Evolutionary Ecology **15:** 15–35, 2001.

Research article

Trait evolution in an individual-based model of herbaceous vegetation

JOHN WARREN[1]* and CHRIS TOPPING[2]
[1]*Institute of Rural Studies, University of Wales, Llanbadarn Fawr, Aberystwyth, Ceredigion, SY23 3AL, Wales;* [2]*Department of Landscape Ecology, NERI, Kalø, Grenåvej 14, DK - 8410 Rønde, Denmark*
*(*author for correspondence, e-mail: jhw@aber.ac.uk)*

Received 9 May 2000; accepted 30 May 2001

Co-ordinating editor: J. Stuefer

Abstract. Many theoretical studies of evolution are based upon the concepts of the evolutionary stable strategy and optimal life-history solutions. An individual based model of vegetation is used to simulate life-history evolution under two different sets of environmental conditions. At one level the results suggest that optimal life-history solutions do appear to evolve. At the end of the simulations the vegetation that evolved in a fertile and uncut environment was taller, thinner and germinated later than that which developed in a less fertile and cut habitat. However, between simulation variation was observed to be high, particularly for the parameter regulating the timing of reproduction, and it showed no indication of reaching fixation. When this trait was prevented from mutating, the variances of other traits were seen to increase. Although at the population level between simulation variation was high, some traits achieved a degree of stability within simulations, suggesting that multiple adaptive peaks may be being approached. However, there was little evidence of trait fixation occurring within the most abundant 'genotype'. It is considered that frequency dependent selection/Red Queen dynamics may be acting to prevent the most abundant 'genotype' from reaching fixation. It is argued that if such processes prevent optimal genetic solutions from being achieved then the search for evolutionary stable strategies within the evolution of life-histories may be over simplistic.

Key words: competition, evolutionary stable strategy, individual-based model, life-history evolution, Red Queen dynamics

Introduction

The traits of age specific growth, reproduction and death etc. which define an organism's life-history are not randomly distributed (Deevey, 1947; Mac Arthur, 1962; Southwood, 1988). It appears common sense that life-histories are compromise positions, as individuals allocate more resources to any structure or function they must be 'traded off' against others. The evolution of life-histories has been studied by geneticists and ecologists (Anderson and King, 1970; Charlesworth and Giesel, 1972) with current theory encompassing both disciplines (Sibly, 1996). Theoretical studies of life-history evolution have been many and various (Klinkhamer *et al.*, 1997; Scheiner, 1998; Teriokhin, 1998) but tend to include the concept of the evolutionary stable strategy (ESS), genetic equilibrium or optimal life-history solutions. However, recent studies have suggested that under some conditions several equilibrium positions may be possible (Law *et al.*, 1997; Geritz *et al.*, 1998). By necessity most of the theories of life-history evolution are model based. Because of the long-term nature of the subject the testing of such models is reliant upon demonstrating that their assumptions are correct and/or that the predictions actually occur (Sibly and Antonovics, 1992). A further complication in testing life-history theory is the difficulty of defining 'species' limits around trait variation both within populations and over time (Maynard Smith, 1991). Considering the evolution of individual traits independently (Iwasa and Levin, 1995; Takada and Nakajima, 1996) often surmounts this difficulty. However, this approach cannot be considered as studying life-history evolution in its pure sense, as this must include the co-evolution of several traits or holistic ecological concepts such as functional types.

In this paper, we use a computer model of vegetation, which defines individual plants as three-dimensional (3D) entities whose behaviour is regulated by life-history rules, to study the evolution of these rules. Within the model individuals compete for above and below ground resources with other individuals about which they have no information about their competitive ability. Individual plant growth, reproduction and death are determined by the season and by plant size which in turn is determined by how successful it has been in capturing resources with a specified arena or 'habitat'. Life-history rules can be considered as 'genes', which are limited by trade-offs, such that 'resources' cannot be directed towards a trait without them being withdrawn from another. The model was developed earlier and applied to predict vegetation changes in the field (Warren and Topping, 1999).

In this study we allow stochastic mutations to occur in the life-history rules, resulting advantageous mutations auto-select as they compete over time with one another. This approach was used to investigate if within a particular 'habitat' specific combinations of life-history rules repeatedly evolve to become most abundant.

The model

Within the model growth, reproduction and death of individual plants are limited by rules based upon known life-history attributes. These rules can be considered as analogous to genes, with different parameter values being alleles. The life-history traits of size (both vertical and horizontal), reproduction and defence are linked by 'trade-off' via a series of parameters, which determine the partitioning of resources within each individual. Similarly the ability to grow under shaded conditions is 'traded-off' against growth rate in full light. Model simulation calculates the 3D above-ground space occupied by each individual on a month-by-month basis. Individuals have no information about the competitive abilities of the other individuals present; growth and reproduction are limited indirectly by below grown resources, shading or competition for space. A full description of the modelling approach used can be found in (Warren and Topping, 1999) and the life-history parameters are presented in Table 1. The model used here has been modified from (Warren and Topping, 1999) in that it contains two additional life-history parameters, one that defines the calendar month in which individuals large enough to reproduce do so, and a second which determines the month of germination. Mutations have been introduced into the model by allowing 11 of the life-history parameter values the ability to change each time reproduction occurs. To prevent run-away selective advantages, only those parameters regulated by 'trade-off' were allowed to mutate. The number of offspring produced in which mutations have occurred is determined by an additional parameter. Within these randomly chosen mutating propagules one, two or three randomly selected parameter values were altered, thus making it possible but unlikely that the same parameter be selected three times. These parameter values were allowed to change by plus or minus 1–10% from their previous value, parameters defined as integers were varied by plus or minus one integer unit. The binary state variable of reproductive state was allowed to switch from vegetative to seed producing or the back (Table 1). In non-mutating individuals reproductive

Table 1. Life-history parameter used in the model

Parameter	Those allowed to mutate
1. Initial number of propagules	–
2. Ramet life span	–
3. Max. height	M
4. Max. width	M
5. Shade tolerance	M
6. Below ground extraction efficiency	–
7. Extent of monthly winter die-back	–
8. Reproduction vegetative or seed	–
9. Propagule number	M
10. Size at reproducing	M
11. Resources allocated to growing tall	M
12. Resources allocated to growing wide	M
13. Resources allocated to reproduction	M
14. Resources allocated to herbivore defence	M
15. Month of reproduction	M
16. Month of germination	M

propagules, parameter values remained unchanged, they are 'genetically' identical to their parent.

The simulations

To investigate the evolution of life-histories within the model, vegetation dynamics were simulated in two contrasting competitive arenas or 'habitats'. One of these 'habitats' was defined as being of high below-ground fertility and uncut (with competition for light expected to be important), while the second arena contained half the below-ground resources of the first and the vegetation was cut annually in the 6 month (with competition for below-ground resources expected to be more important than competition for light). Both 'habitats' were defined as containing no initial spatial variation in below-ground resources, and with no disturbance events or herbivory. Simulations were initiated with equal numbers of three different 'genotypes'; these were based on a tall vegetatively reproducing grass, a short seed reproducing forb, and a short vegetatively spreading forb. The taller growing individuals were expected to dominate in the first arena where competition for light was most important, while lower growing forms may be more successful in the cut habitat.

Model simulations of each 'habitat' were replicated 10 times with mutations occurring in 1 of every 250 propagules. All simulations were run for 5000 years. In every 500 year of the simulation the life-history parameter values of the most abundant 'genotype' (defined as the unique set of life-history parameters with the highest percentage cover) at the time were recorded from the 6 month. Simultaneously, the mean parameter values of all individuals present were calculated. This approach was designed to detect possible ESS if it occurred at the population level or at the level of the most abundant solution within the population. All data were transformed by multiplication or division by multiples of 10, such that the mean values for each parameter over the 10 replicates fell between zero and one. This avoided biasing the data in favour of parameters with large values such as seed number per plant and against those with low values such as those defined as proportion.

To determine if different life-histories had evolved in the two 'habitats' principal components analyses (PCA) were performed on the life-history parameter values of the individuals present after 5000 years. The binary state variable of reproductive state was excluded from the analysis as were shade tolerance and resources partitioned into defence, because these traits were close to fixation at zero in both habitats. PCA was carried out on the parameter values of the 'genotype' that were most abundant at the end of the 20 simulations. Similarly PCA was carried out on the population mean of the life-

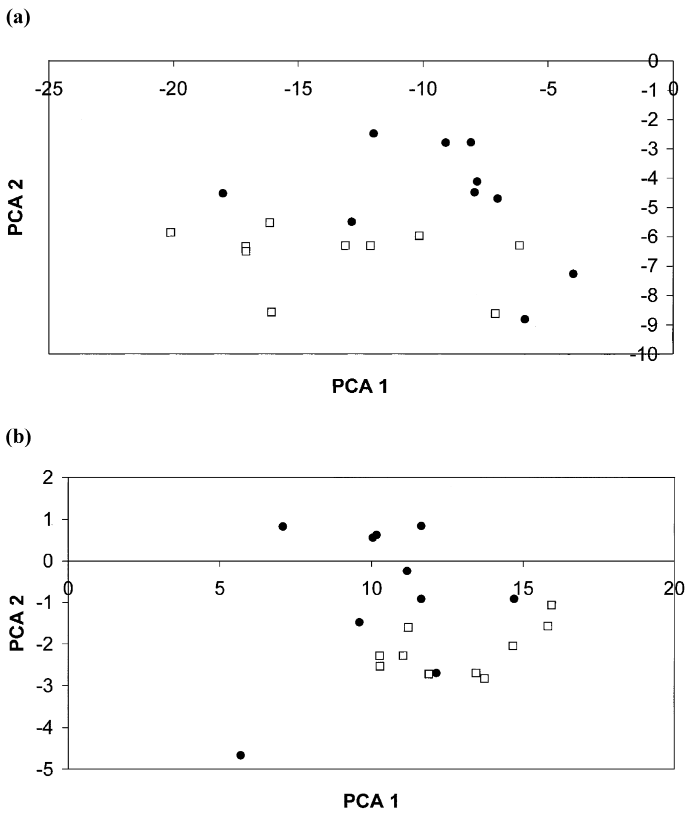


Figure 1. (a) The first and second principle components from a PCA of parameter values from the most abundant 'genotypes' after 5000 years of 10 replicate simulation for each of two different 'habitats'. Solid circles represent the fertile uncut habitat and the open squares represent the unfertile cut habitat. (b) The first and second principle components from a PCA of mean parameter values of all individuals present after 5000 years of 10 replicate simulation for each of two different 'habitats'. Solid circles represent the fertile uncut habitat and the open squares represent the unfertile cut habitat.

history parameter values, calculated over all individuals present after 5000 years of simulation (Fig. 1).

To determine if the life-history parameters were evolving towards an ESS within each 'habitat' we plotted the standard deviation of each parameter value (calculated from the 10 replicates) against time. This was carried out separately for the most abundant 'genotypes' and the population means (Figs 2 and 3). We used regression analysis to determine if the standard deviation of each parameter value was changing over time (Tables 2 and 3). To help identify the source of this variation, population means for all non-fixed traits were plotted

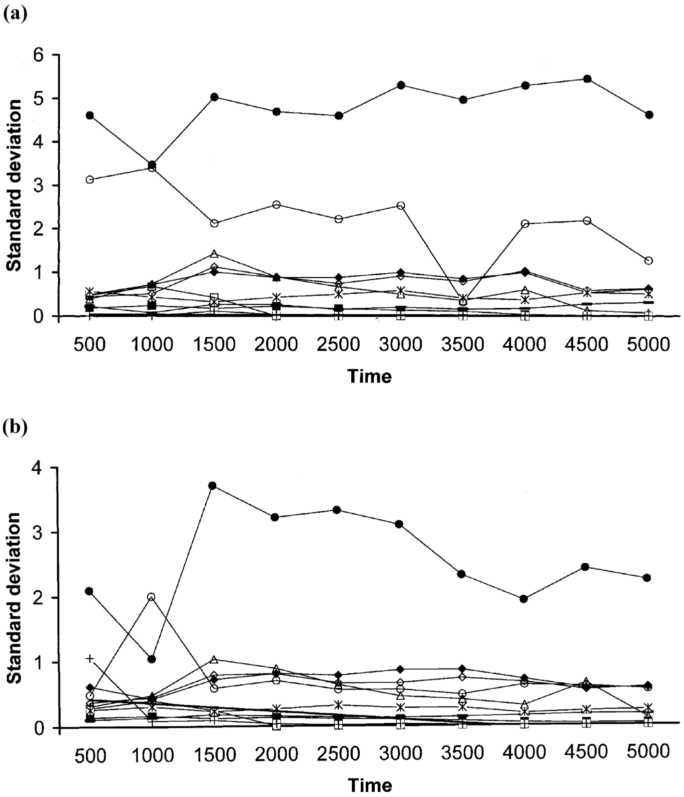


Figure 2. Between simulation variation plotted as change in the standard deviation of the trait parameter values with time: traits values from (a) the most abundant 'genotype' from the fertile habitat and (b) the population means from the fertile habitat. Solid squares: plant height, hollow squares: plant width, hollow triangles: resources partitioned into seeds, solid diamonds: resources partitioned into growing tall, a horizontal cross: resources partitioned into defence, solid circles: the timing of reproduction, a dash: the threshold size at which reproduction occurs, diagonal crosses: propagule number, and hollow circles: germination time.

against time (with 50 year intervals) for the first three simulations of the low fertility cut 'habitat' (Fig. 4). Similarly trait values of all non-fixed traits were plotted against time for the most abundant 'genotype' within the low fertility cut 'habitat'. For clarity just the first two simulations were plotted (Fig. 5).

The greatest run-to-run variation was found in the parameter determining timing of reproduction, with no indication of its standard deviation decreasing with time (see Results). It was therefore decided to prevent this parameter from mutating from its initial value and rerun the 10 simulations of the low fertility cut 'habitat' to determine if this enabled ESS to be achieved more readily. Again we plotted standard deviations against time and used regression analysis to determine if these were changing over time (Fig. 6 and Table 4).

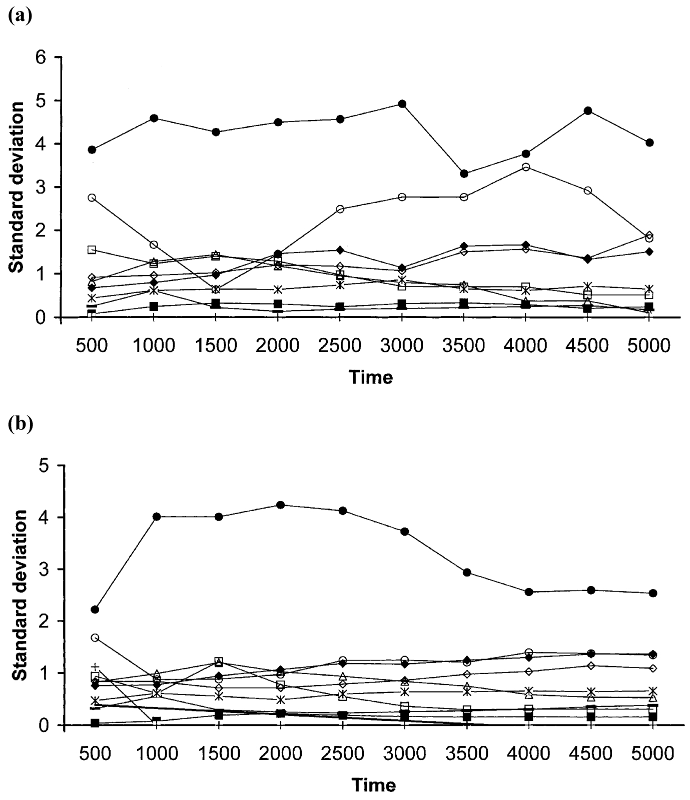


Figure 3. Same as in Figure 2, but for traits values from (a) the most abundant 'genotype' from the unfertile habitat and (b) the population means from the unfertile habitat. Solid squares: plant height, hollow squares: plant width, hollow triangles: resources partitioned into seeds, solid diamonds: resources partitioned into growing tall, a horizontal cross: resources partitioned into defence, solid circles: the timing of reproduction, a dash: the threshold size at which reproduction occurs, diagonal crosses: propagule number, and hollow circles: germination time.

Results

After 5000 years of simulation the vegetation that evolved in the fertile uncut environment was taller, thinner and germinated later than that which developed in the less fertile cut habitat, with mean canopy heights = 2.38 and 1.12, mean plant widths = 3.0 and 4.53 and mean germination times = 6.71 and 5.47 respectively. One-way analysis of variance revealed that these differences were highly significant ($F = 231.54$, $p < 0.001$, $F = 247.95$, $p < 0.001$, and $F = 29.09$, $p < 0.001$ respectively). The vegetation in the two habitats did not differ significantly in any of the other life-history traits.

The PCAs over all non-fixed parameter values (Fig. 1a and b) revealed that for the vegetation as a whole and for the most abundant genotype, different life-history strategies could be said to have evolved after 5000 years within the

Table 2. Regression analysis of trait standard deviations against time. For the fertile habitat and most abundant 'genotype' (Panel A) and fertile habitat and population means (Panel B)

Trait	Intercept	Slope	R^2	p
Panel A				
Height	0.2706	−0.0000529	82.8	0.0001
Width	0.5260	−0.000134	61.0	0.008
Resources into seeds	1.0105	−0.000158	36.6	0.064
Resources into width	0.8020	−0.0000025	0.01	0.957
Resources into height	0.7098	0.0000195	1.7	0.718
Resources into defence	0.0372	−0.0000075	10.7	0.356
Time of reproduction	4.2410	0.000204	29.8	0.102
Threshold of reproduction	0.1575	0.0000183	15.2	0.233
Propagule number	0.4467	0.0000063	1.3	0.757
Time of germination	3.2378	−0.000384	43.7	0.037
Panel B				
Height	0.1761	−0.000029	91.9	0.0001
Width	0.3101	−0.0000792	61.3	0.007
Resources into seeds	0.7190	−0.0000715	15.2	0.266
Resources into width	0.6618	0.00000875	0.9	0.798
Resources into height	0.5651	0.0000202	4.8	0.543
Resources into defence	0.4845	−0.000128	35.3	0.070
Time of reproduction	2.5650	−0.0000137	0.1	0.945
Threshold of reproduction	0.1233	0.00000805	25.9	0.133
Propagule number	0.2893	−0.0000125	23.8	0.153
Time of germination	1.0363	−0.000188	15.1	0.261

two environments. These two PCA were very similar with the first components accounting for 82% (Fig. 1a) and 87% (Fig. 1b) of the variation, which was comprised primarily of the timing of reproduction. In both cases the second principal component appeared to separate the two habitats and in both case this component was comprised primarily of resources partitioned into growing wide and the timing of germination. In both PCAs the same two low fertility simulations clustered with the high fertility group. These two simulations were unusual in that about 20% of the vegetation that developed, reproduced vegetatively whilst in all other simulations reproduction via seed was the norm, occurring in more than 98% of all individuals.

Plotting the standard deviations of all the traits against time (Figs 2 and 3) revealed little tendency for the between simulation variance to decline. However, regression analysis of the fertile environment data (Table 2) revealed that between simulation variation declined significantly in the traits of plant height and width for the population as a whole and additionally for germination time in the most abundant genotype. In the unfertile and cut environment (Table 3) between simulation variation was seen to decline significantly in the traits of plant width and resources partitioned into seed production. However, in the most abundant 'genotype' a significant increase in standard deviation over time

Table 3. Regression analysis of trait standard deviations against time: For the unfertile, cut habitat and most abundant 'genotype' (Panel A) and unfertile, cut habitat and population means (Panel B)

Trait	Intercept	Slope	R^2	p
Panel A				
Height	0.2160	0.000015	8.9	0.402
Width	1.6168	−0.0002	90.6	0.0001
Resources into seeds	1.4554	−0.00236	70.0	0.003
Resources into width	0.7744	0.00018	58.3	0.01
Resources into height	0.7599	0.000183	79.2	0.0001
Resources into defence	−0.000042	0.0000006	12.1	0.324
Time of reproduction	4.3563	−0.000035	1.1	0.772
Threshold of reproduction	0.3394	−0.000032	13.8	0.291
Propagule number	0.5678	0.0000318	20.1	0.194
Time of germination	1.6449	0.0002278	16.3	0.247
Panel B				
Height	0.1091	0.000015	18.4	0.216
Width	1.0341	−0.000169	63.8	0.006
Resources into seeds	1.1481	−0.000119	64.5	0.005
Resources into width	0.7204	0.00014	93.3	0.0001
Resources into height	0.6707	0.0000824	68.3	0.003
Resources into defence	0.4491	−0.00012	26.9	0.124
Time of reproduction	3.9168	−0.000226	18.6	0.213
Threshold of reproduction	0.343	−0.0000085	1.9	0.707
Propagule number	0.4989	0.0000347	58.9	0.01
Time of germination	1.0967	0.0000449	7.2	0.452

was seen for the traits of resources partitioned into growing tall and growing wide. This was also seen for the population as a whole, where there was also a significant increase in the variation observed in the number of seeds produced. In all cases where a significant change in the standard deviation was observed, (both increasing and decreasing) the rate of change was slight.

Individual simulations were observed to vary greatly (Fig. 4). Plotting population means of just three simulations revealed little tendency for replicates to converge on identical endpoints. However, within simulations some traits did appear to achieve a degree of stability at the population level. Even after 5000 years, unidirectional change was still apparent in the resources into growing tall (Fig. 4e), producing seeds (Fig. 4c) and in the timing of reproduction (Fig. 4f). At the year-to-year scale population means of all non-fixed traits appeared to fluctuate by around plus or minus 1% of the previous value. At the level of the most abundant 'genotype', there was little evidence that the traits were evolving towards stable endpoints (Fig. 5). The two simulations plotted in Figure 5 both show trait values, which are highly dynamic. The traits of reproductive threshold (Fig. 5g), numbers of propagules (Fig. 5h) and germination time (Fig. 5i) appear to be fluctuating around stable limits, while

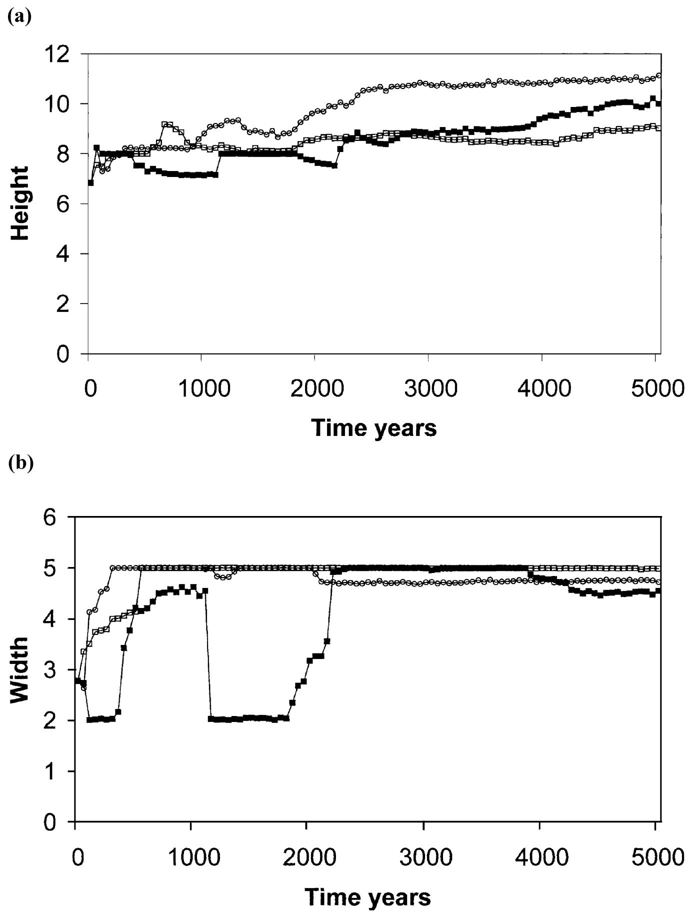


Figure 4. Changes in mean trait values within populations over time. Solid squares represent simulation 1, hollow squares represent simulation 2 and hollow circles represent simulation 3, all from the low fertility cut habitat. Data for the parameter regulating plant height (a), plant width (b), plant resources allocated to seed (c), plant resources allocated to width (d), plant resources allocated to height (e), the timing of reproduction (f), the threshold size of reproduction (g), the number of propagules produced (h) and the timing of seed germination (i).

those of resources allocated to seeds and height (Fig. 5c and e) appear to vary against a background of unidirectional change.

For most traits no relationship was found between simulation variation and time. This was marked in the timing of reproduction, where most simulation to simulation variation was observed but with no apparent trend (Figs 2 and 3). When this trait was prevented from mutating there was no indication ESS was approached more quickly. Regression analysis revealed that between simulation variation only declined significantly in the trait of plant width for the most

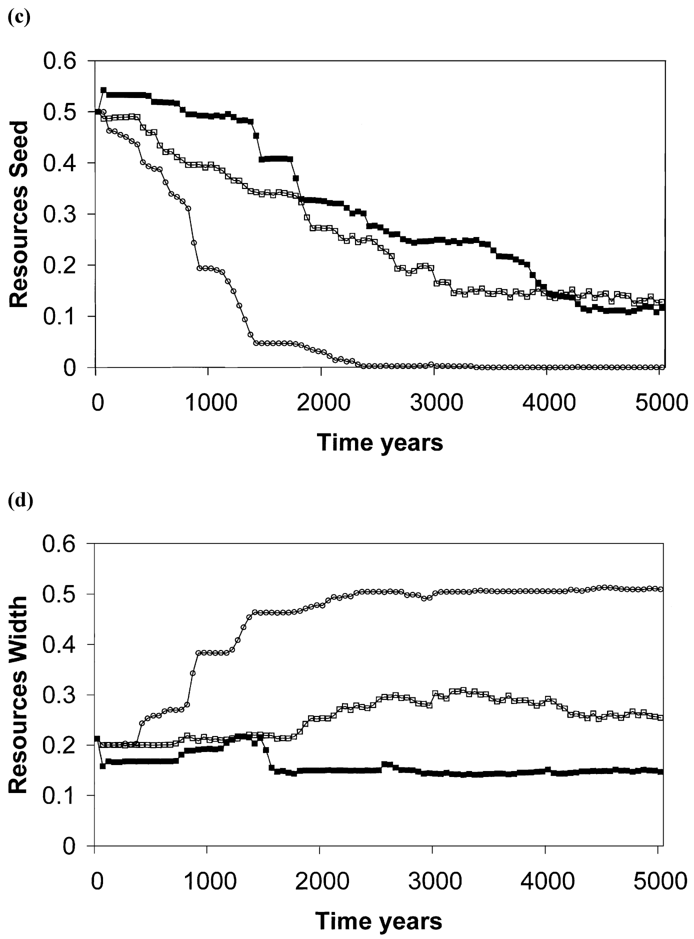
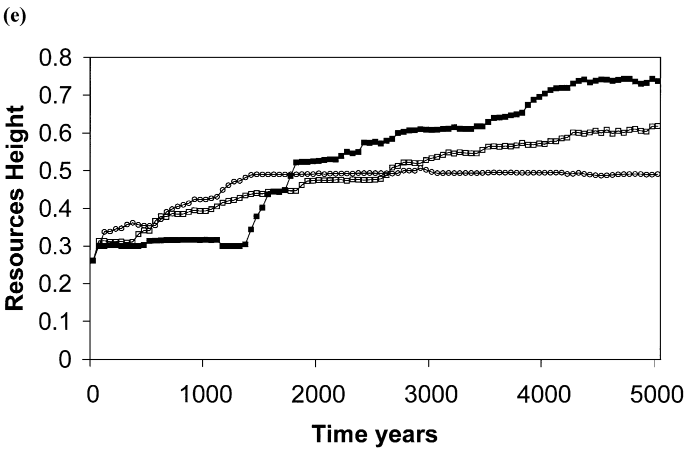


Figure 4. Continued.

abundant 'genotype' and for that of plant height for the population as a whole (Table 4).

Discussion

The results show that different life-history strategies do appear to evolve under different sets of environmental conditions (Fig. 1). As might be expected taller individuals appear to be selected for under fertile uncut conditions, while shorter, wider and earlier growing individuals became most abundant in the less fertile and cut habitat. However, when individual traits are considered, very few could be said to have achieved ESS as between simulation variation



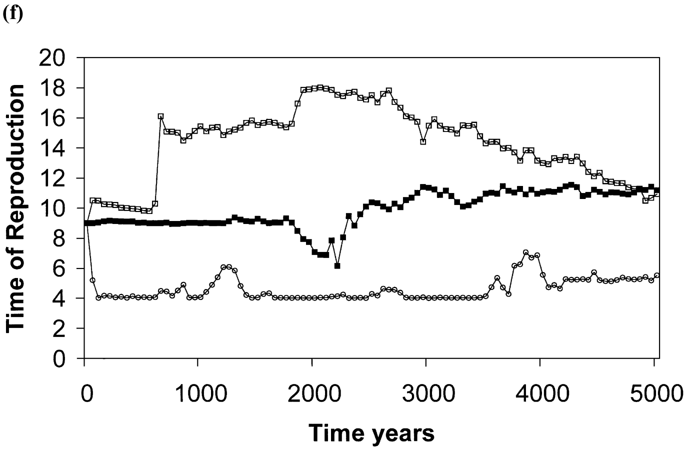


Figure 4. Continued.

was found to be unrelated to time for most traits (Tables 2, 3 and 4). In the traits where selection appeared to have been most strong, those of plant height and width, variance did appear to decline over time.

Three possible explanations exist for the observed maintenance of variation over 5000 years of simulation: Firstly selection may be rather weak compared to mutation and drift. Secondly different simulations within the same 'habitat' may end up on different adaptive peaks as per Wright's (1931) shifting balance theory. Thirdly, simulations may be prevented from going to fixation by frequency dependent selection driven by intra-specific competition (Red Queen dynamics). The first of these explanations can be dismissed as Figure 4 reveals that most population means within simulations achieve a degree of stability or

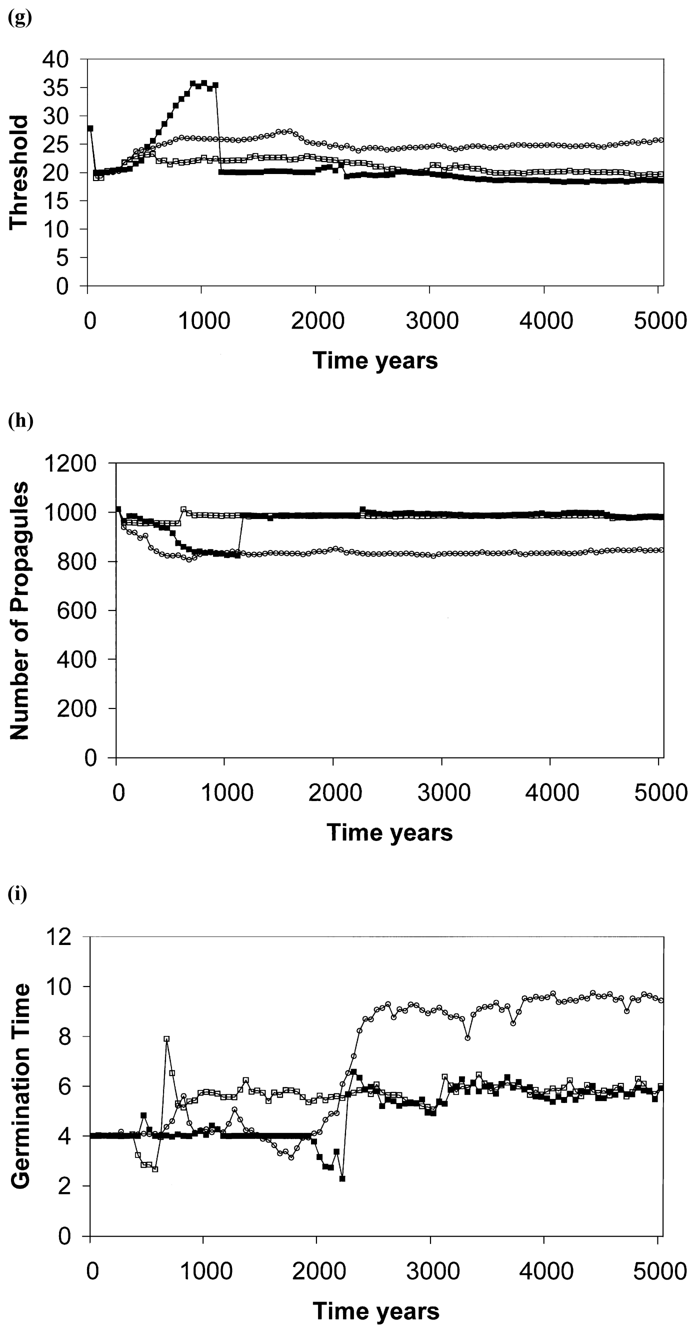
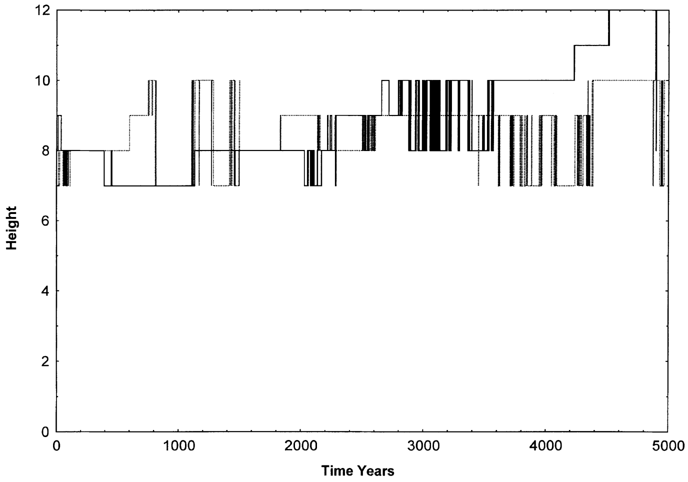


Figure 4. Continued.

(a)



(b)

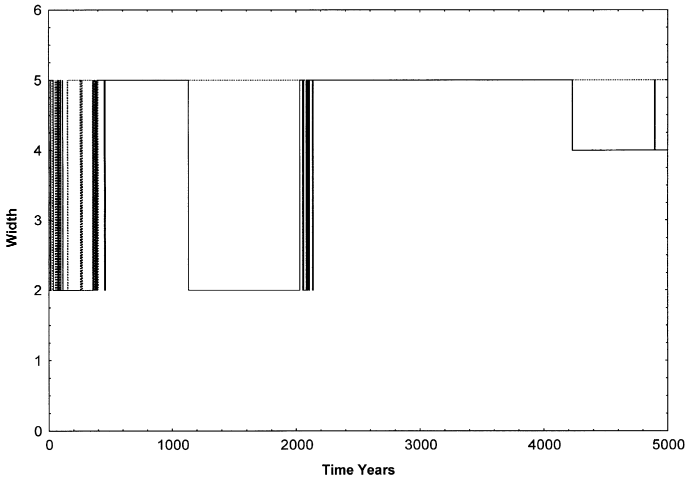


Figure 5. Changes in trait values of the most abundant 'genotype' over time. Solid lines represent simulation 1, broken lines represent simulation 2 both from the low fertility cut habitat. Data for the parameter regulating plant height (a), plant width (b), plant resources allocated to seed (c), plant resources allocated to width (d), plant resources allocated to height (e), the timing of reproduction (f), the threshold size of reproduction (g), the number of propagules produced (h) and the timing of seed germination (i).

exhibit unidirectional change, implying strong selection rather than drift. Additional evidence that selection is stronger than random drift is apparent when looking at the germination time of the most abundant 'genotype' (Fig. 5i).

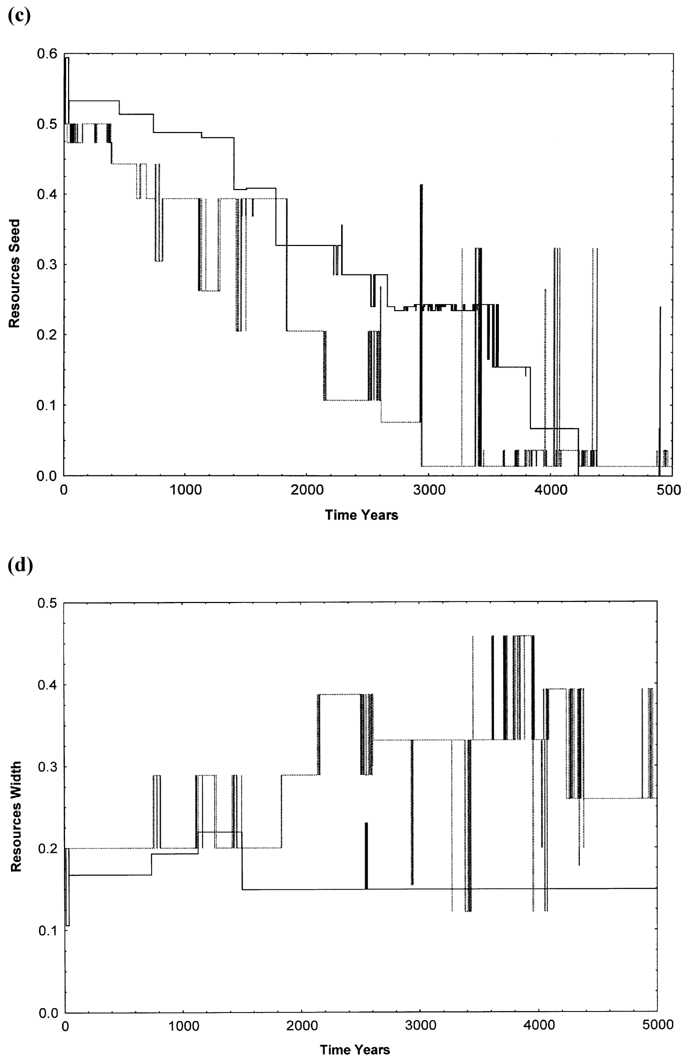
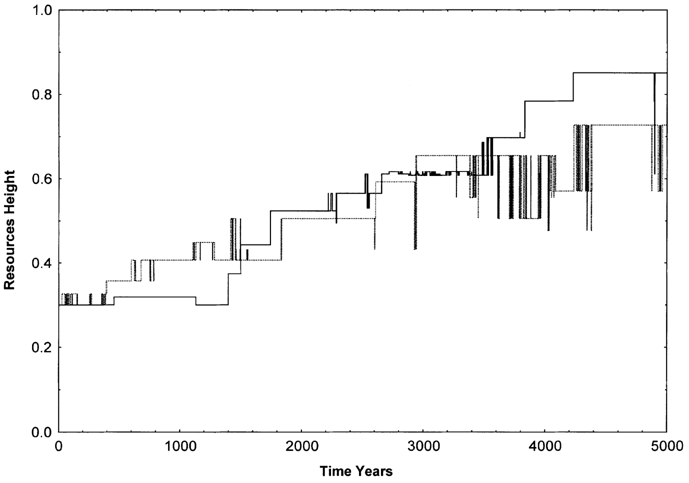


Figure 5. Continued.

Although germination time was seen to vary, germination in the 3 and 5 months was never seen; implying strong selection against germination in these months. The second explanation (that of multiple adaptive peaks) is consistent with the within simulation stability seen in some traits in combination with the run-to-run variation revealed at the population level in Figure 4. However, Wright's shifting balance theory applies only to large random mating populations and would not be expected to occur in the small populations simulated here (although the model usually contain in excess of a 1000 individuals at any one

(e)



(f)

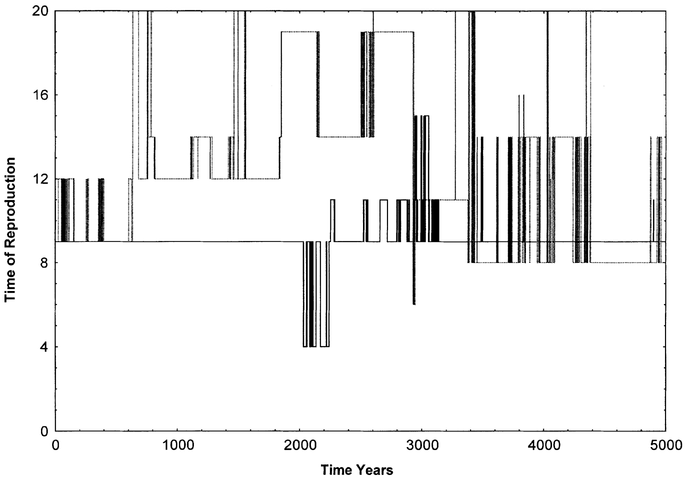


Figure 5. Continued.

time, it rarely contains more than 30 different 'genotypes'). The traits of, resources allocated to seeds and growing tall, and that regulating the time of reproduction (Fig. 4c, e, and f) all showed little sign of becoming fixed within simulations, so for these traits at least, adaptive peaks or ESS had not been attained after 5000 years. The fact that the simulations remained dynamic for so long suggests that selection had not had sufficient time for fixation to be achieved, or another factor such as Red Queen dynamics was actively maintaining/generating variation. The lack of fixation of parameter values within the

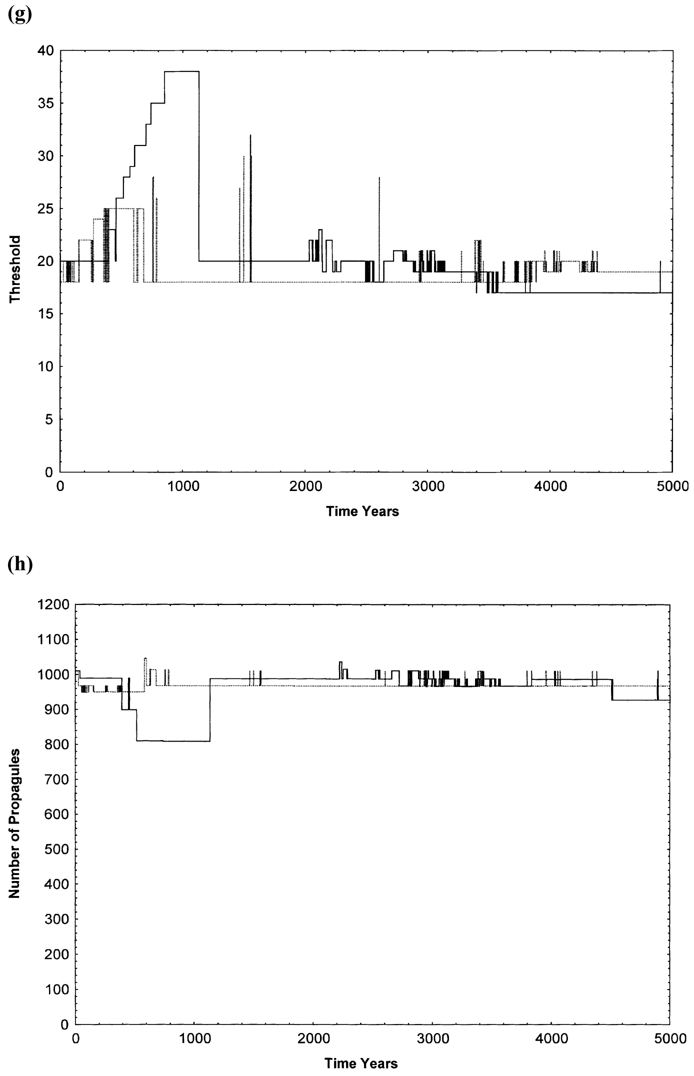


Figure 5. Continued.

most abundant ‘genotype’ (Fig. 5) suggests that Red Queen dynamics may be operating in our system. ESS is a property of the population as a whole (Maynard Smith, 1982) and not the individual; this could explain the relative stability at the population level (Fig. 4). In contrast, Red Queen dynamics operate at the level of the most abundant genotype (Van Valen, 1973) and may be responsible for the lack of fixation observed in Figure 5.

The parameter value regulating the timing of reproduction was seen to vary greatly between simulations and showed no tendency to change over time. There

(i)

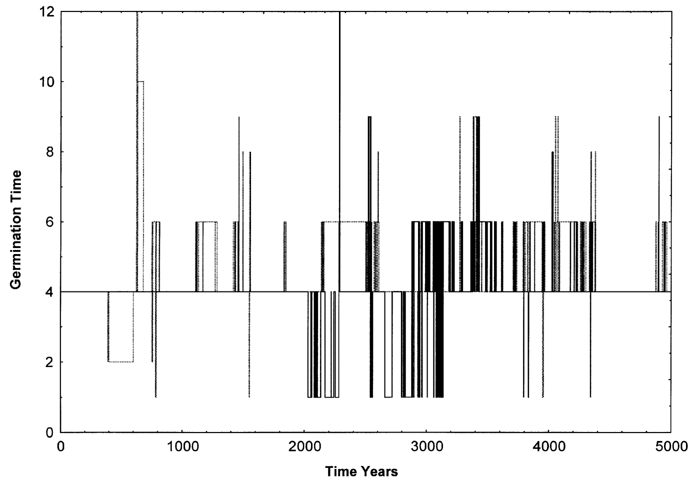


Figure 5. Continued.

are a number of possible explanations for this. Firstly, months as the units of time are not linear in the same sense, as are those of space. Two individuals, who reproduce a year apart in the same month, are likely to be ecologically more similar than those that reproduce 6 months apart are. Even within those reproducing 6 months apart, the 6 months summer to winter are likely to be more different that the 6 months from spring to autumn. Alternatively Red Queen dynamics (Van Valen, 1973) could be operating intensely on this trait. Such dynamics have usually been associated with predator–prey interactions (Dieckmann *et al.*, 1995) or host–parasite systems (Lively *et al.*, 1990). For Red Queen dynamics to occur in this system (without parasites or predators) would imply intense intra-specific competition. Specifically offering selective advantages to individuals that reproduce at a different time from the majority. This possibility might be expected to produce cyclical changes in parameter values as reported by Law *et al.* (1997). Although fluctuations in the timing of reproduction are apparent (Fig. 5f) there is no indication of regular cyclic behaviour in this system.

Further evidence to support the occurrence of Red Queen dynamics is provided by the fact that when the highly variable trait of timing of reproduction was prevented from mutating, the system did not approach apparent ESS more quickly. Instead, the number of seeds produced by the most abundant 'genotype', (Fig. 6a) which had previously been relatively stable, became increasingly dynamic. This effect was only apparent when looking at the most abundant 'genotype', at the level of the population as a whole the traits were generally less variable (Fig. 6b). As above this is consistent with Red Queen dynamics applying at the level of the most abundant genotype rather than on

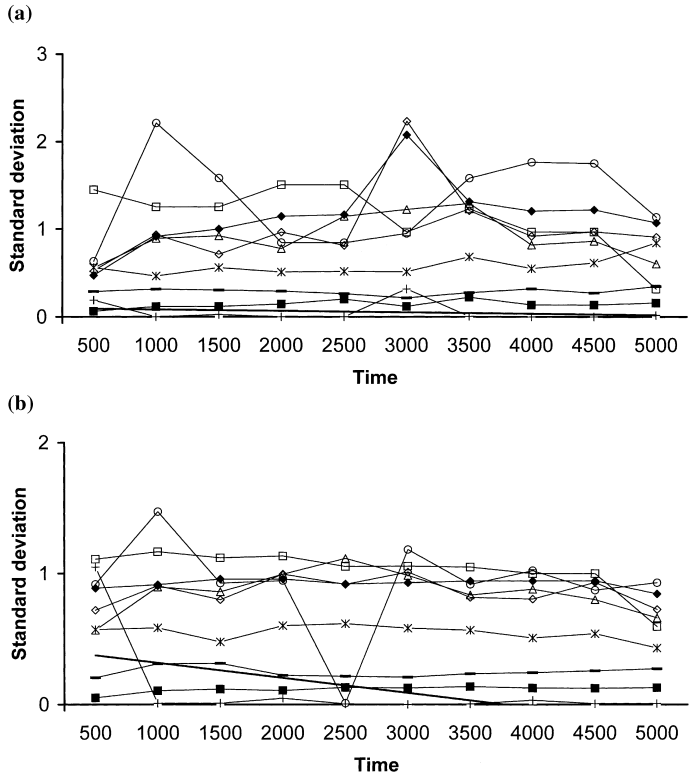


Figure 6. Same as in Fig. 2 but for traits values from (a) the most abundant ‘genotype’ from the unfertile habitat, with the timing of reproduction unable to mutate and (b) population means from the unfertile habitat, with the timing of reproduction unable to mutate. Solid squares: plant height, hollow squares: plant width, hollow triangles: resources partitioned into seeds, solid diamonds: resources partitioned into growing horizontally, hollow diamonds: resources partitioned into growing tall, a horizontal cross: resources partitioned into defence, solid circles: the timing of reproduction, a dash: the threshold size at which reproduction occurs, diagonal crosses: propagule number, and hollow circles: germination time.

the population as a whole. Punctuated equilibria theory (Gould and Eldredge, 1977) also predicts that ESS are not maintained, with evolutionary shifts assumed to result from changes in the abiotic environment but equally they could be driven by dynamic biotic environments. The lack of ESS observed here seems to result from dynamic properties of the biotic component of the environment as the abiotic environment was unperturbed.

The apparent occurrence of Red Queen dynamics in such a simple system is important for a number of reasons: it suggests that the search for absolutely stable endpoints (ESS) within the evolution of life-histories may be over simplistic. It also suggests that Red Queen dynamics may be important even in systems without predators, parasites or pathogens and that the dynamics produced may not always be cyclic.

Table 4. Regression analysis of trait standard deviations against time: For the unfertile, cut habitat and most abundant 'genotype' (with time of reproduction fixed) (Panel A) and unfertile, cut habitat and population means (with time of reproduction fixed) (Panel B)

	Intercept	Slope	R^2	p
Panel A				
Height	0.1003	0.000014	24.6	0.145
Width	1.6401	−0.000181	58.5	0.01
Resources into seeds	0.8644	0.000159	1.0	0.799
Resources into width	0.8253	0.00012	20.9	0.185
Resources into height	0.7891	0.0000832	7.4	0.447
Resources into defence	0.1002	−0.0000162	5.1	0.528
Threshold of reproduction	0.2815	0.0000022	0.9	0.794
Propagule number	0.4459	0.0000489	45.3	0.003
Time of germination	1.1782	0.000054	2.6	0.658
Panel B				
Height	0.0823	0.000011	51.3	0.020
Width	1.2489	−0.0000806	56.5	0.012
Resources into seeds	0.8692	−0.0000039	0.1	0.918
Resources into width	0.9328	−0.0000035	2.3	0.674
Resources into height	0.8675	−0.0000022	0.1	0.931
Resources into defence	0.4305	−0.000114	27.8	0.117
Threshold of reproduction	0.2491	−0.0000009	0.1	0.926
Propagule number	0.5982	−0.0000189	23.6	0.154
Time of germination	1.0032	−0.0000307	1.6	0.728

Acknowledgments

We would like to thank Anita Diaz and Jonas Lawesson for commenting on the manuscript, and two anonymous referees for their suggestions.

References

Anderson, W.W. and King, C.E. (1970) Age-specific selection. *Proceedings of the National Academy of Sciences, USA*, **132**, 437–447.

Charlesworth, B. and Giesel, J.T. (1972) Selection in populations with overlapping generation. II Relations between gene frequency and overlapping generations. *Am. Nat.* **106**, 388–401.

Deevey, E.S. (1947) Life tables for natural populations. *Quart. Rev. Biol.* **22**, 283–314.

Dieckmann, U., Marrow, P. and Law, R. (1995) Evolutionary cycling in predator–prey interactions: population dynamics and the Red Queen. *J. Theor. Biol.* **176**, 91–102.

Geritz, S.A.H., Kisdi, E., Meszena, G. and Metz, J.A.J. (1998) Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**, 35–57.

Gould, S.J. and Eldredge, N. (1977) Punctuated equilibria: on the tempo and mode of evolution reconsidered. *Paleobiol.* **3**, 115–151.

Iwasa, Y. and Levin, S.A. (1995) The timing of life-history events. *J. Theor. Biol.* **172**, 33–42.

Klinkhamer, P.G.L., Kubo, T. and Iwasa, Y. (1997) Herbivores and the evolution of the semelparous perennial life-history of plants. *J. Evol. Biol.* **10**, 529–550.

Law, R., Marrow, P. and Dieckmann, U. (1997) On evolution under asymmetric competition. *Evol. Ecol.* **11**, 485–501.

Lively, C.J., Craddock, C. and Vrijenhoek, R.C. (1990) Red Queen hypothesis supported by parasitism in sexual and clonal fish. *Nature*, **344**, 864–866.

MacArthur, R.H. (1962) Some generalised theorems of natural selection. *Proceedings of the Natural Academy of Sciences, USA*, **38**, 1893–1987.

Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

Maynard Smith, J. (1991) The evolution of reproductive strategies: a commentary. *Philos. Trans. Royal Soc. Lond. B* **332**, 103–104.

Sibly, R.M. (1996) Life-history evolution in heterogeneous environments – A review of theory. *Philos. Trans. Royal Soc. Lond. B* **351**, 1349–1359.

Sibly, R. and Antonovics, J. (1992) Life-history evolution. In R.J. Berry, T.J. Crawford and G.M. Hewitt (eds) *Genes in Ecology*. Blackwells, Oxford.

Scheiner, S.M. (1998) The genetics of phenotypic plasticity. VII. Evolution in spatially structured environments. *J. Evol. Biol.* **3**, 303–320.

Southwood, T.R.E. (1988) Tactics, strategies and templets. *Oikos*, **52**, 3–18.

Takada, T. and Nakajima, H. (1996) The optimal allocation for seed reproduction and vegetative reproduction in perennial plants – an application to the density dependent transition matrix model. *J. Theor. Biol.* **182**, 179–191.

Teriokhin, A.T. (1998) Evolutionarily optimal age schedule of repair: computer modelling of energy partition between current and future survival and reproduction. *Evol. Ecol.* **12**, 291–307.

Van Valen, L. (1973) A new evolutionary law. *Evol. Theory* **1**, 1–30.

Warren, J.M. and Topping, C.J. (1999) A space occupancy model for the vegetation succession that occurs on set-aside. *Agri. Ecosyst. Environ.* **72**, 119–129.

Wright, S. (1931) Evolution in Mendelian populations. *Genetics* **16**, 97–159.