

POPULATION MATRIX MODELS OF *AESCHYNOMENE VIRGINICA*, A RARE ANNUAL PLANT: IMPLICATIONS FOR CONSERVATION

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Abstract. Matrix models are valuable tools for comparing population growth rates (λ) in different environments. Life table response experiments (LTRE) can then be used to identify those life history stages that are most important to observed population growth rate differences. We used matrix models of population growth and LTREs to analyze the effects of standing vegetation and seed dispersal on the population growth rate of *Aeschynomene virginica*, a rare, tidal, wetland annual. We combined seedling establishment, seedling survival to adulthood, adult fecundity, winter seed survival, probability of seeds entering a seed bank, and seed dispersal rates to calculate the matrix elements in a matrix model. Experimental removal of other plant species from field plots increased *A. virginica* fecundity, seedling establishment, and survival. The magnitude of these changes doubled between 1998 and 1999. Removal of interspecific competitors from population patches of *A. virginica* explained 54% of the variability of λ , while environmental variation between 1998 and 1999 explained only 1%. An additional 9% of the variability in λ was explained by adding the interaction of interspecific removal and year to the regression. Sensitivities of λ to changes in lower-level parameters varied over several orders of magnitude. Fecundity had the smallest sensitivity, while seedling establishment made the largest contribution to λ in 1998, and seedling survival to adulthood made the largest contribution in 1999. Simulations indicated that changes in seed dispersal would have small effects on λ . Eighty percent (1998) to 90% (1999) of the seeds produced in local patches growing without interspecific vegetation would have to disperse before patch population growth rates would become negative. Although seed dispersal had little impact on within-patch population dynamics, it may make seeds available to establish populations in nearby, open habitat patches. In population patches with interspecific vegetation, 30 seeds per plant (1998) and 80 seeds per plant (1999) would have to be added before patch population growth rates were positive. The most efficacious treatment to increase population sizes of this rare plant would be creating disturbed patches and not adding seeds.

Key words: annual plant; conservation and management; demography; elasticity analysis; fecundity; hydrochory; life table response experiments; seed bank; seed dispersal; sensitivity analysis.

INTRODUCTION

Recent ecological research on rare plant species has addressed the importance of a variety of ecological factors (Schemske et al. 1994), including competitive interactions (Batty et al. 1984, Gawler et al. 1987), habitat requirements (Buchele et al. 1989), and reproductive ecology (Mehrhoff 1983, Kevan et al. 1991, Buchele et al. 1992). Much of this research has focused on the impacts of ecological factors on just one or a few stages of a plant's life cycle, which falls short of projecting effects on population dynamics. For example, increasing plant cover could cause a decrease in seed production (Gawler et al. 1987), but ultimately have a negligible effect on population growth rates. Different life stages can vary in their effects on the overall rate of population growth (Caswell 2000, 2001,

de Kroon et al. 2000). Hence, changing a particular life stage that has little ultimate impact on population growth rates is of little conservation and management value (Ehrlén and van Groenendael 1998, Caswell 2000). A broader demographic approach is essential in order to estimate and project population growth rates and the status (e.g., growing, stable, or declining) of rare plant populations (Menges 1986, Schemske et al. 1994, Caswell 2001).

Population matrix modeling is one method to project changes in population growth rate (λ) in response to different environmental conditions. Population matrix models are derived from life cycle graphs depicting important ages (Leslie 1945) or stages (Lefkovich 1965) of an organism. The vital rates of life cycle graphs are the probabilities of surviving between different ages/stages or the fecundities of reproductive ages/stages. Vital rates are represented by the matrix elements of the population matrix model and are used to determine the overall population dynamics from year to year. Age- or stage-based matrix models have been

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used to analyze the population dynamics of rare animals (Brault and Caswell 1993, Crooks et al. 1998), perennial plants (Menges 1986, Fiedler 1987), and invasive plants (Parker 2000). Matrix models have also explored the significance of seed age (Schmidt and Lawlor 1983) and spatial and temporal variability of seeds in the seed banks of annual species (Kalisz and McPeck 1992).

Year-to-year population dynamics of annual plants have historically been modeled using the probability that a seed in a soil seed bank will germinate and produce more seeds that then return to the soil seed bank (Schmidt and Lawlor 1983, Kalisz and McPeck 1992). This model collapses to tracking the dynamics of a single stage, the seed in the soil (Schmidt and Lawlor 1983) with a single vital rate for an annual cycle. The model does not account for the different phases of the life cycle that the plant passes through within the course of a year (Kalisz and McPeck 1992).

This approach ignores potentially important within-year dynamics that may affect population growth rates (Caswell 1989, 2000, 2001, Brault and Caswell 1993, Wisdom and Mills 1997). Several processes combine in the vital rate for the single stage annual plant model. We can view this vital rate as arising from the probability of the seed germinating, the probability of the seedling surviving to reproduce, the fecundity of each plant, and the probability of a seed surviving over winter. Vital rates, clearly, can be made up of several lower-level parameters, which are not explicitly shown by the matrix elements of a population matrix model. Determining whether one or more of these lower-level parameters are a limiting factor to the overall vital rate may be essential in devising a management plan for the maintenance of the population.

Similarly, if a vital rate in a multistage life cycle has a small effect on the overall population growth rate, limited management resources should be invested in promoting a different vital rate in the life cycle. It is critical to look at vital rates and lower-level parameters hand in hand, in order to fully understand the drivers of population dynamics and their implications for management.

Life table response experiments (LTRE) exploit information in population matrix models by decomposing the variability of λ into the component variability due to changes in vital rates caused by experimental treatments or environmental conditions (Caswell 1989, 2000, Ehrlén and van Groenendael 1998). In this paper, we combined matrix transition models and LTRE analysis to determine the effects of standing vegetation and seed dispersal on the population growth rate of *Aeschynomene virginica* L. (Fabaceae), a rare, annual plant which is listed as a federally threatened species (U.S. Fish and Wildlife Service 1992). *A. virginica* is a freshwater tidal wetland plant associated with areas of little or no standing vegetation (U.S. Fish and Wildlife Service 1995, Griffith and Forseth 2003), and whose seeds

disperse from population patches with tidal flow (Griffith and Forseth 2002). These traits may have implications for the conservation and management of this threatened plant. For example, is the association of this plant with open habitats due to the failure of its seeds to germinate in the shade of standing vegetation, or is it due to reduced seedling and/or adult survivorship in the presence of standing vegetation? To address this question, we experimentally manipulated the standing vegetation, creating two treatment categories: cut and uncut. We measured the complete pattern of demographic responses of the plants, including several lower-level parameters. Then, we evaluated the resulting effects of the treatments on matrix elements and finally on asymptotic population dynamics. We used an LTRE approach to determine which components of the life cycle made the largest contribution to the variance in the asymptotic population growth rate between the treatments. We also estimated seed dispersal from populations and simulated the impact of changing dispersal on population growth rates. Our objective was to estimate the importance of some of the intra-annual dynamics in the life history of *A. virginica* that are not captured by composite vital rates. Specifically, we asked: (1) What is the contribution of different life history stages, i.e., seedling establishment, seedling survival to adulthood, and seed production to changes in λ ? (2) What is the effect of standing vegetation on local patch population growth rate (λ)? (3) Does year-to-year environmental variability affect the relative role of different vital rates on λ ? (4) How many seeds can disperse out of a patch before patch population growth ceases? (5) How many seeds need to immigrate into a patch to sustain population sizes in the presence of interspecific competitors?

METHODS

Study system

A. virginica or sensitive joint-vetch's global distribution is in the freshwater, tidal wetlands of the east coast of the United States, from southern New Jersey to central North Carolina. *A. virginica* grows in patchily distributed populations along stream and small tributary edges in areas of decreased standing vegetation on the levee or high marsh (U.S. Fish and Wildlife Service 1995; A. Griffith, *personal observation*). Tides typically inundate *A. virginica* populations twice daily. Its stream edge distribution and association with tidal influences are consistent with a reliance on secondary seed dispersal by water, or hydrochory (U.S. Fish and Wildlife Service 1995, Griffith 2002, Griffith and Forseth 2002). The experimental removal of interspecific vegetation from patches of *A. virginica* has been found to increase seedling establishment (germinated seed to first true leaf stage), seedling survival (seedling to adult plant stage), and seed production (fecundity) of *A. virginica* (Griffith and Forseth 2003).

TABLE 1. Values (mean \pm 1 SE) for lower-level parameters used to construct matrix elements in the matrix model; all data are presented as proportions, except for seed production, which is expressed as mean seeds produced per adult plant.

Parameter	Demography experiment†				Dispersal experiment‡ (2000)	Seed bank experiment§ (1999–2000)
	1998		1999			
	Cut plots	Uncut plots	Cut plots	Uncut plots		
Seedling establishment	0.23 ± 0.19	0.08 ± 0.08	0.45 ± 0.21	0.26 ± 0.13		
Seedling survival	0.61 ± 0.33	0.38 ± 0.31	0.51 ± 0.34	0.06 ± 0.05		
Adult seed production	121.9 ± 117.2	51.5 ± 41.9	157.4 ± 91.5	7 ± 21		
Proportion of seeds not dispersing					0.66 ± 0.14	
Winter survival						0.379 ± 0.092
Germination						0.789 ± 0.093
Viable seeds not germinating						0.039 ± 0.025

[†] Data are from Griffith and Forseth (2003).[‡] Data are from Griffith and Forseth (2002).[§] Data are from Griffith (2002).

Experimental conditions

We conducted this research on the Cumberland Marsh Preserve in New Kent County, Virginia, USA. Seedling establishment, seedling survival, and seed production, three of the lower-level parameters in this study, were estimated using experimental removal of all aboveground vegetation in plots located near extant populations of *A. virginica* (Table 1). These experiments were repeated in two different years, 1998 and 1999. Experimental design and analysis are described in detail in Griffith and Forseth (2003). Briefly, four sets of experimental plots were set up at each of three locations along Holt's Creek on the Cumberland Marsh Preserve. Each plot had all aboveground vegetation either removed or not removed. One hundred *A. virginica* seeds collected from nearby populations were added to each plot in the spring of the year. Plots were checked several times during the summer, all newly emergent vegetation aside from *A. virginica* was clipped at the soil surface in vegetation removed plots, new *A. virginica* individuals were marked, presence or absence of previously marked plants was noted, and plant sizes were measured. All seeds were counted on surviving plants at the end of the summer in 1998 and the number of seeds per plant was estimated in 1999 using the relationship between plant size and seed production (Griffith and Forseth 2003).

Seed dispersal out of a local population patch was estimated using a second set of experiments repeated 11 times in one year (Table 1). The design and analysis of these experiments are described in detail in Griffith and Forseth (2002). Briefly, a set of four plots was established at three different sites on the stream edge at the Cumberland Marsh Preserve. Each plot was enclosed by screen on the three sides of the plot not facing the stream. Half of the plots were also closed on the side facing the stream, to control for seeds that were in the plot but could not be found. Forty *A. virginica* seeds were added to each plot and a week later we counted the seeds remaining in the plots.

Soil samples taken before seed dispersal in the fall have verified the presence of a persistent seed bank for *A. virginica*. Seed density was spatially variable, but densities as high as 300 viable seeds/m² (calculated from data in Griffith 2002) suggest the importance of a seed bank. Seed survival over winter and the probability that seeds remain dormant in the soil for greater than a year were estimated from artificial seed banks constructed following the procedures of Kalisz (1991) (Table 1). Details are given in Griffith (2002), but are described briefly here. Nylon screen bags were filled with autoclaved soil and 125 *A. virginica* seeds were sealed in each bag. Nine bags were buried flush with the soil surface at each of three sites on the Cumberland Marsh Preserve on 25 October 1999, to coincide with natural seed fall from plants. Seed bags were retrieved the next spring, all hard seeds were removed from the bags, and placed on moist sand to germinate. *A. virginica* seeds exhibit physical seed dormancy (Baskin and Baskin 1995), and viable seeds germinate when the seed coat allows water imbibition. After seven months, the seed coat of nongerminated seeds was scored to facilitate imbibition. If the radicle of a seed grew after scoring, it was considered viable.

Matrix model and LTRE analysis

Transition matrix models project population size using a model of the general form

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

where, \mathbf{n} is a vector of the number of individuals in different plant stages and \mathbf{A} is a matrix of probabilities and fecundities that defines the survival and reproduction of individuals in each stage between time (t) and ($t + 1$) (i.e., matrix elements).

The transition matrix (\mathbf{A}) is derived from a life cycle graph that shows the possible transitions between stages of a given species (Caswell 2001). Our model system, *A. virginica*, is an annual plant with a seed bank, so we have adopted the life cycle graph proposed by

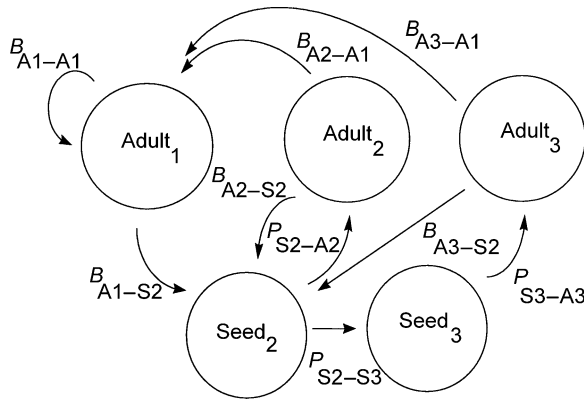


FIG. 1. Life cycle graph of an annual plant with a two-year seed bank. Each arrow represents a fall-to-fall transition or a vital rate. $Adult_1$, $Adult_2$, and $Adult_3$ are adult plants at the time of seed set. $Seed_2$ and $Seed_3$ are seeds that have remained alive in the soil for two and three winters, respectively. $Adult_1$, $Adult_2$, and $Adult_3$ are one-, two-, or three-year-olds, respectively, depending upon the age of the seed from which they germinated. The B_{i-j} 's are the products of survival probabilities and a fecundity. P_{i-j} 's are the products of survival probabilities. The $i-j$ subscripts are abbreviations for the adult or seed stages at the beginning and end of a transition.

Kalisz and McPeck (1992) which, in essence, turns an annual plant into a perennial through a multiyear seed bank (Fig. 1). This model is a more complex version of a simple annual plant model discussed by Caswell (2001). In our model, the stages in the model are standing adults or dormant seeds in a seed bank, as in Caswell. However our model is more complex in that adults can have different ages based upon the age of the seed from which they germinated. $Adult_1$, $Adult_2$, and $Adult_3$ are adult plants censused at the time of seed set. A one-year-old adult ($Adult_1$), for example, is a plant that germinated from a seed produced on an adult plant ($Adult_1$, $Adult_2$, $Adult_3$) the previous season. A two-year-old adult ($Adult_2$) is a plant that germinated from a seed produced two seasons ago ($Seed_2$) that did not germinate, remained dormant through a second winter, and germinated the second spring after it was

produced. The projected population growth rates of the simple (Caswell 2001) and complex models (Fig. 1) were essentially the same. However, the more complex model allowed us to distinguish the importance of different aged seeds in the seed bank to local population growth.

The life cycle graph depicts the nonzero transitions or vital rates (Caswell 2001) of a population projection matrix (Table 2). The matrix elements in the matrix represent transitions from the life stages in one year, shown across the top of the matrix, to the life stages in the next year, shown down the side of the matrix. All seed-to-adult transitions are presented as probabilities. Adult-to-adult or adult-to-seed transitions include both probabilities and fecundities (seeds per plant). We derived these probabilities and fecundities using parameter estimates from the experiments described previously. The equations in Table 3 represent matrix elements and the lower-level parameters that make up each matrix element. We have no estimates of differences in matrix elements between different aged plants or seeds, so we assumed that $B_{A1-S2} = B_{A2-S2} = B_{A3-S2}$, $B_{A1-A1} = B_{A2-A1} = B_{A3-A1}$, and $P_{S2-A2} = P_{S3-A3}$. Seeds remaining in the soil for different times could have different seed survival or germination probabilities. However, due to the difficulty in obtaining these estimates the assumption of no differences in these parameters is commonly used (see also Kalisz and McPeck 1992). Even though we assume equal values for these matrix elements, it is interesting and important to include these different aged seeds in the model because population growth rates may be more or less sensitive to changes in each age's matrix element, and these sensitivities may change in different environments.

Population parameters calculated from population projection matrix models include the annual growth rate (λ), matrix element sensitivities (S_{ij}), and matrix element elasticities (E_{ij}). λ is the dominant right eigenvalue of matrix A (Caswell 2001). When $\lambda = 1$, the population size does not change from year to year. If $\lambda > 1$ or $\lambda < 1$, the population is increasing or

TABLE 2. Matrix of stage transitions (i.e., matrix elements) for an annual plant with a two-year seed bank.

Stage	$Seed_2$	$Seed_3$	$Adult_1$	$Adult_2$	$Adult_3$
$Seed_2$	0	0	B_{A1-S2}	B_{A2-S2}	B_{A3-S2}
$Seed_3$	P_{S2-S3}	0	0	0	0
$Adult_1$	0	0	B_{A1-A1}	B_{A2-A1}	B_{A3-A1}
$Adult_2$	P_{S2-A2}	0	0	0	0
$Adult_3$	0	P_{S3-A3}	0	0	0

Notes: The adult-to-adult transition (B_{A1-A1}) is a typical annual cycle. Adult-to-seed transitions, B_{A1-S2} , B_{A2-S2} , and B_{A3-S2} , are the rates at which seeds remain viable in the soil for two winters. The seed-to-seed transition, P_{S2-S3} , is the rate at which a two-year-old seed remains viable in the seed bank for a third year. Seed-to-adult transitions, B_{S2-A2} and B_{S3-A3} , are the rates at which two- or three-year-old seeds, respectively, germinate and emerge from the seed bank. All symbols match those in Fig. 1. The subscript numbers are age in years. For example $Seed_2$ is a seed that has remained in the soil for two winters.

TABLE 3. Matrix elements and their lower-level parameters for a matrix model of an annual plant with a seed bank.

Matrix element	Matrix element descriptions	Lower-level parameters
$B_{A1-S2} = B_{A2-S2} = B_{A3-S2}$	rate at which adults at time (t) produce dormant seeds in the soil at time ($t + 1$)	Seeds \times NoD $\times P_{\text{bank}}$
$B_{A1-A1} = B_{A2-A1} = B_{A3-A1}$	rate at which adults at time (t) produce adults at time ($t + 1$)	Seeds \times NoD $\times P_{\text{germ}} \times P_{\text{estab}}$ $\times P_{\text{surv}}$
P_{S2-S3}	rate at which dormant seeds in the soil at time (t) remain dormant at time ($t + 1$)	$P_{\text{winter}} \times P_{\text{bank}}$
$P_{S2-A2} = P_{S3-A3}$	rate at which dormant seeds in the soil germinate and produce adults at time ($t + 1$)	$P_{\text{germ}} \times P_{\text{estab}} \times P_{\text{surv}}$

Notes: Matrix elements were calculated by multiplying the lower-level parameters as indicated. "Seeds" is the mean number of seeds produced per plant. "NoD" is the fraction of seeds that do not disperse on the tide. " P_{bank} " is the probability of a seed remaining in soil without germinating. " P_{estab} " is the probability of seed germinating and surviving to the first true leaf stage. " P_{surv} " is the probability of a seedling surviving from the first true leaf stage to the time of reproduction. " P_{winter} " is the probability of a seed on the ground surviving overwinter to germination time. " P_{germ} " is the probability of a seed germinating once it has survived the winter.

decreasing in size, respectively. Matrix element sensitivity is the change in λ due to a small change in a matrix element (e.g., $\delta\lambda/\delta a_{ij}$) and can be calculated as

$$S_{ij} = v_i w_j / \langle \mathbf{w}, \mathbf{v} \rangle \quad (2)$$

where a_{ij} is the matrix element in the i th row and j th column of the matrix, v_i is the reproductive value of the i th stage of the life cycle, w_j is the stable stage distribution of the j th stage of the life cycle, and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of the vectors of the stable stage distribution and reproductive values (Caswell 2001). Sensitivities of different matrix elements are not directly comparable because they can vary over several orders of magnitude (i.e., probabilities vs. fecundities). Matrix element elasticities are the proportional change in λ due to a change in a matrix element relative to the magnitude of λ and can be calculated as

$$E_{ij} = S_{ij}(a_{ij}/\lambda). \quad (3)$$

Elasticities are comparable between different matrix elements in the same matrix or between the same matrix elements in different matrices from the same population model. The sum of elasticities in each column of a matrix gives the proportional influence of that stage/age class on changes in λ (Kalisz and McPeck 1992, Caswell 2001).

A life table response experiment (LTRE) is conducted when different sets of matrix elements are derived under different experimental conditions (Hansen et al. 1999, Caswell 2000, 2001). Differences in matrix elements (or the lower-level parameters that make up each matrix element), produce variability in λ [$\text{var}(\lambda)$]. LTRE analysis allows us to decompose $\text{var}(\lambda)$ into contributions from different matrix elements. The decomposition of $\text{var}(\lambda)$ can be calculated for the effect α caused by the differences between two treatments as

$$\alpha^{1-2} = \sum (a_{ij}^1 - a_{ij}^2) \delta\lambda / \delta a_{ij} \Big|_{(1/2)(\mathbf{A}^1 + \mathbf{A}^2)} \quad (4)$$

or the sum of the differences between the matrix element derived under the treatment 1 conditions and the matrix element under treatment 2 conditions multiplied

by the matrix element sensitivity (Caswell 1989, 2000, 2001). The sensitivities are evaluated for the set of matrix elements at the mean of the two treatment conditions [$\frac{1}{2}(\mathbf{A}^1 + \mathbf{A}^2)$] (Brault and Caswell 1993, Levin et al. 1996, Caswell 2000). The actual contribution of a change in a matrix element to $\text{var}(\lambda)$ is the product of the difference and sensitivity. We performed LTRE analyses for the cut and uncut treatments from our demography experiments. The sensitivities for the demography LTRE were evaluated at the set of matrix elements from cut and uncut treatment matrices.

Because each lower-level parameter (X_a) can impact more than one matrix element, the sensitivity of λ to changes in these X_a comes additively through the effect of the X_a on matrix element, a_{ij} :

$$d\lambda/dX_a = \sum (S_{ij}) \delta a_{ij} / \delta X_a. \quad (5)$$

This is by application of the chain rule (Brault and Caswell 1993, Levin et al. 1996, Caswell 2001). This is analogous to the matrix element sensitivities, but shows the effects on λ as a result of changes in within-year dynamics. We calculated the effects of lower-level parameters by implicitly differentiating the characteristic equation of the population matrix. The characteristic equation states λ as a function of the matrix elements in the transition matrix and therefore as a function of the lower-level parameters (Caswell 2001). The characteristic equation for our model is $B_1 P_2 P_{4,5} \lambda^2 + B_1 P_{4,5} \lambda^3 + B_3 \lambda^4 - \lambda^5 = 0$. Solutions of the implicit differentiation of this characteristic equation, for changes in λ with respect to each of the lower-level parameters, are shown in the Appendix.

Randomizations

Low experimental replication limited our ability to use typical randomization techniques like bootstrapping to distinguish statistically significant differences between population λ 's under different experimental treatments (i.e., standing vegetation and year-to-year parameter differences). Therefore, we generated a data set of lower-level parameters using the estimated means, variances, and covariances of these parameters.

Covariances were calculated for parameters generated from the same experiment. Each observation was randomly drawn from a normal distribution with the mean, variance, and covariance of each variable estimated from our data. One thousand observations were generated for each treatment level of our experiments, but only biologically possible (i.e., positive) values were allowed. This produced a distribution of lower-level parameters for each treatment level (i.e., cut and uncut plots) and each year (i.e., 1998 and 1999) of our demography experiments and the seed survival and seed dormancy variables. We regressed the cut–uncut treatment (vegetation), year (date) and vegetation \times date interaction on λ (SAS, 1996). Changes in R^2 values indicate the changes in the percentage of variability of the dependent variable λ explained by additional independent variables in the regression model. λ was natural log-transformed ($\ln \lambda$) to improve homogeneity of variances. Log-transformed values were back transformed for data presentations.

Simulations

In *A. virginica*'s tidal habitat, seed dispersal may vary from week to week and year to year, as tidal inundation and flow rates vary (Griffith and Forseth 2002). Tidal variability, in turn, causes variability in seed dispersal out of patches (Griffith and Forseth 2002). We could not experimentally manipulate this variable to estimate its impact on λ . Therefore, we simulated the effects of changes in the lower-level parameter "NoD" (i.e., the fraction of seeds that do not disperse on the tide) to investigate the impacts of changes in dispersal on λ . We started at the estimated NoD = 0.66 and incrementally increased the fraction of seeds leaving populations. For each of these dispersal fractions, we projected λ . We increased the fraction of seed dispersal until λ dropped below 1. In each case, we used 1998 and 1999 transition matrices that were the mean of parameters from the cut experimental plots.

For conservation and management reasons, we wished to know the impacts of hypothetical seed production increases on λ in uncut plots. These data estimated the efficacy of seed additions to *A. virginica* populations found in patches with established vegetation. We started by calculating λ using estimated parameters from uncut plots. We incrementally increased seed production by multiples of the estimated seed production parameter until λ was >1 . Seed additions were modeled as if seeds were added in the spring, so that no added seeds were lost over the winter.

RESULTS

Differences in matrix elements, caused by vegetation removal, that include fecundity (e.g., those signified with a *B*) were generally larger than differences in matrix elements that only included survival probabilities (e.g., those signified with a *P*; Fig. 2, top graphs). The

matrix element sensitivities for the transition of two-year-old seed to adults (P_{S2-A2}) and first year adults to adults the next year (B_{A1-A1}) were much greater than all other sensitivities (Fig. 2, middle graphs). The relative sensitivity of the most sensitive matrix elements changed between 1998 and 1999, but the overall pattern of sensitivities did not change (Fig. 2, middle graphs). In both 1998 and 1999, the greatest contribution to a change in λ came from the matrix element B_{A1-A1} (Fig. 2, bottom graphs). The transition of first year adults to adults the next year (B_{A1-A1}) was the largest of the adult to adult transitions (B_{A1-A1} , B_{A2-A1} , and B_{A3-A1}), in both 1998 and 1999, as both differences and sensitivities for B_{A1-A1} were large.

Underlying these changes in matrix elements are changes in lower-level parameters. Our experimental treatments caused differences in fecundity, the seed to seedling establishment transition, and the seedling to adult survival transition (Fig. 3). The size of these differences approximately doubled between 1998 and 1999 (Fig. 3). Population growth rates were least sensitive to fecundity, most sensitive to the seed to seedling transition in 1998, and most sensitive to the seedling to adult transition in 1999 (Fig. 3). The probabilities of dispersal, seed dormancy, and overwinter survival were not changed by our experimental treatments, but λ would be sensitive to changes in these parameters (Fig. 3).

Summed elasticities of each stage/age class varied between year and treatment (Table 4). The Adult₁ stage had at least a 98% influence on λ in cut plots in both 1998 and 1999. However, the elasticities for this stage in uncut plots decreased to 79% and 20% in 1998 and 1999, respectively. In the 1998 uncut plots, the Seed₁ and Adult₂ stages increased their total influence on λ to 10% and 9%, respectively, compared to 1% for each in 1998. In the 1999 uncut plots, Seed₁ replaced Adult₁ as having the highest elasticity, while the balance of the influences on λ came relatively evenly from the Seed₂, Adult₂, and Adult₃ stages.

The removal of standing vegetation from population patches of *A. virginica* significantly affected the population growth rate (λ). In the linear regression of randomized data, the dependent variable vegetation explained 54% of the variability of λ . The two main effects vegetation and date explained 55% of the variability of λ . The addition of the interaction of vegetation \times date to the regression explained 63% of the variability in λ (Table 5). In plots where vegetation was not removed, λ was <1 in 1998 ($t_{999} = -24.9$, $P < 0.001$; Fig. 4) and in 1999 ($t_{999} = -94.6$, $P < 0.001$; Fig. 4), implying a decreasing population growth rate. λ in plots with vegetation removed was >1 in 1998 ($t_{999} = 19.1$, $P < 0.001$; Fig. 4) and in 1999 ($t_{999} = 35.8$, $P < 0.001$; Fig. 4), indicating increasing population size. The interaction between vegetation and date arose because λ in cut plots increased from 1998 to

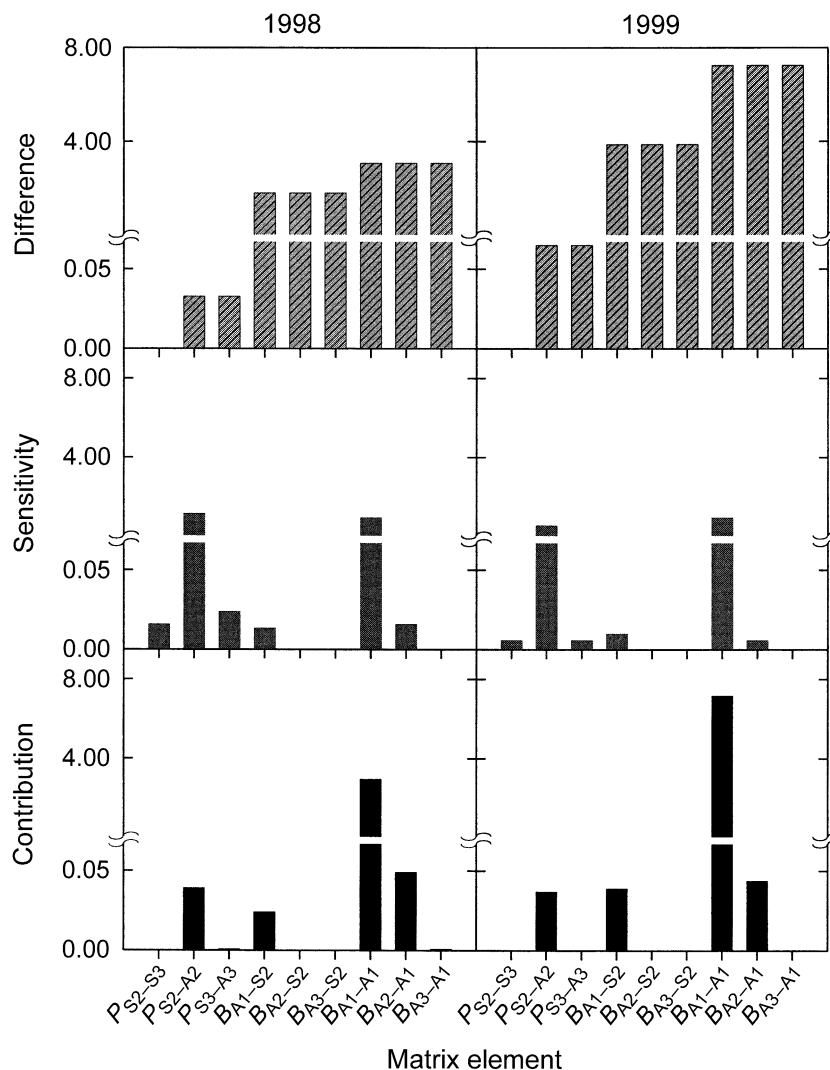


FIG. 2. Contribution of changes in matrix elements to changes in population growth rate (λ) with the removal of competing vegetation. "Difference" is the difference between matrix elements for cut and uncut demography plot means. "Sensitivity" is the amount that λ changes with a small change in the matrix element. Sensitivity was calculated for the set of matrix elements at the mean of the cut and uncut matrix elements. "Contribution" of a matrix element is the product of difference and sensitivity.

1999, while λ in uncut plots decreased from 1998 to 1999 (Fig. 4).

Given the measured population parameters in experimental plots in which vegetation was removed and the estimated seed dispersal rate of 0.34, the 1998 λ was 3.42 and the 1999 λ was 7.32 (Fig. 5). An increase in the percentage of seeds dispersing out of these patches would cause a decrease in λ for the local population patch. Our simulations in 1998 show the population would stop increasing ($\lambda = 1$) when $\sim 80\%$ of the seeds left the population patch. The 1999 estimated parameters would require that just over 90% of the seeds leave a population patch before population growth fell below 1.0. In comparison, the 1998 λ was 0.35 and the 1999 λ was 0.05 in experimental plots in which veg-

etation was not removed. Using the measured fecundity from these plots, 51.4 seeds/plant and 7 seeds/plant, in 1998 and 1999, respectively (Table 1), an additional 30 seeds/plant would be needed to raise λ above 1.0 in 1998 (Fig. 6). In 1999, an addition of 80 seeds/plant was required for λ to reach 1.0 (Fig. 6).

DISCUSSION

The removal of interspecific competitors from around *A. virginica* plants increased local asymptotic population growth rates in both years of our study. In contrast in plots where vegetation was not removed, matrix analysis indicated that population size was decreasing. Observations of this plant's association with disturbances, open habitat patches, and the decrease in

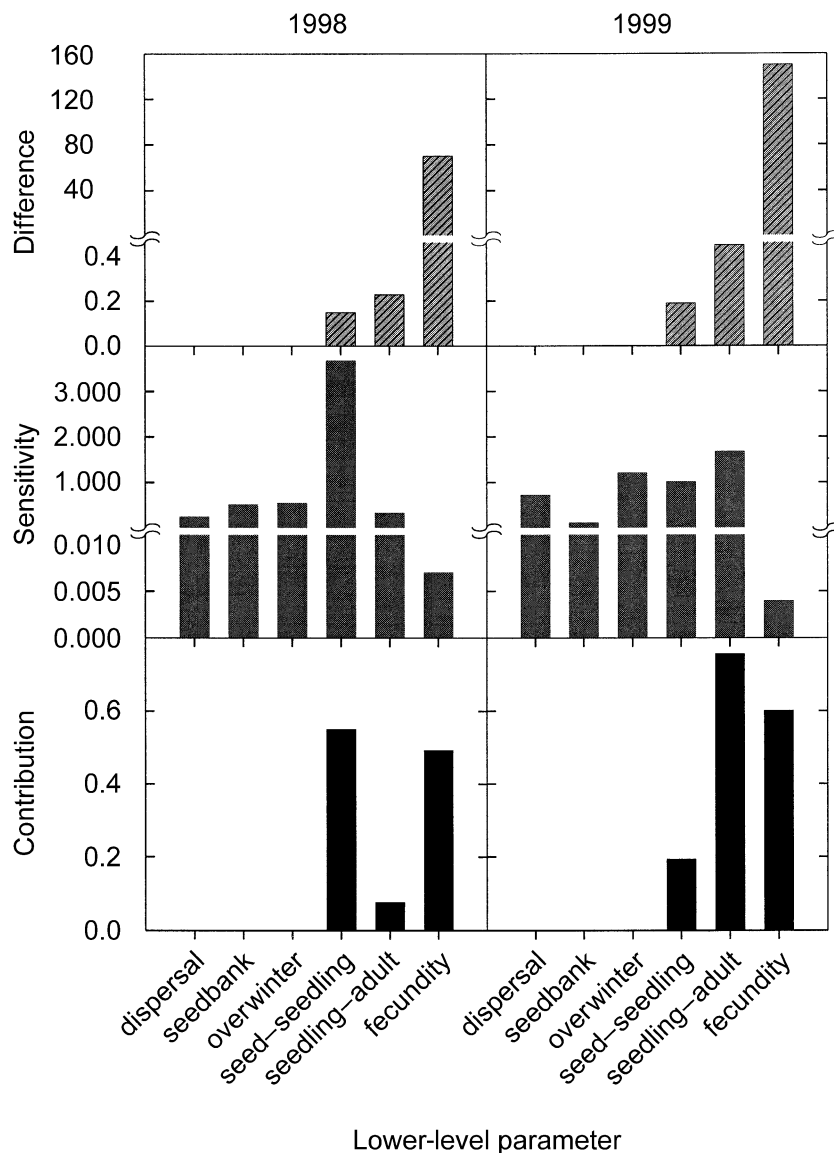


FIG. 3. Contribution of changes in lower-level parameters to changes in population growth rate (λ). "Difference" is the difference between parameters estimated in cut and uncut experimental plots. Total contribution of a lower-level parameter is the product of difference and sensitivity.

population growth rates in areas with standing vegetation strongly suggest a dependence of *A. virginica* on wetland processes that remove or decrease standing vegetation. Freshwater tidal wetlands are characterized by high annual primary productivities ranging from 1000 to 3500 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Pickett et al. 1989, Whigham and Simpson 1992) and have high species diversity compared to other wetlands (Odum et al. 1984, Whigham and Simpson 1992). This high biomass would impose a highly competitive environment on species growing in these wetlands. This is especially critical for annual plants that must establish from seeds each year, while competing perennials would benefit from prior year's belowground resources. *A. virginica*'s de-

TABLE 4. Summed elasticities for each column (i.e., stage/age class) in the elasticity matrix for each year and vegetation treatment.

Stage/age class	1998		1999	
	Cut plots	Uncut plots	Cut plots	Uncut plots
Seed ₁	1	10	1	32
Seed ₂	0	1	0	14
Adult ₁	98	79	99	23
Adult ₂	1	9	1	18
Adult ₃	0	1	0	14

Notes: All numbers are percentages. Columns may not add to 100% due to rounding error.

TABLE 5. Regression results from randomization of estimated data.

Variable	SS		R^2	df
	Model	Additional		
Vegetation	9186	NA	0.54	1
Date	234	NA	0.01	1
Vegetation and date	9420	245	0.55	2
Vegetation, date, and vegetation \times date	10736	1316	0.63	3

Notes: The dependent variable is $\ln \lambda$. Vegetation is the independent variable for data from either cut or uncut plots. Date is the independent variable for data from 1998 or 1999.

creased population growth rates in the presence of standing vegetation suggest that this plant is a poor competitor, specializing in the colonization of open habitat patches.

Designing conservation plans for a rare plant requires data about which stages in the life cycle contribute the most to the response of population growth rate to competition. Ideally, these measurements would encompass multiple years, due to year-to-year variation in local climate. For *A. virginica*, the mean population growth rates were similar in 1998 and 1999 but, the difference between λ in populations with and without vegetation increased in 1999, compared to 1998. This indicates that year-to-year variation in environmental conditions acts primarily in an interactive fashion with local patch conditions to affect population growth in *A. virginica*. Vegetation removal directly affected seedling establishment, seedling survival to maturity, and seed production. However, seed production changes impacted λ about equally in 1998 and 1999, while the relative contribution of seedling establishment and seedling survival to λ reversed between years. In 1998, of the three parameters, seedling establishment was the least responsive to the treatment. Nevertheless, the difference in seedling establishment made a large contri-

bution to the difference in population growth rates between the treatments because population growth rate was very sensitive to this parameter. In 1999, a large difference in seedling survival and moderate sensitivity of λ to this parameter combined to create the larger contribution. As others have stressed (Ehrlén and van Groenendael 1998, Caswell 2000), these perturbation analyses (sensu Caswell 1997) focus attention on two separate factors (i.e., changes in vital rates or lower-level parameters and the sensitivity of population growth rates to these changes) that combine to impact population growth rates. Management actions may cause a change in vital rates or lower-level parameters, but such actions will not affect population growth rates if λ is not sensitive to the change (Caswell 2000). For example, actions affecting the chance of an adult plant producing adult plants the following year would have a much greater impact on the population growth rate than actions affecting seeds entering a seed bank (Fig. 2).

Our results suggest standing vegetation may affect the population growth of *A. virginica* in several ways. Seedling establishment may increase in cut plots because of increased seed germination under these conditions. Dormancy is often broken in this family when a plug in the seed coat is removed and the seeds imbibe water (Baskin and Baskin 1998). Vegetation removal above dormant seeds would increase the soil temperature variation, expansion and contraction of seeds, and thus facilitate removal of the seed coat plug (J. Baskin, *personal communication*). At the same time, decreased seedling survival and seed production in standing vegetation is consistent with competition for light. *A. virginica* seedlings growing among dense vegetation develop weak and spindly stems (A. Griffith, *personal observation*) and the resulting smaller individuals produce fewer seeds (Griffith and Forseth 2003).

Our life table response experiments showed that all vital rates, except one, changed in response to removal of standing vegetation. In both years, the vital rates for transitions from adult plants to adult plants were affected the most by vegetation removal. However, only one of the lower-level components of the adult to adult transition made a large contribution to λ . The contribution of the $Adult_1$ to $Adult_1$ (B_{A1-A1}) transition was larger than transitions that depend upon a seed bank (B_{A2-A1} and B_{A3-A1}). The impact of the seed bank was small because of the small numbers of seeds emerging

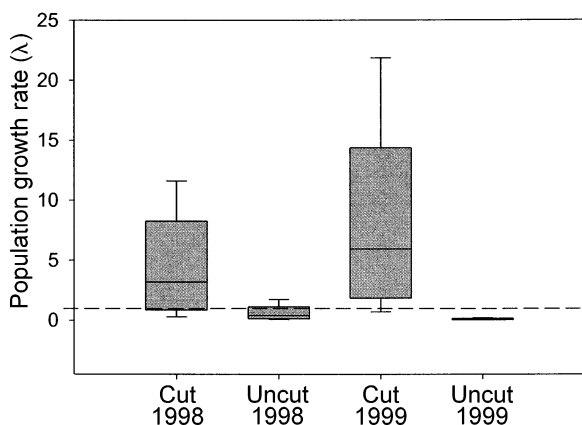


FIG. 4. Box plot of population growth rates (λ) from randomizations of estimated data in 1998 and 1999. The horizontal line in the box is the median value. The top and bottom of the box are 75th and 25th percentiles, respectively. The top and bottom bars are 90th and 10th percentiles, respectively. Some bars are too small to see. The dashed line marks $\lambda = 1$.

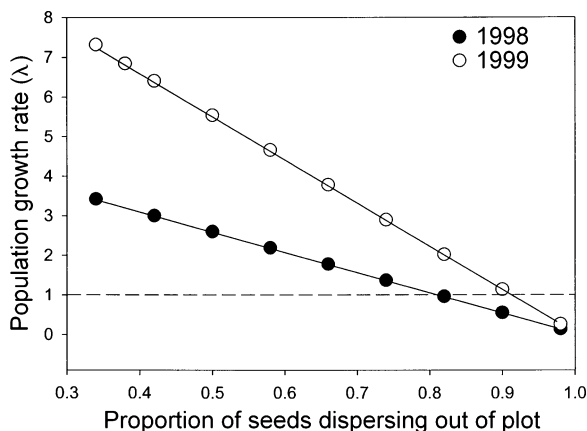


FIG. 5. Population growth rate as a function of simulated increase in dispersal of seeds from a population in which standing vegetation was removed. Results are from mean matrix elements of cut experimental plots in 1998 and 1999.

from the seed bank relative to plants germinating from seeds produced the previous fall. A seed had only a 4% chance of entering the seed bank and then about a 30% chance of surviving and germinating the next spring. Nevertheless, the sensitivity of λ to the emergence of adult plants from a two-year-old seed bank (P_{S2-A2}), can actually be larger than its sensitivity to B_{A1-A1} . This sensitivity will not result in large changes in λ unless the number of first year seeds is low, i.e., unfavorable years for growth or large competitive suppression of adults by interspecific vegetation.

The importance of seeds entering or emerging from the seed bank is made clearer by our elasticity analysis. Only the youngest adult to adult transition had a notable influence on λ in patches with little or no standing vegetation. When the population growth rate was high, the seed bank played practically no role in population growth. But, in lower-quality patches, the importance of the seed bank increased greatly as these seed bank classes had a much greater influence on λ . In the first year, the $Adult_1$ class transitions determined >90% of λ . In the second year, the $Adult_1$ influence on λ dropped to 62% while 30% of the remaining influence was split between the $Seed_1$ and $Adult_2$ stages. These results parallel the results of Kalisz and McPeck (1992). The population growth rate of *Collinsia verna*, a winter annual, increased in one year and then decreased in the following year. During the poor year, the seed bank stages had much larger summed elasticities, when compared to the good growth year of *C. verna*. In general, these results highlight the importance of estimating and modeling seed banks in the population dynamics of annual plants, especially when current year's fecundity is reduced by unfavorable environmental conditions. Short-term seed banks, even those low in absolute number may play a significant role in buffering an annual plant's population changes when fecundities are reduced. This year-to-year variation in stage elasticities

also sheds light on the importance of our assumptions about parameter value equalities (Table 3). As long as the model's parameter values lead to a relatively large elasticity for the $Adult_1$ class, the small elasticity values of the remaining matrix elements means they have very little influence on λ and our assumptions have negligible impacts on matrix projections. But, poor quality habitat patches like those of uncut plots in 1999 produced elasticities that were more evenly distributed among the stage/age classes (Table 5). This means assumptions about parameters will be more likely to produce incorrect projections for those matrices because of the more even distribution of elasticities.

Our simulations showed that the impact of seed dispersal on local population growth rates was minor compared to the impacts of vegetation removal. Seed dispersal would have to increase considerably, up to ~80% of all seeds emigrating, before local populations decrease in size. Similar results to these were found in a matrix model of scallop populations (Barbeau and Caswell 1999), where losses due to dispersal were secondary to losses from predation.

Established population patches may be relatively insensitive to dispersal rates, but metapopulation dynamics may be highly sensitive. For example, increased seed dispersal from local population patches of the forest herb *Primula vulgaris* increased metapopulation growth rates (Valverde and Silvertown 1997). This was due to the connection between increased dispersal and increased colonization of suitable forest patches occupied by *Primula vulgaris*. The patchy distribution of local populations of *A. virginica* in the New Cumberland marsh also comprises a metapopulation. Local populations disappear and reappear from year to year (U.S. Fish and Wildlife Service 1995; A. Griffith, *personal observation*). Since this species appears to be a fugitive species (*sensu* Hutchinson 1951), specializing in disturbed and/or open habitat patches, increases in

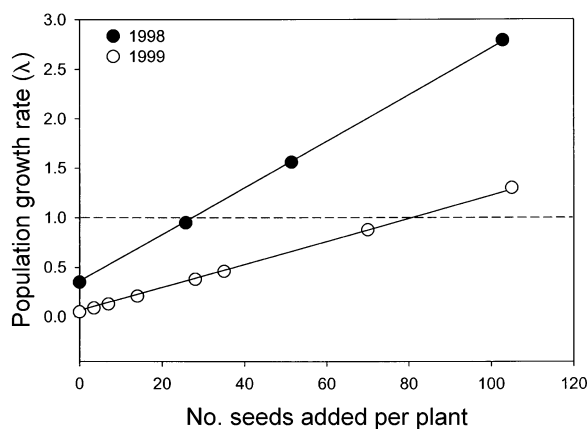


FIG. 6. Population growth rate as a function of simulated seed additions into plots where standing vegetation was not removed. Results are from mean matrix elements of uncut experimental plots in 1998 and 1999.

seed dispersal may be essential to the maintenance of a healthy metapopulation by establishing populations in newly created open patches. *A. virginica* seeds that move into adjacent stream flows have the potential to move significant distances (Griffith and Forseth 2002). Hence, dispersing seeds may leave source population patches and potentially colonize empty habitat patches or augment existing populations. Since populations in high quality, open patches can place a high percentage of their seeds into this floating seed pool and continue to grow in size, they may act as source populations (Watkinson and Sutherland 1995, Hanski and Simberloff 1997) in a metapopulation.

Conservation and management

One effective management approach may be to restore or increase natural patch creation processes in freshwater tidal wetlands. This would increase the number of high quality sites for the establishment of local population patches of *A. virginica* that, in turn, would serve as source populations in the regional metapopulation. There are a variety of methods that could be used to increase the availability of open habitat patches. In areas where human populations are not a constraint, natural disturbance regimes could be reestablished. This may include the establishment or promotion of animal populations, such as muskrat, that create openings in the marsh, and reduction of flood control measures to increase variability in stream flow rates. In areas where these measures are impractical, manual removal of common dominants in small, spatially dispersed patches may be more practical.

Our matrix models show that adding seeds to plots with established vegetation would be an ineffective means of promoting the continued existence and/or expansion of this plant. Additions of seeds produced in the greenhouse or in a common garden have the added problem of placing unknown genes into existing or established populations. Little is known about the population genetics of *A. virginica* (but see Carulli and Fairbrothers 1988) and additions of unknown genes could dilute genes or gene combinations important for any local adaptations (Templeton 1986, Hogbin and Peakall 1999). However, artificial seed dispersal of local seed stock to suitable, open habitat patches may be an effective way of establishing new population patches and extending the range of the current metapopulation.

The removal of standing vegetation in known *A. virginica* populations would increase population growth rates by increasing the number of plants surviving to reproduce, as well as, the average fecundity of each surviving plant. Additionally, the removal of standing vegetation in potential *A. virginica* populations may help establish a viable population with the addition of only a few *A. virginica* seeds. If material and human resources are limited, our results suggest that removal of standing vegetation would be the most efficacious

step in the conservation and management of *A. virginica* populations. Vegetation removal impacts seedling establishment, seedling survival, and seed production which in turn make a large contribution to increasing λ , relative to seed additions.

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APPENDIX

A characteristic equation of an annual plant matrix model and solutions of the implicit differentiation of this characteristic equation with respect to the lower-level parameters that make up matrix elements is available in ESA's Electronic Data Archive: *Ecological Archives* A015-006-A1.