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"Life cycle models for plants"

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These are preliminary lecture notes, intended only for distribution to participants.

Life cycle models for plants
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Abstract

This paper reviews the use of matrix population models in the study of plant demography. Because of their modular architecture, growth plasticity, and multiple modes of reproduction, plant life cycles usually violate the assumptions of classical age-specific demography. Using a directed graph description of the life cycle, it is easy to derive matrix projection models for complex life cycles. Linear time-invariant models can be used for population projection (distinguished from prediction), and provide valuable insight into the population consequences of environmental conditions. The ergodicity of such models, their asymptotic and transient behavior, and their sensitivity properties depend on the eigenvalues and eigenvectors of the projection matrix. The characteristic equation for the eigenvalues and formulas for the eigenvectors can be derived directly from the life cycle graph.

Sensitivity analysis connects demography with evolution. Since Darwinian fitness is a fundamentally demographic notion, the sensitivity of population growth rate measures the selective pressure on life history traits, and can be used to predict the results of trade-offs arising from genetic correlations between traits. Examples are presented using data from the literature on populations of trees and herbaceous plants.

1 Life Cycle Complexity

The life cycle is the fundamental unit of demographic analysis. Evaluating the demographic consequences of the vital rates (a general term

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subsuming rates of growth, survival, development, reproduction, and so on), requires an analytical framework that can include the entire life cycle. Evaluating the evolutionary consequences of changes in the vital rates requires a relation between the vital rates and a measure of fitness, and a perturbation analysis which reveals the effects on fitness of possible modifications of the rates. Fitness, being a measure of the relative rate of incorporation of genotypes into future generations, is itself a fundamentally demogaphic idea. Demographic and evolutionary considerations thus converge upon the need for a description of the life cycle from which analytical conclusions can be drawn.

Classical demographic theory, developed in the first half of the 20th century for human populations, satisfies this need for life cycles which can be defined by a specific set of age-dependent vital rates: the survivorship function $l(x)$ and the maternity function $m(x)$, where x denotes age. Together $l(x)$ and $m(x)$ determine the eventual rate of population increase (r or its discrete time version λ), the stable age distribution, the reproductive value distribution, the rate of convergence to the stable age distribution, the period of the oscillations produced en route to the stable age distribution, and so on. This theory was applied to animal populations early on (Pearl 1928, Leslie and Ransom 1940, Deevey 1947, Birch 1948, Leslie and Park 1949, Evans and Smith 1951), and at least the rudiments of it are now included in beginning ecology texts.

Unfortunately, the life cycles of most plants violate the assumptions of classical demography. The age of an individual plant says little about its likely demographic fate, so the vital rates cannot be written as functions of age. Multiple modes of reproduction make it impossible to describe reproduction by a simple maternity function. Such "complex" life cycles (my use of the term is wider than that of Wilbur (1980)) require a more general demographic theory.

It is only fair to acknowledge that even human demographers recognise that demographic characteristics are affected by variables other than age (e.g., Clark and Spuhler (1959) for body size effects on human fertility). "Multidimensional" demographic models, in which individuals are classified by multiple criteria such as age and sex, age and location, or age and nuptiality are an active area of current investigation (Land and Rogers 1982).

1.1   The sources of life cycle complexity

An examination of some of the reasons that plant life cycles fail to meet the assumptions of classical demography is revealing. Many of them reflect the modular architecture of plants (Harper 1981). Because individual plants are often collections of modules, each potentially capable of reproduction, fertility is usually strongly dependent on size. The growth plasticity which follows from modular construction, however, tends to decouple age and size. Survival probabilities are also strongly dependent on size, and there are often multiple modes of reproduction.

1.1.1   Size dependent demography

That survival and reproduction in plants are strongly dependent on size is now widely appreciated. Here I consider some examples, in order to suggest some powerful statistical methods for examining the dependence of vital rates on size and age. These methods have yet to be widely applied in plant demography.

Reproduction in trees is strongly affected by size (Baker 1950). Figure 1 shows the proportion of Western White pine (*Pinus monticola*) trees bearing cones as a function of diameter. The significance of trends in such binary data can be assessed by logistic regression (Cox 1970); in this case there is a highly significant ($P < .001$) size effect. The overall effect of size on fertility is even greater than indicated by this curve, since large trees are not only more likely to bear cones, but bear more and larger cones and produce more seed with a higher germination rate (Zon 1915).

Size dependence *per se* does not violate the assumptions of classical demography. If size is closely related to age, then a simple transformation can express size-dependent vital rates as a function of age. However, in most plants the dependence of fertility on size is accompanied by a plasticity of growth that makes age a very poor predictor of size. This uncertainty in the size of individuals is obscured by the common practice of plotting "growth curves" showing mean size as a function of age, without any indication of the degree of variation.

Figure 2 is a typical example of the relation between age and size in trees, based on data from Meyer (1930) on Douglas fir (*Pseudotsuga taxifolia*) in even aged stands. Although mean size is clearly related to age, following a von Bertalanffy growth curve ($y = a(1 - exp(-bx))$)quite closely, the variability in size at a given age increases continuously. Thus age becomes a poorer and poorer predictor of size as the trees reach the
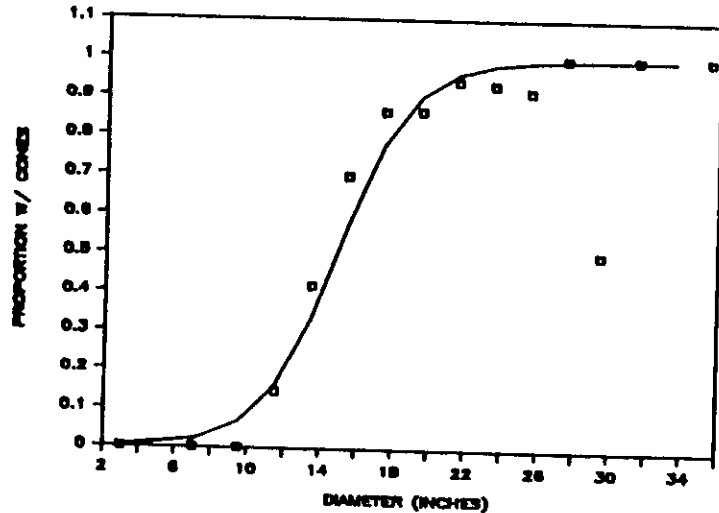
WHITE PINE REPRODUCTION

Figure 1: The proportion of individuals bearing cones as a function of diameter in the Western white pine (*Pinus monticola*). The logistic regression is highly significant (improvement in $\chi^2 = 248.22$, df $= 1$, $P < .001$). Data from Zon (1915).

larger sizes at which reproduction is most likely to occur.

The "stand tables" produced by foresters for trees present frequency distributions of size at age, for even-aged populations, in the form of a 2-dimensional contingency table. Table 1 is an example. The relation between age and size is highly significant ($\chi^2 = 646.14$, df $= 80$, $P < .0001$). However, age is still an extremely poor predictor of size. The extent to which knowledge of one variable (e.g., age) permits prediction of the other (e.g., size) in such a table is measured by Goodman and Kruskal's (1954) r, which measures the decrease in the proportion of incorrect predictions of the size class of a randomly selected individual when knowledge of age class is taken into account (Bishop et al. 1975, Ch.11). It also measures the proportion of the variation in variable (size) explained by the other (age), in a fashion analogous to the coefficient of determination (R^2) in regression (Light and Margolin 1971). For the data of Table 1, $r = .073$,
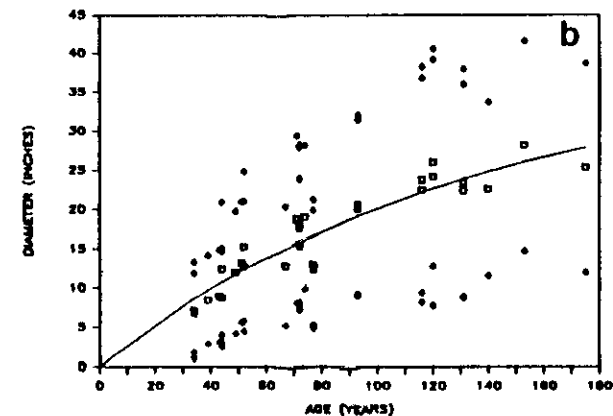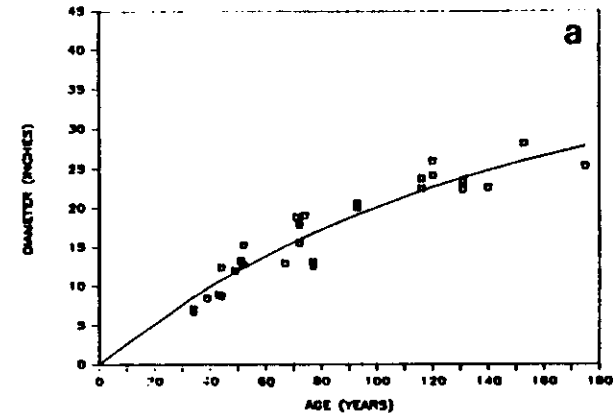
DOUGLAS FIR: SIZE VS. AGE

Figure 2: (a) The mean size (dbh in inches) as a function of age, for even-aged stands of Douglas fir (*Pseudotsuga taxifolia*). The curve is a von Bertalanffy growth curve fitted to the points; it explains 88% of the variance. (b) The same fitted curve, with approximate 95% confidence intervals indicated by diamonds. Data from Meyer (1930).

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Table 1: The number of longleaf pine trees per acre, in even aged stands, by age and diameter. Data from Forbes (1930).

	Diameter (in.)					
Age	8	10	12	14	16	18
15	0	0	0	0	0	0
20	11	0	0	0	0	0
25	46	0	0	0	0	0
30	80	14	0	0	0	0
35	101	24	6	0	0	0
40	117	36	10	0	0	0
45	119	55	18	0	0	0
50	120	65	21	0	0	0
55	113	67	30	8	0	0
60	106	73	35	11	0	0
65	93	74	39	13	3	0
70	81	76	42	18	3	0
75	73	74	45	19	6	0
80	64	70	48	24	8	0
85	55	66	50	28	10	0
90	51	63	50	29	15	0
95	44	58	51	33	14	2

so knowledge of an individual's age improves the ability to predict its size by only 7.3%.

This is not atypical. Meyer (1938) presents a series of stand tables for *Pinus ponderosa* as a function of a "site index" (the height in feet of an average diameter dominant tree at age 100 years) which measures the quality of the site. In no case (Figure 3) does age explain more than 21% of the variance in size, and in most cases it explains less than 10%. There is an interesting suggestion that size and age may be more closely related on intermediate quality sites. This might reflect the processes by which size distributions become more skewed as a cohort grows, under the influence of variability in growth rate and competitive ability (e.g., Turner and Rabinowitz 1983).

Size dependent mortality is common in plants (e.g., Harper 1977, Cook 1980, Solbrig 1981, Sarukhan et al. 1984, Jimenez and Lugo 1985
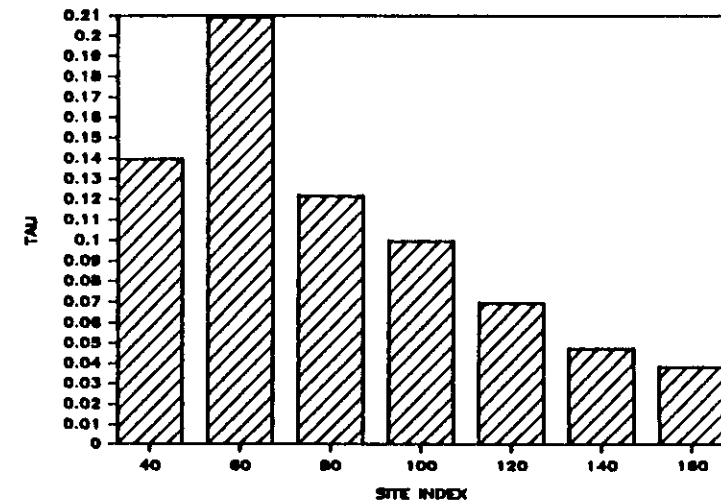

PREDICTION OF SIZE FROM AGE

Figure 3: Goodman and Kruskal's r as a function of site index for Ponderosa pine *Pinus ponderosa*. The standard error of r for these data was between .003 and .004, so the differences between sites are highly significant. Data from yield tables in Meyer (1938).

and many others). Data for two monocarpic perennial herbs, *Dipsacus sylvestris* and *Arctium minus* are shown in Figure 4. The effect of size on survival probability is highly significant, even in *A. minus*, where the overall survival probability is quite high. The relation between size and survival probability in these data is noticeably less abrupt than that between size and reproductive status in Figure 1.

Ideally, the relative importance of age and size should be decided on the basis of data in which both age and size are known, and in which as many demographic transitions as possible (not just survival) are recorded. Data are seldom reported in this form, and even more seldom analysed so as to take advantage of it. Tables 2 and 4 show one approach to such analyses, for two monocarpic perennials, *Dipsacus sylvestris* and *Verbascum thapsis* (data kindly supplied by P.A. Werner and K. Gross). In each
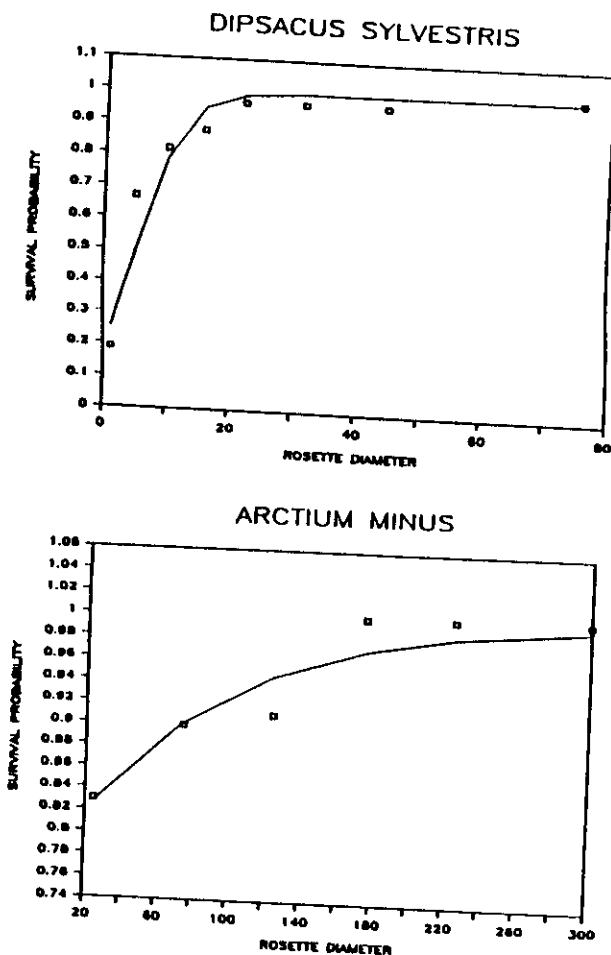
DIPSACUS SYLVESTRIS

ARCTIUM MINUS

Figure 4: Logistic regression of survival probability as a function of rosette diameter in *Dipsacus sylvestris* and *Arctium minus*, two monocarpic perennials. The effect of size in both cases is significant ($P < .0001$). Data from Werner (1975) and Gross and Werner (1983), respectively.

case, the fate (death, survival as a vegetative rosette, or flowering) in year $t + 1$ of individuals of known age and size in year t is recorded.

In the literature, such data are often converted into proportions and subjected to analysis of variance (e.g., Werner 1975, Gross 1981). However, log-linear contingency table analyses (e.g., Bishop et al. 1975, Fienberg 1978, Fingleton 1984) are more appropriate and much more powerful. The data of Tables 2 and 4 can be treated as 3-way contingency tables (Age × Size × Fate). The significance of the effects of age and size on demographic fate is evaluated by testing the two way AF and SF interactions. Tests of the three way interaction (ASF) evaluate the importance of the interaction of age and size in determining fate. A significant three-way interaction implies that the size-specific (age-specific) transition pattern differs for different aged (sized) individuals. This effect is obscured when the proportions are subjected to analysis of variance, because reducing the transition data to proportions leaves only a single observation per cell. Its significance would suggest that *both* age and size be included in a projection model, as in Law (1983) and Caswell (1983).

The significance of an interaction is measured by the reduction in the log-likelihood ratio (distributed as χ^2) when the interaction is added to the log-linear model. The "partial" association test adds the interaction to the model containing all the other interactions of the same order; the "marginal" association test adds it to the model containing only all lower-order interactions involving the variables in question. Other comparisons can be made; here the partial association tests are most relevant.

The results of the analyses are shown in Tables 3 and 5. In both species, the effect of size on demographic fate is highly significant. The fate of *D. sylvestris* is also affected by age (mainly an increase in survival and flowering probabilities among older plants), but comparison of the partial χ^2 values shows the effect to be much smaller than that of size. The interaction between age and size in determining fate is not significant. For *V. thapsis*, however, the three-way interaction is significant while the interaction of age and fate is not. Thus there is no direct effect of age on demographic fate, but the size-specific transition pattern differs between the two age classes.

For contrast, Tables 6 and 7 show a similar analysis for reproductive output of a large mammal, the moose (*Alces alces*; data from Saether and Haagenrud (1983)). Individuals were classified by age and size, and their reproductive output (no calfs, one calf, or twins) recorded. In this case, although there is a significant association of age and size (older animals tend to be larger), there is no significant interaction of size and reproductive

output, once age is taken into account. The differences between Tables 2-5 and 6-7 are typical of the differences between size- and age-dependent demography.

The decoupling of age and demography that results from size-dependent vital rates and growth plasticity also arises when individuals are classified by developmental stages (e.g., the "age-states" developed by the Russian school of plant population biology, e.g., Gatsuk et al. 1980).

1.1.2 Modes of reproduction

The second major violation of the assumptions of classical demography by most plant populations concerns reproduction. The classical maternity function $m(x)$ gives the expected number of offspring produced, per unit time, by an individual of age x. All these offspring are assumed to be demographically identical. Many plants, however, possess multiple modes of reproduction, and hence their analysis requires models capable of including multiple reproductive pathways.

For example, as a consequence of their modular architecture, many plants reproduce clonally by rhizomes, budding, tillers, etc. as well as by seed (e.g., Abrahamson 1980, Cook 1983, Jackson et al. 1985). There are important genetic differences between clonally and sexually produced offspring. These differences make the definition of an individual (equivalently, the definition of the life cycle) ambiguous, and raise questions about the operation of selection (e.g., Jansen 1977, Lynch and Gabriel 1983, Caswell 1985, Jackson et al. 1985). However, there are often demographic differences as well; new seedlings may have very different survival, growth and reproductive probabilities than newly produced vegetative shoots.

Other examples of multiple modes of reproduction include seed heteromorphism (Venable 1985) and sex change (Policansky 1982).

Age-specific survivorship and maternity functions simply cannot incorporate the demographic properties of complex life cycles. The problems for evolutionary demography are even more profound, for life cycle complexity creates the need to analyse the effects on fitness of traits which simply do not appear in the classical theory.

Table 2: A three way contingency table relating fate (death, survival as a vegetative rosette, or flowering) to rosette diameter and age in *Dipsacus sylvestris*. Data from Werner (1975).

Age	Fate	Size Class						Total
		1	2	3	4	5	6-8	
2	Rosette	170	165	61	21	10	0	427
	Flower	0	0	0	0	2	0	2
	Death	725	81	10	0	1	0	817
	Total	895	246	71	21	13	0	1246
3	Rosette	0	80	75	84	28	12	279
	Flower	0	0	1	3	14	68	86
	Death	0	41	19	14	1	1	76
	Total	0	121	95	101	43	81	441
4	Rosette	0	6	7	17	15	0	45
	Flower	0	0	0	0	8	16	24
	Death	0	3	3	3	0	0	9
	Total	0	9	10	20	15	16	78
5	Rosette	0	0	0	3	4	4	11
	Flower	0	0	0	0	2	3	5
	Death	0	0	0	1	1	2	4
	Total	0	0	0	4	7	9	20

2 Matrix Projection Models and Their Analysis

Matrix projection models were introduced by Bernardelli (1941), Lewis (1942), and especially Leslie (1945, 1948). These initial models were age-classified, and were subsequently adopted and widely utilised by human demographers (e.g., Keyfitz 1967, Goodman 1967). They are now a basic tool in that field (e.g., Keyfitz 1968, 1977).

Matrix models were extended to complex life cycles by Lefkovitch (1965), and have been developed by Caswell (1978, 1980, 1982a,b, 1983, 1985, Werner and Caswell 1977, Caswell and Werner 1978), Usher (1976),

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Table 3: Log-linear analysis of the effect of age and size on demographic fate of *Dipsacus sylvestris*, using data in Table 2. F=fate, S=size, A=age. Calculated using BMDP procedure P4F (Dixon 1985).

Effect	df	Partial Assoc χ^2	Prob	Marginal Assoc χ^2	Prob
F	2	736.16	0.0000		
S	5	1297.27	0.0000		
A	3	2087.15	0.0000		
FS	10	679.67	0.0000	1198.16	0.0000
FA	6	16.48	0.0114	534.97	0.0000
SA	15	768.34	0.0000	1286.83	0.0000
FSA	30	38.56	0.1360		

Table 4: A three way contingency table relating fate (vegetative rosette, death, or flowering) to rosette diameter and age in *Verbascum thapsis*. Data from Gross (1981) and *personal communication*.

Age	Fate	Size Class						Total
		1	2	3	4	5	6-8	
2	Rosette	19	18	21	3	4	0	65
	Flower	0	0	17	30	25	56	128
	Death	639	70	25	12	7	8	761
	Total	658	88	63	45	36	64	954
3	Rosette	0	1	2	1	0	0	4
	Flower	0	2	2	6	4	4	18
	Death	3	10	7	6	2	2	30
	Total	3	13	11	13	6	6	52

Hubbell and Werner (1979), Law (1983), Hughes (1984) and others. In this section, I summarize the development and analysis of these models.

Table 5: The results of log-linear analysis of the data in Table 4. Statistics as in Table 3.

Effect	df	Partial Assoc χ^2	Prob	Marginal Assoc χ^2	Prob
F	2	878.47	0.0000		
S	5	1209.10	0.0000		
A	1	957.16	0.0000		
FS	10	612.07	0.0000	628.71	0.0000
FA	2	2.37	0.3052	19.01	0.0001
SA	5	83.74	0.0000	100.38	0.0000
FSA	10	17.72	0.0598		

2.1 The life cycle graph

The relationship of the projection matrix and the life cycle is clarified by the use of the *life cycle graph* (Hubbell and Werner 1979, Caswell 1982a). In its simplest form, a life cycle graph (Figure 5) is a directed graph, the nodes of which $(n_i, i = 1, \ldots, k)$ denote the abundance of each of k stages in the life cycle. The arcs indicate the transitions possible from one time to the next. Thus the graph should be understood to follow from both the description of the life cycle and from the choice of a time step for projection of the population. The coefficient on the arc from n_j to n_i gives the number of individuals of stage i at time $t + 1$ per individual in stage j at time t.

2.2 The population projection matrix

The matrix projection model corresponding to the life cycle graph is

$$n(t + 1) = A(t)n(t) \qquad (1)$$

where $n(t)$ is a k-vector whose entries are the n_i and A a $k \times k$ matrix with $a_{ij}(t)$ equal to the coefficient on the arc from n_j to n_i. For example, graph (a) in Figure 5 produces a standard Leslie matrix, graph (b) a size-classified matrix like that used by Hartshorn (1975), Enright and Ogden (1979), Pinero et al. (1984), and Burns and Ogden (1985) for tree
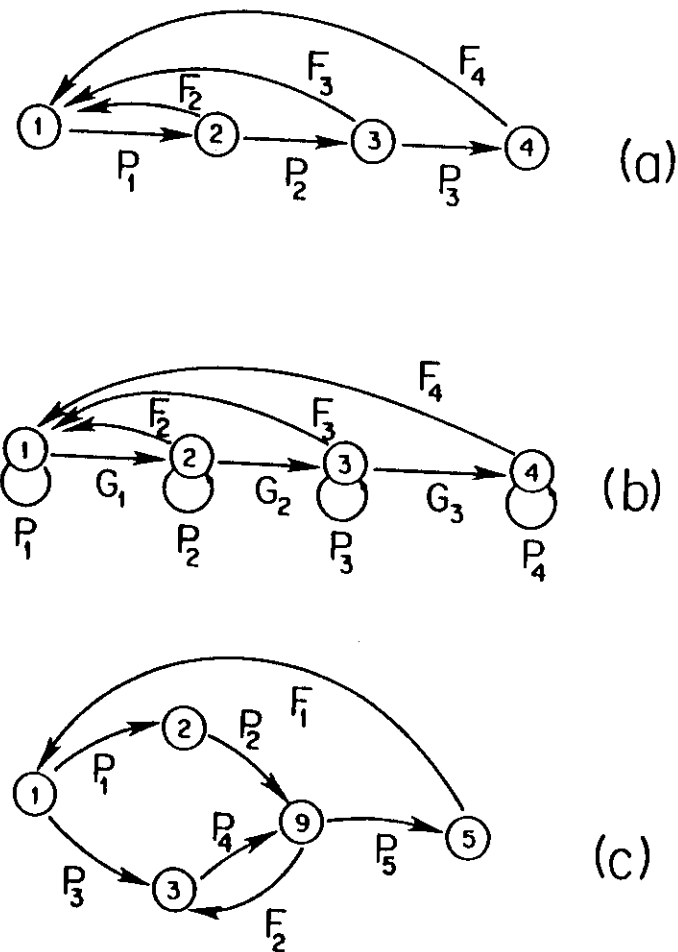
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Table 6: A three way contingency table relating reproductive output (no calves, one calf, or twins) to age and body weight in the moose *Alces alces*. Data from Saether and Haagenrud (1983).

Age	Weight	Reproduction			Total
		Zero	One	Twins	
2.5	-170	55	35	3	93
	170-200	70	44	5	119
	200+	22	9	0	31
	Total	147	88	8	243
3.5	-170	8	21	4	33
	170-200	10	23	9	42
	200+	7	13	4	24
	Total	25	57	17	99
4.5-6.5	-170	3	15	16	34
	170-200	2	27	22	51
	200+	3	23	6	32
	Total	8	65	44	117
6.5-8.5	-170	1	14	4	19
	170-200	5	26	22	53
	100+	2	20	9	31
	Total	8	60	35	103
9.5+	-170	3	18	6	27
	170-200	3	18	11	32
	200+	6	46	27	79

Figure 5: Three simple life cycle graphs. (a) An age-classified life cycle, (b) a simple size-classified life cycle, (c) a hypothetical life cycle including both sexual and vegetative reproduction. From "Stable population structure and reproductive value for populations with complex life cycles" by H. Caswell, Ecology 1982, 63:1223-1221. Copyright 1982 by Ecological Society of America. Reprinted by permission.

populations:

$$\begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix} \quad (2)$$

and graph (c) a matrix containing both sexual (F_1) and vegetative (F_2) reproduction:

Table 7: The results of log-linear analysis of the data in Table 6. R = reproductive output, W = weight, A = age; statistics as in Table 3.

Effect	df	Partial Assoc χ^2	Prob	Marginal Assoc χ^2	Prob
R	2	78.86	0.0000		
W	2	57.81	0.0000		
A	4	113.03	0.0000		
RW	4	4.17	0.3836	6.31	0.1768
RA	8	215.83	0.0000	217.98	0.0000
WA	8	25.52	0.0013	27.66	0.0005
RWA	16	15.69	0.4748		

$$\begin{pmatrix} 0 & 0 & 0 & 0 & F_1 \\ P_1 & 0 & 0 & 0 & 0 \\ P_3 & 0 & 0 & F_2 & 0 \\ 0 & P_2 & P_4 & 0 & 0 \\ 0 & 0 & 0 & P_5 & 0 \end{pmatrix} \tag{3}$$

The life cycle graph and projection matrix are intuitive expressions of the structure of the life cycle. The only subtlety is the role of the time step. The transitions open to an individual depend on the time step used for projection. If the time step is long enough, every stage may contribute to every other stage, and A becomes totally positive. At shorter time steps, some of the transitions are impossible, and the structure of the matrix A will be richer. In general, the choice of a time step for investigation is as much a part of the biology of the problem as is the choice of a set of stages with which to describe the life cycle.

The dynamics resulting from (1) depend on the nature of the coefficients. In the simplest case they are constant, and (1) is a linear system of constant-coefficient difference equations. The analysis of such systems is as well developed as their biological reality is doubtful. I will return to the issue of assumptions shortly.

Projection models with time-varying coefficients have been studied by a number of authors, in both periodic (e.g. Skellam 1966, Gourley and Lawrence 1977, Tuljapurkar 1985) and stochastic environments (e.g., Cohen 1976, 1979a,b, Tuljapurkar 1982a,b, Tuljapurkar and Orsack 1980).

If the coefficients are functions of the entries in $n(t)$, the dynamic equations become nonlinear. This may result from density-dependence, in which $A(t)$ depends on the absolute abundance of the various stages (Beddington 1974, Guckenheimer et al. 1977, Levin and Goodyear 1980), or frequency-dependence, in which $A(t)$ depends only on the relative values of the n_i. Frequency-dependence is important in two-sex models, in which reproductive output depends on the relative abundance of males and females in appropriate stages (Caswell and Weeks 1986).

2.3   Analysis

This paper concentrates on the analysis of linear, time-invariant projection models. I propose to survey their analysis in fairly complete fashion, using as examples a variety of published data for plant populations. The analysis of time-invariant matrix models has four major parts: the problem of ergodicity, asymptotic analysis, transient analysis and sensitivity analysis. The rest of this section summarises the major results in each of these areas.

I am restricting attention to linear models for three reasons. First, they have been extensively used on plant populations. Table 8 lists all the studies of which I am aware applying matrix models to plant populations. My apologies in advance to anyone whose work I have missed! This body of work is an important contribution to plant population biology, even though it has rarely (Biersychudek 1982, Meagher 1982, Cochran 1986) gone beyond the linear time-invariant case.

A notable feature of this set of papers is their use of matrix models for interspecies or interpopulation comparisons. Schmidt and Levin's (1985) reciprocal transplant experiment with *Phlox drummondii* is the most elaborate analysis, but even excluding this case the average number of populations compared is over 5. My second reason for focusing on these models is that much more comparative information can be had from them than is usually obtained. Most of the studies in Table 8 have calculated population growth rates. Many have calculated the stable stage distribution and manipulated the matrices numerically to investigate the sensitivity of population growth rate. Only a few have reported reproductive values, and fewer still have used analytical sensitivity methods. None has approached a complete analysis of the information included in the population projection matrix. My goal here is to lay out some of the possibilities for such analysis using examples from plant populations, and to indicate the kinds of information such an analysis might provide.

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Author	Date	Species	No.	Form	Habit	Class	λ	w	v	Sen
Usher	1966	Scots pine		H	P	SI	1.2043	Y		N
Sarukhan and Gadgil	1974	Ranunculus spp.	46	H	P	ST	.093 - 4.665	Y		N
Hartshorn	1975	Pentaclethra macroloba	1	H	P	SI	1.002	Y		
Werner and Caswell	1977	Dipsacus sylvestris	8	H	MP	A,SI,ST	0.63 - 2.60	Y	Y	A
Caswell and Werner	1978	Dipsacus sylvestris	8	H	MP	A,SI	0.63 - 2.60	Y	Y	
Enright and Ogden	1979	Nothofagus fusca	3	T	P	ST	.9996 - 1.0279	Y		N
Enright and Ogden	1979	Araucaria cunninghamii	1	T	P	SI	1.0204	Y		N
Bullock	1980	Podococcus barteri	1	H	P	ST	1.0125	Y		N
Bierzychudek	1981	Arisaema triphyllum	4	H	P	SI	0.85 - 1.32	Y		N
Sverdlove	1981	Panax quinquefolium	1	H	P	SI	.95	Y	Y	
Meagher	1982	Chamaelirium luteum	3	H	P	SI,SE	.990 - 1.056	Y	Y	A
Fetcher and Shaver	1983	Eriophorum vaginatum	5	S	P	A	.77 - 1.65	Y	Y	A
Silander	1983	Cassia nemophila	3	S	P	A	.897 - 1.177	Y	Y	
Pinero et al.	1984	Astrocaryum mexicanum	6	T	P	SI	.9932 - 1.0399	Y	Y	A
Burns and Ogden	1985	Avicennia marina	1	T	P	SI	1.2228	Y	Y	N
Schmidt and Levin	1985	Phlox drummondii	120	H	A	ST	0 - 34.06	Y		
Taylor and Inouye	1985	Frasera speciosa	1	H	MP	SI		Y		A
van Groenendael	1985	Plantago lanceolata	2	H	P	A,SI		Y	Y	
Cochran, M.E.	1986	Cypripedium acaule	3	H	P	SI,ST	1.035 - 1.931	Y	Y	A

Table 8: Demographic studies of plant populations using projection matrix methodology. No.: number of populations analysed; Form: H=herb, S=shrub, T=tree; Habit: P=perennial, A=annual, MP=monocarpic perennial; Class: A=age-classified, SE=sex-classified, SI=size-classified, ST=stage-classified; λ: population growth rate; w (stable population structure); v (reproductive value): Y=yes; Sen (sensitivity): A=analytical, N=numerical.

The comparative use of matrix models leads to my final justification for focusing on the linear model, which requires a brief digression on the widely misunderstood distinction between *projection* and *forecasting* (or prediction; Keyfitz 1972) in demographic analysis.

2.3.1 Projection, forecasting and assumptions

A forecast is an attempt to predict what will happen to a population. A projection is an attempt to describe what would happen to the population, given certain hypotheses. Gramatically, forecasting uses a matrix model in the indicative mood, projection in the subjunctive. For example, a linear time invariant matrix model yields an estimate of population growth rate λ and stable stage distribution w (see below). A population following the model eventually grows at a rate λ with a structure proportional to w. Ecological use of this purely analytical result is often criticised for assuming that the environment is constant and that density or frequency effects are unimportant. Since environmental variability and density-dependent vital rates are trivially obvious biological facts, how can one possibly accept such assumptions? And if the analysis truly depends on them, what use can it be?

The answer is, of course, that one must assume these conditions as facts about the world only if the model is being used to forecast actual future population dynamics. This is rarely if ever done with such models (for good reason). Instead, most biologists are interested in population projection, in which the values of λ and w (and other indices) answer the hypothetical question "how *would* the population behave *if* the present conditions were to be maintained indefinitely?" To assert that "The present demographic properties of this population are such that, were they to remain constant, the population would eventually come to grow at a rate λ with a structure w" is not to claim that the first, hypothetical clause is true.

Projection, in other words, is a way to say something about present conditions (more precisely, about the relation between present conditions and the population experiencing them), *not* about the future behavior of the population. As Keyfitz (1972) has pointed out, one of the most powerful ways to study present conditions is to examine their eventual consequences were they to remain as they are.

Demographic parameters have the important property of integrating the impact of environmental conditions on vital rates throughout the life cycle. Properly interpreted as projections, then, they are extremely valu-

able in comparative studies of the sort that plant demographers have tended to conduct. They shed light on the response of populations to different environmental conditions. They do not require absurd assumptions about the constancy of the environment.

2.3.2 Ergodicity

A projection matrix model is said to be *ergodic* if, roughly speaking, its eventual behavior is independent of initial conditions. Cohen (1979b) reviews the ergodic theorems for both time invariant and time varying matrix models; here we will discuss only the time invariant case.

The solution to (1) can be written in terms of the eigenvalues (λ_i) and eigenvectors (w_i) of A:

$$n(t) = \sum_i c_i w_i \lambda_i^t, \qquad (4)$$

where the eigenvalues of A are assumed distinct and the c_i are determined by the initial conditions. A sufficient condition for ergodicity is the existence of a positive eigenvalue λ_1 which exceeds in magnitude all the other eigenvalues, and which has associated with it a non-negative eigenvector w_1. Even in the absence of such a dominant eigenvalue, a certain degree of convergence can be guaranteed.

The eigenvalue spectrum of a non-negative matrix is described by the Perron-Frobenius theorem (e.g., Gantmacher 1959, Seneta 1981). That $a_{ij} \geq 0$ can be assumed on demographic grounds, since otherwise there would exist populations capable of producing negative numbers of individuals. The ergodic properties of the population depend on the *irreducibility* and *primitivity* of A.

These conditions are easily specified in terms of the life cycle graph (Rosenblatt 1957). A matrix is irreducible if its life cycle graph is strongly connected, i.e., if there exists a directed path between any two nodes. An irreducible matrix is primitive if the greatest common divisor of the length of the loops in the life cycle graph is one. An imprimitive matrix is said to be cyclic with an index of imprimitivity (d) equal to the greatest common divisor of the loop lengths in the life cycle graph.

Most population projection matrices (including all those in Table 8) are irreducible, because it is a rare description of the life cycle which contains stages which cannot contribute, directly or indirectly, to the rest of the life cycle. Reducible matrices do occur if post-reproductive individuals are included in the life cycle, since by definition they do not contribute to

any of the reproductive stages. However, the post-reproductive stages are irrelevant to the dynamics of the reproductive stages, and can hence be ignored in the analysis. This is traditionally done in age-classified models for human populations. More interesting reducible matrices may arise in the analysis of spatially subdivided populations if they include subpopulations which do not contribute to other subpopulations but, unlike the post-reproductive stages in an age-classified model, do reproduce locally.

An age-classified life cycle with only a single reproductive age class (e.g., monocarpic perennials, such as some bamboos (Jansen 1976), with a fixed age at reproduction) produces a primitive life cycle graph with an index of imprimitivity equal to the age of reproduction.

The ergodic properties of projection matrices may be summarized as follows:

1. If A is either totally positive, or nonnegative, irreducible and primitive, there exists a real eigenvalue $\lambda_1 > 0$ which is a simple root of the characteristic equation. The eigenvalues satisfy $\lambda_1 > |\lambda_i|$ for all $i > 1$. The right and left eigenvectors, w and v, corresponding to λ_1 are real and strictly positive. The eigenvalue λ_1 may not be the only real positive eigenvalue, although if there are others they do not have non-negative eigenvectors.

   The population will converge to the stable structure w from any non-zero initial population, and will eventually grow at the rate λ_1.

2. If A is nonnegative and irreducible but imprimitive (cyclic) with index d, then there exists a real eigenvalue $\lambda_1 > 0$ which is a simple root of the characteristic equation, and which has associated right and left eigenvectors w and $v > 0$. The eigenvalues satisfy $\lambda_1 \geq |\lambda_i|$ for all $i > 1$, however, there are $d - 1$ eigenvalues equal in magnitude to λ_1, given by $\lambda_1 \exp(i2\pi k/d), k = 1, 2, \ldots, d - 1$.

   The dynamics of populations governed by primitive matrices have been investigated in detail by Cull and Vogt (1973, 1974, 1976). Because there are d eigenvalues of equal magnitude the stage distribution does not converge, but oscillates with period d, as does total population size. The population sampled every d time units grows at the rate λ_1^d.

3. If A is non-negative but reducible, there exists a real eigenvalue $\lambda_1 \geq 0$ with corresponding eigenvectors w and $v \geq 0$. The eigenvalues satisfy $\lambda_1 \geq |\lambda_i|$ for all $i > 1$. A reducible matrix can be rearranged

(by renumbering the nodes of the life cycle graph) into a normal form:

$$A = \begin{pmatrix} B & 0 \\ C & D \end{pmatrix} \qquad (5)$$

where the diagonal blocks B and D are irreducible (or can be further subdivided to yield a series of irreducible diagonal blocks; see Gantmacher 1959). Let S_1 and S_2 denote the sets of stages involved in B and D, respectively. The stages in S_1 communicate with each other, and may (if C is non-zero) contribute to the stages in S_2, but S_2 does not contribute to S_1. Thus the dynamics of the stages in S_1 can be treated independently, by analysing the irreducible matrix B.

Alternatively, the entire system described by A may be analysed. The ergodicity of A is complicated by a dependence on initial conditions which is absent in the irreducible case. The rearrangement of A generates a decomposition of the state space into a set of invariant coordinate subspaces (Gantmacher 1959), given in this case by S_2 and $S_2 + S_1$. An initial vector in S_2 (e.g., an initial population consisting solely of post-reproductive individuals) will not converge to w. This phenomenon may generate interesting problems in complex spatially subdivided populations, but has not arisen in any applications of matrix models to date.

2.3.3 Asymptotic behavior

The asymptotic dynamics of an ergodic matrix are determined by its maximal eigenvalue and its corresponding eigenvectors. From (2),

$$\lim_{t \to \infty} n(t)/\lambda_1^t = c_1 w_1 \qquad (6)$$

Since the subscript identifying λ_1 as the maximal eigenvalue is not needed for this discussion, we drop them for the rest of this section.

The eventual population growth rate is given by λ, where $\lambda = 1$ is the critical value separating extinction ($\lambda < 1$) from growth ($\lambda > 1$). The values of λ calculated from plant life cycles (Table 8) range widely, and agree with biological intuition. Long-lived herbaceous perennials and trees have values of λ clustered tightly around 1; values of λ for short-lived herbaceous plants vary much more widely.

The form of the stable stage distribution w depends strongly on the structure of the life cycle (see Section 3). In contrast with stable age distributions, which are monotonically decreasing (unless $\lambda \leq 1$), stable size

or stage distributions may increase or decrease. Thus the peaks commonly observed in size distributions (e.g., Lorimer and Krug 1983 for trees) may be part of the stable size distribution, rather than reflecting perturbations from that distribution as they would if it were an age distribution.

The coefficients c_i appearing in (4) permit us to introduce the important notion of *reproductive value*, given by the left eigenvector v_1 corresponding to λ_1 (i.e., v_1 satisfies $v_1' A = \lambda v_1'$). First introduced by Fisher (1931) using an obscure (to me, at least) analogy with the present value of a loan, reproductive value measures the relative contribution of a given stage to future population growth. From (4), the initial population $n(0)$ can be written

$$n(0) = \sum_i c_i w_i = Wc \qquad (7)$$

where W is a matrix whose columns are the w_i and c is a vector whose elements are the c_i. Thus

$$c = W^{-1}n(0). \qquad (8)$$

From the definition of W, $W^{-1}AW = A$, where A is a matrix with the λ_i on the diagonal and zeros elsewhere. However, this implies that

$$W^{-1}A = AW^{-1}, \qquad (9)$$

that is, the *rows* of W^{-1} are the *left* eigenvectors v_i of A. Let $W^{-1} = V$. Then (8) gives the coefficients c:

$$c = Vn(0) \qquad (10)$$

In particular, c_1 is given by $v_1'n(0)$. Since $n(t)$ eventually grows as $c_1 \lambda_1^t w_1$, the populations resulting from two different initial conditions are, at any given time, larger or smaller depending on c_1. The coefficient c_1 is, from (10), a weighted sum of the initial population sizes of each stage; the weights are the reproductive values of the stages in the sense that they give the relative contribution of the those stages in the initial population to eventual population size.

2.3.4 Transient behavior

Prior to convergence to the stable stage distribution, a population's dynamics are determined by the complete eigenvalue spectrum. These transient dynamics have seldom been analysed (cf. Caswell and Werner 1978), but can be investigated by examining the subdominant eigenvalues of A.

The rate of convergence to the stable structure w depends on the initial conditions and on the subdominant eigenvalues (see Equation 4). Convergence is more rapid, the larger λ_1 is in comparison to the other eigenvalues. This leads to the definition of the *damping ratio*

$$\rho = \lambda_1/|\lambda_2| \tag{11}$$

where λ_2 is the second largest (in magnitude) eigenvalue.

The subdominant eigenvalues are often complex numbers. When raised to powers, as they are in the solution (4), they produce oscillations, since

$$\lambda^t = |\lambda|^t(\cos t\theta + i \sin t\theta) \tag{12}$$

where θ is the angle defined by λ in the complex plane. The period of these oscillations is

$$P = 2\pi/\tan^{-1}(\Im(\lambda)/\Re(\lambda)) \tag{13}$$

where $\Re(\lambda)$ and $\Im(\lambda)$ are the real and imaginary parts of λ, respectively.

The most important of these periods is that corresponding to λ_2. In age-classified models, P corresponds approximately to the generation time (Lotka 1945, Coale 1972). In complex life cycles P is still an important measure of the time scale on which the population responds to perturbations. A perturbation in the stage structure can be expected to set up oscillations with a period P which will die out at a rate proportional to ρ.

These measures of transient behavior have not been extensively investigated. Figure 6 shows the relation between ρ, P, and λ for 7 populations of *Dipsacus sylvestris* (Werner and Caswell 1977, Caswell and Werner 1978). Both regressions are significant, but that for ρ explains little of the variance. They suggest that populations with higher growth rates are characterised by slower convergence to the stable stage distribution and higher frequency oscillations. The generality of these patterns is unknown.

Although λ_2 produces the most long lasting effects of any of the subdominant eigenvalues, and hence gives an upper bound on the eventual rate of convergence, one can define a set of damping ratios

$$\rho_i = \lambda_1/|\lambda_i| \tag{14}$$

and periods

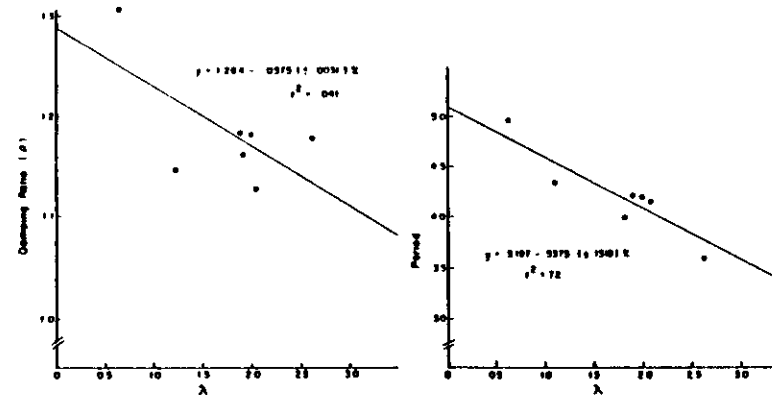$$P_i = 2\pi/\tan^{-1}(\Im(\lambda_i)/\Re(\lambda_i)). \tag{15}$$

Figure 6: The relation of the damping ratio ρ and the period of oscillation P of the second largest eigenvalue to the magnitude of the dominant eigenvalue for 7 populations of *Dipsacus sylvestris*. Based on data in Werner and Caswell (1977).

corresponding to each of the λ_i. The initial conditions may increase the importance, in the short run, of some of the subdominant eigenvalues. The coefficients c_i in (4) are determined by the initial conditions. Suppose that $\lambda_i > \lambda_j$, but that a particular initial condition produces $c_i < c_j$. Eventually the contribution of λ_j becomes negligible in comparison with that of λ_i, but in the short run $c_j\lambda_j^t$ may be much larger than $c_i\lambda_i^t$. Certain initial populations, i.e., those resulting from colonisation by a single stage (usually seeds), may occur frequently in colonising species. Figure 7 shows two examples of the set of c_i (calculated from Equation 8) resulting from such an initial condition, based on projection matrices for *Arctium minus* (Hawthorne unpub.) and *Pentaclethra macroloba* (Hartshorn 1975). In the case of *A. minus*, the smaller eigenvalues also have smaller values of c_i, but in *P. macroloba* the opposite is true. Thus the transient dynamics following colonisation in the latter species will be more influenced by the smaller eigenvalues than is true for *A. minus*.
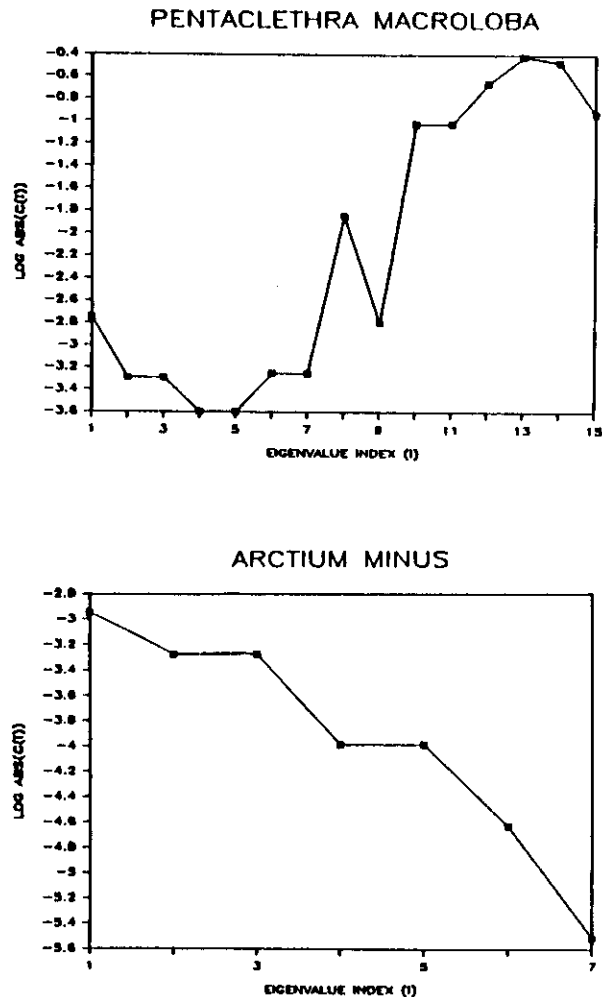
PENTACLETHRA MACROLOBA

ARCTIUM MINUS

Figure 7: The coefficients c_i corresponding to the eigenvalues λ_i, arranged in decreasing order of magnitude, for *Arctium minus* (Hawthorn unpub.) and *Pentaclethra macroloba* (Hartshorn 1975). The absolute values of the c_i are plotted on a log scale. The initial conditions are an initial input of propagules in size class 1.

2.4   Sensitivity analysis

I turn now to the effect on population growth of perturbations of the life cycle parameters. Such perturbations can arise in several ways. Changes in the external environment may change the vital rates directly, or genetic variation may lead to changes in the rates due to changes in gene frequency under the impact of natural selection

Many authors have approached the perturbation analysis of matrix models numerically (Table 8), manipulating the entries in the matrix and reporting the resulting changes in λ. Analytical methods are available, however, that provide much more powerful insights into the results of changes in the vital rates. The next sections summarize some of these.

Examples. As examples of the sensitivity analyses to be discussed here, I have chosen a set of five size-classified projection matrices for tree populations, taken from:

- Hartshorn's (1975) study of a population of *Pentaclethra macroloba*, a wet forest canopy tree in Costa Rica.

- Enright and Ogden's (1979) study of one population of *Araucaria cunninghami* in New Guinea and three stands (each with two fecundity estimates) of *Nothofagus fusca* in New Zealand.

- Pinero et al.'s (1984) study of six populations (two stands at each of three densities) of the palm *Astrocaryum mexicanum* in Mexico.

- Burns and Ogden's (1985) study of a population of the mangrove *Avicennia marina* in New Zealand.

The projection matrices used in these studies all have the same form (Figure 5b), so that sensitivities can be expressed in terms of the G_i, P_i, and F_i. As a group they also permit both inter- and intra-specific comparisons.

2.4.1   Growth rate sensitivity

The most demographically important sensitivity analysis is that of population growth rate λ. A number of authors had considered this problem in the context of age-classified demography (Demetrius 1969, Goodman 1971, Keyfitz 1971) before a general formula was presented by Caswell (1978; the formula in question dates back at least to Jacobi (1846) and

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has been rederived many times since):

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{<\mathbf{v}, \mathbf{w}>} \qquad (16)$$

where v_i and w_j are the ith element of the reproductive value vector and the jth element of the stable structure vector, respectively, and $<>$ denotes the scalar product. (Cohen (1978) takes another approach to the problem, and also considers the second derivatives of λ.)

Several conclusions follow from (16). First, the sensitivities are non-negative; increasing a_{ij} never decreases λ. Obvious evolutionary considerations suggest that, at some point, further increases in, e.g., reproduction must actually decrease the growth rate. Such phenomena are due to correlations between traits, and will be examined within the context of (16) in a subsequent section.

Second, since a_{ij} denotes the transition from n_j to n_i, the importance of changes in that transition depends on the abundance of the source stage and the reproductive value of the destination stage.

Sensitivities have been calculated using this formula for plant populations by a number of authors (see Table 8). Examples for the five tree populations are shown in Figures 8, 9, and 10. Two results are immediately apparent. First, the sensitivity of λ to changes in the matrix elements varies by many orders of magnitude over the life cycle. Second, there is no universal trend for size-specific sensitivities to decrease with increasing size. This is a sharp contrast to the situation in age-classified models, and has potentially important implications for the evolution of senescence (Caswell 1978, 1985).

The sensitivity structure of the entire life cycle can be summarized by an overall sensitivity index S, which gives an upper bound on the norm of the change in λ produced by a change in $\mathbf{A}$ of unit magnitude (Caswell 1978). Assuming that $<\mathbf{w}, \mathbf{v}> = 1$,

$$S = \sqrt{(\mathbf{v}'\mathbf{v})(\mathbf{w}'\mathbf{w})} \qquad (17)$$

$$= \left(\sum_i \sum_j \left(\frac{\partial \lambda}{\partial a_{ij}}\right)^2\right)^{1/2} \qquad (18)$$

Rewriting (17) in the form of (18) reveals it as a root-mean square measure of overall sensitivity of λ. An intuitive interpretation of S is as follows. Suppose that the a_{ij} are subject to small independent random perturbations with variance $V(a_{ij})$. The resulting variance of λ is
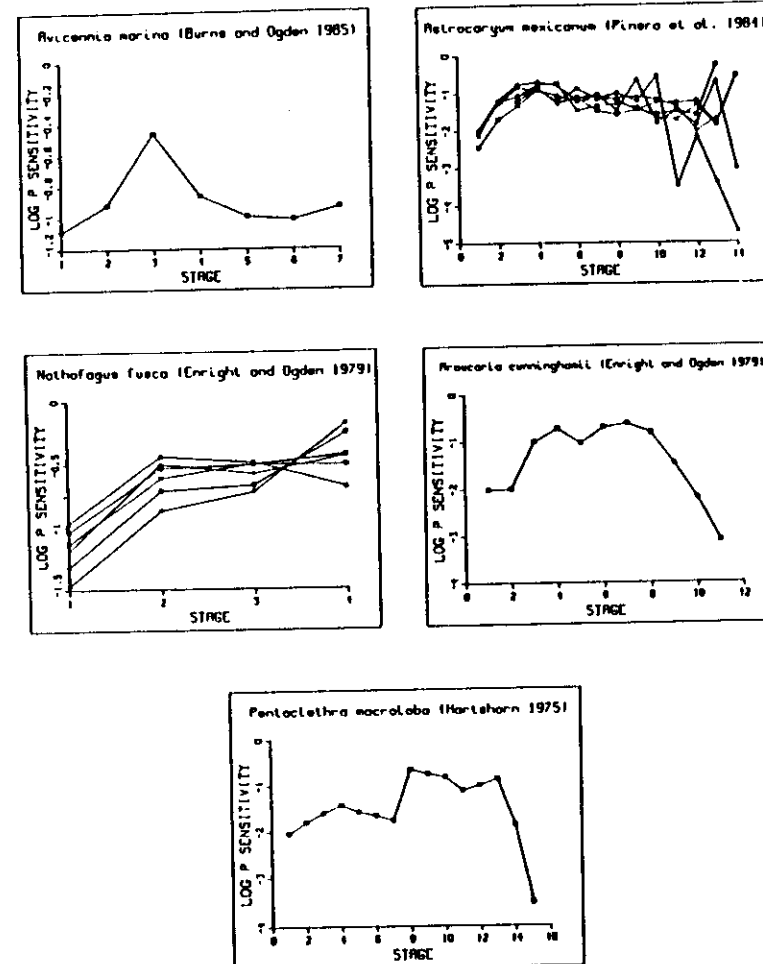

Figure 8: Sensitivities of λ to changes in P_i, the probability of remaining in size class i, for five tree populations.
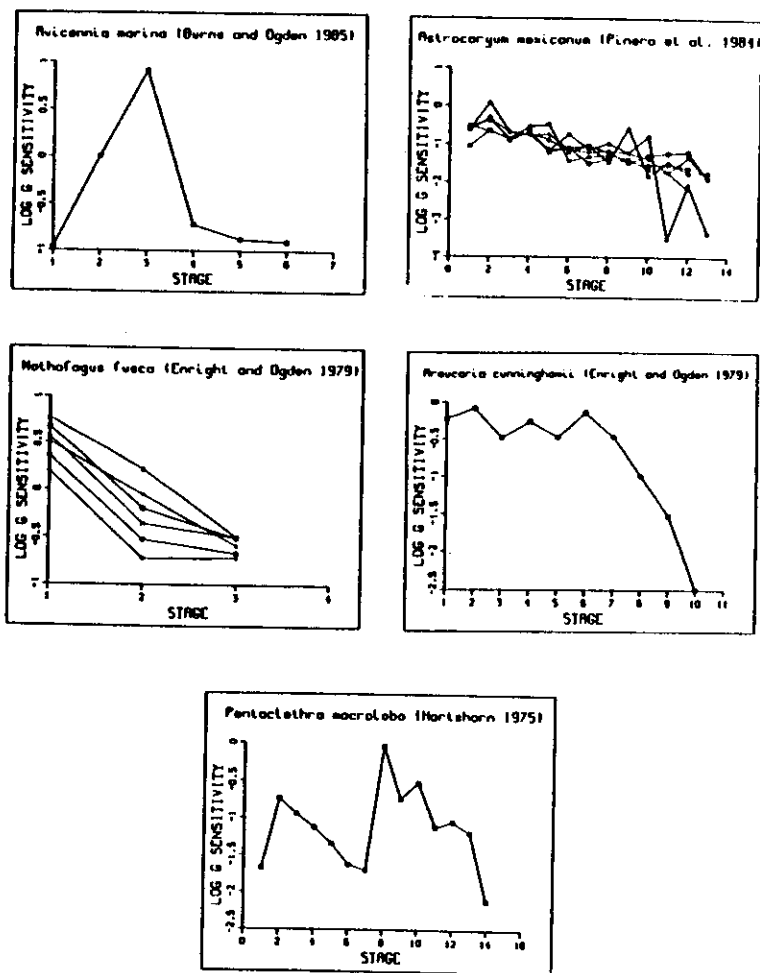
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Figure 9: Sensitivities of λ to changes in G_i, the probability of surviving and growing from size class i to $i + 1$, for five tree populations.
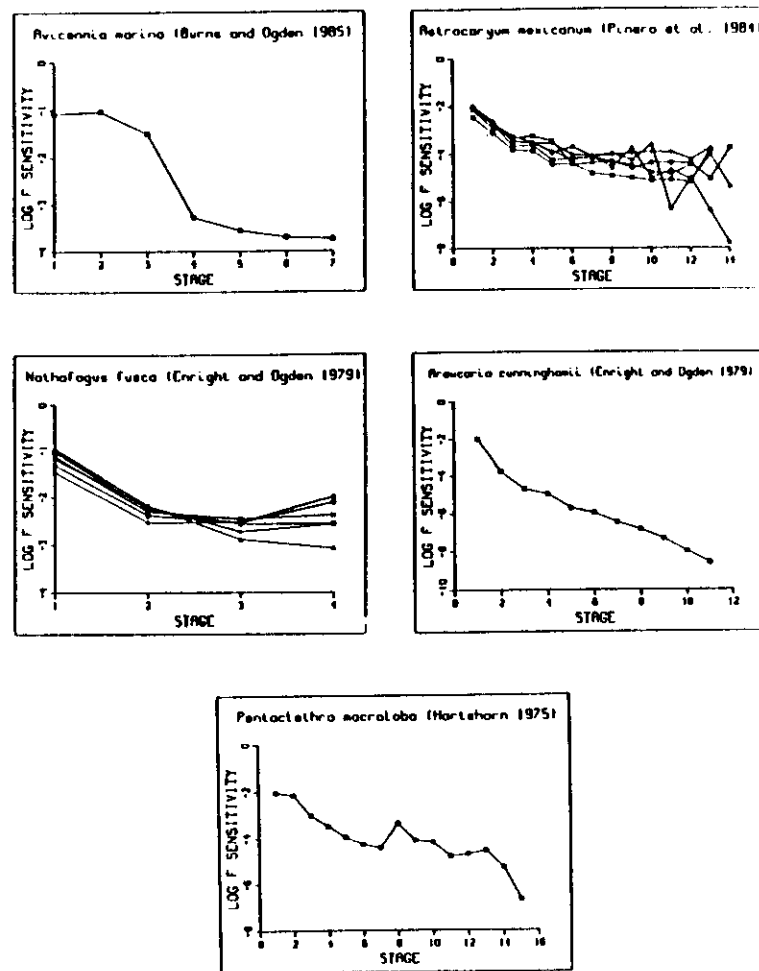

Figure 10: Sensitivities of λ to changes in F_i, the reproductive output of size class i, for five tree populations.

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approximately

$$V(\lambda) \approx \sum_{i,j} \left(\frac{\partial\lambda}{\partial a_{ij}}\right)^2 V(a_{ij})$$

$$= S^2 V(a_{ij}). \tag{19}$$

Thus the overall sensitivity index S approximates the standard deviation of λ resulting from a unit variance in each of the a_{ij}. In this sense, it measures the overall sensitivity of population growth rate to changes in the life cycle.

A few values of S were tabulated by Caswell (1978), but it has not been widely applied. One of its problems, particularly apparent in (18) is its incorporation of sensitivities to changes in *all* the a_{ij}, including changes which are biologically impossible. A more realistic index can be obtained by restricting the summations in (18) and (19) to those a_{ij} in which change is considered possible.

Elasticities. Most numerical sensitivity investigations (Table 8) have examined the result of perturbations which change the matrix elements by fixed *proportions* (e.g., 10%), rather than fixed amounts, and express the results as a proportional change in λ. This method has an obvious advantgage when comparing parameters measured on different scales, such as survival probabilities (which must lie between 0 and 1) and fertilities (Caswell and Werner 1978).

Equation (16) can be modified to give a proportional sensitivity or *elasticity* index (a term borrowed from microeconomics) which solves this problem. Let e_{ij} denote the proportional change in λ resulting from a proportional change in a_{ij}. Then

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} \tag{20}$$

$$= \frac{\partial \ln\lambda}{\partial \ln a_{ij}} \tag{21}$$

(see Schmidt and Lawlor 1983, Caswell et al. 1984, DeKroon et al. 1986). Table 9 compares a sensitivity matrix and an elasticity matrix for a population of *Dipsacus sylvestris*. Note that the sensitivity of λ to fertility changes (a_{17}) is much smaller (.001) than the corresponding elasticity (.25).

This index has several interesting properties. It is not difficult to show

Table 9: The sensitivity and elasticity matrices for a population of *Dipsacus sylvestris* (Field A, stage-classified matrix from Werner and Caswell (1977). The (i,j) entries of the two matrices give $\partial\lambda/\partial a_{ij}$ and e_{ij}, respectively.

Sensitivity Matrix

0.25	0.10	0.05	.00	0.01	.00	.001
0.04	0.02	0.01	.00	.00	.00	.00
0.01	.00	.00	.00	.00	.00	.00
0.99	0.41	0.22	0.01	0.05	0.01	.00
5.10	2.11	1.13	0.05	0.24	0.04	0.02
27.09	11.20	5.99	0.25	1.28	0.23	0.11
59.28	24.52	13.10	0.55	2.80	0.51	0.25

Elasticity Matrix

0.00	0.00	0.00	0.00	0.00	0.00	0.25
0.02	0.00	0.00	0.00	0.00	0.00	0.00
0.00	.00	0.00	0.00	0.00	0.00	0.00
.00	.00	.00	.00	0.00	0.00	0.00
0.20	0.01	0.00	.00	0.03	0.00	0.00
0.03	.00	0.00	0.01	0.17	0.02	0.00
0.00	0.00	0.00	0.00	0.04	0.21	0.00

(DeKroon et al. 1986) that

$$\sum_i\sum_j e_{ij} = 1. \tag{22}$$

This implies that e_{ij} gives the proportion of the overall elasticity contributed by a_{ij}. This makes elasticity matrices particularly easy to compare across populations.

More interesting still, e_{ij} provides a direct measure of the relative contribution of the a_{ij} to λ, i.e. of the proportion of λ "contributed by" the coefficient a_{ij}. Define b_{ij} as the contribution of a_{ij} to λ, satisfying

$$\lambda = \sum_i\sum_j a_{ij}b_{ij}, \tag{23}$$

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and suppose that b_{ij} can be written $b_{ij} = \alpha_i\beta_j$ for some α_i and β_j. That is, assume that the contribution of a_{ij} can be written as a product of a term specific to the "source" stage and a term specific to the "sink" stage. The only b_{ij} satisfying these requirements is $b_{ij} = e_{ij}$. To see this, note from (9) that $\mathbf{VAW} = \mathbf{A}$, where $\mathbf{VW} = \mathbf{I}$; this similarity transformation of $\mathbf{A}$ is unique. Thus λ_1 can be uniquely written:

$$\lambda_1 = \mathbf{v}_1'\mathbf{Aw}_1 \tag{24}$$

$$= \sum_i \sum_j a_{ij} v_i w_j. \tag{25}$$

Dividing both sides of (25) by λ_1 yields (22).

In the elasticity matrix of Table 9, 83% of the value of λ is accounted for by a_{61} (seeds → medium rosettes), a_{66} (medium rosettes → large rosettes), a_{76} (large rosettes → flowering plants) and a_{17} (flowering plants → seeds). This is a great simplification of the total life cycle, and clearly indicates the most important developmental pathways in this population.

It is possible to calculate elasticities of λ with respect to other variables which themselves contribute to the a_{ij}. While such elasticities give the proportional sensitivity of λ to the variables in question, they do not sum to unity and do not give the relative contribution of those variables to λ.

The elasticities of λ with respect to P_i, G_i and F_i are shown in Figures 11, 12 and 13. The different species differ among themselves in the extent to which they rely on survival, growth and reproduction in achieving their observed rates of population growth. Overall, though, the P_i make by far the biggest contribution to λ, the G_i much less and the F_i even less. This is perhaps reasonable, considering that these are relatively long-lived, slow-growing species; the pattern for the herbaceaous *Dipsacus sylvestris* is quite different. These patterns deserve further study.

2.4.2   Transient sensitivities

The damping ratio and the period of oscillation are functions of eigenvalues. Since the sensitivity formula (16) applies to any eigenvalue (using he appropriate eigenvectors), it is not difficult to develop sensitivity formulae for the indices of transient behavior (Caswell, unpublished.). Let $\lambda_2 = x \pm iy$. Then

$$\frac{\partial \rho}{\partial a_{ij}} = \frac{1}{|\lambda_2|}\left(\frac{\partial \lambda_1}{\partial a_{ij}} - \frac{\rho}{|\lambda_2|}\left(x\frac{\partial x}{\partial a_{ij}} + y\frac{\partial y}{\partial a_{ij}}\right)\right) \tag{26}$$
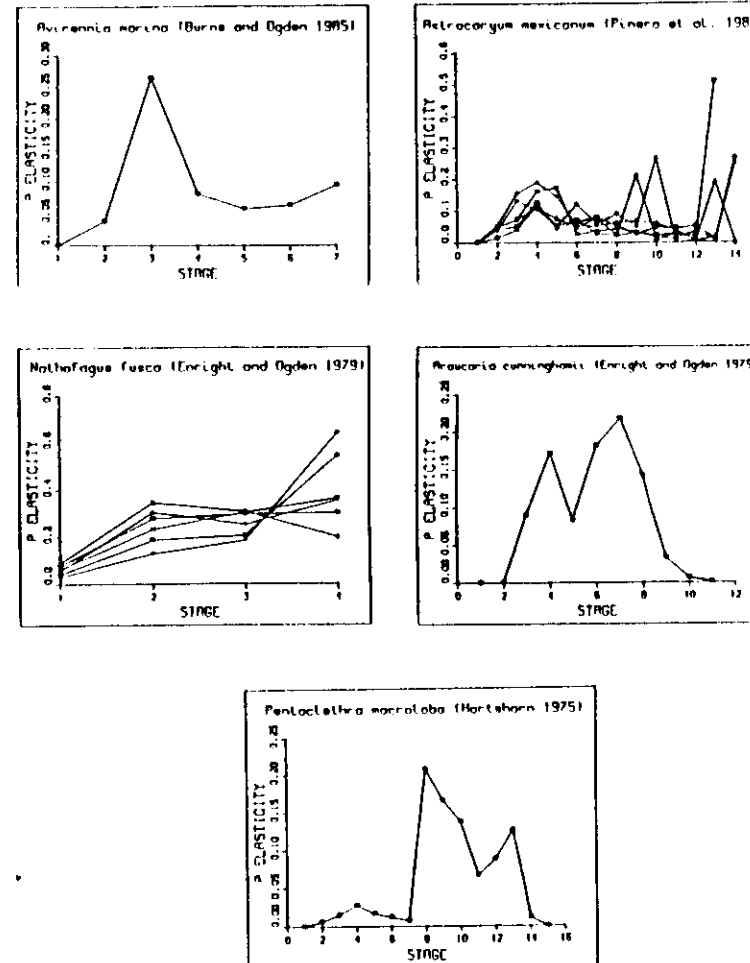
Figure 11: The elasticity of λ with respect to P_i as a function of size class i, for five tree populations.
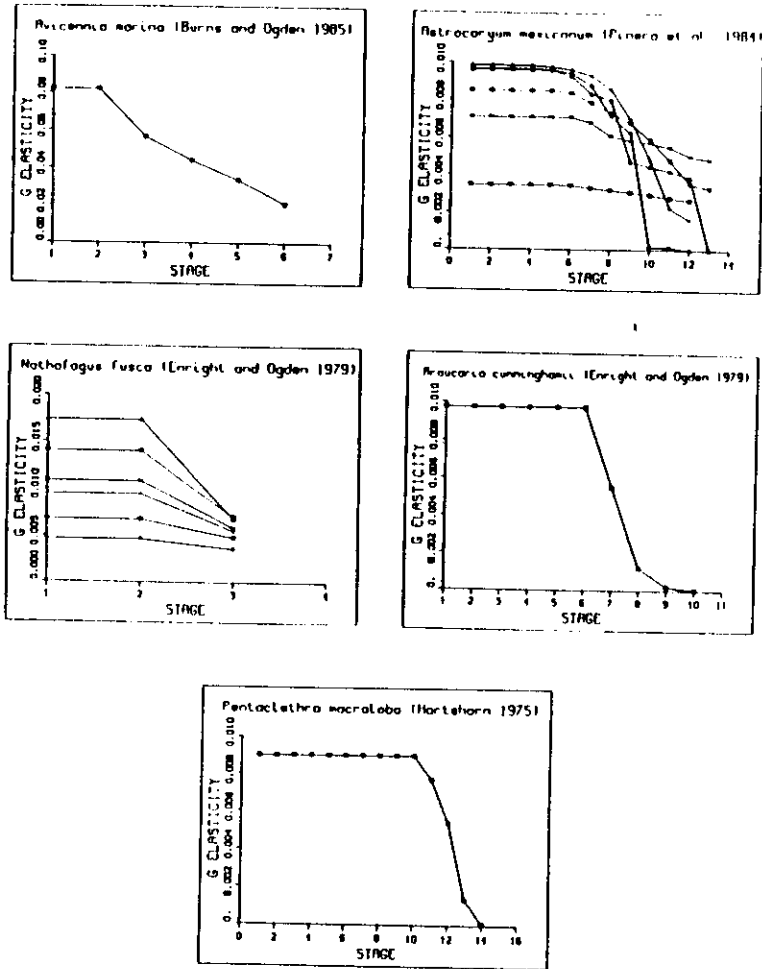
Figure 12: The elasticity of λ with respect to G_i as a function of size class i, for five tree populations.
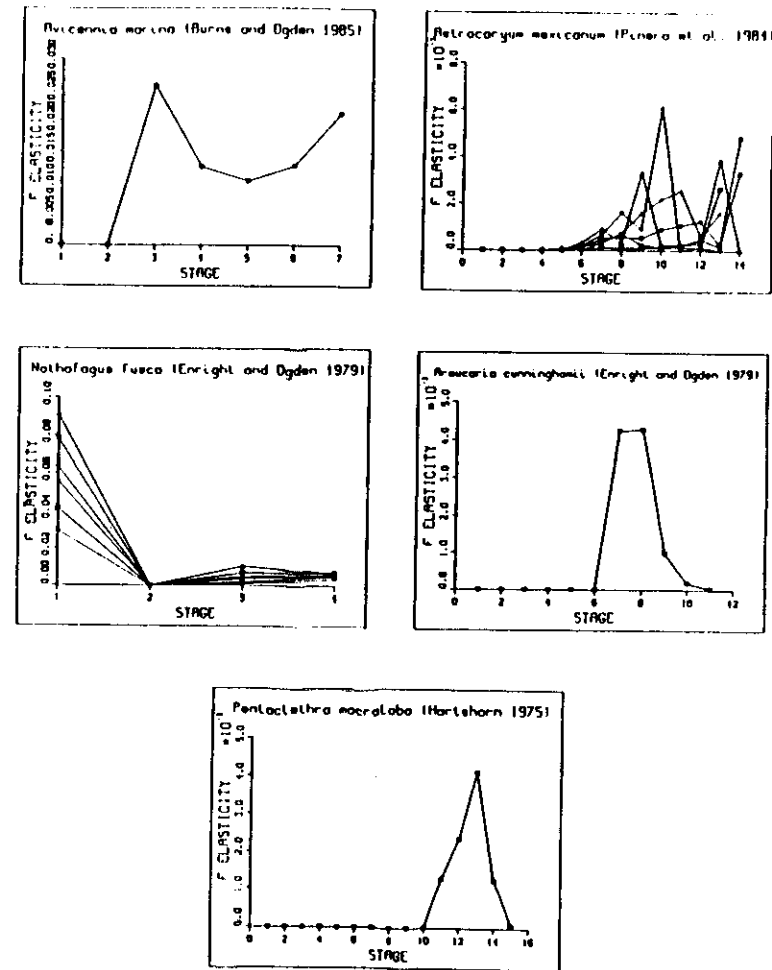

Figure 13: The elasticity of λ with respect to F_i as a function of size class i, for five tree populations.

and

$$\frac{\partial P}{\partial a_{ij}} = \frac{-2\pi}{\theta^2 |\lambda_2|^2} \left(x \frac{\partial y}{\partial a_{ij}} - y \frac{\partial x}{\partial a_{ij}} \right). \qquad (27)$$

These formulae have yet to be systematically applied.

2.4.3 Eigenvector sensitivities

Formulae for the sensitivity of the eigenvectors **w** and **v** to changes in the a_{ij} were presented by Caswell (1980). Let dA be the matrix of perturbations da_{ij}, and assume that $< w, v >= 1$. Then

$$dw_i = \sum_{j \neq i} \left(\frac{< (dA)w_i, v_j >}{\lambda_i - \lambda_j} \right) w_j \qquad (28)$$

$$dv_i = \sum_{j \neq i} \left(\frac{< (dA')v_i, w_j >}{\lambda_i - \lambda_j} \right) v_j. \qquad (29)$$

These formulae can be simplified to give sensitivities of the dominant eigenvectors w_1 and v_1 respectively:

$$\frac{\partial w_1(i)}{\partial a_{kl}} = w_1(l) \sum_{m \neq 1} \frac{v_m(k) w_m(i)}{\lambda_1 - \lambda_m} \qquad (30)$$

$$\frac{\partial v_1(i)}{\partial a_{kl}} = v_1(k) \sum_{m \neq 1} \frac{v_m(i) w_m(l)}{\lambda_1 - \lambda_m}. \qquad (31)$$

Note that, unlike the eigenvalue formulae, the eigenvector sensitivities depend on the entire eigenvalue spectrum. The presence of $(\lambda_1 - \lambda_m)$ terms in the denominator means that the eigenvectors are particularly sensitive to perturbations when two of the eigenvalues are nearly equal.

3 Graphical Derivation of Eigenvectors

It is clear from the preceeding section that most of the demographic interpretation of a life cycle graph can be expressed in terms of the eigenvalues and eigenvectors of **A**. The eigenvectors are particularly important, since they are the key to the sensitivity analysis of the life cycle.

   Given numerical values for the a_{ij}, the evaluation of the eigenvalues and eigenvectors of **A** is simple, provided only that one has access to numerical routines for eigenanalysis, which are now widely available.

However, for many theoretical applications, algebraic formulae for the eigenvectors in terms of the a_{ij} are much more useful. Such formulae have been provided by Caswell (1982a), following Hubbell and Werner (1979). They make use of the z-transform (the discrete analogue of the Laplace transform; see Jury (1964)) and have the additional advantage of permitting some useful simplifications of the life cycle graph. The formulae are derived in Caswell (1982a); here I present the results without proof and then apply them to some questions in life history evolution.

3.1   The z-transformed life cycle graph

The z-transform of a basic life cycle graph is obtained by replacing a_{ij} by $a_{ij}\lambda^{-1}$, where λ is a complex variable. (In the engineering literature it is customary to use z for this variable; hence the name. In our case, the solution to a particular equation in λ will be identified with the maximal eigenvalue of the matrix; hence it seems best to stick with the symbol λ.)

   Transitions which require more than a single time step can also be included in the life cycle graph. The z-transform of a transition requiring α time steps replaces a_{ij} with $a_{ij}\lambda^{-\alpha}$ (see Figure 14). It is, of course, possible to write such a graph without using such transitions, by identifying α intermediate stages between n_1 and n_2, for example, and assigning them survival probabilities whose product is P_1. Indeed, the α-step transition is the simplification of the expanded graph, following the rules of Mason and Zimmerman (1960). Since the eigenvalues and eigenvectors are independent of what happens between n_1 and n_2, except for the values of α and P_1, it is convenient to specify the transitions this way.

   Terminology. For our formulae we shall need the following terms. A *path* between n_i and n_j is a sequence of arcs connecting the two nodes, following the directions of the arrows, without passing through any node more than once. A *loop* is a closed sequence of arcs, following the directions of the arrows, passing through no node more than once per cycle. The length of a loop is the number of distinct nodes through which it passes. A *self-loop* is a loop of length one. Paths or loops are said to be disjoint if they share no nodes in common.

   The *transmission* of a path or loop is the product of the coefficients along that path or loop, usually with special treatment (described below) reserved for self-loops.

3.2 The characteristic equation

The eigenvalues λ_i are the solutions to the characteristic equation

$$\det(\mathbf{A} - \lambda \mathbf{I}) = 0, \tag{32}$$

which is, in general, a kth order polynomial in λ, with k complex roots. For the special case of the age-classified Leslie matrix, (32) has a well-known special form, a discrete version of Lotka's integral equation for r in the continuous time model. For complex life cycles, the characteristic equation can be written down directly from the life cycle graph (Hubbell and Werner 1979, Caswell 1982a):

$$1 = \sum_i L_i + \sum_{i,j}^* L_i L_j - \sum_{i,j,k}^* L_i L_j L_k + \cdots \tag{33}$$

where L_i denotes the transmission of the ith loop, and the summations marked with asterisks add the products of all pairs, triplets, etc. of disjoint loops.

Since the transmissions L_i contain λ^{-1} terms, (33) is a polynomial in λ^{-1}; solutions of (33) are eigenvalues of the matrix corresponding to the life cycle graph.

Self-loops are most easily handled by absorbing them (Mason and Zimmerman 1960) into the transmissions between nodes. A self-loop of strength $a_{jj}\lambda^{-1}$ at node j can be removed by dividing the transmission of all incoming arcs at node j by $1 - a_{jj}\lambda^{-1}$. This greatly simplifies the resulting calculations because unabsorbed self-loops are always disjoint. When self-loops are absorbed, most life cycles retain no disjoint loops, and only the first summation appears in (33).

3.2.1 Sensitivity of λ to changes in development time

The possession of a formula for the characteristic equation is of relatively little computational use. If one has values for the coefficients it is easier to find the eigenvalues directly with matrix routines; if one does not, it is not usually possible to solve the equation (certainly not for $k > 4$).

However, the characteristic equation can be used to derive the sensitivity of λ to changes in development time (Caswell unpublished). A special case of this problem, the effect of changes in age at maturity on population growth rate, has been studied by Lewontin (1965), Mertz (1971), Caswell and Hastings (1980), Hoogendyk and Estabrook (1984) and others. The following results, however, are more general.
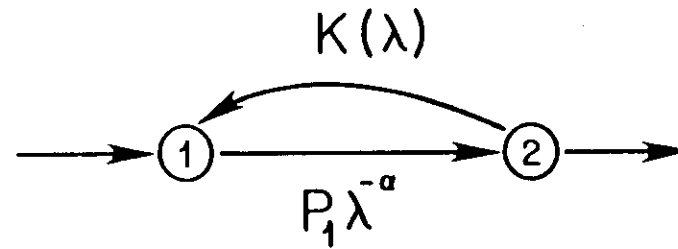

Figure 14: A segment of a life cycle graph connecting two arbitrary developmental stages, n_1 and n_2, with a delay of α time units. The arc $K(\lambda)$ represents the aggregate of all pathways from n_2 back to n_1.

Consider the transition shown in the z-transformed life cycle graph of Figure 14. It links two arbitrary stages (n_1 and n_2), with a survival probability P_1 over α time units. The single arc labelled $K(\lambda)$ incorporates all the possible pathways from n_2 back to n_1. $K(\lambda)$ is the transmission of this combined path, and can be written

$$K(\lambda) = \sum_i k_i \lambda^{-i} \tag{34}$$

where k_i is the sum of the transmissions of all pathways from n_2 to n_1 requiring exactly i time steps.

The characteristic equation, assuming that the life cycle contains no disjoint loops, is

$$f(\lambda) = P_1 \lambda^{-\alpha} K(\lambda) = 1 \tag{35}$$

from which $\partial\lambda/\partial\alpha$ can be derived by implicit differentiation:

$$\frac{\partial\lambda}{\partial\alpha} = \frac{-\partial f/\partial\alpha}{\partial f/\partial\lambda}. \tag{36}$$

Two cases arise, depending on the relation of P_1 and α. In the first, P_1 is a constant independent of α. In the second, the instantaneous mortality rate μ is constant, and P_1 is obtained by applying this rate over α time units:

$$P_1 = e^{-\mu\alpha}. \tag{37}$$

It is not clear which case is more realistic. The second case is easily visualised: during their development from n_1 to n_2 individuals are exposed to a constant risk, and their survival probability is determined by how long they are exposed. However, Taylor and Williams (1984) have suggested that this scenario does not apply to fish populations. In general, the dependence of P_1 on α will depend on the details of the survivorship curve between n_1 and n_2.

Case 1. Carrying out the differentiations in (36) we obtain

$$\partial f/\partial \alpha = -ln(\lambda) \tag{38}$$

$$\partial f/\partial \lambda = -\alpha\lambda^{-1} - \lambda^{-1}P_1\lambda^{-\alpha}\sum_i ik_i\lambda^{-i}$$

$$= -(\alpha + M)/\lambda \tag{39}$$

The quantity $M = P_1\lambda^{-\alpha}\sum_i ik_i\lambda^{-i}$ is a weighted mean of the lengths of the paths from n_2 back to n_1. To see this, note that $P_1\lambda^{-\alpha}\sum_i k_i\lambda^{-i} = 1$, so that the terms in the summation can be treated as a probability distribution. The weighting in M is a function of the transmissions along the various paths. M is thus a measure of the length of the most important pathways from n_2 back to n_1.

Combining (38) and (39) we obtain, for Case 1:

$$\frac{\partial\lambda}{\partial\alpha} = \frac{-\lambda ln\lambda}{\alpha + M}. \tag{40}$$

The elasticity of λ with respect to α, giving the proportional change in λ resulting from a proportional change in α, follows immediately from (40):

$$\frac{\partial\ln\lambda}{\partial\ln\alpha} = \frac{-\alpha\ln\lambda}{\alpha + M}. \tag{41}$$

From (40) and (41) it is clear that increases in development time α always decrease λ unless $\lambda \leq 1$, and that if $\lambda = 1$, α is neutral. It is also clear that the sensitivity of λ to changes in development time is inversely related to M.

Case 2. In this case

$$\partial f/\partial\alpha = -(\mu + \ln\lambda), \tag{42}$$

while $\partial f/\partial\lambda$ is still given by (39). Thus we have

$$\frac{\partial\lambda}{\partial\alpha} = \frac{-\lambda(\mu + ln\lambda)}{\alpha + M} \tag{43}$$

and

$$\frac{\partial\ln\lambda}{\partial\ln\alpha} = \frac{-\alpha(\mu + \ln\lambda)}{\alpha + M} \tag{44}$$

Now the critical value of λ, below which $\partial\lambda/\partial\alpha$ becomes positive is

$$\lambda = e^{-\mu} < 1. \tag{45}$$

Thus, in Case 2, the selective pressure on α is negative even in an equilibrium population ($\lambda = 1$). However, it is possible for selection to favor increases in α, contrary to the assertion of Hoogendyk and Estabrook (1984) that $\partial\lambda/\partial\alpha \geq 0$. Their claim applies only to the special case of age-independent survival in an age-classified life cycle, in which λ can never be less than $e^{-\mu}$, even in the absence of reproduction. If this assumption is not made, then when the population is decreasing sufficiently fast, selection favors delayed development.

Equations (40-45) show that changes in timing within the life cycle can be very important, and that the factors governing their importance are the λ itself, M and α.

3.3   Eigenvector formulae

Rather more useful than the characteristic equation are the formulae for the eigenvectors. Define the following transmissions in the z-transformed life cycle graph.

- T^i_{1x}: the transmission of the ith directed path from n_1 to n_x.

- $L_j(n_1)$: the transmission of the jth loop which is disjoint with n_1.

- $L_j(T^i_{1x})$: the transmission of the jth loop which is disjoint with the path T^i_{1x}.

In terms of these quantities, the elements of the right eigenvector w are given by

$$w_1 = 1 - \sum_j L_j(n_1) + \sum_{j,k} L_j(n_1)L_k(n_1) - \cdots \tag{46}$$

and

$$w_x = \sum_i T^i_{1x}\left(1 - \sum_j L_j(T^i_{1x}) + \sum_{j,k} L_j(T^i_{1x})L_k(T^i_{1x}) - \cdots\right) \tag{47}$$

for $x > 1$. Again, the summations marked with asterisks are taken over all products of disjoint pairs, triplets, etc. of loops.

The left eigenvector **v** is the right eigenvector of the transposed matrix **A'**. It can be developed most easily in terms of the *transposed transmissions*. The transposed transmission differs from the transmission only in the treatment of self-loops; instead of dividing all incoming arcs by $1 - a_{ii}\lambda^{-1}$ one divides all outgoing arcs. Defining

- $\hat{T}_{x1}^i$: the transposed transmission of the ith path from stage x to stage 1,

the entries of the eigenvector **v** are given by

$$v_1 = 1 - \sum_j L_j(n_1) + \sum_{j,k}^* L_j(n_1)L_k(n_1) - \cdots \qquad (48)$$

and

$$v_x = \sum_i \hat{T}_{x1}^i \left(1 - \sum_j L_j(\hat{T}_{x1}^i) + \sum_{j,k}^* L_j(\hat{T}_{x1}^i)L_k(\hat{T}_{x1}^i) - \cdots \right) \qquad (49)$$

for $x > 1$.

Many life cycles contain no disjoint loops (once self-loops have been absorbed). In particular, life cycles containing one stage through which all individuals must pass contain no such loops. For these life cycles the eigenvector formulae (46-49) simplify to

$$w_1 = 1 \qquad (50)$$

$$w_x = \sum_i T_{1x}^i \qquad (51)$$

and

$$v_1 = 1 \qquad (52)$$

$$v_x = \sum_i \hat{T}_{x1}^i. \qquad (53)$$

3.3.1 Sensitivity formula for multi-step transitions

Multi-step transitions such as those shown in Figure 14 do not correspond to a single entry a_{ij} in the projection matrix, and the sensitivity of λ to
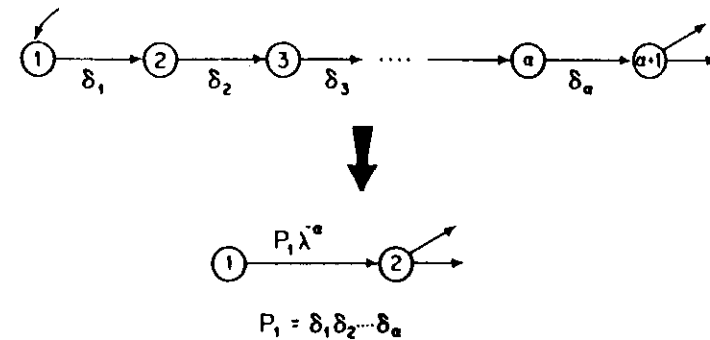
Figure 15: The process of reduction generating a life cycle transition requiring multiple time steps. From Caswell (1985). Reprinted by permission of Yale University Press.

changes in such parameters requires slightly different treatment (Caswell 1985). A transition like P_1 in Figure 14 is a reduction (Mason and Zimmerman 1960) of a graph segment like that shown in Figure 15, where the δ_i are the survival probabilities over each of the steps from n_1 to n_2. The survival probability $P_1 = \Pi \delta_i$. From the point of view of the reduced graph, all the δ_i might as well be identical, in which case $P_1 = \delta^\alpha$.

Without loss of generality, we assume that the change in P_1 results from a change in δ_1. Since $P_1 = \delta_1 \delta^{\alpha-1}$,

$$\frac{\partial \lambda}{\partial P_1} = \delta^{-\alpha+1} \frac{\partial \lambda}{\partial \delta_1}$$

$$= \delta^{-\alpha+1} \frac{w_1 v_2}{<\mathbf{w},\mathbf{v}>}. \qquad (54)$$

In (54), w_1 and v_2 refer to the unreduced graph. Stage 2 (and hence v_2) does not even appear in the reduced graph. However, v_2 can be rewritten as

$$v_2 = \delta^{\alpha-1}\lambda^{-\alpha+1}v_{\alpha+1}. \qquad (55)$$

Thus (54) reduces to

$$\frac{\partial \lambda}{\partial P_1} = \lambda^{-\alpha+1} \frac{w_1 v_{\alpha+1}}{<\mathbf{w},\mathbf{v}>}. \qquad (56)$$

23

Notice that, if $\alpha = 1$, (56) converges to the single-step sensitivity formula (16), as it should.

In (56), the scalar product term in the denominator still refers to the unreduced graph. However, for $1 < i < \alpha+1$ in the unreduced graph, $w_i = (\lambda^{\alpha+1-i}/\delta_i\delta_{i+1}\cdots\delta_\alpha)w_{\alpha+1}$ and $v_i = \delta_i\delta_{i+1}\cdots\delta_\alpha\lambda^{-\alpha-1+i}v_{\alpha+1}$. Thus, in this range,

$$w_i v_i = w_{\alpha+1} v_{\alpha+1}, \tag{57}$$

and the scalar product can be expressed in terms of the eigenvectors of the reduced graph:

$$< \mathbf{w}, \mathbf{v} > = w_1 v_1 + \alpha w_2 v_2 + \cdots. \tag{58}$$

4   Evolutionary interpretation

One of the major uses of the sensitivity formulae is in evolutionary calculations. This requires a demographic definition of fitness, a relation between this definition of fitness and the parameters defining the life cycle, and a description of natural selection incorporating all these elements.

4.1   Fitness

We equate fitness with λ, either as a property of a genotype or as a population average. The assumptions required to justify this usage (primarily slow selection and approximate stability of population structure) have been discussed in detail by Roughgarden (1979) and Charlesworth (1980) in the context of age-dependent models. I conjecture that the extension of those results to complex life cycles will produce no major changes. This definition lets us take advantage of the demographic framework outlined above to relate fitness to the structure of the life cycle.

4.2   The secondary theorem and selective pressure

The connection between fitness and selection is provided by the so-called Secondary Theorem of Natural Selection (Robertson 1968), which states that the rate of change in a quantitative trait under selection is proportional to the genetic covariance of that trait with fitness. (The Fundamental Theorem (Fisher 1958) states that the rate of increase of mean fitness is proportional to the genetic variance in fitness. It may be fundamental, but it is of much less use in predicting the results of selection on life history traits.)

The best statement of the Secondary Theorem is due to Lande (1982a,b). Let $\mathbf{z}$ denote an m-vector of quantitative traits (survival probabilities, clutch sizes, resource allocations, development rates, etc.) and let G denote the additive genetic covariance matrix (i.e. $g_{ij} = Cov_g(z_i, z_j)$). Then Lande shows that

$$\Delta\mathbf{z} = \lambda^{-1}\mathbf{G}\nabla\lambda \tag{59}$$

where $\Delta\mathbf{z}$ is the change in the average value of $\mathbf{z}$ due to natural selection and $\nabla\lambda = (\frac{\partial\lambda}{\partial z_1} \cdots \frac{\partial\lambda}{\partial z_m})'$.

Focusing on any one trait, z_i, (59) reduces to

$$\Delta\bar{z}_i = \lambda^{-1}\sum_{j=1}^{m}\left(\frac{\partial\lambda}{\partial z_j}\right)Cov_g(z_i, z_j). \tag{60}$$

If z_i is independent of the other traits, (60) reduces still further to

$$\Delta\bar{z}_i = \lambda^{-1}\frac{\partial\lambda}{\partial z_i}V_g(z_i) \tag{61}$$

(cf. Emlen 1970), where $V_g(z_i)$ is the additive genetic variance in z_i. In the simplest case, then, the direction of natural selection on any trait is determined by the sensitivity of λ to changes in the value of that trait. If one assumes (as is becoming increasingly clear that one cannot always do (Istock 1983)) that the genetic variance in different traits is effectively equal, then the sensitivities determine the rate as well as the direction of selection. Emlen (1970) introduced the term *selective pressure* for the sensitivity term in (61).

4.3   Correlated traits and trade-offs

When genetic correlations exist between different traits, as can be expected to the extent that any of them are under the control of genetic systems with pleiotropic effects (Templeton 1980), the change in $\bar{z}_i$ is influenced by the selective pressure on the other traits as well. Consider two traits, z_1 and z_2. From (60),

$$\Delta\bar{z}_1 = \lambda^{-1}\left(\frac{\partial\lambda}{\partial z_1}V_g(z_1) + \frac{\partial\lambda}{\partial z_2}Cov_g(z_1, z_2)\right). \tag{62}$$

But since $\partial z_1/\partial z_2 \approx Cov_g(z_1, z_2)/V_g(z_1)$, (62) can be rewritten

$$\Delta\bar{z}_1 = \lambda^{-1}\left(\frac{\partial\lambda}{\partial z_1} + \frac{\partial\lambda}{\partial z_2}\frac{\partial z_2}{\partial z_1}\right)V_g(z_1). \tag{63}$$

The bracketed terms in (63) give the "net selective pressure" on z_1, incorporating both the direct and indirect (through z_2) effects of changes in z_1 on λ.

Negative correlations between traits ("antagonistic pleiotropy" (Rose 1982) or "tradeoffs") are the most interesting cases. They can arise because of energetic constraints (resources allocated to one function cannot be allocated to another), architectural constraints (modules devoted to reproduction are not available for growth), or as a result of the genetic system.

When the traits in question can be expressed in terms of the elements a_{ij} of a projection matrix, the selective pressure terms in (63) can be obtained from the eigenvalue sensitivity formulae. The resulting expressions can be used to predict conditions under which selection should favor increases in one trait at the expense of another, as a function of the (usually unknown) correlations (e.g., Caswell 1983, 1985, Caswell et al. 1984). If it is assumed that λ is maximised as a function of z_1 and z_2, the value of $\partial z_2 / \partial z_1$ can be calculated in terms of the sensitivities (Caswell 1982c, 1984). Some other general conclusions arise from consideration of certain correlation patterns.

4.3.1   Tradeoffs between pathways

The preceeding results can be used to derive conditions under which selection should favor increasing investment in one developmental pathway at the expense of another.

Divergent pathways. Suppose, as in Figure 16b, that the choice is between two divergent pathways, and suppose that the cost of an increase in P_2 at the expense of P_1 is c; i.e. that

$$\partial P_2 / \partial P_1 = -c. \tag{64}$$

The net effect of an increase in P_1 is then

$$\frac{d\lambda}{dP_1} = \frac{\partial \lambda}{\partial P_1} - c \frac{\partial \lambda}{\partial P_2}$$

$$= \frac{w_3(v_1 - cv_2)}{<w,v>}. \tag{65}$$

Selection thus favors increasing P_1 if and only if
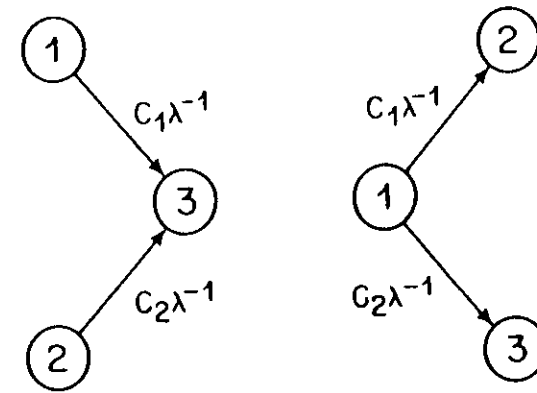
$$v_1 / v_2 > c. \tag{66}$$

Figure 16: (a) Two convergent pathways in a life cycle graph. (b) Two divergent pathways in a life cycle graph.

That is, the direction of selection on divergent pathways depends on the relative reproductive values of the destination stages.

Convergent pathways. Figure 16a shows two convegent pathways. By an argument analogous to (64-66), selection favors increasing P_1 at the expense of P_2 if and only if

$$w_1 / w_2 > c. \tag{67}$$

The direction of selection in a choice between convergent pathways depends only on the abundance in the stable stage distribution of the two source stages.

4.3.2   Survival and growth in size-classified populations

The size-classified life cycle graph (Figure 5b) can be directly analysed to obtain the selective pressures on P_i, F_i and G_i. However, the P_i and the G_i can be also be expressed in terms of lower level demographic parameters describing survival and growth. Let σ_i and γ_i denote the survival probability and growth probability, respectively, of an individual in size class i. Then

$$P_i = \sigma_i(1 - \gamma_i) \tag{68}$$

$$G_i = \sigma_i \gamma_i. \tag{69}$$

We can now calculate the selective pressures on σ_i and γ_i:

$$\frac{\partial \lambda}{\partial \sigma_i} = w_i \left(\frac{(1 - \gamma_i)v_i + \gamma_i v_{i+1}}{< \mathbf{w}, \mathbf{v} >} \right) \tag{70}$$

$$\frac{\partial \lambda}{\partial \gamma_i} = w_i \sigma_i \left(\frac{v_{i+1} - v_i}{< \mathbf{w}, \mathbf{v} >} \right). \tag{71}$$

Examples are shown in Figures 17 and 18.

The survival probability σ_i affects both the transition from n_i to n_{i+1} and the transition from n_i to itself, so the selective pressure on σ_i is proportional to the weighted average of v_i and v_{i+1}. The selective pressure on γ_i is interesting because, unlike the other selective pressures in this life cycle, it may be negative (if $v_{i+1} < v_i$). In such a situation, selection should favor decreases in γ_i, until n_{i+1} is effectively dropped from the life cycle. This implies that, in size-classified life cycles, the reproductive value distribution should increase monotonically up to the largest size class. This is a striking contrast to the pattern of reproductive value as a function of *age*, which tends to increase until early in reproductive life and then decline dramatically. Figure 19 shows several examples. They tend to support the prediction. While there are occasional declines in reproductive value at the largest sizes, they are small compared to those observed in age-classified life cycles.

5   Conclusions

It is perhaps fair to say that the life cycle is *the* description of the organism (Bonner 1965). This paper has reviewed some of the purely demographic information that can be obtained from a specification of the life cycle. The amount of that information is greater than most biologists have realized. The complexity of plant life cycles (size- or stage-dependent demography, multiple reproductive modes, and so on) is no longer a hindrance to this analysis.

It is worth considering here what lies beyond the linear time-invariant *projection* models on which this review has focused. There are other possibilities. The few studies that have tested projection matrices for temporal variability have found it (Bierzychudek 1982, Cochran 1986). This invites the application of recently developed theory on inhomogeneous matrix projection models (Cohen 1976, 1979a, Tuljapurkar 1982a,b, 1985) to
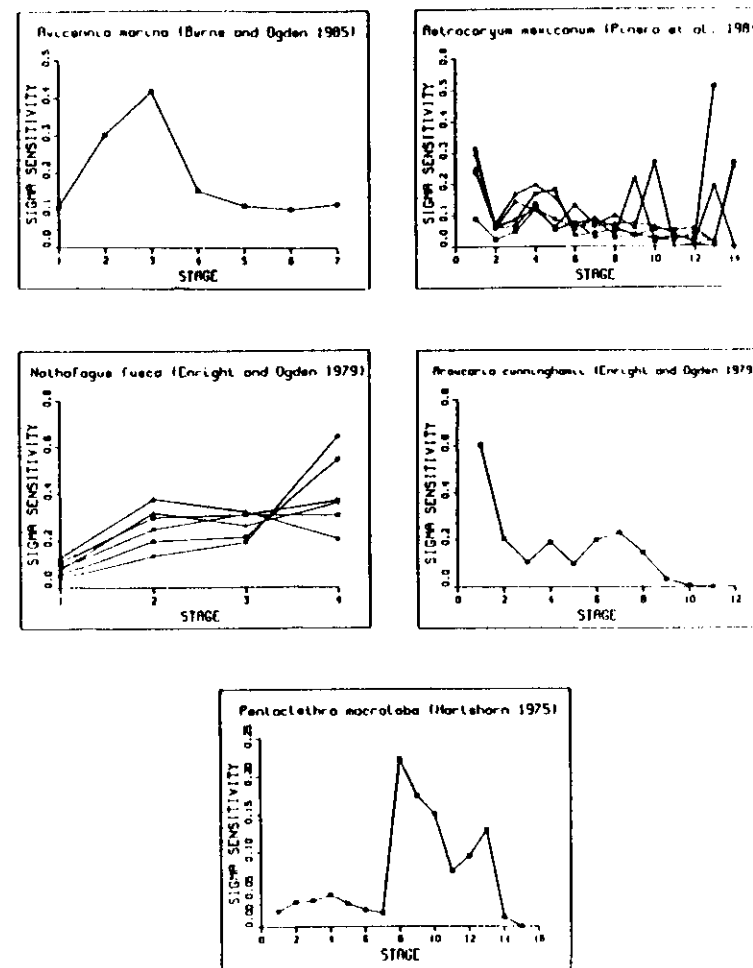

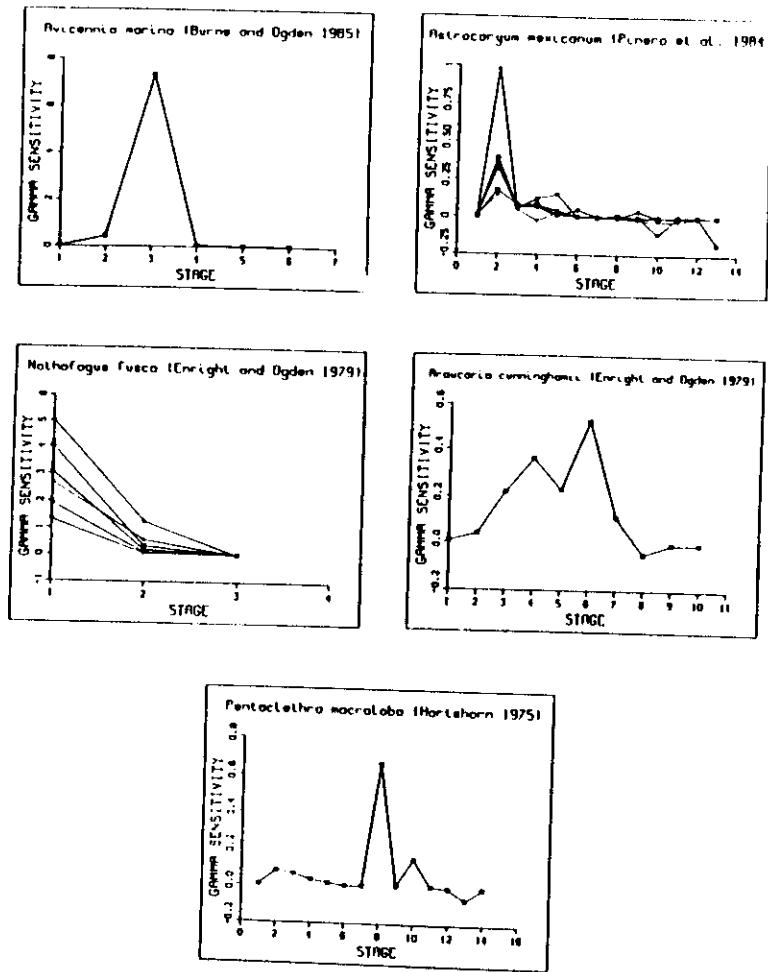Figure 17: The sensitivity of λ to σ_i as a function of size class i, for five tree populations.

Figure 18: The sensitivity of λ to γ_i as a function of size class i, for five tree populations.
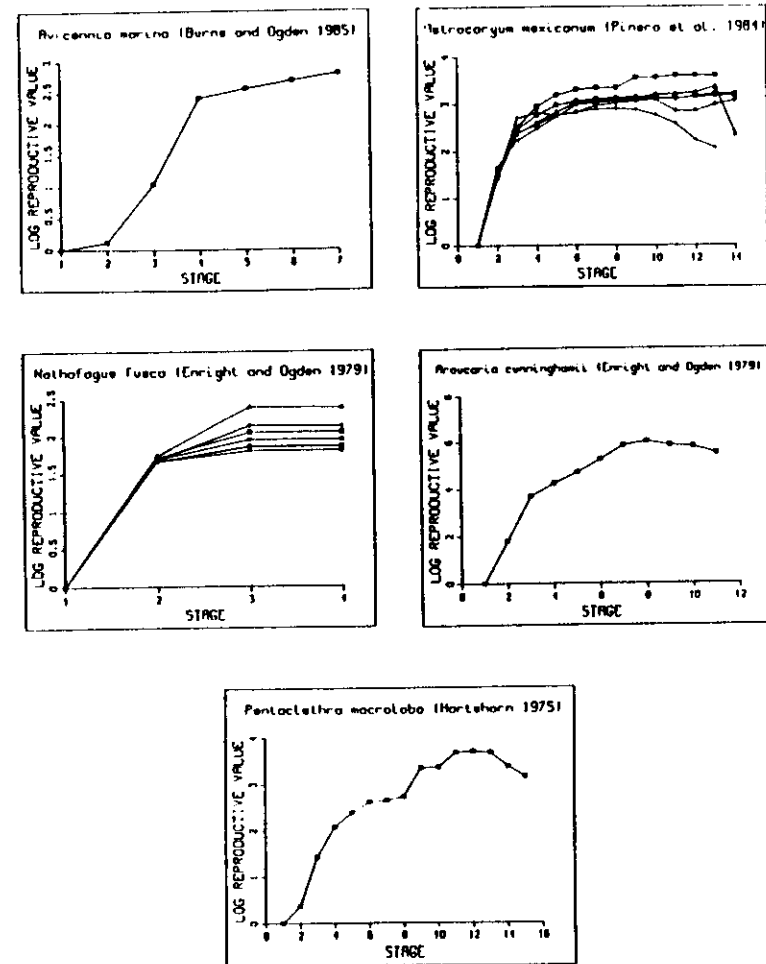
Figure 19: The reproductive value v_i as a function of size class i, for five tree populations.

plant populations. It is not yet clear how much data, or what sort of data, will be required for this, but a good example is the work of Cohen et al. (1983) on striped bass populations with stochastic reproduction.

Nonlinear systems, in which the elements of the projection matrix depend on the state of the population, also warrant investigation. It is now known that extremely complex dynamics can be produced by density-dependent matrix models arising as a result of competition (Guckenheimer et al. 1977, Levin and Goodyear 1980) and by frequency-dependent models arising as a result of the interaction of the sexes (Caswell and Weeks 1986). What is not clear is whether or not these complex dynamics result from the parameter values typical of actual populations.

Plants are modular organisms, and can thus the growth of individual genets can often be modelled as the dynamics of a population of modules (Harper 1981). Maillette (1982) and McGraw and Antonovics (1983) have constructed matrix models for the dynamics of modules (buds of the silver birch *Betula pendula* and branches of the shrub *Dryas octopetala*, respectively). A major unsolved problem is the construction and analysis of *hierarchical* models which would describe the the population dynamics of both genets and of modules within genets. Such models would be a particularly valuable way to study the population dynamic and evolutionary consequences of patterns of individual growth.

6 Acknowledgements

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