

A demographic interpretation of Grime's triangle

J. SILVERTOWN, M. FRANCO* and K. McCONWAY†

Biology Department and †Statistics Department, Open University, Milton Keynes, MK7 6AA, UK and *Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275 04510, México, D.F., México

Summary

1. The CSR theory of life-history strategies of Grime, and demographically based theories of life history represent strongly contrasting approaches that have yet to be reconciled.

2. It is argued that there are a priori grounds for analogy between Grime's three primary strategies of the established phase in plants and the demographic processes of growth ($\approx C$), survival ($\approx S$), and fecundity ($\approx R$).

3. The contribution of growth, fecundity and survival to the finite rate of population increase λ was calculated for populations of 18 plant species that have also been classified according to Grime's CSR scheme. The match between the demographic classification of species based on these data and their CSR status was determined using a randomization test, and no significant match between the two was found. The reasons for this result are discussed, and it is concluded that it would be premature to abandon attempts to reconcile these two important approaches to plant life history.

Key-words: Competition, elasticity analysis, finite rate of increase, growth, life-history strategies, survival
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Introduction

For many years plant ecology has been riven by a difference of opinion between those with a demographic approach and those who find utility in Grime's triangular classification of plant life-history strategies (Grime 1977, 1979). Harper (1982) has characterized the former as a mechanistic approach and criticized the latter for being merely descriptive. Grime (1984) has used the golfing metaphor of 'putting from the tee' to describe the futility of attempting to explain vegetation processes by a reductionist research programme of plant demography. By proposing a simple demographic interpretation of Grime's triangle we wish to argue that the two approaches might be reconciled, and that a recognition of the link could produce important new insights into the ecology of plants. Although Grime has recently argued that the triangular model applies to woody plants and to animals as well, this discussion is confined to herbaceous species and communities since it is to these that the model has been most extensively fitted (Grime, Hodgson & Hunt 1988).

Grime (1977, 1979) argues that there are three basic life-history strategies that plants may adopt in the established phase: competitive (C), stress-tolerant (S) and ruderal (R). Each strategy is characterized by a distinct set of ecological, morphological and physiological traits and is found in species

occupying habitats of a particular kind (Grime *et al.* 1988). The lists of traits Grime (1984; Grime *et al.* 1988) uses to separate the different strategies contains many with a direct bearing on plant demography such as perennation, shoot turnover and fragmentation, and flowering precocity. The case for the CSR model has been made largely on empirical grounds, and lacks a formal theoretical basis. A demographic interpretation may provide one.

A demographic triangle

The virtue of a demographic approach to life-history strategies is that demographic variables can be used to calculate the fitness of a life-history phenotype. Three demographic processes contribute to the finite rate of increase (λ) of a population: fecundity (F), growth (G) and survival (L). Because λ is the annual rate at which individuals, on average, multiply, it can also be interpreted as the fitness of an average individual.

There is at least a superficial similarity between the optimization of the demographic variables G , L and F and Grime's CSR strategies. Competitors maximize growth ($C \approx G$). Stress tolerators must maximize survival ($S \approx L$). Ruderals, which are essentially fugitive species, clearly rely upon maximizing fecundity ($R \approx F$). The relative contributions

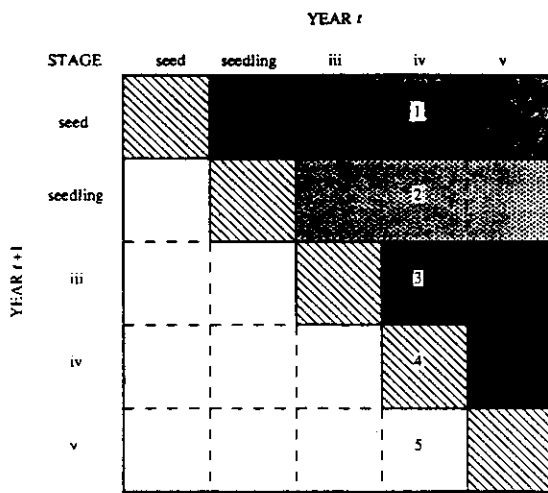


Fig. 1. A stage-projection matrix with five stages (seed, seedling, iii, iv, v), showing the five regions discussed in the text.

of G , L and F to λ and fitness for any particular population can be calculated, and the correspondence with the CSR status of the species tested.

However, before this test can be applied we must consider the relationships between the life-history variables G , L and F . If they are to be considered alternative strategies they should trade-off against each other. Trade-offs between growth and seed reproduction (G vs F), and survival and seed reproduction (L vs F) have been frequently observed in plant demographic studies (Silvertown 1987), and these costs of reproduction are a fundamental component of the demographic theory of life-history evolution (Bell & Koufopanou 1986). Growth and survival, on the other hand, have a more complex relationship. At sites where plant growth is not resource limited, growth and survival will be positively correlated because in these competitive situations larger plants survive and smaller ones die. At high densities this relationship underlies the self-thinning rule. At 'stressful' sites where resources do limit plant growth, survival may be uncorrelated or even negatively correlated with growth. There is no demographic evidence pertaining to this so we must treat a G vs L trade-off as an assumption of the model, to be tested by its fit to CSR.

To ordinate plant populations in G - L - F space and to compare the position of a species on this ordination with that plotted by Grime in the CSR triangle we need estimates of the relative contributions of G , L and F to λ for a range of populations and species. To permit the ordination to be plotted in a triangle, the contributions of G , L and F must sum to unity.

The demography of a plant population may be summarized by the stage-specific rates at which individuals develop from one life-history stage to another (by growth), rates of survival in each stage, rates of vegetative reproduction, fecundity and

regeneration from seed (Caswell 1989). For the purposes of analysis, these stage-specific rates may be used to construct a population projection matrix of the kind shown in Fig. 1. The design of the matrix allows us to separate life-history processes into different compartments. Matrix elements in the top two rows represent fecundity, elements between the second row and the leading diagonal contain rates of vegetative reproduction, elements in the leading diagonal contain rates of survival in the same stage class ('stasis'), and elements in the triangular region below the diagonal contain rates of development from smaller to larger stage classes (growth or 'progression').

A test

Stage projection matrices for 18 herb species, whose CSR status has been classified by Grime *et al.* (1988), were taken from the literature or compiled from published demographic data. Corrections to matrices from published sources were necessary in a number of cases where authors' models incorrectly allowed a whole year for the transition between seeds and seedling recruits (Caswell 1989, p.49). Full details of the matrices that we compiled ourselves will be published elsewhere. The contribution of G , L and F to λ was estimated by elasticity analysis of the matrices (de Kroon *et al.* 1986; Caswell 1989). For the purposes of this analysis F = the sum of elements in regions 1, 2 and 3 of the matrix (Fig. 1), L = region 4 (the leading diagonal) and G = region 5. The offshoots produced by clonal plants may be considered a contribution to reproduction (F) or growth (G). In the latter case $F = 1 + 2$ and $G = 3 + 5$. The elements of the elasticity matrix sum to unity, giving the useful constraint that $G + L + F = 1$. This constraint embodies the assumption that G and L , L and F , and G and F trade-off against each other perfectly.

Elasticity values and CSR status for the 18 species are given in Table 1, and the relative positions of each species in the CSR/GLF triangle are shown in Fig. 2. CSR statuses were converted to numerical scores using the schematic ordination given by Grime *et al.* (1988, p.4). Correspondence between CSR and GLF is generally poor, although there are three species (*Dipsacus sylvestris*, *Ranunculus acris* and *Scabiosa columbaria*) where the two classifications are in close agreement.

The degree of relationship between the CSR status and GLF scores was assessed statistically using a permutation test (Pitman 1937; Cox & Hinkley 1974, pp.182w-187; see also Sokal & Rohlf 1981, pp.787-795). Such a test avoids making any parametric assumptions about the distributions of CSR or GLF scores. The squared Euclidean distance $(C-G)^2 + (S-L)^2 + (R-F)^2$ was taken as a measure of discrepancy between the CSR and GLF scores for each species. The sum D of the squared Euclidean dis-

tances for all 18 species was calculated and used as an overall measure of discrepancy. If the CSR and *GLF* scores matched perfectly, *D* would take the value of zero; the larger the value of *D*, the less likely it is that CSR and *GLF* scores are measuring the same thing. The actual values of *D* were 3.699 for *GLF* with vegetative reproduction contributing to R and 3.862 for *GLF* with vegetative reproduction contributing to *G*.

Consider the null hypothesis that there is no relationship between CSR and *GLF* scores. Under this hypothesis, for instance, it is just as likely that the *GLF* scores of 0.56, 0.07 and 0.37 observed for *Anthyllis vulneraria* would occur with an S/SR strategy as, say, a CR strategy. It would therefore be possible in principle to assess the distribution of the overall measure of discrepancy *D* under the null hypothesis by calculating its value for each of the 18! ($=6.4 \times 10^{15}$) ways of pairing the 18 observed sets of CSR scores with the 18 sets of *GLF* scores. In practice, this is not feasible, but the distribution can be approximated by drawing a large number of permutations at random from the 18! possibilities and

by calculating the value of *D* for each one. The observed value of *D* can then be compared with this approximate null distribution to give a *P*-value. This procedure was carried out using 10000 random permutations and the results are given in Table 2. The *P*-values presented are lower tail one-tailed values, because the procedure is testing for similarity in values between CSR and *GLF* scores.

The null distribution for *D* turns out to be symmetrical but somewhat shorter-tailed than a normal distribution. Both observed values of *D* lie in the middle of the corresponding null distributions; in fact both are rather larger than the mean. The *P*-values are large. There is therefore no evidence that the CSR and *GLF* values are related.

Discussion

This is not the first paper to suggest that there are demographic correlates of C, S and R strategies. Starting from an independent set of assumptions to those of Grime (1977) or the present paper,

Table 1. The CSR status and elasticities of *G*, *L* and *F* for 18 species of herbs. The value of *F* shown includes a component for vegetative reproduction, which is also shown separately. If clonal reproduction is treated as growth rather than reproduction, its elasticity should be subtracted from *F* and added to *G*

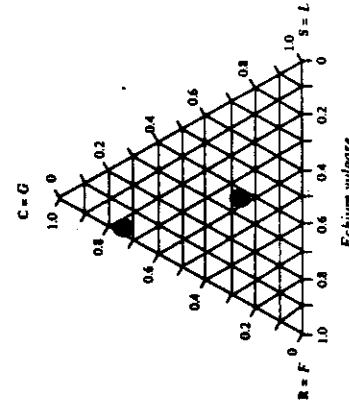
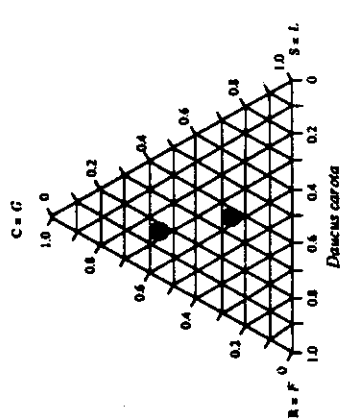
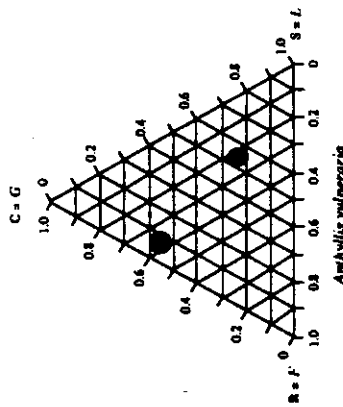
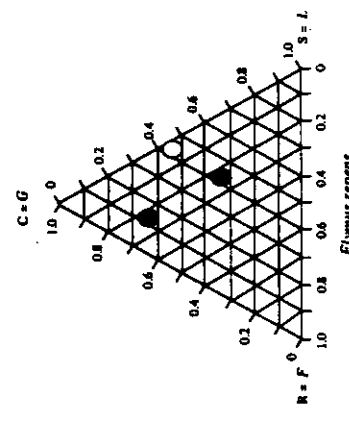
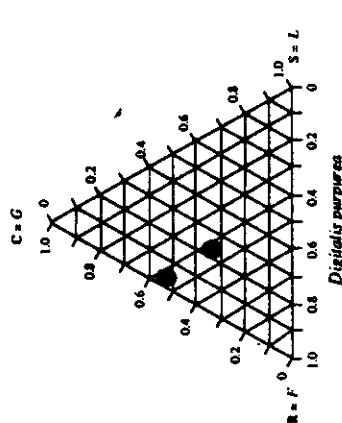
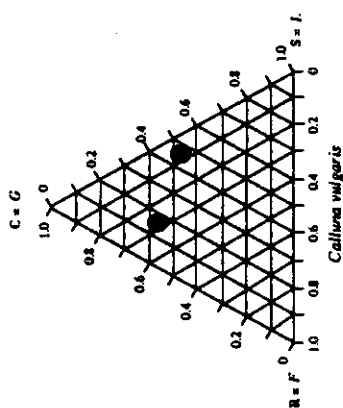
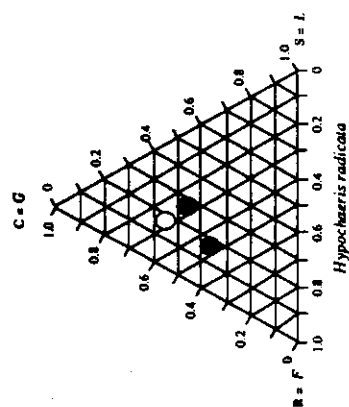
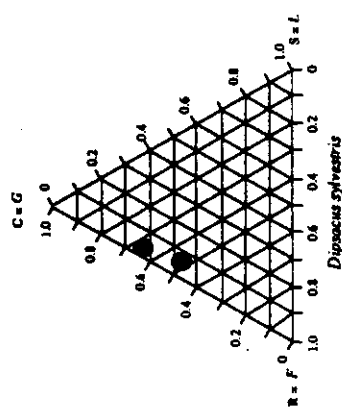
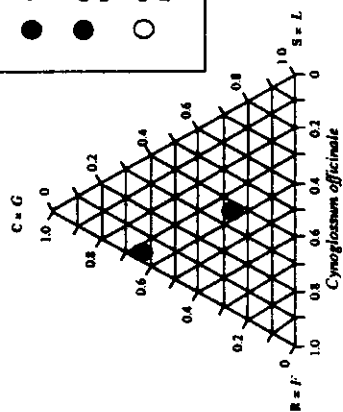
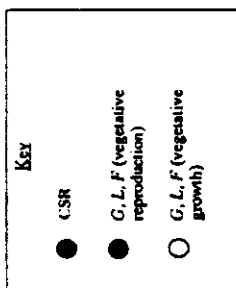
Species	Elasticities					Source of demographic data
	CSR strategy	<i>G</i>	<i>L</i>	<i>F</i>	Vegetative reproduction	
<i>Anthyllis vulneraria</i>	S/SR	0.56	0.07	0.37	0	Sterk 1975; Sterk <i>et al.</i> 1982
<i>Calluna vulgaris</i>	SC	0.51	0.2	0.29	0.001	Scandrett & Gimingham 1989
<i>Cynoglossum officinale</i> *	SR/CSR	0.63	0.06	0.31	0	de Jong & Klinkhamer 1988
<i>Daucus carota</i>	SR/CSR	0.55	0.18	0.27	0	Verkaar & Schenkveld 1984
<i>Digitalis purpurea</i>	CR/CSR	0.52	0.01	0.48	0	van Baalen & Prins 1983
<i>Dipsacus sylvestris</i> *	CR	0.6	0.05	0.34	0	Caswell 1989
<i>Echium vulgare</i> *	SR/CSR	0.72	0	0.28	0	Klemow & Raynal 1985
<i>Elymus repens</i>	C/CR	0.28	0.49	0.23	0.23	Mortimer 1983
<i>Hypochaeris radicata</i>	CSR	0.36	0.16	0.47	0.190	de Kroon, Plaiser & Groenendaal 1987
<i>Linum catharticum</i>	SR	0.06	0.83	0.11	0	Verkaar & Schenkveld 1984
<i>Picris hieracoides</i> *	R/CSR	0.73	0	0.27	0	Klemow & Raynal 1985
<i>Plantago coronopus</i>	S/SR	0.42	0.17	0.42	0.012	Waite 1984
<i>Potentilla anserina</i>	CR/CSR	0.29	0.51	0.19	0.190	Eriksson 1988
<i>Ranunculus acris</i>	CSR	0.39	0.31	0.31	0.027	Sarukhán & Harper 1973
<i>Ranunculus bulbosus</i>	SR/CSR	0.49	0.24	0.27	0	Sarukhán & Harper 1973
<i>Ranunculus repens</i>	CR	0.14	0.79	0.08	0.017	Sarukhán & Harper 1973
<i>Scabiosa columbaria</i>	S/SR	0.32	0.51	0.17	0	Verkaar & Schenkveld 1984
<i>Senecio jacobaea</i>	R/CR	0.68	0.04	0.28	0.078	Forbes 1977

* Species classified by K. Thompson of Unit of Comparative Plant Ecology, University of Sheffield (personal communication).

Table 2. Observed values of the discrepancy measure *D*, its mean and standard deviation under the null hypothesis of no relationship between CSR and *GLF* scores, and one-tailed *P*-values

Vegetative reproduction contributing to:	Observed <i>D</i>	Mean <i>D</i> under null hypothesis	Standard deviation of <i>D</i> under null hypothesis	<i>P</i> -value
<i>Fecundity</i>	3.699	3.377	0.521	0.724
<i>Growth</i>	3.862	3.757	0.516	0.579

Demographic
interpretation of
Grime's triangle



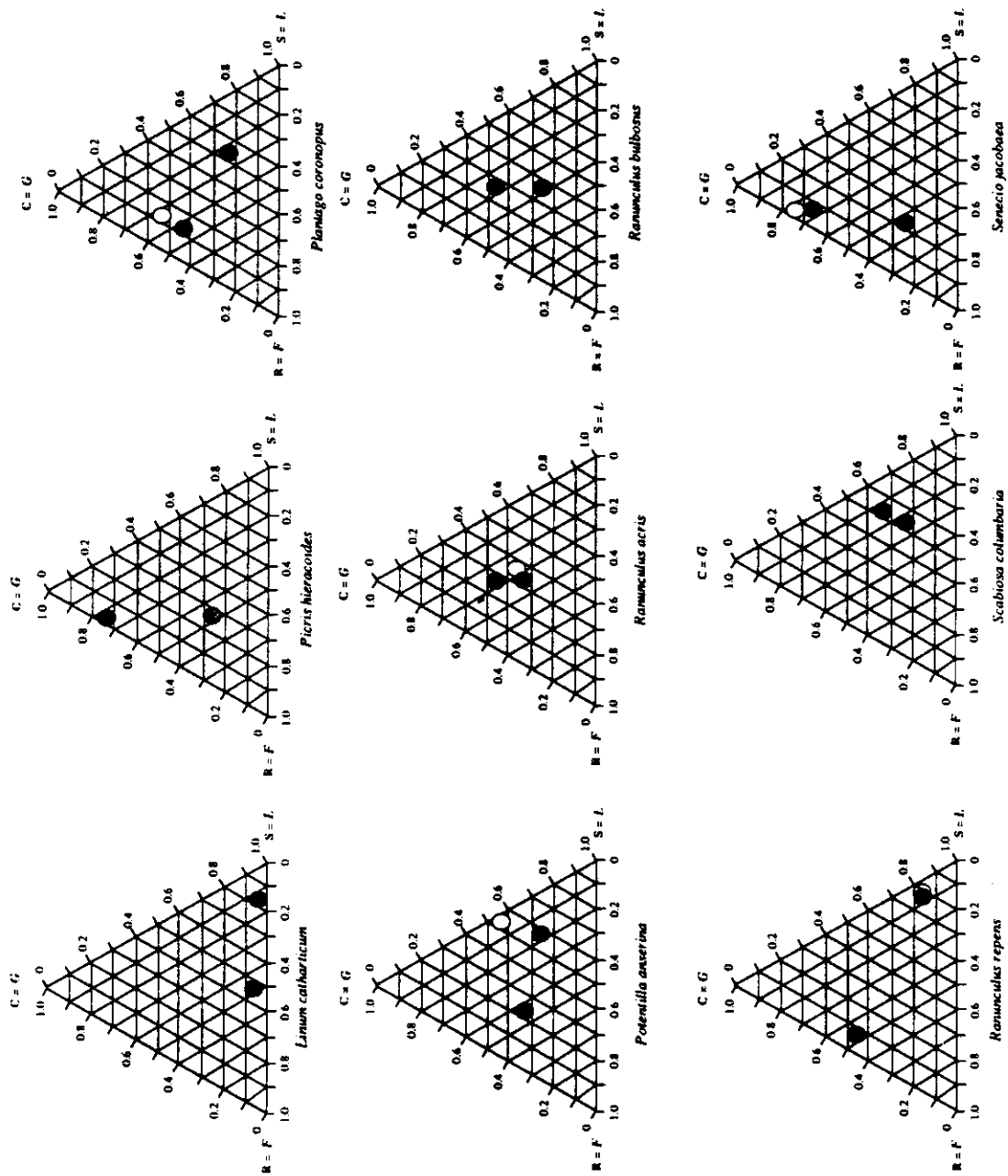


Fig. 2. Triangular ordinations of 18 herb species using CSR and GLF. The vertices of each triangle are C/G, S/L, R/F. The positions of species according to the CSR classification were determined from the data in Table 1 and the schematic diagram given by Grime *et al.* (1988; Fig. 1.2).

Whittaker & Goodman (1979) concluded from a simulation model based upon the logistic equation that there were three patterns of life-history strategy corresponding to the operation of saturation selection (=competitive strategy), adversity selection (=stress-tolerant strategy), and exploitation selection (=ruderal strategy). Unfortunately, as the authors admitted, the model was not very 'accessible to empirical investigation'. While the present paper was in review, we had sight of the proof of a paper by Enright & Watson (1991) who also propose an analogy between CSR and *GLF* based upon elasticity analysis. They do not discuss the idea in any detail, but tentatively apply it to a sample of seven trees and one herb (*Dipsacus sylvestris*).

The present demographic interpretation of CSR overcomes a number of objections that have been lodged against the triangular model in its original form. Harper (1982) has criticized Grime's use of the term 'stress', but the demographic interpretation of CSR does not rely upon the semantics of this term since it substitutes it for a demographic variable that can be directly measured. Indeed, all three variables of interest can be estimated directly in a way that is not possible for 'competitiveness', 'stress tolerance', or 'ruderalness', which are imprecise concepts (Grubb 1985). Because the variables *G*, *L* and *F* can be estimated, so too can the trade-offs between them that provide another difficulty for CSR (Grubb 1985; Loehle 1988). Loehle (1988) has criticized the triangular model on the grounds that *C*, *S* and *R* should be measured on three independent axes and that forcing all points in the three-dimensional space defined by these axes into only two dimensions creates distortion. However, this distortion does not occur when the three variables always sum to unity, as *G*, *L* and *F* do when measured as proportional contributions to λ .

On present evidence, there is no correspondence between CSR and *GLF*. This could be because: (1) CSR has no demographic basis; (2) the demographic interpretation of CSR offered here is incorrect or inadequate; or (3) the interpretation is correct but the data available to test it are inaccurate. Since this is the first attempt to find a demographic basis for CSR that is testable, it would be premature to accept the first explanation. As far as the second explanation is concerned, it was argued above that the correspondence between *GLF* and CSR is plausible, though superficial. One possible problem is that the CSR classification of a species is based upon its ecology in the established phase, whereas the projection matrix summarizes the entire life cycles. Grime *et al.* (1988) identify five regeneration strategies, but these are not closely coupled to the three strategies of the established phase. In our analysis there is no distinction between strategies of the established and the regeneration phase so, for example, a long-term seed pool or a pool of persistent juveniles, which are two

of Grime's regeneration strategies, will both contribute to *L*. Elasticity analysis can, of course, be used to make much finer distinctions between strategies than the simple partition into *G*, *L* and *F*, and a more sophisticated study based upon a much larger sample of species, including trees and shrubs, will be published elsewhere.

The division of the projection matrix into three regions, representing fecundity, survival and growth, is pragmatic rather than absolute. Vegetative reproduction, which was included in *F* (ruderalness), can be regarded as clonal *growth*, when it should be included in *G*. However, allowing for this does not improve the overall fit (Table 2). Plants that grow from one size class to another are included in *G* (competitiveness), but of course these plants are also survivors and could make a contribution to 'stress tolerance' that is ignored by equating survival solely with the principal diagonal (region 4). As has already been observed, it is not certain that there is a trade-off between *G* and *L*, in which case species should not be expected to sort neatly on this axis. If *GLF* has been correctly analogized with CSR, this failing applies as much to the CSR theory itself as to the demographic interpretation of it.

Finally, we must consider the demographic data on which the test of correspondence between CSR and *GLF* was based. None of these data were collected in the Sheffield region where CSR classifications of the species in question were made. Since the CSR theory is founded on the assumption that it is legitimate to generalize about the ecology of species, the use of demographic data from outside the Sheffield region, and indeed in many cases from outside the British Isles, constitutes a rigorous but not unreasonable test. A more serious objection to these data is that they may be unrepresentative of 'average' populations of the species in question due to sampling error. Though some of the data in Table 2 derive from matrices that were averaged over several sites and years, demographic studies are typically conducted at a few small, carefully selected sites. Only more studies can solve this problem. In an ideal world, λ should be unity for all species if averaged over sufficient time. In the real world the actual value of λ varies, and its value at the time we happen to study a population will affect the relative values of *G*, *L* and *F*. If it were possible to restrict a test of the hypothesis that $GLF \approx CSR$ to populations at demographic equilibrium, in which $\lambda=1$, this problem would be obviated.

Even though the present attempt to interpret CSR in a demographic manner failed to find a correspondence between CSR and the chosen demographic variables, it seems obvious that plant demography could benefit from a comparative approach and that any viable theory of life-history strategies must ultimately be founded on demography.

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