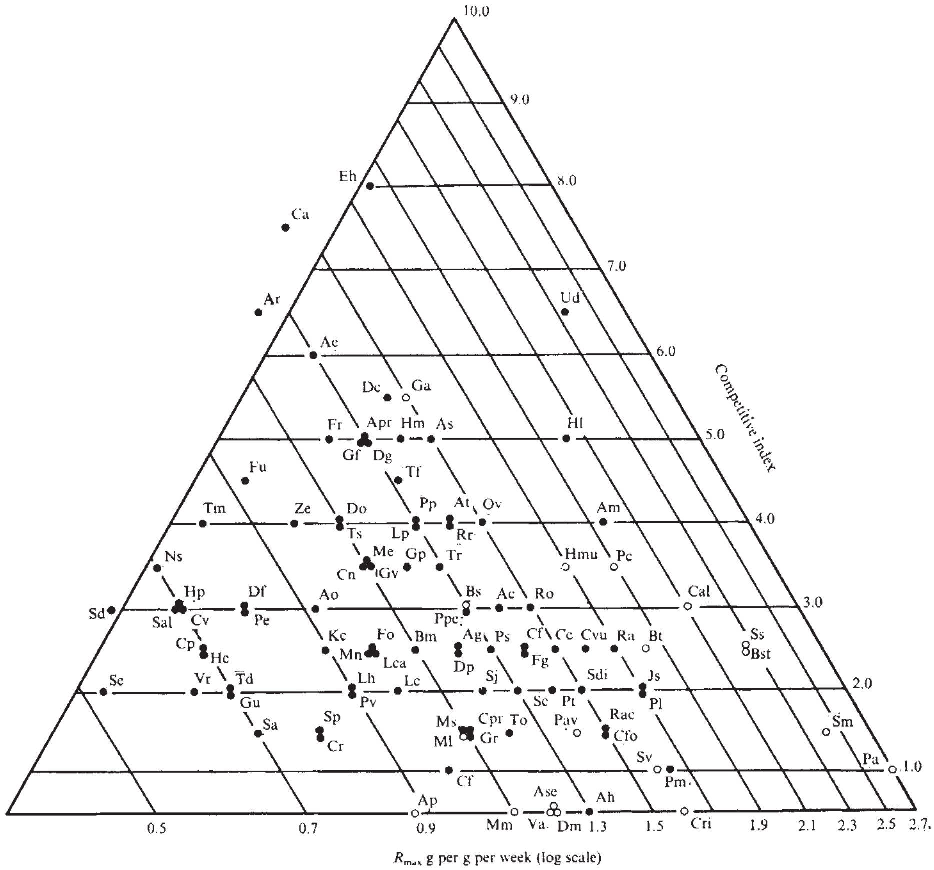

Fig. 2 A triangular ordination of herbaceous species. ○, Annuals; ●, perennials (including biennials). The competitive index (CI) was calculated from the formula CI = $(a+b+c)/2$ where a, estimated maximum height of leaf canopy (1, < 12 cm; 2, 12–25 cm; 3, 25–37 cm; 4, 37–50 cm; 5, 50–62 cm; 6, 62–75 cm; 7, 75–87 cm; 8, 87–100 cm; 9, 100–112 cm; 10, > 112 cm); b, 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, 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).

Key to species: The value in brackets refers to the 95% confidence limit for R_{max}.

Ac, *Agrostis canina*, ssp. *canina* (± 0.18); Ae, *Arrhenatherum elatius* (± 0.16); Ag, *Alopecurus geniculatus* (± 0.14); Ah, *Arabis hirsuta* (± 0.28); Am, *Achillea millefolium* (± 0.57); Ao, *Anthoxanthum odoratum* (± 0.17); Ap, *Aira praecox* (± 0.14); Apr, *Alopecurus pratensis* (± 0.22); Ar, *Agropyron repens* (± 0.11); As, *Agrostis stolonifera* (± 0.22); Ase, *Arenaria serpyllifolia* (± 0.30); At, *Agrostis tenuis* (± 0.25). Bm, *Briza media* (± 0.14); Bs, *Brachypodium sylvaticum* (± 0.28); Bst, *Bromus sterilis* (± 0.25); Bt, *Bidens tripartita* (± 0.28). Ca, *Chamaenerion angustifolium* (± 0.17); Cal. *Chenopodium album* (± 0.73); Cc, *Cynosurus cristatus* (± 0.13); Cf, *Carex flacca* (± 0.24); Cfl, *Cardamine flexuosa* (± 0.18); Cfo, *Cerastium fontanum* (± 0.19); Cn, *Centaurea nigra* (± 0.15); Cp, *Carex panicea* (± 0.25); Cpr. *Cardamine pratensis* (± 0.18); Cr. *Campanula rotundifolia* (± 0.36); Cri, *Catapodium rigidum* (± 0.38); Cv, *Clinopodium vulgare* (± 0.09); Cvu, *Cirsium vulgare* (± 0.56). Dc, *Deschampsia cespitosa* (± 0.12); Df, *Deschampsia flexuosa* (± 0.18); Dg, *Dactylis glomerata* (± 0.14); Dm, *Draba muralis* (± 0.15); Do, *Dryas octopetala* (± 0.47); Dp, *Digitalis purpurea* (± 0.34; Eh, *Epilobium hirsutum* (± 0.13). Fg, *Festuca gigantea* (± 0.41); Fo, *Festuca ovina* (± 0.14); Fr, *Festuca rubra* (± 0.16); Fu, *Filipendula ulmaria* (± 0.26). Ga, *Galium aparine* (± 0.21); Gf, *Glyceria fluitans* (± 0.19); Gp, *Galium palustre* (± 0.15); Gr, *Geranium robertianum* (± 0.13); Gu, *Geum urbanum* (± 0.38); Gv, *Galium verum* (± 0.30). Hc, *Helianthemum chamaecistus* (± 0.24); Hl, *Holcus lanatus* (± 0.28); Hm, *Holcus mollis* (± 0.16); Hmu, *Hordeum murinum* (± 0.35); Hp, *Helictotrichon pratense* (± 0.09). Js, *Juncus squarrosus* (± 0.17). Kc, *Koeleria cristata* (± 0.11). Lc, *Lotus corniculatus* (± 0.14); Lca, *Luzula campestris* (± 0.13); Lh, *Leontodon hispidus* (± 0.14); Lp, *Lolium perenne* (± 0.13). Me, *Milium effusum* (± 0.16); Ml, *Medicago lupulina* (± 0.13); Mm, *Matricaria matricarioides* (± 0.22); Mn, *Melica nutans* (± 0.11); Ms, *Myosotis sylvatica* (± 0.12). Ns, *Nardus stricta* (± 0.16). Ov, *Origanum vulgare* (± 0.22). Pa, *Poa annua* (± 0.42); *Pav*, *Polygonum aviculare* (± 0.12); Pc, *Polygonum convolvulus* (± 0.56); Pe, *Potentilla erecta* (± 0.23); Pl, *Plantago lanceolata* (± 0.13); Pm, *Plantago major* (± 0.19); Pp, *Poa pratensis* (± 0.14); Ppe, *Polygonum persicaria* (± 0.13); Ps, *Poterium sanguisorba* (± 0.38); Pt, *Poa trivialis* (± 0.25); Pv, *Prunella vulgaris* (± 0.14). Ra, *Rumex acetosa* (± 0.33); Rac, *Rumex acetosella* (± 0.17); Ro, *Rumex obtusifolius* (± 0.29); Rr, *Ranunculus repens* (± 0.35). Sa, *Sedum acre* (± 0.17); Sal, *Sesleria albicans* (± 0.11); Sc, *Scabiosa columbaria* (± 0.16); Sd, *Sieglingia decumbens* (± 0.14); Sdi, *Silene dioica* (± 0.17); Sj, *Senecio jacobaea* (± 0.13); Sm, *Stellaria media* (± 0.23); Sp, *Succisa pratensis* (± 0.15); Ss, *Senecio squalidus* (± 0.17); Sv, *Senecio vulgaris* (± 0.36). Td, *Thymus drucei* (± 0.20); Tf, *Tussilago farfara* (± 0.17); Tm, *Trifolium medium* (± 0.08); To, *Taraxacum officinalis* (± 0.12); Tr, *Trifolium repens* (± 0.16); Ts, *Teucrium scorodonia* (± 0.21). Ud, *Urtica dioica* (± 0.13). Va, *Veronica arvensis* (± 0.28); Vr, *Viola riviniana* (± 0.16). Ze, *Zernaerecta* (± 0.08).

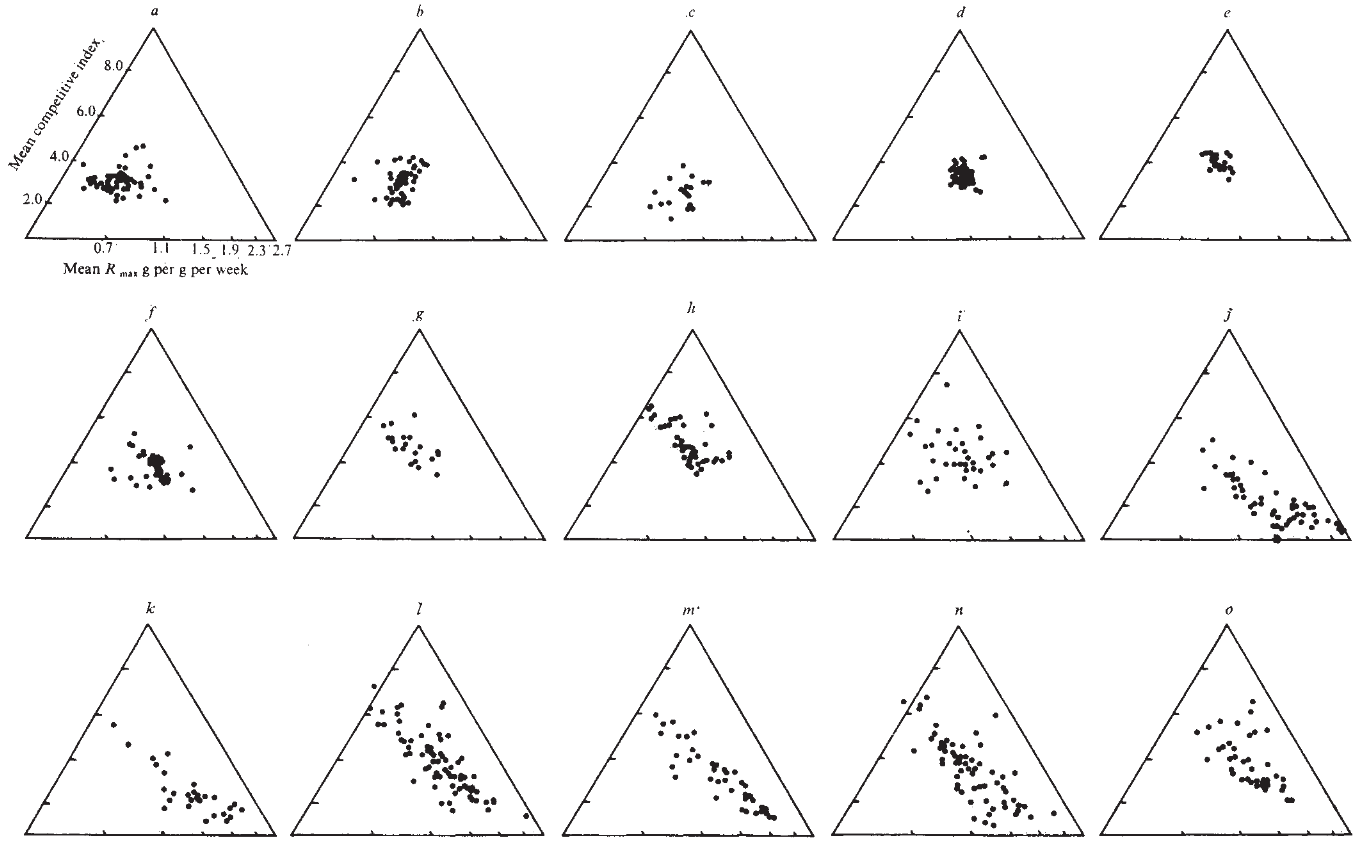

Fig. 3 Triangular ordinations of m² samples of herbaceous vegetation from fifteen habitats. Axes are mean competitive index and mean R_{max} each derived as in Fig. 2 and weighted according to the relative frequency of the species in the sample. *a*, Unenclosed sheep pastures on acidic strata; *b*, Unenclosed 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.

desiccation[23]. In marked contrast, both the competitive and the ruderal strategies are associated with high potential relative growth rates[23,26,27].

The ruderal strategy. The majority of herbaceous species in highly disturbed habitats are annuals or short-lived perennials. A result of disturbance is the release of space and relief from stress and competition. It is not surprising, therefore, to find that a characteristic of many ruderals is the capacity for rapid seedling establishment and growth[23]. A related feature is the tendency for a high proportion of the photosynthate to be directed into seeds and, under conditions of stress, for seed production to be maintained at the expense of vegetative growth[28,29].

Ordination of species

To test the practical value of ordination by strategy, tests were carried out using data from an unpublished survey of the vegetation of the Sheffield region. As a first step, a triangular ordination was carried out on 100 herbaceous plants prominent in the data. One axis in the ordination was designed to correspond to the relative importance of the competitive strategy and was a numerical index based upon estimates of the maxima in height of canopy, lateral spread and litter accumulation derived from the field observations of Dr J. G. Hodgson and myself. The results of numerous investigations (for example refs 5–8, 11 and 13) suggest that in a majority of competitive species height of canopy is of greatest importance. For the purposes of this investigation, therefore, the maximum possible score for height of canopy was arranged to be twice that allowed for either lateral spread or litter accumulation (legend of Fig. 2). The competitive index used here differs from a predecessor[16] both in the introduction of a weighting system and in the fact that relative growth rate is not incorporated. The second axis, on a log scale, referred to stress tolerance and was R_{max}, the maximum relative growth rate of the species recorded during the period 2–5 weeks after germination in a standardised, productive growth-room environment[23]. The values of R_{max} should be regarded as first estimates and may be subject to revision as data become available for other seed sources and conditions of growth.

In view of the provisional nature of the data, it is reassuring to find that the majority of the species fall within the triangle (Fig. 2) and, with certain exceptions, for example, *Origanum vulgare*, *Scabiosa columbaria* and *Tussilago farfara*, lie in close proximity to species with which they have strong ecological affinities. The left-hand corner is occupied by species tolerant of desiccation, for example *Sedum acre*, or shade, for example *Sanicula europaea*, or frequent in nutrient-deficient habitats whether acidic (*Deschampsia flexuosa*, *Nardus stricta*), calcareous (*Helictotrichon pratense*, *Sesleria albicans*) or associated with a wider range in soil *p*H (*Sieglingia decumbens*, *Viola riviniana*). Annual plants are concentrated in the 'ruderal corner' and show a significant ($P < 0.001$) and anticipated[30] rise in seed weight with increasing competitive index. Species of productive, derelict habitats occur towards the apex of the triangle. The unique position in the ordination of *Urtica dioica* is due to the unusually rapid growth rate of the species and is consistent with the sensitivity of the species to mineral-nutritional stress[21,23,31]. The location of the winter annuals *Aira praecox*, *Veronica arvensis*, *Arenaria serpyllifolia* and *Draba muralis* coincides with that predicted for disturbed, unproductive habitats (Fig. 1*g*) and is quite distinct from that of the perennial plants such as *Festuca ovina* and *Koeleria cristata*, with which the annuals occur on limestone outcrops. This suggests that in such habitats the patches of bare soil occupied by the annuals constitute a distinct spatial and temporal niche.

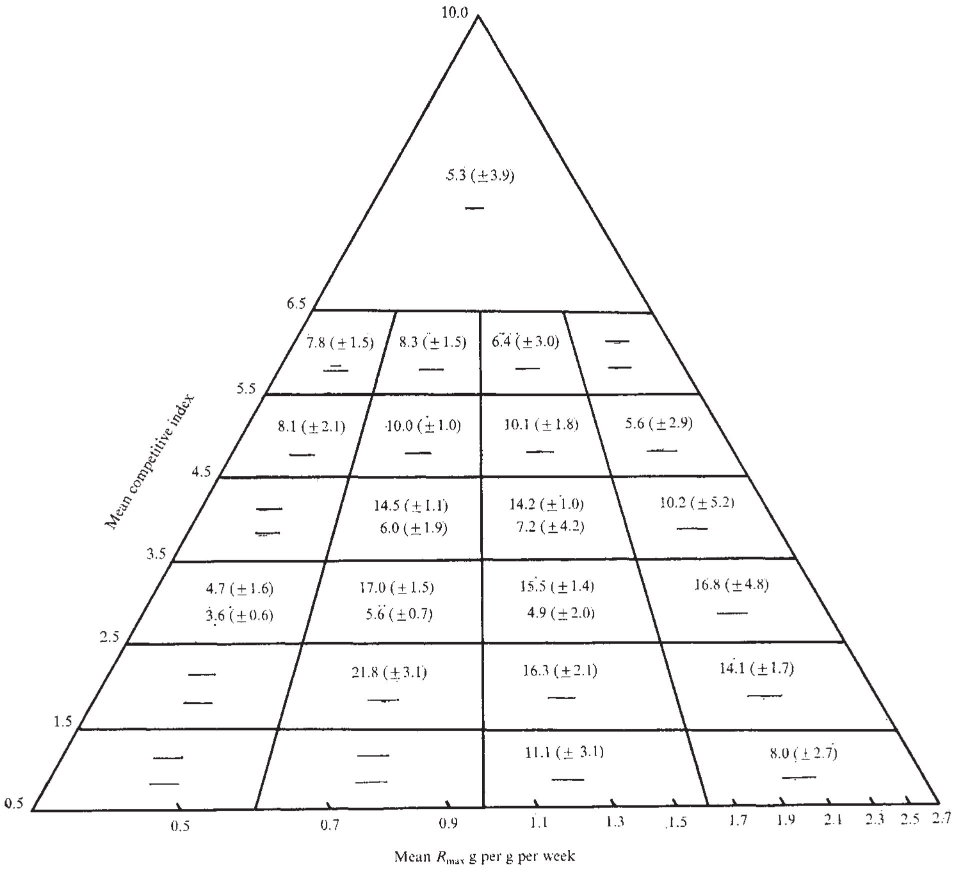

Fig. 4 Pattern of species density (number of species m^{-2}) obtained by ordination of 925 samples of herbaceous vegetation from a wide range of habitats. Axes are the same as in Fig. 3. In each cell the uppermost values are the mean and 95% confidence limit for samples from sites with a surface soil pH > 4.0. The lower values refer to samples of pH < 4.1.

* Cells containing less than five samples.

Ordination of vegetation samples

The second step in evaluating the approach was to ordinate vegetation samples from a wide variety of habitats. The axes were based on mean values for individual quadrats of both the competitive index and R_{max}, with R_{max} again plotted on a logarithmic scale. In the case of the competitive index, the values for each species which contributed towards the mean for the quadrat were weighted according to the relative importance of the species in the m^2 sample. An identical system of weighting was applied in the calculation of mean R_{max} for the quadrat although here data were necessarily restricted to those species for which growth analyses had been carried out (> 50% and including the more frequent species in the majority of samples). A selection of the ordinations is presented in Fig. 3. The various types of vegetation occupy positions in quite close agreement with those predicted in Fig. 1*g*. The figures illustrate the tendency of samples from stressed habitats (*a*, *b*, *c*), disturbed environments (*j*, *k*) and semiderelict but productive sites (*g*, *h*, *i*) to extend into respective corners of the triangle. 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 (compare Fig. 1*e*).

Figure 4 illustrates the pattern of species density which was obtained by pooling data from 25 ordinations (925 samples). When 103 samples from extremely acidic soils (surface soil pH < 4.1) are discounted the predicted decline in species density, towards the apex of the triangle, is apparent. The fall in species density in the lowest rank of cells is probably related to the scarcity of species adapted to extremes of stress and disturbance[16].

Future developments

The consistent patterns evident in Fig. 3 are encouraging, particularly in view of the fact that the samples in each ordination have been drawn from localities scattered over a wide geographical area. However, there is obvious scope for refinement of the method. There is a need for more accurate estimations of R_{max} and for an assessment of the extent to which this attribute and others used in the ordination is subject to intraspecific variation. It is also necessary to evaluate alternative criteria with respect to both the competitive and the stress-resistant strategies. In addition, the possibility of a 'ruderal axis', perhaps related to 'reproductive effort'[32] remains to be examined.

None of the species in Fig. 2 occurs within the two areas of the triangle corresponding to extreme competition or severe stress. This may be due to deficiencies in the axes or in the data. An alternative explanation is that it is necessary to explore beyond a temperate herbaceous flora in order to find the necessary conjunctions of R_{max} and competitive index.

The value of this triangular ordination to vegetation management lies at present in the ability to detect the intensity of competition and stress and to predict the intensity of disturbance at particular sites. If the approach is to be put to maximum use, however, it must be complemented by techniques which identify particular forms of competition, stress and disturbance.

I thank Dr J. G. Hodgson and Dr R. Hunt for their helpful criticism of the manuscript and for their permission to draw upon the results of unpublished collaborative projects, and also A. V. Curtis and A. M. Neal for their participation in field and laboratory work. This research was supported by the Natural Environment Research Council.

Received January 24, 1974.

1 Grime, J. P., *Nature*, **244**, 311 (1973).
2 Olsen, C., *J. Ecol.*, **9**, 1 (1921).
3 Greig-Smith, P., *J. Ecol.*, **36**, 339 (1948).
4 Monsi, M., and Saeki, T., *Jap. J. Bot.*, **14**, 22 (1953).
5 Watt, A. S., *J. Ecol.*, **43**, 490 (1955).
6 Black, J. M., *Aust. J. agric. Res.*, **9**, 299 (1958).
7 Donald, C. M., *Aust. J. agric. Res.*, **9**, 421 (1958).
8 Black, J. N., *Aust. J. agric. Res.*, **11**, 277 (1960).
9 Palmer, J. H., and Sagar, G. R., *J. Ecol.*, **51**, 783 (1963).
10 Ellenberg, H., *Vegetation Mitteleuropas mit den Alpen* (Eugen Ulmer, Stuttgart, 1963).

[11] Willis, A. J., *J. Ecol.*, **51**, 353 (1963).
[12] Grime, J. P., *J. Ecol.*, **36**, 339 (1963).
[13] Thurston, J. M., In *Ecological Aspects of the Mineral Nutrition of Plants* (edit. by Rorison, I. H.) (Blackwell, Oxford, 1969).
[14] Smith, C. J., Elston, J., and Bunting, A. H., *J. Br. Grassld Soc.*, **26**, 213 (1971).
[15] Maarel, E. Van der., in *The Scientific Management of Animal and Plant Communities for Conservation* (edit. by Duffey, E. and Watt, A. S.) (Blackwell, Oxford, 1971).
[16] Grime, J. P., *Nature*, **242**, 344 (1973).
[17] Parsons, R. F., *Am. Nat.*, **102**, 595 (1968).
[18] Bradshaw, A. D., Chadwick, M. J., Jowett, D., and Snaydon, R. W., *J. Ecol.*, **52**, 665 (1964).
[19] Clarkson, D. T., *J. Ecol.*, **55**, 111 (1967).
[20] Parsons, R. F., *Oecologia Plantarum*, **3**, 121 (1968).
[21] Rorison, I. H., *New Phytol.*, **67**, 913 (1968).
[22] Higgs, D. E. B., and James, D. B., *J. Ecol.*, **57**, 553 (1969).
[23] Hunt, R., thesis, Univ. Sheffield (1970).
[24] Grime, J. P., *J. Ecol.*, **51**, 391 (1963).
[25] Loach, K., *New Phytol.*, **69**, 273 (1970).
[26] Clatworthy, J. N., and Harper, J. L., *J. exp. Bot.*, **13**, 307 (1961).
[27] Myerscough, P. J., and Whitehead, F. H., *New Phytol.*, **66**, 785 (1967).
[28] Salisbury, E. J., *The Reproductive Capacity of Plants* (Bell, London, 1942).
[29] Harper, J. L., in *Mechanisms in Biological Competition* (edit. by Milthorpe, F. L.), 1 (Cambridge University Press, London, 1961).
[30] Harper, J. L., Lovell, P. H., and Moore, K. G., *Adv. Ecol. Systemat.*, **1**, **237**, (1970).
[31] Pigott C. D., and Taylor, K., *J. Ecol.*, **52**, (suppl.), 175 (1964).
[32] Ogden, J., thesis, Univ. Wales (1968).

Computer-aided three-dimensional reconstruction and quantitative analysis of cells from serial electron microscopic montages of foetal monkey brain

Pasko Rakic,
Department of Neuropathology, Harvard Medical School

Larry J. Stensas
Department of Physiology, University of Utah, Salt Lake City, Utah 84112

Edward P. Sayre & Richard L. Sidman
Department of Neuropathology, Harvard Medical School; Department of Neuroscience, Children's Hospital Medical Center, Boston, Massachusetts 02115

Computer-aided reconstruction of immature brain cells with highly irregular shapes from serial electron microscopic montages gives three-dimensional images and quantitative data on surface areas and volumes, providing new classes of data on cell behaviour during development.

KNOWLEDGE of structural relationships between cells in the central nervous system has reached a level of precision that requires efficient high resolution methods of quantitative three dimensional analysis. The classic Golgi method[1,2] provides a blackened image of the complete silhouette of individual cells against an almost colourless background, and steps have been taken to obtain quantitative cytological data with computer aid[3]. But this method lacks adequate resolution and usually does not facilitate visualisation of relationships between contiguous cells. The transmission electron microscope provides appropriate resolution and facilitates visualisation of the profiles of cell bodies and processes, and their relationships with other cells in a given field of view. Preparation of several hundred consecutive serial sections is now feasible and computer-aided reconstruction methods have been applied to electron microscopic analysis of the organisation of invertebrate neural tissue (refs 4 and 5 and personal communication from S. Brenner). We describe here the application of a quantitative computer-aided method to the analysis of cell shapes, volumes and surface areas as visualised in electron micrographs of a sector of foetal monkey cerebrum.

A 58-d embryo was removed from an anaesthetised *Macacus rhesus* monkey by hysterotomy and perfused through the circulatory system with a mixture of 1% formaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer[6]. Blocks of tissue 1×1×0.5 mm were postfixed in OsO_4, stained with uranyl acetate, dehydrated and embedded in Maraglas. Precisely oriented transverse sections 1 μm thick were cut from a sector of cerebral wall approximately at the border of the occipital and temporal lobes (Fig. 1*a*). The block was remounted and trimmed to a rhomboid shape, yielding a final block face that extended from the ventricular zone to the base of the cortical plate (Fig. 1*b*) and included a sector of subventricular zone about 100 μm thick and intermediate zone 300 μm thick (neuroembrylogical terminology recommended by Boulder Committee[7]). A set of 170 consecutive serial sections, each about 80 nm thick, was mounted on Formvar film on one-hole (1×2 mm) grids and stained with uranyl acetate and lead citrate. From every third section, 16–20 overlapping fields were photographed at ×2,800 with a Hitachi electron microscope and montages were prepared of prints at a final magnification of ×8,400. Selected cells and their nuclei were outlined on transparent acetate sheets, and minor adjustments in alignments were made by reference to nearby transversely cut cell processes and capillaries. Registration marks were placed on each transparency for alignment