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# Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials

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## Summary

**1** Stage projection (Lefkovitch) matrices for 21 species of woody plants and 45 herbaceous perennials were extracted from the plant demographic literature or compiled from published data.

**2** Each matrix was divided into six regions representing: 1, recruitment of seeds to the seed pool; 2, recruitment of seedlings or juveniles from current seed production; 3, clonal growth; 4, retrogression, due to plants decreasing in size or reverting in stage; 5, stasis, (survival from one year to the next in the same stage class); 6, progression to later stage classes.

**3** Matrix analysis was used to calculate the finite rate of increase  $\lambda$  for each population and to calculate the elasticities of each transition coefficient in the matrices. Elasticities were summed within each of the six regions of the matrix to give measures ( $E_1 - E_6$ , respectively) of the importance of each component of the life cycle to  $\lambda$  and fitness.

**4** Herbs as a group differed significantly from woody plants in most of these components. Seedling recruitment was more important in herbs than woody plants. Retrogression occurred only in herbs, particularly those with a tuber. Stasis occurred in nearly all species, but was most important in woody plants. Progression was more important than fecundity in almost all species.

**5** Trade-offs among life cycle components were determined from correlation matrices of  $r$  ( $= \ln \lambda$ ) and elasticities  $E_1 - E_6$  for the whole sample and for herbs and woody plants separately. As a whole,  $r$  was positively correlated with elasticities for fecundity ( $E_1 + E_2$ ) and growth ( $E_3 + E_6$ ) and negatively correlated with survival ( $E_4 + E_5$ ). In clonal herbs, fecundity and clonal growth were negatively correlated.

**6** The division of elasticities into three major components (growth,  $G = E_3 + E_6$ ; fecundity,  $F = E_1 + E_2$ ; and survival,  $L = E_4 + E_5$ ) allowed us to construct triangular plots in  $G-L-F$  space. This was done separately for iteroparous forest herbs, iteroparous herbs from open habitats, semelparous herbs and woody plants. Each of these four groups occupied a distinct position in  $G-L-F$  space. Within woody plants, shrubs of fire-prone habitats occupied the end of the distribution with the lowest survival elasticity.

**7** It is argued that the demographic approach to the classification of distinct ecological groups offers new insights into the relationship between life history and habitat.

**Keywords:** clonal growth, elasticity analysis, Lefkovitch matrix, life-history evolution, matrix analysis, progression, recruitment, retrogression, stasis, trade-off

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## Introduction

The comparative method has a long tradition in biology, particularly in evolutionary studies (Harvey

& Pagel 1991), and is the *modus operandi* of a significant contemporary school of plant ecology (Grime *et al.* 1988). The method is founded on the principle that similar environments exert similar

selective forces on different species, leading to convergent evolution and adaptive patterns that transcend taxonomic boundaries. Dissimilar environments exert different selective forces that may lead to the evolutionary divergence of related taxa.

Since the pioneering study of three *Ranunculus* species by Sarukhán & Harper (1973), the demography of wild plants has often been analysed on a comparative basis, albeit usually for small numbers of related taxa (e.g. Schaffer & Schaffer 1977; Newell, Solbrig & Kincaid 1981; Angevine 1983; Kawano *et al.* 1987; Fone 1989; Young 1990; Boutin & Harper 1991). Wider comparisons between larger numbers of unrelated taxa should allow greater generalization about the evolutionary forces that shape plant life history. However, before any such exercise can be tackled we must establish a meaningful method of comparison for species with life cycles as different as, for example, *Linum catharticum*, a short-lived semelparous herb and *Sequoia sempervirens*, a clonal tree of renowned size and longevity.

The life cycle of a plant can be described by a life-cycle graph (Hubbell & Werner 1979), from which a population projection matrix may be derived (Caswell 1989). The projection matrix allows the quantitative demographic data that describe the life cycle of a population with age or stage structure to be represented in a standard format. The contribution that an average individual belonging to an age, size or stage class (say  $j$ ), makes in a predefined time interval ( $t$  to  $t+1$ ) to another class (say  $i$ ; where  $i$  takes the values 1, 2, ...,  $j$ , ...,  $k$ ) is expressed as a coefficient ( $a_{ij}$ ) of a square matrix ( $A$ ) whose number of rows and columns is equal to the number of classes chosen ( $k$ ). Populations where the individuals are grouped in age classes are described by a Leslie matrix (after Leslie 1945, 1948), where the only non-zero elements are on the first row (fecundities =  $a_{1j}$ ) and on the first subdiagonal (survivorship =  $a_{i,i-1}$ ). When individuals are classified in size or stage classes, any element of the matrix may be positive because each class may potentially (if not biologically) contribute to any other. This is known as a Lefkovitch matrix (Lefkovitch 1965). In most plants fecundity, growth and survivorship are closely related to individual size or stage of growth and are only loosely related to chronological age, so Lefkovitch matrices tend to be more appropriate, and are more often used, than Leslie matrices. Dual classification by age and stage is possible using a Goodman matrix (Goodman 1969), but is rarely used (but see van Groenendael & Slim 1989, Law 1983).

Analysis of population projection matrices provides a range of measures of population structure and behaviour that afford comparison between species (Caswell 1989). First, analysis of a population projection matrix yields the finite rate of increase  $\lambda$ , which may be used as a measure of fitness for

organisms possessing a particular set of traits in a particular environment. Secondly, matrix analysis yields the stable age or stage distribution and a vector of reproductive values. These are of interest in themselves (J. Silvertown & M. Franco, unpublished), and may also be used to calculate the elasticity  $e_{ij}$  of each element  $a_{ij}$  in the matrix. Elasticity is a measure of the sensitivity of  $\lambda$  to small changes in  $a_{ij}$ , standardized to allow for the fact that elements  $a_{ij}$  representing survival probabilities can only range between zero and one, whereas an  $a_{ij}$  representing fecundity can have any value at all. If  $s_{ij}$  is the sensitivity of element  $a_{ij}$ , then the elasticity of the element is:

$$e_{ij} = (a_{ij}/\lambda) \times s_{ij}.$$

Elasticity is a measure of the relative change in the value of  $\lambda$  in response to small changes in the value of a matrix element, and it is also a measure of an element's contribution to fitness (de Kroon, van Groenendael & Caswell 1986). Elasticities sum to unity, and may be summed across selected regions of a matrix in order to compare the relative importance of, say, fecundity with the importance of growth. Caswell (1986) made such a comparison for Lefkovitch matrices of five tree species and found that the probability of remaining in a size class was generally more important than that of growing a size class or of fecundity. This was not so for *Dipsacus sylvestris* (a semelparous herb), and he concluded that 'These patterns deserve further study'.

In a recent comparative study, Silvertown, Franco & McConway (1992) used elasticity analysis of matrices for 18 herb species to test for a correspondence between demographic measures of growth, survival and fecundity and measures of Competitive, Stress-tolerant and Ruderal (CSR) status according to Grime's classification (Grime *et al.* 1988). No correspondence was found. Enright & Watson (1992) made a similar comparison for seven trees and a herb, but their sample was too small to permit any firm conclusions.

It is an axiom of life-history theory that trade-offs between different life history parameters, in particular between reproduction, growth and survival, constrain life-history evolution. The evolutionary constraints created by such trade-offs should lead to negative correlations among the elasticity values representing different components of the life cycle. In particular, one would expect a trade-off between fecundity and survival, with fecundity more important to short-lived herbs and survival more important to long-lived trees. Among clonal plants one might expect a trade-off between the importance of vegetative reproduction and the importance of sexual reproduction.

In this study we use elasticity analysis of matrix projection models for a sample of 45 herbs and 21 woody species to determine the contribution of dif-

ferent components of the life cycle to  $\lambda$  in plants of widely contrasting life history. This sample is large and ecologically diverse enough for us to test for correlation between the importance (elasticity) of life history components and habitat. This is the ultimate test of utility in any comparative study of life history and has not been applied to the results of elasticity analysis before. If this approach to comparative plant demography is successful it should help us understand the relationship between life history and the habitat templet (Southwood 1977, 1988).

## Methods

A comprehensive survey of the literature on plant demography (Franco & Silvertown 1990) was used to identify studies of perennials that presented data in the form of a population projection matrix (43 cases), or which supplied enough information to permit us to construct a projection matrix for the population(s) ourselves (23 cases). Matrices for species studied at more than one site or in more than one year were averaged to give one matrix per species per study. In one case (*Araucaria hunsteinii*) matrices for different populations could not be averaged because stage classifications differed between sites. In this case the population parameters were calculated separately for each matrix and the parameters averaged, using the geometric mean of  $\lambda$ , to obtain a single species' estimate. Most authors gave annual estimates of the coefficients  $a_{ij}$ . When this was not the case we standardized the matrix to apply to a projection interval of one year.

Caswell (1989, p. 49) identified an error in population projection matrices for plants that we found to be frequent in the literature. A proportion of the seeds of many plants pass from production to germination in under one year, so seeds should not appear as a separate stage in matrix models that have a projection interval of one year unless there is a long-term (supra-annual) seed pool. Even when a supra-annual seed pool exists, a proportion of recruits from seed will enter the population without passing through it. The many studies which have not allowed for this give an underestimate of  $\lambda$  because an artificial seed pool delays recruitment. We corrected for this error, which in some cases meant the disappearance altogether of a seed category appearing in the published matrix for a population.

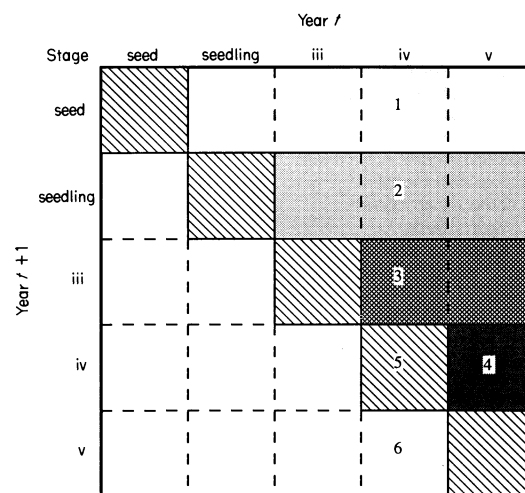
Matrices were analysed by the power method (Caswell 1989, p. 79). Here we report only the results concerning the finite rate of increase of the population ( $\lambda$ ) or its natural logarithm, the intrinsic rate of population increase ( $r$ ), and the elasticity ( $e_{ij}$ ) of the different elements of the matrix. Each of the 66 matrices (Table 1) was divided into six regions, each representing a different part of the life cycle. The regions, shown in Fig. 1, were:

- 1 *recruitment of seeds* to the seed pool;
- 2 *recruitment of seedlings* or juveniles from current seed production;
- 3 *clonal growth*;
- 4 *retrogression* due to plants decreasing in size during the year or reverting from a flowering state to a vegetative one or becoming dormant;
- 5 *stasis*, or survival from one year to the next in the same stage class;
- 6 *progression* to later stage classes.

Elasticities  $e_{ij}$  were summed within each of the six regions to give totals for each life-history process that are termed  $E_1$ – $E_6$ , respectively. For the purpose of the present analysis  $E_1$ + $E_2$  collectively represent *fecundity* ( $F$ ),  $E_4$ + $E_5$  collectively represent *survival* ( $L$ ), and  $E_3$ + $E_6$  collectively represent *growth* ( $G$ ). Not all matrices contained all six components and the relevant matrix elements in published matrices were not always in the positions shown in Fig. 1. Care was taken to assign each elasticity coefficient to its biologically correct component, regardless of its actual position in the matrix.

Trade-offs between the different life history components were sought by compiling a Spearman rank correlation matrix for  $r$ ,  $E_1$ – $E_6$ ,  $F$ ,  $L$ ,  $G$ . Variables  $E_1$ – $E_6$ ,  $F$ ,  $L$ ,  $G$  are directly or indirectly dependent on each other because elasticities sum to unity. Some negative correlations among these variables are therefore to be expected. However, which variables are negatively and which positively correlated, and to some extent the strength of negative correlations, is determined by biological trade-offs. The significance of correlations between elasticities was determined using a randomization test (Manly 1991) that allowed for the mathematical constraints that could produce spurious correlation.

For the whole sample and for herbs and woody plants separately, each observed correlation coefficient



**Fig. 1** The six regions of the stage projection matrix: 1, seed production; 2, seedling recruitment; 3 clonal growth; 4, retrogression to a previous stage or size; 5, stasis-survivorship within the same class; 6, Pprogression to later stages.

**Table 1** Finite rate of increase  $\lambda$  and summed elasticity values in six components  $E_1 - E_6$  of the stage projection matrices for 66 species of herbs, shrubs and trees.  $n$  = dimension of the matrix.

Species	$\lambda$	$E_1$	$E_2$	$E_3$	$E_4$	$E_5$	$E_6$	$n$	Source
<b>Herbs</b>									
1. <i>Agropyron repens</i> <sup>1</sup>	2.963	0.0001	0.0003	0.2302	0	0.4910	0.2773	6	Mortimer (1984)
2. <i>Allium monanthum</i> <sup>1</sup>	1.588	0	0.0003	0.2395	0.0613	0.4416	0.2572	7	Kawano <i>et al.</i> (1987)
3. <i>Anthyllis vulneraria</i> <sup>2</sup>	1.416	0.1306	0.2347	0	0	0.0727	0.5621	4	Sterk (1975), Sterk <i>et al.</i> (1982)
4. <i>Arisaema serratum</i>	0.991	0	0.0680	0.1050	0	0.2640	0.5630	19	Kinoshita (1987)
5. <i>Arisaema triphyllum</i> <sup>3</sup>	1.073	0.0122	0.0691	0.0661	0	0.6533	0.1995	7	Bierzchudeck (1982)
6. <i>Armeria maritima</i> <sup>2</sup>	1.458	0	0.1225	0	0	0.2258	0.6517	11	Lefebvre & Chandler-Mortimer (1984)
7. <i>Calathea ovandensis</i> <sup>1</sup>	1.550	0	0.2659	0	0.0353	0.2677	0.4312	4	Horvitz & Schemske (1986)
8. <i>Calochortus albus</i>	1.542	0	0.1875	0.0067	0	0.4048	0.4011	4	Fiedler (1987)
9. <i>Calochortus obispoensis</i>	1.023	0	0.0411	0.0253	0	0.8314	0.1022	3	Fiedler (1987)
10. <i>Calochortus pulchellus</i>	1.115	0	0.0859	0.0288	0	0.6629	0.2224	4	Fiedler (1987)
11. <i>Calochortus tiburonensis</i>	1.156	0	0.0811	0.0040	0	0.7570	0.1579	3	Fiedler (1987)
12. <i>Chamaelirium luteum</i> <sup>3</sup>	1.004	0	0.0279	0	0.2801	0.2958	0.3961	24	Meagher (1982)
13. <i>Cleome droserifolia</i> <sup>2</sup>	1.118	0.0358	0.0333	0	0	0.5753	0.3557	15	Hegazy (1990)
14. <i>Clintonia borealis</i> <sup>1</sup>	1.128	0	0	0.1754	0	0.6459	0.1787	3	Pitelka <i>et al.</i> (1985)
15. <i>Cynoglossum officinale</i> <sup>2</sup>	1.064	0	0.3148	0	0	0.0557	0.6295	3	Boorman & Fuller (1984)
16. <i>Danthonia sericea</i> <sup>3</sup>	1.196	0	0.1087	0	0.0456	0.4260	0.4197	6	Moloney (1988)
17. <i>Daucus carota</i> <sup>2</sup>	1.367	0	0.2736	0	0	0.1791	0.5473	3	Verkaar & Schenkeveld (1984)
18. <i>Digitalis purpurea</i> <sup>2</sup>	11.815	0.0397	0.4375	0	0	0.0059	0.5169	4	van Baalen (1982), van Baalen & Prins (1983)
19. <i>Dipsacus sylvestris</i>	2.322	0.0659	0.0015	0	0.2773	0.0506	0.6047	6	Caswell (1989)
20. <i>Disporum sessile</i> <sup>1</sup>	0.936	0	0.0224	0.2478	0.0560	0.2089	0.4649	13	Kawano <i>et al.</i> (1987)
21. <i>Disporum smilacinum</i> <sup>1</sup>	1.427	0	0.0054	0.1929	0.1070	0.3761	0.3186	8	Kawano <i>et al.</i> (1987)
22. <i>Echium vulgare</i> <sup>2</sup>	1.548	0	0.2761	0	0	0	0.7239	4	Klemow & Raynal (1985)
23. <i>Erythronium japonicum</i> <sup>1</sup>	1.001	0	0.0437	0.1742	0	0.3547	0.4274	13	Kawano <i>et al.</i> (1987)
24. <i>Fritillaria meleagris</i> <sup>2</sup>	1.018	0	0.0220	0.0770	0.1051	0.5145	0.2814	8	Zhang (1983)
25. <i>Gentiana pneumonanthe</i> <sup>2</sup>	1.335	0.0934	0.1147	0	0	0.3156	0.4763	4	Chapman <i>et al.</i> (1989)
26. <i>Hieracium floribundum</i> <sup>2</sup>	1.012	0.0014	0.0015	0.0716	0	0.8498	0.0758	4	Thomas & Dale (1975)
27. <i>Hypochoeris radicata</i>	1.270	0	0.2840	0.1900	0	0.1640	0.3620	3	de Kroon <i>et al.</i> (1987)
28. <i>Isatis tinctoria</i> <sup>2</sup>	1.237	0	0.3238	0	0	0.0285	0.6477	3	Farah <i>et al.</i> (1988)
29. <i>Linum catharticum</i> <sup>2</sup>	2.159	0	0.9417	0	0	0	0.0584	3	Verkaar & Schenkeveld (1984)
30. <i>Narcissus pseudonarcissus</i> <sup>3</sup>	0.976	0	0.0176	0.0844	0	0.7853	0.1127	3	Barkham (1980)
31. <i>Ophrys sphegodes</i> <sup>1</sup>	1.038	0	0.3204	0	0.0369	0.3865	0.2561	7	Waite & Hutchings (1991)
32. <i>Panax quinquefolium</i> <sup>3</sup>	0.996	0.0750	0	0	0	0.5606	0.3644	6	Charron & Gagnon (1991)
33. <i>Pedicularis furbishiae</i>	1.035	0	0.0778	0.1346	0.0152	0.3565	0.4159	6	Menges (1990)
34. <i>Picris hieracoides</i> <sup>2,3</sup>	0.767	0	0.2678	0	0	0	0.7322	4	Klemow & Raynal (1985)
35. <i>Plantago coronopus</i> <sup>2,3</sup>	1.142	0	0.4055	0.0116	0	0.1659	0.4171	3	Waite (1984)
36. <i>Podophyllum peltatum</i> <sup>2,3</sup>	1.158	0	0.0045	0.1891	0	0.5831	0.2232	4	Sohn & Polikansky (1977), Rust & Roth (1981)
37. <i>Potentilla anserina</i> <sup>3</sup>	0.883	0	0.0022	0.1902	0	0.5166	0.2910	6	Eriksson (1987, 1988)
38. <i>Ranunculus acris</i> <sup>1</sup>	1.206	0.0767	0.2097	0.0217	0	0.3073	0.3847	4	Sarukhán & Harper (1973), Sarukhán (1974), Harper (1977)
39. <i>Ranunculus bulbosus</i> <sup>1</sup>	1.345	0.2219	0.0481	0	0	0.2383	0.4918	3	Sarukhán & Harper (1973), Sarukhán (1974), Harper (1977)
40. <i>Ranunculus repens</i> <sup>1</sup>	0.498	0.0586	0.0025	0.0169	0	0.7853	0.1367	4	Sarukhán & Harper (1973), Sarukhán (1974), Harper (1977)
41. <i>Scabiosa columbaria</i> <sup>2,3</sup>	1.030	0	0.1482	0	0.0228	0.5098	0.3192	3	Verkaar & Schenkeveld (1984)
42. <i>Senecio integrifolius</i> <sup>2,3</sup>	1.446	0	0.1940	0.0119	0	0.3941	0.3999	3	Widen (1987)
43. <i>Senecio jacobaea</i> <sup>2</sup>	0.803	0	0.2012	0.0775	0	0.0444	0.6770	4	Forbes (1977)
44. <i>Swallenia alexandrae</i> <sup>2</sup>	0.997	0	0.0330	0	0	0.8679	0.0991	4	Pavlik & Barbour (1988)
45. <i>Viola fimbriatula</i> <sup>1</sup>	1.484	0.0854	0.0947	0.0457	0	0.2519	0.5223	14	Solbrig <i>et al.</i> (1988)
<b>Trees and shrubs</b>									
46. <i>Alnus incana</i> <sup>3</sup>	0.971	0	0	0.0615	0	0.7411	0.1974	5	Huenneke & Marks (1987)
47. <i>Araucaria cunninghamii</i>	1.009	0	0.0078	0	0	0.9412	0.0510	10	Enright & Watson (1991)
48. <i>Araucaria hunsteinii</i> <sup>1,3</sup>	1.020	0	0.0116	0	0	0.9281	0.0603	7	Enright (1982)
49. <i>Astrocaryum mexicanum</i> <sup>3</sup>	1.014	0.0081	0	0	0	0.9031	0.0889	14	Piñero <i>et al.</i> (1984)
50. <i>Avicennia marina</i> <sup>1</sup>	1.246	0	0.0974	0	0	0.6350	0.2676	6	Burns & Ogden (1985)
51. <i>Banksia ericifolia</i> <sup>2</sup>	1.609	0.0755	0.0728	0	0	0.3875	0.4642	9	Bradstock & O'Connell (1989)
52. <i>Betula nana</i>	0.992	0	0	0.1421	0	0.6740	0.1840	4	Ebert & Ebert (1989)
53. <i>Calluna vulgaris</i> <sup>1</sup>	2.995	0.0853	0.2021	0.0008	0	0.2029	0.5089	6	Barclay-Estrup & Gimingham (1975), Mallik <i>et al.</i> (1984), Scandrett & Gimingham (1989)
54. <i>Carnegiea gigantea</i> <sup>2</sup>	0.540	0	0.0006	0	0	0.9969	0.0024	15	Steenbergh & Lowe (1977, 1983)
55. <i>Cassia nemophila</i> <sup>1</sup>	1.207	0.0479	0.0439	0	0	0.5375	0.3707	12	Silander (1983)
56. <i>Fagus grandifolia</i> <sup>1</sup>	0.939	0	0.0078	0	0	0.9687	0.0235	4	Harcombe (1987)
57. <i>Iriartea deltoidea</i> <sup>3</sup>	1.081	0	0.0324	0	0	0.8402	0.1275	6	Pinard (1992)
58. <i>Nothofagus fusca</i> <sup>3</sup>	1.006	0	0.0084	0	0	0.9696	0.0221	4	Enright & Ogden (1979)
59. <i>Pentaclethra macroloba</i> <sup>1</sup>	1.002	0	0.0091	0	0	0.8946	0.0963	14	Hartshorn (1975)
60. <i>Petrophile pulchella</i> <sup>2</sup>	1.643	0.0600	0.0985	0	0	0.3645	0.4770	9	Bradstock & O'Connell (1989)
61. <i>Pinus palustris</i> <sup>1</sup>	0.998	0	0.0057	0	0	0.9649	0.0294	8	Platt <i>et al.</i> (1988)
62. <i>Podococcus barteri</i> <sup>1</sup>	1.013	0	0.0081	0.0404	0	0.8191	0.1325	6	Bullock (1980)
63. <i>Psidium guajava</i> <sup>1</sup>	0.994	0	0.0020	0	0	0.9767	0.0213	12	Somarrriba (1988)
64. <i>Rhopalostylis sapida</i>	1.007	0	0.0081	0	0	0.9440	0.0478	8	Enright & Watson (1992)
65. <i>Sequoia sempervirens</i> <sup>1</sup>	0.992	0	0	0	0	1	0	5	Namkoong & Roberds (1974)
66. <i>Vatica hainanensis</i> <sup>1</sup>	1.000	0	0.0219	0	0	0.7885	0.1896	12	Hu (1988)

<sup>1</sup>Matrix given by the source, but modified or corrected for this study. <sup>2</sup>Matrix compiled for this study from data in the source. <sup>3</sup>Matrix used in this study was obtained by averaging matrices given in the source.

cient was tested against a distribution of expected values of the statistic generated from a null model. The null models contained the same number of species as each sample (66, 45, 21, respectively) and were based on the observed elasticities of each sample in order to preserve biological realism. In each null model, observed values of the six elasticities were independently permuted among species and then standardized to sum to unity for each species. A correlation matrix was then calculated for the model. This was repeated 5000 times for each sample to generate a frequency distribution of correlation coefficients against which observed values were tested. The test was conservative (i.e. prone to type II error) because null models were generated from the observed data.

Because some species lack certain elasticities (e.g. non-clonal species lack  $E_3$  and species with no seed dormancy lack  $E_1$ ), spurious correlations could be created by including all species in all correlations. To avoid this, cases of zero values in  $E_1 - E_6$  were treated as missing observations, so sample sizes (and degrees of freedom) were determined pairwise within the correlation matrix.

Because  $F + L + G = 1$  there is a mathematical constraint among these variables, but biological constraints determine which species occur where in the space defined by them. The 66 species in the study were plotted in a triangular ordination for each of four groups: iteroparous herbs from closed habitats (forest herbs), iteroparous herbs of open habitats, semelparous herbs and woody species.

## Results

### COMPARISON OF WOODY PLANTS AND HERBS

The parameters calculated for each population are shown in Table 1. Although the intrinsic rate of increase ( $r$ ) varied greatly within each sample it differed at the 5% level between woody plants and herbs (Table 2).

**Table 2** A comparison of the mean values of  $r$ , elasticities  $E_1 - E_6$  and  $G$ ,  $L$ ,  $F$  for herbs and woody plants. Differences between the two groups were tested by Mann-Whitney  $U$ -test

	Herbs		Woody plants		$P <$
	$n$	mean (SD)	$n$	mean (SD)	
$r$	45	0.225 (0.451)	21	0.090 (0.315)	0.05
$E_1$	13	0.069 (0.060)	5	0.055 (0.030)	0.81
$E_2$	43	0.149 (0.175)	17	0.038 (0.053)	0.01
$E_3$	25	0.105 (0.083)	4	0.061 (0.060)	0.29
$E_4$	11	0.095 (0.096)	0	—	—
$E_5$	42	0.402 (0.246)	21	0.785 (0.235)	0.001
$E_6$	45	0.381 (0.184)	20	0.168 (0.165)	0.001
$G$	45	0.439 (0.183)	21	0.172 (0.170)	0.001
$L$	45	0.398 (0.256)	21	0.785 (0.235)	0.001
$F$	45	0.163 (0.175)	21	0.044 (0.074)	0.001

$E_1$ . A supra-annual seed pool existed in 13/45 herb populations and 5/21 woody plants. In only two cases did the seed pool contribute above 10% to changes in  $\lambda$  (*Anthyllis vulneraria* and *Ranunculus bulbosus*; Table 1) and the difference between herbs and woody plants was not significant (Table 2).

$E_2$ . Seedling recruitment occurred in all but two herb populations and in 17/21 woody plants (Table 1). The importance of seedlings varied greatly between herbs, reaching over 40% in the facultatively semelparous perennial *Digitalis purpurea* and 94% in the semelparous biennial *Linum catharticum*. *Digitalis purpurea* also had by far the largest value of  $\lambda$  in the data set (11.815) while *Linum catharticum* occupied fifth place ( $\lambda = 2.159$ ). The importance of seedling recruitment among woody plants was highest in the heathland shrub *Calluna vulgaris* (20%), but 12 herbs had higher values of  $E_2$  and the difference between the two life forms was significant ( $P < 0.01$ , Table 2). *Calluna vulgaris* also had the highest  $\lambda$  among woody plants (2.995).

$E_3$ . Clonal growth was recorded in 25/45 herb populations and in 4/21 woody plants (Table 1, Table 2). Values were highest in *Disporum sessile* (0.2478) and *Allium monanthum* (0.2395), two bulbiferous woodland herbs, and *Agropyron repens* (0.2302), a persistent rhizomatous weed. The two woody plants with the highest values of  $E_3$  were the dwarf arctic shrub *Betula nana* and the shrub *Alnus incana*. No seed or seedling recruitment was recorded in either species, but their clonal growth elasticities were only 0.1421 and 0.0615, respectively. Nine of the 25 clonal herbs had values of  $E_3 > 0.14$ . Clonal growth was not significantly different between herbs and woody plants (Table 2).

$E_4$ . Retrogression was sometimes difficult to separate from clonal growth in published matrices. It was absent from woody plants, but definitely occurred in eleven herbs, including an orchid (*Ophrys sphegodes*) and five species in the Liliaceae (*Allium monanthum*, *Chamaelirium luteum*, *Disporum sessile*, *D. smilacinum*, *Fritillaria meleagris*).

$E_5$ . Stasis occurred in all species except *Echium vulgare*, *Linum catharticum* and *Picris hieracoides* which are all short-lived semelparous perennials. Values of  $E_5$  were particularly high in woody plants, reaching a value of one in the very long-lived tree *Sequoia sempervirens* (Table 1). The difference between herbs and woody plants was highly significant (Table 2).

$E_6$ . Progression was more important than seed or seedling recruitment in all species, with only two exceptions: the short-lived, semelparous, biennial to perennial herb *Linum catharticum*, and the orchid *Ophrys sphegodes*. In general, progression was more important in herbs than woody plants (Table 2).

Overall, growth ( $G$ ) and fecundity ( $F$ ) were significantly more important in herbs than woody plants and the reverse was true for survival ( $L$ ) (Table 2).

#### CORRELATION BETWEEN ELASTICITIES OF LIFE-CYCLE PARAMETERS

Spearman rank correlations were calculated for the whole data set (Table 3) and for herbs and woody plants separately (Tables 4 and 5, respectively). There was a significant positive correlation between the intrinsic rate of increase  $r$  and the elasticity of fecundity ( $F$ , Table 3). This was especially strong in woody plants (Table 5, Fig. 2), but the correlation in herbs (Table 4) depended entirely upon a single outlier with a high value of  $r$ . Seedling recruitment ( $E_2$ ) rather than recruitment from the seed pool ( $E_1$ ) was responsible for this relationship. Significant negative correlations of similar strength occurred between survival ( $L$ ) and  $r$  and between stasis ( $E_5$ ) and  $r$  for all three data sets. Growth elasticity ( $G$ ) and  $r$  were positively correlated in woody plants ( $r = 0.66$ ,  $P < 0.0001$ ,  $n = 21$ ), and in the sample as a whole. Progression ( $E_6$ ) rather than clonal growth ( $E_3$ ) was responsible for the correlation between  $r$  and  $G$ , which was weaker than the correlation between  $r$  and  $E_6$  alone.

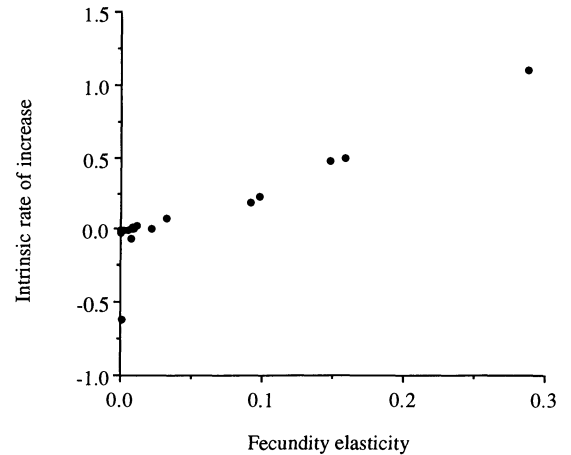


Fig. 2 Relationship between the intrinsic rate of population increase ( $r$ ) and the elasticity of fecundity ( $F$ ) in woody plants.

Seed recruitment ( $E_1$ ) was positively correlated with seedling recruitment ( $E_2$ ), progression ( $E_6$ ), and growth ( $G$ ) and negatively correlated with survival ( $L$ ) in the whole sample (Table 3). These correlations were weaker or not significant for the subsamples (Tables 4 and 5). Despite an overall positive correlation between  $E_2$  and  $G$ , the elasticity of seedling recruitment was significantly negatively correlated with the elasticity of the clonal compo-

Table 3 Spearman rank order correlation matrix for  $r$  ( $= \ln \lambda$ ), elasticity components  $E_1 - E_6$ , fecundity ( $F = E_1 + E_2$ ), survival ( $L = E_4 + E_5$ ) and growth ( $G = E_3 + E_6$ ) for 66 species of herbs and woody plants. Values in *italics* are significant  $P < 0.05$ , values in **bold** are significant  $P < 0.01$ . Except for correlations involving  $r$ , significance levels were determined by a randomization test. Pairwise sample sizes are shown in parentheses

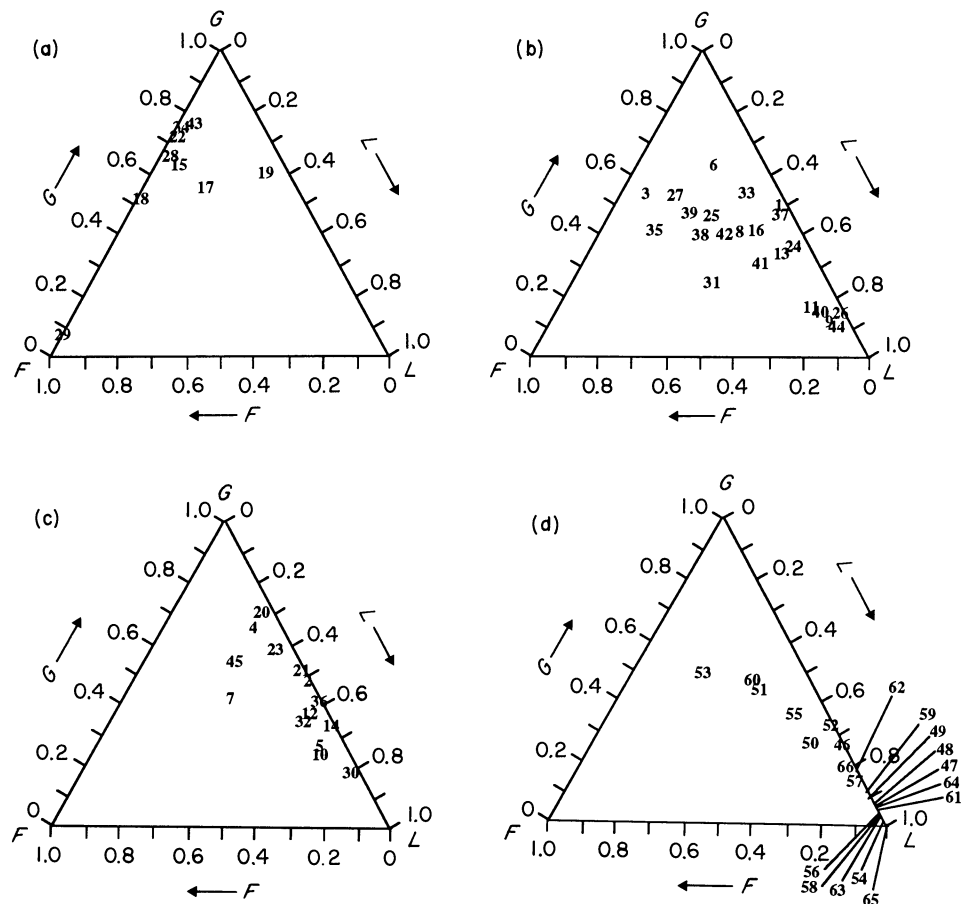
	$r$	$E_1$	$E_2$	$E_3$	$E_4$	$E_5$	$E_6$	$F$	$L$
$E_1$	0.22 (18)								
$E_2$	<b>0.41</b> (60)	0.55 (16)							
$E_3$	-0.14 (29)	-0.75 (7)	-0.55 (26)						
$E_4$	0.06 (11)	— (1)	-0.68 (11)	-0.20 (5)					
$E_5$	<b>-0.55</b> (63)	-0.63 (18)	<b>-0.67</b> (57)	-0.15 (29)	-0.21 (11)				
$E_6$	<b>0.43</b> (65)	<b>0.70</b> (18)	<b>0.60</b> (60)	0.07 (29)	0.02 (11)	<b>-0.95</b> (62)			
$F$	<b>0.51</b> (66)	0.72 (18)	0.95 (60)	<b>-0.60</b> (29)	-0.63 (11)	<b>-0.73</b> (63)	<b>0.66</b> (65)		
$L$	<b>-0.53</b> (66)	-0.70 (18)	<b>-0.76</b> (60)	-0.12 (29)	0.32 (11)	0.98 (63)	<b>-0.89</b> (65)	<b>-0.79</b> (66)	
$G$	<b>0.39</b> (66)	0.53 (18)	<b>0.45</b> (60)	0.46 (29)	0.17 (11)	<b>-0.94</b> (63)	0.94 (65)	<b>0.51</b> (66)	-0.88 (66)

Table 4 Spearman rank order correlation matrix for  $r$  ( $= \ln \lambda$ ), elasticity components  $E_1 - E_6$ , fecundity ( $F = E_1 + E_2$ ), survival ( $L = E_4 + E_5$ ) and growth ( $G = E_3 + E_6$ ) for herbs in the sample. Values in *italics* are significant  $P < 0.05$ , values in **bold** are significant  $P < 0.01$ . Except for correlations involving  $r$ , significance levels were determined by a randomization test. Pairwise sample sizes are shown in parentheses

	$r$	$E_1$	$E_2$	$E_3$	$E_4$	$E_5$	$E_6$	$F$	$L$
$E_1$	0.11 (13)								
$E_2$	0.26 (43)	0.55 (12)							
$E_3$	-0.03 (25)	-0.77 (6)	-0.55 (24)						
$E_4$	0.06 (11)	— (1)	-0.68 (11)	-0.20 (5)					
$E_5$	-0.38 (42)	-0.54 (13)	-0.58 (40)	-0.22 (25)	-0.21 (11)				
$E_6$	0.19 (45)	0.66 (13)	<b>0.44</b> (43)	0.12 (25)	0.02 (11)	<b>-0.91</b> (42)			
$F$	0.33 (45)	0.66 (13)	0.95 (43)	<b>-0.64</b> (25)	-0.63 (11)	-0.63 (42)	<b>0.49</b> (45)		
$L$	-0.38 (45)	-0.65 (13)	<b>-0.72</b> (43)	-0.18 (25)	0.32 (11)	0.96 (42)	-0.79 (45)	<b>-0.74</b> (45)	
$G$	0.16 (45)	0.43 (13)	<b>0.22</b> (43)	0.54 (25)	0.17 (11)	<b>-0.85</b> (42)	0.89 (45)	<b>0.24</b> (45)	-0.75 (45)

**Table 5** Spearman rank order correlation matrix for  $r$  ( $= \ln \lambda$ ), elasticity components  $E_1 - E_6$ , fecundity ( $F = E_1 + E_2$ ), survival ( $L = E_4 + E_5$ ) and growth ( $G = E_3 + E_6$ ) for woody plants in the sample. Values in *italics* are significant  $P < 0.05$ , values in **bold** are significant  $P < 0.01$ . Except for correlations involving  $r$ , significance levels were determined by a randomization test. Pairwise sample sizes are shown in parentheses

	$r$	$E_1$	$E_2$	$E_3$	$E_4$	$E_5$	$E_6$	$F$
$E_1$	0.90 (5)							
$E_2$	<b>0.88</b> (17)	0.80 (4)						
$E_3$	-0.80 (4)	— (1)	— (2)					
$E_4$	-0.67 (21)	-0.90 (5)	-0.90 (17)	0.20 (4)				
$E_5$	<b>0.68</b> (20)	0.90 (5)	<b>0.90</b> (17)	-0.40 (4)	-1.00 (20)			
$F$	<b>0.88</b> (21)	0.90 (5)	<b>1.00</b> (17)	-0.95 (4)	-0.66 (21)	<b>0.64</b> (20)		
$L$	-0.67 (21)	-0.90 (5)	-0.90 (17)	0.20 (4)	1.00 (21)	-1.00 (20)	-0.66 (21)	
$G$	<b>0.66</b> (21)	0.90 (5)	<b>0.90</b> (17)	-0.20 (4)	-1.00 (21)	0.99 (20)	<b>0.64</b> (21)	-1.00 (21)



**Fig. 3** Distribution of 66 perennial species in  $G-L-F$  space: (a) semelparous herbs, (b) iteroparous herbs of open habitats, (c) iteroparous forest herbs, (d) woody plants. Species numbers correspond to those in Table 1.

nent of growth ( $E_3$ ) in herbs ( $r = -0.55$ ,  $P < 0.05$ ,  $n = 24$ ) and in the whole sample. The positive relation between  $E_2$  and  $G$  was due to a strong positive correlation between  $E_2$  and  $E_6$ .  $E_2$  was also negatively correlated with  $L$  and its components  $E_4$  and  $E_5$  although in herbs the latter did not show significance.

The negative relationship between the elasticities of sexual and clonal reproduction was manifest in a strong ( $P < 0.01$ ) negative correlation between fecundity ( $F = E_1 + E_2$ ) and clonal growth ( $E_3$ ) in both the whole sample and herbs, although sample size was too small for woody plants ( $P = 0.10$ ,  $n = 4$ ).

Retrogression to previous stages ( $E_4$ ) had a poor, non-significant correlation with other variables. Woody plants did not have retrogression.

Stasis ( $E_5$ ) and progression ( $E_6$ ) were very strongly negatively correlated with each other. Correlations between  $G$ ,  $L$  and  $F$  are to be expected because of the mathematical constraint referred to, but it is notable that the correlation between fecundity and survival is a negative one while that between fecundity and growth is positive (Table 3).

It is evident from the  $G-L-F$  triangular plots that most populations had low fecundity elasticity (Fig. 3). Nevertheless, the distribution of the 66 species is more or less continuous. Short-lived,

semelparous herbs were distributed along the  $G$  axis (Fig. 3a). Although  $F$  varied from 0.07 for *Dipsacus sylvestris* to 0.94 for *Linum catharticum*, survival elasticity ( $L$ ) was always lower than 0.33. The high mortality of seedlings and the absence of a seed bank in *Linum catharticum* made it dependent on a high recruitment rate. This species was incorrectly placed along the  $L$  axis in a previous paper (Silvertown, Franco & McConway 1992).

Iteroparous herbs of open habitats showed a great deal more variation in the variables  $G$ ,  $L$  and  $F$  (Fig. 3b) but tended to occupy the middle portion of the triangle with low to intermediate values for  $F$  and  $L$  and intermediate  $G$  values. Five of them (nos 9, 11, 26, 40 and 44), however, occurred clumped near the  $L$  axis next to long lived trees (see below). In particular, the high  $L$  value for *Ranunculus repens* was due to seeds remaining in the seed bank with a 'decay rate ... too slow to detect ...' (Sarukhan 1974). The other four plants in this group are characterised by a bulbous (nos 9 and 11), stoloniferous (nos 26 and 40) or hummock-forming (no. 44) habit.

Iteroparous forest herbs were scattered along the survivorship axis from  $L = 0.25$  for *Viola fimbriatula* to  $L = 0.785$  for *Narcissus pseudonarcissus* (Fig. 3c). Plants in this group were characterized by low-fecundity elasticity, the highest value being  $F = 0.266$  for *Calathea ovandensis*. Woody plants tended to occupy the  $L$  corner of the triangle (Fig. 3d). Their population growth rate depends heavily on the survival of established adult individuals. The four species in the lower range of survival elasticity for this group and which had higher values of  $G$  and  $F$  (nos 51, 53, 55 and 60) are all small shrubs of open, sometimes fire-prone habitats.

## Discussion

However ingeniously devised, a study that attempts to compare species that range from *Senecio* to *Sequoia* is in danger of being something of a procrustean exercise. How might this have affected our results? The dimensionality of a matrix, or the number of stages into which a life cycle is divided, will affect values of  $a_{ij}$  and  $e_{ij}$ . Although statistical rules of thumb have been proposed to determine the appropriate dimensionality of a projection matrix (Vandermeer 1978; Moloney 1986), in practice it has been a decision based on the biology of a species (Caswell 1989). Even where we compiled matrices ourselves, matrix dimensionality in this study was largely decided by the authors of our data sources. However, by aggregating values of  $e_{ij}$  into six components, each with a clear biological meaning, we attempted to iron out inaccuracies caused by differing dimensionality.

Dimensionality is important in determining the relative values of stasis and progression. There was

a very strong negative correlation between  $E_5$  and  $E_6$ , which is to be expected if these have a relatively fixed sum. However, within the sum  $E_5 + E_6$  the relative value of these variables in different species may vary either for biological reasons or as an artifact of differing dimensionality. The more dimensions in a matrix, the narrower will be the limits which define each size class and the more likely it is that the annual growth increment of an individual in a particular class will take it out of that size class at the next census. With increasing dimensionality the diagonal matrix elements  $a_{ii}$  will become smaller and the subdiagonal elements larger, causing an associated decrease in  $E_5$  and an increase in  $E_6$ . This artifact will move individual points in the  $G$ - $L$ - $F$  space to varying degrees. To investigate its effect it is necessary to modify the dimensionality of individual matrices and this in turn requires raw data on individual growth or at least information on the number of individual in each stage class (stage distribution). This information was not usually available. Preliminary analyses made by Enright and Franco (unpublished) have, however, shown that for long-lived woody species dimensionality effects are small within the range of dimensions commonly used. An indicative test for the occurrence of this problem in our database may be made. If the negative correlation between  $E_5$  and  $E_6$  is artifactual we would expect a negative correlation between matrix dimensionality ( $n$ ) and  $E_5$ . If there is no such correlation, one can tentatively attribute some biological significance to the partitioning  $E_5:E_6$ . When treated separately, woody plants and herbs did not show significant correlation (Spearman) between  $E_5$  and  $n$  (herbs,  $S = -0.06$ ,  $P = 0.720$ ; woody plants,  $S = 0.02$ ,  $P = 0.937$ ). However, when all species were lumped together, the correlation was significant but positive ( $S = 0.25$ ,  $P < 0.05$ ), i.e. given the range of values for  $n$  in the dataset, long-lived woody plants have high values of stasis. There may be a simple biological explanation of variation in  $E_5$  and  $E_6$ . High values of  $E_5$  are characteristic of woody plants and high values of  $E_6$  are characteristic of herbs (Table 2). This makes intuitive sense and is confirmation that our partitioning of elasticities has biological meaning across the full range of plant life history in our sample.

The distinct separation of species into ecologically different groups in  $G$ - $L$ - $F$  space (Fig. 3) provides a starting point to categorize patterns of demography and life-history in plants. Forest herbs fall along the  $L$ - $G$  axis; semelparous plants along the  $F$ - $G$  axis. Species lying along the  $L$ - $G$  axis, near the  $L = 1$  vertex of the triangle, are mostly (although not exclusively) woody plants of forest habitats. Woody plants of open habitats lie towards the centre of the triangle in the direction of the  $G$  corner. Iteroparous herbs of open habitat are more

broadly scattered but this is to be expected given the wide range of habitats they occupy. Except for the presence of *Linum catharticum*, the distribution of our 66 perennial species in  $G$ – $L$ – $F$  space leaves the region of the triangle with  $F = 1$  at its vertex conspicuously empty. We would expect this region to be occupied by annual species. With some exceptions then, ordination in  $G$ – $L$ – $F$  space produces a clear correspondence between the relative importance of the three major demographic parameters to  $\lambda$  and life form and habitat. This is an important step towards linking a quantitative description of life history with the habitat templet (Southwood 1977, 1988).

The species in our study comprise both genet populations (e.g. most of the trees) and ramet populations (the clonal species). We have treated the two kinds of population equivalently, although it has been argued that a distinction should be made between them because fitness should be measured only at the level of the genet (Harper 1977). The alternative view is that ramet dynamics may be used as an indirect measure of genet fitness (Caswell 1985; de Kroon & van Groenendaal 1990; Eriksson & Jerling 1990), in which case the dominant eigenvalue,  $\lambda$ , of a projection matrix may be used to measure fitness in ramet as well as genet populations. The validity of this approach is confirmed by our finding that there is a correlation between the elasticity of clonal growth and the elasticity of fecundity in the demography of ramets.

A negative correlation between elasticities implies a trade-off between the contributions to fitness of the corresponding components of the life cycle. However, it is important to recognize that this need not imply a precisely parallel trade-off between the phenotypic values of two traits. It is easiest to see the reason for this with an example. *Digitalis purpurea* is a species that produces large numbers of small seeds which can lie dormant for a long time in the seed pool. Only a small proportion of these seeds ever become seedlings (0.15% per year), so one might conclude, on the basis of the numerical allocation of seeds between dormant/nondormant phenotypes, that seed dormancy makes a larger contribution to fitness (or is 'more important') in *D. purpurea* than in a species such as *Ranunculus bulbosus* with a smaller fraction of dormant seed (45% germination per year). In fact this is incorrect and the elasticity for the seed pool ( $E_1$ ) is much greater in *R. bulbosus* (0.2219) than in *D. purpurea* (0.0397) (Table 1). The reason for this is simply that dormant seeds make no contribution to fitness unless they germinate, so the value of a seed in the seed pool cannot be evaluated without taking into account the germination rate and the rest of the life cycle as well. In fact, this is exactly what elasticity does (de Kroon, Plaiser &

van Groenendaal 1987). It might be argued that trade-offs between life-history traits are *better* measured by correlations between elasticity values than by correlations between trait values themselves, because the consequences for fitness can be more directly interpreted in the former.

The literature on the function and evolutionary significance of clonal growth in plants has concentrated on its advantages, and on the costs and benefits of clonal integration with little attention to the potential costs of clonality itself. It has been assumed that the evolution of clonal growth is limited by the long-term disadvantages that are assumed to operate against asexual reproduction in general, but a short-term trade-off between clonal growth and sexual reproduction must also occur. The negative correlation between clonal growth elasticity ( $E_3$ ) and fecundity elasticity ( $F$ ) within the group of clonal plants (Table 3) strongly suggests that there is a trade-off between the contributions to fitness of these two modes of reproduction. Furthermore, there was no correlation whatsoever between  $r$  and  $E_3$ , so there is no evidence here either that clonal growth confers an absolute fitness advantage.

The relative importance of life-cycle parameters to  $\lambda$  is expected to vary with the value of  $\lambda$  (e.g. Caswell 1982), and the correlations we found between  $r$  ( $= \ln \lambda$ ) and various elasticities confirm this (Tables 3 and 4). The strongest correlation was between  $\lambda$  and the value of  $F$  among woody plants (Fig. 2). Using sensitivity analysis of model populations Caswell (1982) found that the relative importance of fecundity *increased* as  $\lambda$  decreased, whereas we found the reverse pattern for actual populations.

The matrices used in this study were stationary ones, and therefore the elasticities derived from them project the relative contributions of life history components to fitness in an environment that does not vary with time and in which  $\lambda$  is constant. This may have a variety of effects. For species which recruit only infrequently, our matrices may not portray the full importance of fecundity or a seed pool to population dynamics. The importance of a seed pool to fitness ( $E_1$ ) is very likely to be underestimated, because selection operates strongly in favour of this character when  $\lambda$  varies (Cohen 1966; Silvertown 1988; Venable 1990). The effects of environmental variation can be incorporated in a matrix approach to life history evolution (e.g. Tuljapurkar 1990).

This paper is only the first step towards a comparative demography of plants. We have demonstrated that the approach can reveal meaningful relationships between life history variables, between life history and life form and between life history and habitat, but there is still much to do. With a sample containing more species it would be possible to look for the influence of taxonomic

constraints on demographic patterns. We are also acutely aware that demographic parameters for most species vary greatly in time and in space, and future studies should attempt to compare intra-specific patterns with interspecific ones. Future papers will look at this and other topics in comparative plant demography using our dataset.

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