Life History Variation in Plants: An Exploration of the Fast-Slow Continuum Hypothesis

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Life history variation in plants: an exploration of the fast-slow continuum hypothesis

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SUMMARY

Several empirical models have attempted to account for the covariation among life history traits observed in a variety of organisms. One of these models, the fast-slow continuum hypothesis, emphasizes the role played by mortality at different stages of the life cycle in shaping the large array of life history variation. Under this scheme, species can be arranged from those suffering high adult mortality levels to those undergoing relatively low adult mortality. This differential mortality is responsible for the evolution of contrasting life histories on either end of the continuum. Species undergoing high adult mortality are expected to have shorter life cycles, faster development rates and higher fecundity than those experiencing lower adult mortality. The theory has proved accurate in describing the evolution of life histories in several animal groups but has previously not been tested in plants. Here we test this theory using demographic information for 83 species of perennial plants. In accordance with the fast-slow continuum, plants undergoing high adult mortality have shorter lifespans and reach sexual maturity at an earlier age. However, demographic traits related to reproduction (the intrinsic rate of natural increase, the net reproductive rate and the average rate of decrease in the intensity of natural selection on fecundity) do not show the covariation expected with longevity, age at first reproducion and life expectancy at sexual maturity. Contrary to the situation in animals, plants with multiple meristems continuously increase their size and, consequently, their fecundity and reproductive value. This may balance the negative effect of mortality on fitness, thus having no apparent effect in the sign of the covariation between these two goups of life history traits.

1. INTRODUCTION

(*a*) *The comparative study of plant life histories*

The comparative study of life histories has received considerable attention in the zoological literature (see Harvey & Pagel 1991; Stearns 1992). In plants, however, it has concentrated on traits related to reproductive systems and seed traits (e.g. Mazer 1990, Casper *et al.* 1992; Jordano 1995; Renner & Ricklefs 1995). The scarcity of studies of the whole life cycle of plants has meant that comparative studies of life history traits based on demographic information have mainly been attempted with closely related species (e.g. Sarukhán & Gadgil 1974; Fiedler 1987; Kawano *et al.* 1987; Fone 1989; Svensson *et al.* 1993). More than 20 years have gone by since the publication of Harper & White's (1974) *The demography of plants* and it is only now that we can attempt a comparative analysis of demographic traits based on a wider sample of detailed population studies.

(i) *A demographic classification of life histories*

A usual approach in exploring the diversity of life histories is to look for patterns of correlation between life history and habitat. The existence of such correlation leads to the classification of life histories into a descriptive framework. Several authors (reviewed by Southwood 1988) have proposed classification schemes of life history variation. What these schemes have in common is the recognition of the role played by two environmental axes, productivity and disturbance. Following this approach, we have suggested that elasticities may be useful in classifying species according to the relative importance that fecundity, stasis (survival without growth) and progression through the life cycle play in different species and in different habitats (Silvertown *et al.* 1992, 1993). In a model of population dynamics where individuals are classified into n life stages and the demographic information is represented as contributions and transitions among all life stages in a square matrix ($\mathbf{A} = \{a_{ij}\}$ where i,j = 1, 2, …, n), elasticity is defined as the proportional change in the finite rate of increase (λ_1) produced by a proportional change in each of the elements of the matrix (a_{ij}). That is, there exists a square matrix of elasticities ($\mathbf{E} = \{e_{ij}\}$) corresponding to the population matrix $\mathbf{A}$ such that $e_{ij} = \delta \ln(\lambda_1)/\delta \ln(a_{ij})$ (de Kroon *et al.* 1986). Once the elasticity matrix has been obtained, the individual coefficients may be summed into identifiable demographic components. We have found it convenient to reduce the various demographic

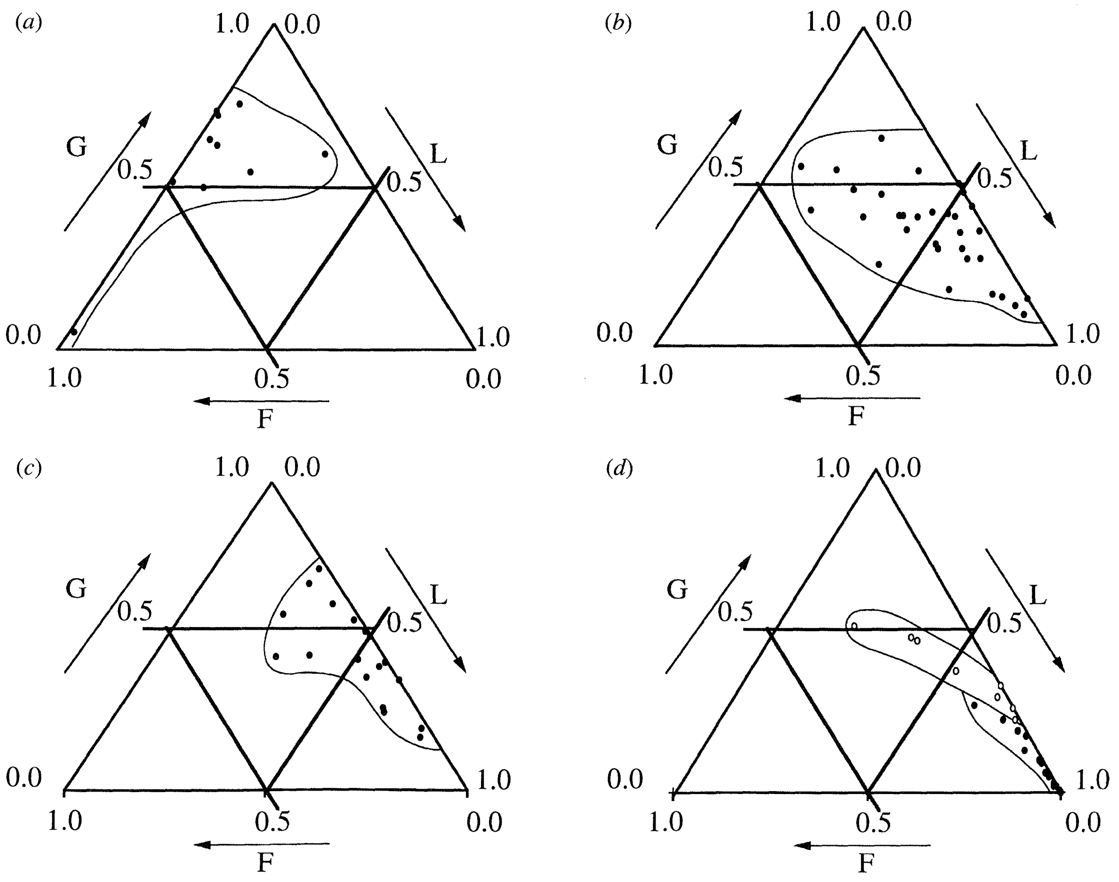

Figure 1. Ordination of species in the demographic triangle, updated from Silvertown *et al* (1993). The relative importance (elasticity) of stasis (L), fecundity (F) and growth (G) derived from the analysis of population projection matrices is shown for different groups of species: (a) semelparous herbs, (b) iteroparous herbs of open habitats, (c) iteroparous forest herbs, (d) woody plants (closed circles denote trees; open circles denote shrubs).

phenomena (progression to further stages of the life cycle, clonal growth, stasis or permanence in the same stage, retrogression to previous stages, seed production and seedling recruitment) into three main components: survival with positive growth (progression + clonal growth), survival without positive growth (stasis + retrogression) and fecundity (seed production and seedling recruitment). Because for each particular population matrix elasticities add up to unity (de Kroon *et al.* 1986; Mesterton-Gibbons 1993), species can be ordinated in a triangular space defined by these three demographic components (figure 1; 'The demographic triangle'). Despite the fact that this ordination is limited by the mathematical constraints imposed upon the definition of elasticity itself (Shea *et al.* 1994; Enright *et al.* 1995) and that it does not take into account the indirect effects that demographic parameters have on each other (Franco & Silvertown 1994; van Tienderen 1995), the triangular classification of plant populations is a first, heuristic step in framing the large variety of life histories. Using an increasing sample of demographic information for perennial plant species has allowed us to conclude that the relative importance (elasticity) of these three population processes describes important dimensions of life history variation (Silvertown *et al.* 1992, 1993; Silvertown & Franco 1993). Specifically, the position of individual populations of the same species in the demographic triangle follows a gradient correlated both with successional stage (figure 2, after Silvertown & Franco 1993) and with the population's rate of increase (Silvertown *et al.* 1996). Among species, this position is correlated with life form and habitat, but is also

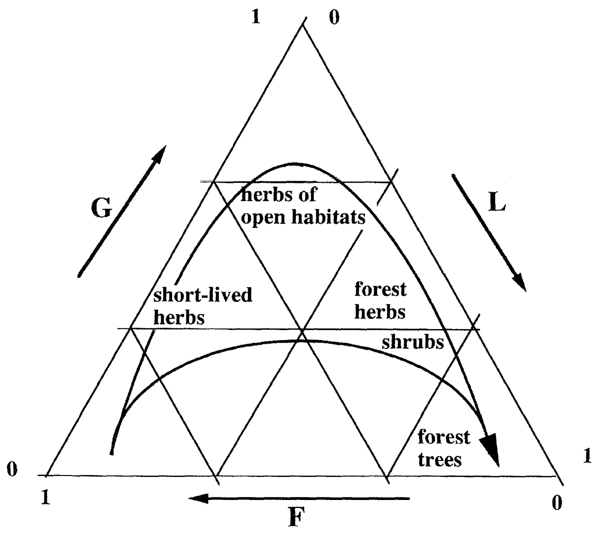

Figure 2. The successional trajectories suggested by the distribution of species in the demographic triangle in Fig. 1, after Silvertown & Franco (1993).

affected by longevity, relative growth rate and the number of life stages used to classify individuals in the population (Silvertown *et al* 1993; Enright *et al.* 1995). Evidently, covariation among life history traits is largely responsible for the position that species or populations occupy in the triangle.

(ii) *The fast-slow continuum hypothesis of life history variation*

The best known scheme of life history covariation is the r-K selection theory. Because of its emphasis on the relative roles of density-dependent and density-independent mortality, and its sometimes conflicting predictions, the theory has been repeatedly attacked and defended (see Boyce 1984). More recently, however, the emphasis of this discussion has moved from the kind of mortality (and habitat) encountered by organisms to the role played by mortality, whatever its cause, on other life history traits (e.g. Harvey & Zammuto 1985; Read & Harvey 1989; Promislow & Harvey 1990). In this respect, among other relationships Harvey and co-workers have found a negative relationship between adult mortality rate and age at sexual maturity, and a positive relationship between adult mortality rate and annual fecundity in mammals. This has led to the confirmation of a 'fast-slow' continuum, with organisms undergoing high adult mortality evolving fast development rates, high fecundity and short life cycles, on the one hand, and organisms subject to low adult mortality developing slow growth rates, low fecundity and long life cycles. Due to the inevitable covariation of demographic traits when populations are stationary (Sutherland *et al.* 1986), but also to the mathematical constraints imposed by the very definition of some of these traits, it becomes difficult to assign a unidirectional cause-effect relationship among them. Nevertheless, employing a combination of dimensional analysis, natural selection theory and stable demography, Charnov (1991) has derived a theoretical justification for the covariation of some of these demographic traits. In agreement with the evidence in animals (Harvey and co-workers' studies; Charnov & Berrigan 1990; Blackburn 1991; Charnov 1993; Berrigan *et al.* 1993; see also Roff 1992; Stearns 1992), Charnov's model predicts the signs found empirically in the relationships between adult mortality rate and age at sexual maturity (negative) and between adult mortality rate and fecundity (positive). This provides a theoretical justification of the fast-slow continuum which is free of the problems created by the interaction of external causes which have plagued previous models. Charnov's model is based on three assumptions: (i) there is a trade-off between growth and reproduction; (ii) once the adult stage is reached, mortality is constant and independent of reproduction; and (iii) growth is determinate and annual fecundity is constant. While the second assumption defines the ecological setting, the other two refer to the organisms' morphological or physiological limitations and trade-offs. With these simple assumptions, Charnov's model strongly supports the idea that organisms can be ordinated between those living 'at a fast pace' (high mortality, short age at sexual maturity and lifespan, high fecundity), on one extreme, and those leading 'slower' ways of life (low mortality, long age at sexual maturity and lifespan, low fecundity), on the other. This is the simplest way of stating the fast-slow continuum hypothesis of life history variation.

In this paper, we ask whether the fast-slow continuum hypothesis is applicable to plants. We show that a high rate of adult mortality is associated with a younger age at sexual maturity and shorter lifespan in genets of non-clonal plants and ramets of clonal plants. This is in agreement with the fast-slow continuum theory. However, because most plants monotonically increase their fecundity throughout adult life, the presumed positive relationship between mortality and fecundity cannot be tested. We therefore employ other demographic traits to explore the possible significance of this difference between unitary animals and modular plants.

2. METHODS

(*a*) *Life history data*

The dataset comes from published studies on plant demography. The original dataset containing information for 66 species is described by Silvertown *et al.* (1993). Eighteen more species were added (12 in Silvertown & Franco 1993 and a further six in Silvertown *et al.*1997) and one deleted to give the 83 species used here. The paper for the deleted species (*Hypochoeris radicata*) did not contain the information necessary for the projection described below. The demographic information applies to genets of aclonal plants (53) but to ramets of clonal ones (30). Nine of the 83 species were semelparous. A more complete description of the dataset may be found in the papers cited above. An average matrix population model (see Caswell 1989) was projected for each of the 83 species using the program STAGECOACH (Cochran & Ellner 1992). This program yields a series of scalars, vectors and matrices useful in population studies, such as eigenvalue and eigenvector spectra, sensitivity and elasticity matrices, and several age-related life history parameters including survival and fecundity schedules. The parameters (traits) that we use in this paper are:

1. r, the population's intrinsic rate of natural increase, calculated as the natural logarithm of λ_1, the dominant eigenvalue of each matrix;
2. L, total lifespan (the expected age at death for individuals that have already reached the last stage of the life cycle, equation (6) in Cochran & Ellner's paper);
3. α, age at sexual maturity (the expected age at which a newborn first enters the set of stages with positive fecundity; Cochran & Ellner's equation (15));
4. G, generation time (the mean age of parents of offspring produced at stable stage distribution; Cochran & Ellner's equation (26));
5. R_0, net reproductive rate (the total number of descendants in the lifetime of an average individual; Cochran & Ellner's equation (18)).

In cases where there was more than one type of recruit (e.g. seed, seedling and vegetative ramet) we used the population averages of these parameters provided by STAGECOACH.

The survival schedules generated by STAGECOACH were in turn used to calculate life expectancy at different ages. Because survival approaches zero asymptotically, the life cycle was assumed to end at the calculated average lifespan. Thus,

6. E_α, life expectancy at age at maturity, was used as an inverse estimate of adult mortality, M, $E_\alpha = 1/M$ (Harvey & Zammuto 1985; Sutherland *et al.* 1986).

Finally, the life table survival and fecundity schedules were used to calculate the sensitivity of the intrinsic rate of natural increase to changes in age-specific survival and fecundity, employing the formulae given by Hamilton (1966; equations (1.6) and (1.7) in Rose 1991). These sensitivities measure the intensity of natural selection on these two parameters as the individuals age. The slope of the regression of the logarithm of each of these two sensitivities on age provided two scalars:

7. Hp_x, the exponential rate of decrease in the intensity of natural selection on survival;
8. Hm_x, the exponential rate of decrease in the intensity of natural selection on fecundity.

(*b*) *Taxonomic distribution and phylogeny of the species in the dataset*

To account for the possible phylogenetic bias in our dataset we employed two classification systems. The first one corresponds to the taxonomic classification of Cronquist (Woodland 1991, after Cronquist 1981, for angiosperms, and Cronquist *et al.* 1966, for gymnosperms). In this system, the 83 species in our dataset were grouped into 70 genera, 39 families, 29 orders and 10 subclasses of angiosperms and gymnosperms. The second system used corresponds to the combined phylogeny of angiosperm (search II, Chase *et al.* 1993) and gymnosperm (Chaw *et al.* 1995) families obtained through the analysis of nucleotide sequences from the plastid gene *rbc*L and the 18S rRNA gene, respectively. The position of the Plantaginaceae, which was not present in Chase *et al.*'s phylogeny, next to the Scrophulariaceae was supported by both classical taxonomy (e.g. Cronquist 1981) and the results of Olmstead & Reeves (1995) who sequenced the chloroplast genes *rbc*L and *ndh*F. The same justification was made for the Cactaceae, next to the Plumbaginaceae (among the 39 families in the dataset) within the Caryophyllids (sensu Chase *et al.* 1993), and the Capparaceae near the Cruciferae.

(*c*) *Data analyses*

To identify the taxonomic level at which most variation occurs, a hierarchical analysis of variance was performed on all life history variables employing Cronquist classification. Furthermore, to incorporate the effect of taxonomic relatedness on the covariation of life history parameters, a comparative analysis by independent contrasts for each pair of relevant life history traits was conducted using each of the two classification systems. This was done with the help of the program CAIC (Purvis & Rambaut 1995). The method, due to Felsenstein (1985), assumes a Brownian motion model of divergence among clades and, as a consequence, that the variance of the traits in question increases with the sum of branch lengths along the cladogram. Thus, given a phylogenetic tree, CAIC calculates a series of contrasts along the tree and, if information on branch lengths exists, the contrasts can be standardized by dividing them by the square root of the sum of those branch lengths, i.e. by their standard deviation (Felsenstein 1985, Garland 1992, Purvis & Rambaut 1995). If branch lengths are not available these can be assumed equal (an implicit view of punctuated evolution) or made proportional to the number of taxa below each node. The latter, however, requires that the full phylogeny be known. In our comparative analyses, we assumed equal branch lengths. This is because in the case of the Cronquist system, having the same number of accepted taxonomic levels above each species implies equivalence within each level. In the other case, the phylogeny reconstructed from Chase *et al.* (1993) and Chaw *et al.* (1995) is based on two different genes with likely differences in their rates of evolution among lineages (e.g. Bousquet *et al.* 1992; Chase *et al.* 1993; Frascaria *et al.* 1993; Gunter *et al.* 1994). Furthermore, the reconstructed phylogeny for our dataset can only be applied down to the family level, after which the tree divides into as many genera and species as we had. Thus, the taxonomic diversity in our dataset is a measure of the diversity of authors' preferences.

3. RESULTS

Three distinct patterns in the level where most of the variation is found can be distinguished in the life history parameters investigated (table 1): (i) traits that are age-dependent (L, α, G and E_α) had their variation concentrated at the division level; (ii) traits that can be described as time-dependent (r and R_0) had their variation concentrated at the species level; (iii) traits that describe the rate of decrease in the intensity of natural selection with age (Hp_x and Hm_x) concentrated their variation at intermediate (genus and order, respectively) levels. In the first case, this is clearly a consequence of long-lived gymnosperms (*Sequoia*, *Araucaria* and *Pinus*) being contrasted with angiosperms which, although containing some trees, are dominated in the dataset by short-lived herbs. When calculating cross-species correlations, traits in the second group tended not to show covariation with those in the first group, except with G and Hp_x (table 2). Of the two traits in the third group Hp_x showed significant correlation with all traits, except Hm_x. The latter, on the other hand, only showed a weak correlation with E_α.

For the vast majority, these correlations remained the same when either taxonomy or phylogeny were incorporated into the analysis (tables 2 and 3). Cross-

Table 1. *Percentage of variance accounted for by different taxonomic levels in a hierarchical analysis of variance of life history traits employing Cronquist classification*

(For definition of traits, see text. For each trait, the highest value is represented in bold; second highest in italics.)

	taxonomic level						
life history trait	division	class	subclass	order	family	genus	species
r	0.0	0.0	1.4	*36.4*	0.0	4.5	**57.7**
log (R_0)	21.7	0.0	1.1	*33.4*	0.0	0.0	**43.9**
log (L)	**69.4**	1.7	2.6	0.0	*10.4*	7.0	8.9
log (α)	**39.0**	0.0	16.0	0.0	*24.3*	5.0	15.7
log (G)	**74.9**	0.0	4.9	0.0	4.8	6.7	*8.6*
log (E_α)	**41.1**	0.6	2.6	15.4	0.0	*29.5*	10.8
Hp_x	0.0	0.0	14.1	*16.2*	0.0	**58.3**	11.3
Hm_x	0.0	3.8	0.0	**86.5**	0.0	*9.6*	0.0

Table 2. *Pairwise correlations between life history traits taking individual species as independent points (lower diagonals) and as contrasts employing Chase–Chaw phylogeny (upper diagonals).*

(In the latter analysis, the correlations on rows for r and $\log(R_0)$ correspond to these traits treated as *dependent*, while variables in rows $\log(L)$ to Hm_x were assumed *independent*. Values in parenthesis represent sample size, i.e. number of species and number of contrasts, respectively. Values in bold are significant at $P < 0.01$, usually $P < 0.001$; values in italics $0.01 < P < 0.05$.)

	r	$\log(R_0)$	$\log(L)$	$\log(\alpha)$	$\log(G)$	$\log(E_\alpha)$	Hp_x	Hm_x
r		**0.63**	−0.14	−0.09	*−0.32*	−0.16	**0.75**	0.22
		(49)	(53)	(49)	(52)	(47)	(31)	(31)
$\mathrm{Log}(R_0)$	**0.73**		0.11	0.01	−0.26	0.05	0.07	0.31
	(74)		(49)	(49)	(48)	(47)	(29)	(29)
$\log(L)$	−0.21	0.01		**0.60**	**0.68**	**0.74**	**−0.60**	−0.04
	(81)	(74)		(49)	(52)	(47)	(31)	(31)
$\log(\alpha)$	−0.19	−0.01	**0.70**		**0.61**	*0.36*	*−0.38*	*−0.37*
	(74)	(74)	(74)		(48)	(47)	(29)	(29)
$\log(G)$	**−0.45**	**−0.34**	**0.86**	**0.75**		**0.60**	**−0.56**	−0.25
	(80)	(73)	(80)	(73)		(46)	(31)	(31)
$\log(E_\alpha)$	−0.20	0.01	**0.90**	**0.64**	**0.78**		**−0.50**	−0.29
	(64)	(64)	(64)	(64)	(63)		(26)	(26)
Hp_x	**0.84**	*0.34*	**−0.54**	**−0.46**	**−0.67**	**−0.54**		0.06
	(45)	(43)	(45)	(43)	(45)	(33)		(31)
Hm_x	0.26	0.21	−0.13	−0.22	−0.19	*−0.38*	0.18	
	(45)	(43)	(45)	(43)	(45)	(33)	(45)	

Table 3. *Comparison of the regression results obtained between selected pairs of life history traits employing individual species data (cross-species comparison) or independent contrasts using Cronquist classification and the Chase–Chaw phylogeny*

(In the latter two cases, equal phylogenetic distances were assumed and the relationship was forced through the origin. Values in bold, $P < 0.01$, usually $P < 0.001$; values in italics $0.01 < P < 0.05$.)

		cross-species			Cronquist			Chase–Chaw		
independent	dependent	r	n	b	r	n	b	r	n	b
log (α)	log (E_α)	**0.64**	64	0.721	ns	33		*0.36*	47	0.607
log (L)	log (G)	**0.86**	80	0.974	**0.67**	36	0.844	**0.68**	52	0.873
log (L)	r	ns	81		ns	37		ns	53	
log (L)	log (R_0)	ns	74		ns	35		ns	49	
log (L)	Hp_x	**−0.54**	45	−0.169	**−0.56**	22	−0.195	**−0.60**	31	−0.194
log (L)	Hm_x	ns	45		ns	22		ns	31	

species comparisons tended to yield higher slopes than comparisons using phylogeny and these in turn gave higher slopes than comparisons employing taxonomy. As predicted, the relationship between life expectancy at maturity (E_α) and age at maturity (α), was positive and significant in cross-species $(P < 0.001)$ and phylogenetic comparisons $(P < 0.05)$.

4. DISCUSSION

(*a*) *Fast-slow continuum hypothesis*

The positive relationship between the inverse of adult mortality – life expectancy at maturity (E_α) – and age at sexual maturity (α) supports the hypothesis of a shorter life in species (or populations) that invest in

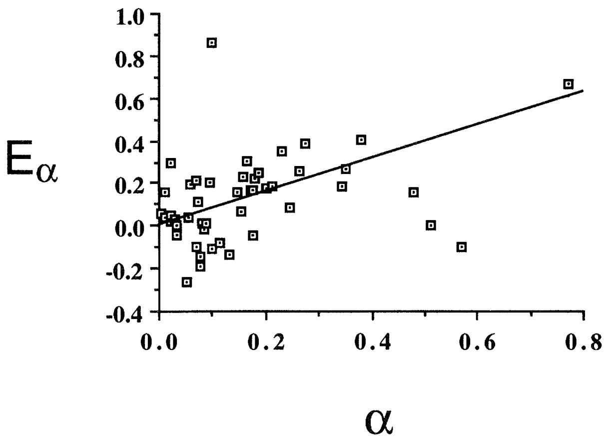

Figure 3. The relationship between life expectancy at maturity (E_α) and age at maturity (α), employing independent contrasts on the Chase-Chaw phylogeny ($n = 47$; $r = 0.36$; $P < 0.05$).

sexual reproduction at an earlier age – or alternatively, that high risks of adult mortality favour those individuals that reproduce earlier (figure 3, table 3). This is also consistent with the positive relationship between age at maturity and adult lifespan found by Silvertown *et al.* (1997). The inclusion of perennial plants among the groups of organisms on which these two relationships have been documented (see Stearns 1992; Charnov 1993) further supports the generality of the fast-slow continuum. It must be stressed, however, that Charnov's model of the fast-slow continuum was developed with mammals in mind and therefore his assumptions may not be totally appropriate for other organisms. As stated in the introduction, these assumptions are: (i) there is a trade-off between growth and reproduction; (ii) once the adult stage is reached, mortality is constant an independent of reproduction; and (iii) growth is determinate and annual fecundity is constant. The first two assumptions are tenable in plants. There is ample evidence in the literature of a compromise between growth and reproduction in plants (e.g. Piñero *et al.* 1982; Bishop & Davy 1985; Eriksson 1985; Calvo & Horvitz 1990; Dick *et al.*1990, Geber 1990; Pyke 1991; Gren & Willson 1994). Similarly, many species in our dataset show approximately constant mortality during adulthood. The third assumption, however, is simply not true for the majority of plants. With the exception of plants with a single terminal meristem, which maintain a relatively constant annual fecundity during the adult stage, most plants show indeterminate growth through the iteration of multiple terminal meristems and, consequently, increasing fecundity with age (Watkinson & White 1985). Nevertheless, and in spite of the fact that plants violate the third assumption of Charnov's model, our data still conform to the expected negative correlation between adult mortality ($1/E_\alpha$) and age at maturity (α). However, because of their increasing fecundity with age/size/longevity, the expected positive relationship between mortality and fecundity cannot be tested.

In this respect, it is interesting to note that, contrary to what is observed in unitary animals neither the intrinsic rate of population increase (r) nor the net reproductive rate (R_0) show the expected, significant negative correlations with longevity (L), age at maturity (α) and life expectancy at maturity (E_α), but, as ought to be expected, they do show correlation with generation time (G) (table 2). The latter correlation, however, may be a trivial one as it is subject to the mathematical constraint of the definition of the traits themselves. Nevertheless, the result that the average rate at which the intensity of natural selection on survival diminishes with age (Hp_x) decreases with the lifespan of the species (L), and is correlated with all the other traits investigated, but the same rate measured on fecundity (Hm_x) shows no relationship with all these variables (table 2) adds to the evidence that the evolution of the reproductive schedules of plants does not have the same kind of restrictions imposed upon unitary organisms with a ceiling fecundity.

It is important to recognize that r and R_0 (but not Hm_x) could have any value between zero and the maximum attainable under ideal conditions. Earlier workers clearly understood this and compared the maximum attainable rate (r_{max}) of different species under ideal conditions (e.g. Evans & Smith 1952) or something approaching this under field conditions (e.g. Ross 1992). Until this information is available, we cannot be certain that the lack of correlation observed between these two traits and others in table 2 is real or not. Nevertheless, the lack of relationship between Hm_x and all other parameters, coupled with the correlation between either r or R_0 and G, makes us feel confident that the effects are real and not a consequence of r and R_0 being labile. In the case of animals with ceiling fecundity and decreasing reproductive value during adulthood, the trade-off between size and number of offspring implies that animals that are large at birth can only be produced in small numbers. The negative relationship between body size and fecundity and between body size and generation time implies that large animals will have smaller r than small, short-living animals. Although with notable exceptions (lilies in temperate forests, the pioneer tropical tree *Cecropia obtusifolia*), the demography of plants has tended to concentrate on invasive short-lived herbs that, because of the absence of density-dependence and interspecific competition, have large r, and on long-lived trees, inhabiting stable communities, with $r \approx 0$. Despite this, the lack of relationship between r and L is remarkable and reinforces the view that the evolution of reproductive schedules does not follow the same rules in plants and animals. This is in agreement with the simulation study of Sackville-Hamilton *et al.* (1987) of a diversity of life histories evolving under similar environmental conditions, and of similar life histories evolving in different environments, depending on the architectural organization and allocation schedules between growth and reproduction of plants.

(*b*) *Cross-species vs comparative analyses*

Recent comparative studies have found contrasting results to those employing cross-species analyses (e.g. Kelly & Purvis 1993; Kelly 1995*a*; Kelly & Beerling

1995). We believe that the similar results obtained here with the three schemes employed (cross-species, Cronquist classification and Chase–Chaw phylogeny) simply points to the limited scope of our dataset. For example, with the exception of the Alismatidae (reflecting the lack of demographic studies of aquatic plants; Franco & Silvertown 1990), all subclasses of angiosperms are represented in the dataset, but there is at present no way of knowing if the variation found at lower taxonomic levels is representative of the subclass as a whole. Most likely it is not. Having 83 species distributed in 39 families means that each family is, on average, represented by two species. Similarly, with 39 families and 29 orders, most orders are represented by a single family. Whether or not taxonomic relatedness affects the results of a comparative analysis depends on the completeness/diversity of the dataset (and obviously on the phylogeny employed; Coddington 1992) but, to make things worse, this possibly may also depend on the kind of information being analysed (Kelly & Woodward, this issue). A wider dataset may be necessary before we can work our way down to investigate the covariation of demographic traits at lower taxonomic levels, particularly if we want to investigate the effect of categorical variables like habitat, life form and parity.

(*c*) *The future of comparative studies*

We have only scratched the surface of life history variation in plants. Despite differences in the reproductive schedules of unitary animals and most perennial plants, the similarities found in the covariation of life history traits are consistent with theoretical expectations. Those differences, and the way they may affect other traits not considered here, are worthy of further investigation. Certainly, those differences have to do not only with the modular construction of plants but with the hierarchical organisation of the whole plant body. For example, it would be interesting to investigate how different degrees of morphological and physiological integration (see Kelly 1995*b*), different degrees of branching, and different degrees of rooting capabilities affect the covariation of demographic life history traits.

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