

## ORIGINAL PAPER

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**Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages**

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**Abstract** Recent studies have used transition matrix elasticity analysis to investigate the relative role of survival (L), growth (G) and fecundity (F) in determining the estimated rate of population increase for perennial plants. The relative importance of these three variables has then been used as a framework for comparing patterns of plant life history in a triangular parameter space. Here we analyse the ways in which the number of life-cycle stages chosen to describe a species (transition matrix dimensionality) might influence the interpretation of such comparisons. Because transition matrix elements describing survival (“stasis”) and growth are not independent, the number of stages used to describe a species influences their relative contribution to the population growth rate. Reduction in the number of stages increases the apparent importance of stasis relative to growth, since each becomes broader and fewer individuals make the transition to the next stage per unit time period. Analysis of a test matrix for a hypothetical tree species divided into 4–32 life-cycle stages confirms this. If the number of stages were defined in relation to species longevity so that mean residence time in each stage were approximately constant, then the elasticity of G would reflect the importance of relative growth rate to  $\lambda$ . An alternative, and simpler, approach to ensure comparability of results between species may be to use the same number of stages regardless of species longevity. Published studies for both herbaceous and woody species have tended

to use relatively few stages to describe life cycles (herbs:  $n = 45$ ,  $\bar{x} = 6.16 \pm 4.63$ ; woody plants:  $n = 21$ ,  $\bar{x} = 8.38 \pm 3.57$ ) and so approximate this approach. By using the same number of stages regardless of longevities, the position of species along the G-L side of the triangular parameter space largely reflects differences in longevity. The extent of variation in elasticity for L, G and F within and between species may also be related to factors such as successional status and habitat. For example, the shade-tolerant woody species, *Araucaria cunninghamii*, shows greater importance for stasis (L), while the gap-phase congener species, *Araucaria hunsteinii*, shows higher values for G (although values are likely to vary with the stage of stand development).

**Key words** Transition matrix · Elasticity analysis · Plant life history · Survival · Life-cycle stages

**Introduction**

The analysis of plant demographic data using matrix algebra provides a powerful tool for both describing and understanding the population dynamic behaviour of organisms from widely differing taxa, life forms and habitats. From a stage-classified life table describing the life-history properties of a sample population, a transition matrix can be constructed, the elements of which typically identify mean rates of fecundity (F), transition (growth) from one stage to the next (G), and survival without transition, or “stasis” (L). Given the abundance of each stage class at time  $t$ , one can make a projection of the population at time  $t + 1$  (Caswell 1989):

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t)$$

where the matrix  $\mathbf{A}$  is a projection matrix and  $\mathbf{n}(t)$  is a column vector describing abundances in each stage class (Fig. 1). If the population is projected forward far enough by continued multiplication of the matrix  $\mathbf{A}$  by

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each newly derived column vector,  $\mathbf{n}(t+1)$ ,  $\mathbf{n}(t+2)$ ,..., both the rate of population increase and the relative abundances of individuals in each stage class become stable, providing estimates of the finite rate of natural increase ( $\lambda$ ) and the stable stage distribution (SSD). These, and other, useful demographic parameters can be derived algebraically from the transition matrix (Caswell 1978, 1982):  $\lambda$  (the dominant eigenvalue of the transition matrix), SSD (the right eigenvector), reproductive values (left eigenvector), and the sensitivity of  $\lambda$  to absolute changes in individual matrix elements. de Kroon et al. (1986) further enhanced the power of the matrix method with their definition of elasticity, a relative measure of the contribution to  $\lambda$  made by each matrix element. Elasticities for each element ( $e_{ij}$ ) are defined as:

$$e_{ij} = \frac{\delta \lambda}{\lambda} \frac{a_{ij}}{\lambda} = \frac{\delta \ln \lambda}{\delta \ln a_{ij}}$$

where  $a_{ij}$ 's are the transition matrix elements, and  $\lambda$  is the finite rate of natural increase (Caswell 1989). Since each  $e_{ij}$  identifies the proportional contribution of transition matrix element  $a_{ij}$  to variation in  $\lambda$ , the elements of the elasticity matrix always sum to unity (de Kroon et al. 1986; Mesterton-Gibbons 1993).

Several authors have now used elasticity to describe the relative contribution made to population growth by individual elements of the matrix, different life stages, and different life-history parameters (typically fecundity, survival and growth) in the population dynamic behaviour of a number of plant and animal species (e.g. Caswell 1986, 1989; Moloney 1988; Gotelli 1991; Enright and Watson 1991, 1992; Silvertown et al. 1992, 1993).

Enright and Watson (1991) and Silvertown et al. (1992) independently proposed the possible relationship between these quantitative measures of life-history parameter contributions to population growth ("fitness" *sensu* Stearns 1992) calculated using transition matrix procedures, and the C-S-R theory of plant

life-history strategies of Grime (1977, 1979). They outlined the analogy between (stage-classified) transition matrix measures of elasticity for fecundity, growth and survival, and the three primary strategies of Grime: selection on competitive (C) strategists is argued to prioritize rapid growth (G in this paper), selection on stress-tolerators (S) should prioritize survival (L in this paper), and that on ruderals (R) should favour high fecundity (F in this paper). The potential appeared to exist for an independent and quantitative assessment of the idea of three primary strategies in plants, and perhaps other kinds of organisms.

Silvertown et al. (1992) conducted a preliminary test of the relationship, comparing the location of 18 herb species in triangular ordination space based both on elasticity analysis and classification into C-S-R space by Grime et al. (1988). There was no significant correlation between the two methods. However, Silvertown and Franco (1994) found that elasticity analysis did predict successional trajectories in G-L-F space similar to those predicted by Grime (1977) in C-S-R space. Elasticity analyses for a total of 66 plant species led Silvertown et al. (1993) to conclude that the transition matrix approach revealed distinctive patterns of the relative importance of stasis (survival), growth and fecundity for different kinds of plants (e.g. semelparous herbs, iteroparous herbs, long-lived woody species).

Published matrices vary in the number of life-cycle stages used to describe different plant species [e.g. from 3 (Sarukhán and Gadgil 1974) to 24 (Meagher 1982); for populations classified into a simple, linear life cycle]. Large and/or long-lived organisms are often divided into more stages than small and/or short-lived organisms. In some species, or for some life-cycle stages, boundaries clearly reflect visible stages in organism development such as the onset of reproduction, appearance of woody stem tissue, or change from juvenile to adult foliage. In other cases, boundaries may be arbitrarily defined according to stem diameter, plant height, number of tillers, etc. Both Vandermeer (1978) and Moloney (1986) have suggested objective methods for determining the number of life-cycle stages which should be used based on sample size and distribution. However, since these studies pre-date the definition of elasticity by de Kroon et al. (1986), they do not address issues pertaining to life-cycle-stage contribution to  $\lambda$ .

Here, we identify the chosen number of life-cycle stages as a factor which might influence the results of elasticity analyses based on the transition matrix method. While it is assumed that authors choose biologically meaningful stages to describe a particular species (Caswell 1986), these different choices may affect between-species comparisons. Silvertown et al. (1993) argued in their comparative study of 66 plant species that the aggregation of elasticities for individual elements of the transition matrices into components reflecting the overall contribution of fecundity, growth and stasis to population growth might "iron

**Fig. 1** Matrix representation of the equation:  $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$  showing how the projected population at  $(t+1)$  is derived by multiplication of the transition matrix,  $\mathbf{A}$ , and column vector,  $\mathbf{n}(t)$ , which describes abundances in each stage class. This projection matrix is divided into five life-cycle stages showing the location of elements which describe survival ( $L$ ), growth ( $G$ ) and fecundity ( $F$ ). Retrogression ( $D$ ), which may occur in some species, is included as a component of  $L$  rather than  $G$  in the interpretation of elasticities in this paper, since it represents the holding of existing resources rather than the capture of new ones. Where no transitions between stages occur, the relevant matrix elements are set to zero

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix} (t+1) = \begin{bmatrix} L_1+F_1 & F_2+D_2 & F_3 & F_4 & F_5 \\ G_1 & L_2 & D_3 & 0 & 0 \\ 0 & G_2 & L_3 & D_4 & 0 \\ 0 & 0 & G_3 & L_4 & D_5 \\ 0 & 0 & 0 & G_4 & L_5 \end{bmatrix} \times \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix} (t)$$

out" inaccuracies caused by the use of different numbers of life-cycle stages. A more appropriate way to address this problem is to analyse the same species data using different numbers of stages. We test this by comparing the elasticities of F, L and G for three species and an artificial data set when life cycles are divided into many stages with the elasticities when life cycles are divided into only four stages. Further, we compare the number of stages and mean time spent in each stage for woody versus herbaceous species for the species data set analysed by Silvertown et al. (1993). This is done since it is not clear how the numbers of life-cycle stages used in the literature are related to species longevity.

**Materials and methods**

Transition matrices based on contrived data for an imaginary tree species, and matrices for several species published elsewhere and compared in Silvertown et al. (1993), were used to test the above question. These species were chosen since data were available which allowed calculation of new transition matrices with a reduced number of life-cycle stages. In addition, they enabled comparison of elasticities between species of both similar and different longevity and habit. These species were: the emergent tropical conifers *Araucaria cunninghamii* (Enright and Watson 1991) and *Araucaria hunsteinii* (Enright 1982), the New Zealand rainforest tree *Nothofagus fusca* (Enright and Ogden 1979) and the North American perennial bunchgrass *Danthonia sericea* (Moloney 1988).

To produce matrices with a reduced number of life-cycle stages, information was required on the number of individuals in each stage. The number of stages for each matrix was reduced by combining information for adjacent stages. New estimates of average fecundity (F), survival without progression to the next stage (L), and survival with progression (G), were entered as the elements of the reduced matrices. If  $n_i$  and  $n_{i+1}$  represent the number of individuals in two successive stages to be combined into one, and if L, G and F are the coefficients for stasis, growth and fecundity, their new values for the combined stages are calculated as:

$$L = \frac{n_i(L_i + G_i) + n_{i+1}L_{i+1}}{n_i + n_{i+1}}$$

$$G = \frac{n_{i+1}G_{i+1}}{n_i + n_{i+1}}$$

$$F = \frac{n_iF_i + n_{i+1}F_{i+1}}{n_i + n_{i+1}}$$

**Table 1** Transition matrices for *Danthonia sericea*: (a) original, six life-cycle stage matrix D 1983–1984 from Moloney (1988); (b) reduced four-stage matrix. Note that matrix elements in (b) are not a simple average of elements in (a), as these have been weighted by the number of individuals in each class

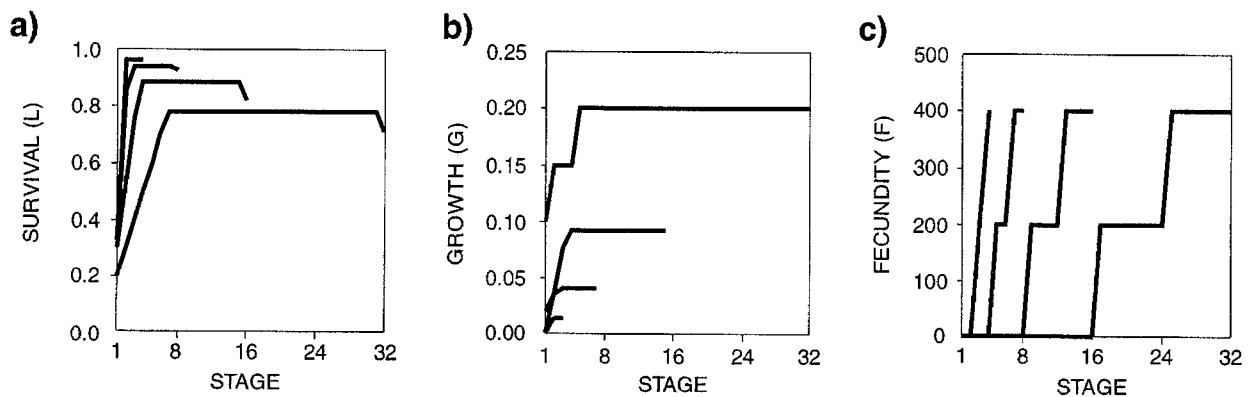
(a) Six-category matrix						(b) Four-category matrix			
0.07	0.89	1.76	4.09	9.21	21.15	0.07	1.25	6.14	21.15
0.17	0.39	0.17	0.00	0.00	0.00	0.30	0.62	0.12	0.00
0.13	0.23	0.46	0.20	0.00	0.00	0.00	0.15	0.75	0.11
0.00	0.05	0.29	0.50	0.05	0.00	0.00	0.00	0.10	0.89
0.00	0.00	0.00	0.27	0.68	0.11				
0.00	0.00	0.00	0.00	0.26	0.89				

In the case of *D. sericea* retrogression (i.e. reduction in size) to a previous life-cycle stage (D) and progression through two stages also had to be taken into account (Table 1).  $\lambda$  and elasticities were calculated using standard matrix techniques (Caswell 1989) and the sum of elasticities associated with L (including D), G and F was compared with those obtained from the original matrices.

A transition matrix describing an imaginary tree species divided into 32 life-cycle stages, having a longevity of about 150 years and  $\lambda$  close to 1.0, was artificially constructed and analysed (Fig. 2). The stable stage distribution provided the values of  $n_i$  and  $n_{i+1}$  necessary for calculating a new transition matrix using only 16 life-cycle stages. This process was repeated to produce transition matrices based on division of the life cycle into eight and four stages (Fig. 2). Elasticities for L, G and F of each of these four matrices were calculated and compared. This allowed analysis of the importance of number of life-cycle stages over a wider range than that available in the published literature.

Mean number of life-cycle stages for herbs and woody plants and mean time to first passage were calculated for the 66 species compared by Silvertown et al. (1993). The average of time to first passage for each matrix describes the mean time spent in each life-cycle stage. This parameter was calculated using the Stagecoach program of Cochran and Ellner (1992), which estimates a variety of both stage- and age-related demographic parameters. These data allowed us to explore further the effect of number of stages on elasticities. Because not all matrices from Silvertown et al. (1993) meet the conditions required by the Stagecoach program to calculate time to first passage, sample sizes differ in the calculation of mean dimension and time spent in each category.

**Fig. 2a–c** Calculated values of transition matrix elements for a survival, b growth, and c fecundity for the imaginary tree species described in the text based on division of the species life cycle into 32, 16, 8 and 4 life-cycle stages respectively



## Results and discussion

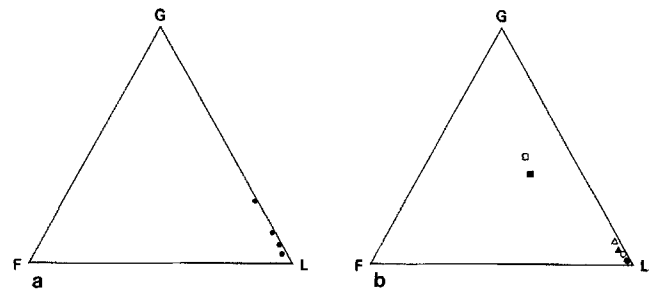
A general consequence of reducing the number of life-cycle stages used to construct the transition matrix for any species is that more individuals remain within the same stage per unit time and fewer proceed to the next stage. Thus, values of  $L$  rise while values of  $G$  fall (Fig. 2). The impact on elasticities of reduced number of stages is an increase in the apparent contribution (importance) of stasis to fitness, even though the sample life-table data are the same. Results are presented for each of the sample species datasets in turn.

### *D. sericea* site D 1983/1984 matrix (Moloney 1988)

The original matrix described division of this perennial grass into six life-cycle stages based on number of tillers: 1–2, 3–6, 7–13, 14–27, 28–56, >56.  $\lambda$  was 1.43 and elasticities for  $L$ ,  $G$  and  $F$  were 0.36, 0.45 and 0.18, respectively. A new matrix with only four stages (tillers: 1–2, 3–13, 14–56, >56) was constructed and analysed (Table 1).  $\lambda$  remained unchanged at 1.43 while elasticities were 0.42 for  $L$ , 0.38 for  $G$  and 0.20 for  $F$  (Table 2, Fig. 3). Stasis now appears to be more important than growth in determining the rate of population increase.

### *A. cunninghamii* 1977–1982 matrix (Enright and Watson 1991)

*A. cunninghamii* is a long-lived, emergent conifer of tropical forests in New Guinea and north-eastern Australia. The sample population described here is from a closed forest stand near Bulolo, Papua New Guinea. The original matrix divided data for this tree species into ten stages according to height for seedlings and stem diameter for individuals more than 2 cm diameter at breast height.  $\lambda$  was 1.009 and elasticities were  $L = 0.94$ ,  $G = 0.05$  and  $F = 0.01$  (Table 2). A new



**Fig. 3a, b** The change in species position within the elasticity triangle following reduction in the number of life-cycle stages used to calculate transition matrices: **a** for the artificial data set, and **b** for species described in the text. For **b** open symbols represent the position of species based on the original matrix, and filled symbols their position based on reduced number of life-cycle stages; (□, ■) *Danthonia sericea*; (○, ●) *Araucaria cunninghamii*; (△, ▲) *A. hunsteinii*. See Table 2 for details of numerical results. Letters at triangle apices refer to positions of 100% elasticity for fecundity ( $F$ ), growth ( $G$ ) and stasis ( $L$ )

matrix with four stages was constructed and analysed.  $\lambda$  increased slightly to 1.010 and elasticities were  $L = 0.97$ ,  $G = 0.02$  and  $F = 0.01$  (Table 2, Fig. 3). Again, elasticity for stasis assumed greater apparent importance and that for growth declined. The slight increase in  $\lambda$  and in fecundity elasticity (although not apparent here due to rounding) was due to more precocious reproduction, an artefact of combining stages for pre-reproductive and newly reproductive individuals (clearly a practice which should be avoided).

### *A. hunsteinii* versus *N. fusca* (Enright & Ogden 1979)

Both species are long-lived forest trees with similar longevities (about 400 years) and recruitment favoured in tree-fall gaps. In the original publication these species were divided into eight and four stages, respectively. Thus the mean residence time of surviving individuals in each stage is twice as long for *N. fusca*. Elasticity analysis for the *N. fusca* stand having the highest  $\lambda$

**Table 2** Summary of transition matrix results for species discussed in the text. Sites are identified as described in source publications. *Stages* refers to the number of life-cycle stages into which the population was divided. For each species, results on the first row are for the unmodified matrix and those on subsequent rows are for matrices based on division of the life cycle into a smaller number of stages

Species	Site	Stages	Elasticity			
			$\lambda$	$L$	$G$	$F$
<i>A. hunsteinii</i> <sup>a</sup>	13	7	1.055	0.88	0.10	0.02
	13	4	1.055	0.92	0.06	0.02
<i>A. cunninghamii</i> <sup>b</sup>	20	10	1.009	0.94	0.05	0.01
	20	4	1.010	0.97	0.02	0.01
<i>D. sericea</i> <sup>c</sup>	D	6	1.430	0.36	0.45	0.18
	D	4	1.430	0.42	0.38	0.20
<i>N. fusca</i> <sup>d</sup>	Middle	4	1.028	0.94	0.04	0.02
Imaginary tree species		32	1.011	0.73	0.26	0.01
		16	1.011	0.85	0.14	0.01
		8	1.011	0.91	0.08	0.01
		4	1.011	0.94	0.04	0.02

Sources of original matrices: <sup>a</sup>Enright (1982); <sup>b</sup>Enright and Watson (1991); <sup>c</sup>Moloney (1988); <sup>d</sup>Enright and Ogden (1979)

(middle stand,  $\lambda = 1.028$ ) produced values of  $L = 0.94$ ,  $G = 0.04$  and  $F = 0.02$  (Table 2). Analysis of the "gap" *A. hunsteinii* stand was first repeated with the number of life-cycle stages adjusted to seven to eliminate the error inherent in assigning a stage to seeds in species which show no dormancy. Caswell (1989, page 49) notes that use of a "seeds" stage introduces an artefactual delay of 1 year in the process of reproduction for such species. Analysis of the seven-stage matrix gave  $\lambda = 1.055$  and elasticities of 0.88, 0.10 and 0.02 for L, G and F, respectively. From both the higher  $\lambda$  and higher elasticity for growth, we might conclude that the latter species needs gaps more than the former. However, when analysed using only four stages of approximately the same dimensions used for *N. fusca*, elasticities change to  $L = 0.92$ ,  $G = 0.06$  and  $F = 0.02$ . There is then little apparent difference between the two species (Fig. 3).

### Imaginary tree species

Analysis of the artificially constructed matrices shows more dramatic change in elasticities as the number of life-cycle stages is reduced.  $\lambda$  remained constant at 1.011 for all four matrices while both the elasticity of L and F increased (0.733–0.938, and 0.013–0.018 respectively) and that of G decreased (0.255–0.044) as the number of life-cycle stages was reduced from 32 to 4 (Table 2, Fig. 3). Age-related parameters calculated using Stagecoach (Cochran and Ellner 1992), such as mean age at maturity and mean generation time, also decreased systematically with reduction in the number of stages used to describe the life cycle. The instability of these measures in relation to number of stages warrants further investigation before age-related parameters calculated from stage-classified population data can be recommended.

Regardless of species, elasticities changed consistently in the expected direction as number of stages was reduced (Table 2). In contrast, comparing different species (matrices), Silvertown et al. (1993) found either no correlation (for herbs and woody plants taken separately) or a significant positive correlation (for herbs and woody plants combined) between number of stages and the apparent importance of stasis elasticity. This is due to the fact that, in their study, category number for woody species was only marginally larger ( $n = 21$ ,  $\bar{x} = 8.38 \pm 3.57$ ) than that for herbs ( $n = 45$ ,  $\bar{x} = 6.16 \pm 4.63$ ;  $t = 0.38$ , not significant) resulting in markedly different mean residence time per stage (woody species  $n = 16$ ,  $\bar{x} = 17.0 \pm 6.2$  years; herbs  $n = 34$ ,  $\bar{x} = 2.5 \pm 1.4$  years;  $t = 2.27$ ,  $P < 0.05$ ).

If we want to compare population dynamic processes in absolute time, then the number of life-cycle stages should be proportional to longevity. Transitions from one stage to the next (G) would then be proportional to relative growth rate (RGR), thus making growth

elasticity a quantitative index of the importance of RGR to the population's rate of increase. However, to compare a short-lived species with a long-lived one, the latter would need to be classified into 10–100 times as many life-cycle stages as the former. Both a huge sample size (number of individuals), and sample area, would be required to justify so many stages.

An alternative, and simpler, approach to ensure comparability of results between species may be to use the same number of life-cycle stages regardless of species longevity. The examples used here allow comparison of several different kinds of plants each classified into just four stages. Differences in elasticities between *A. cunninghamii*, on the one hand, and *A. hunsteinii* and *N. fusca*, on the other, reflect variation in shade tolerance between tree species of similar longevity. Elasticities for the perennial bunchgrass, *D. sericea*, are quite different than those for the long-lived tree species. The apparent importance of G and F is much higher, and that for L is much lower. Variation between species exists for all three parameters and allows classification of life histories into a triangular ordination space (e.g. Silvertown et al. 1992, 1993). The position of species within the demographic triangle is strongly influenced by longevity and all woody species living for more than 200 years are tightly clustered in the L corner of the triangle. Semelparous and iteroparous short-lived perennials show greater importance for G and F (Silvertown et al. 1993). However, some other parts of the triangle appear empty (e.g. no published transition matrix for a plant species shows high elasticity for both L and F relative to G) and may represent impossible combinations of plant life-history attributes.

### Conclusion

The triangular ordination of plant species based on elasticity analysis of demographic information in transition matrices promised the opportunity to explore the patterns and causes of particular kinds of plant life history (Enright and Watson 1991; Silvertown et al. 1992, 1993). However, the dependence of elasticities (and other parameters) on the number of life-cycle stages chosen to describe a sample population means that conclusions based on between-species comparisons of existing data sets are imprecise. There are two ways to make elasticity values comparable both between and within species; first, by using the same number of stages regardless of species attributes, and second, by using whatever number of stages is necessary to equalize the mean residence time of individuals in each stage for the species or populations under comparison. The first approach tends to separate species largely on the basis of longevity, while the second separates species according to relative growth rate. Comparisons among plant groups published thus far use a limited range of stages to describe species and so approximate the first approach.

Under the conditions described above, this quantitative approach to comparing life histories may play a part in complementing, clarifying or challenging existing models, such as Grime's C-S-R classification of species. We therefore believe this to be a promising avenue of inquiry, and consider that comparisons based on the results of transition matrix analyses are worthy of further investigation.

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