Comparing the direct and community-mediated effects of disturbance on plant population dynamics: flooding, herbivory and *Mimulus guttatus*

BRET D. ELDERD and DAN F. DOAK*

*Center for Integrating Statistical and Environmental Science, University of Chicago, Chicago, IL 60637, USA, and *Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA*

Summary

1 Competition, trophic interactions and abiotic disturbances play important roles in governing plant population dynamics, yet few studies have addressed their relative contributions or interacting effects.

2 We used Life Table Response Experiment (LTRE) analysis, coupled with stochastic analyses, to examine how a major abiotic disturbance, flooding, influences the fitness and population growth of a common riparian plant, *Mimulus guttatus*, and how this effect compares and interacts with that exerted by herbivory.

3 We also extended LTRE analysis to include nested factors, which enabled us to examine differences across experimental sites. These spatial contributions to changes in population growth rate, λ, were compared and contrasted with those derived for year and experimental treatments.

4 Flooding had direct positive impacts on population growth, while protection from herbivory benefited plants in both flooded and non-flooded areas. Spatial variation in plant performance was also substantial, with greater variation across experimental sites than temporal variation across years.

5 Our stochastic analysis revealed that the impact of herbivores on population growth was much greater when the environment fluctuated between years with and without flooding than in more constant environments.

6 Both flooding and herbivory exerted the majority of their impacts on plant performance via changes in adult summer survival. For flooded sites, this was surprising, given the small difference in summer survival between control and herbivore-exclusion treatments, and results from the high sensitivity of population growth to adult survival.

7 The importance of herbivory in flooded sites would have not been discerned had we not considered how adult survival interacts with other stages of the *M. guttatus* life cycle. Thus, in order to increase ecological understanding associated with shifts in community dynamics, experimental results should be placed in a life-history context.

8 Within disturbance-driven systems, the direct abiotic effects of factors such as flooding play a critical role in determining population dynamics. However, the biotic interactions that change as a consequence of disturbance can have equal and lasting impacts on population growth.

Key-words: disturbance, flooding, herbivory, matrix models, *Mimulus guttatus* DC, nested LTRE

Correspondence: Bret D. Elderd, Department of Ecology and Evolution, University of Chicago, Chicago, IL, USA (tel. +1 773 834 7690; fax +1 773 702 9740; email belderd@uchicago.edu).

Introduction

The importance of disturbance for maintaining community composition has been studied in a variety of ecosystems (Paine & Levin 1981; White & Pickett 1985; Hobbs & Mooney 1991; Wootton *et al.* 1996). In many

of these systems, either increasing or decreasing disturbance changes overall community structure (Sousa 1979; Collins 2000; Shafroth *et al*. 2002), which, in turn, can ultimately affect community and population dynamics in two different ways. Disturbance can directly impact populations via an abiotic pathway dictated by the type of disturbance. For instance, a hurricane can clear an area and allow for the colonization by plant species that require new light gaps (Pascarella & Horvitz 1998). Disturbance can also indirectly affect community and population dynamics via biotic pathways. For example, changes in the herbivore community in flooded and non-flooded areas have been shown to be a potential limiting factor for riparian plants (Elderd 2005). Because disturbances can dramatically shift community structure and composition, these indirect influences of disturbance are likely to have a substantial influence on population dynamics (Menges 1990; Silva *et al*. 1990; Gross *et al*. 1998), either re-enforcing or weakening direct disturbance effects. However, disentangling these effects has seldom been examined at the level of population growth (but see McEvoy & Coombs 1999).

The importance of disturbance for maintaining community composition (Elderd 2003) and determining population dynamics (Menges 1990; Rood *et al*. 1998; Smith *et al*. 2005) is especially crucial in floodplains. Flooding within the riparian zone directly affects both community composition and population dynamics by providing increased water availability and by scouring riparian bank-side communities. Those species that can withstand frequent disturbance and survive the impacts of scouring during annual floods will flourish. Conversely, control of flooding through engineered structures such as dams can decrease both the frequency and the magnitude of flooding, allowing a different suite of species to colonize riparian areas (Elderd 2003) and potentially altering community interactions. This, in turn, can change community composition, ultimately excluding some species from the riparian area. Within riparian zones, these indirect biotic effects can have a dramatic impact on species survival (Elderd 2005) and potentially on population growth rate. By understanding the degree to which abiotic and biotic factors impact population growth rates, a better understanding of disturbance and community interactions can emerge.

Changes in the herbivore community represent an important biotic pathway by which flooding can impact riparian plants. In many non-flooded areas, grasshoppers (Order: Orthoptera), which are often negatively impacted by increased moisture (Dempster 1963; Ritchie 2000), comprise an important element of the herbivore community. By contrast, leafhoppers (Family: Cicadellidae) are a major component of the insect community in riparian floodplains (Elderd 2002). Thus, flooding creates a spatial mosaic of insect herbivore community types that may differentially affect plant growth and survival.

In order to determine the impacts of abiotic and biotic factors on population-level processes, we conducted a series of field and glasshouse experiments along with a suite of field surveys on the growth, survival and reproduction of a common riparian species, *Mimulus guttatus* (Family: Scrophulariaceae), the common large-leafed monkeyflower, under flooded and non-flooded conditions. For large-scale experimental designs, such as those addressing flooding, nested designs are often used and typically analysed only with conventional statistical techniques. To estimate the population-level implications of year, differences in flooding between experimental areas, herbivory manipulations and site contributions to changes in population growth rate, λ, we extended Life Table Response Experiment (LTRE) analysis methods (Caswell 2001) to include nested designs. Using both LTRE analysis and stochastic demographic analyses, we estimated the separate and interacting impacts of changes in herbivore community and flooding probability on population growth rate, allowing assessment of both abiotic and biotic contributions of flooding to changes in population growth.

Materials and methods

STUDY SYSTEM AND SPECIES

All experimental and survey work was conducted at the University of California Natural Reserve System's Sagehen Creek Field Station (39°25′ N, 120°14′ W) located 14 km north of Truckee, CA, at an elevation of 1920 m. Snowmelt during the late spring and early summer provides most of the base-flow for the creek and is responsible for the annual flooding experienced within the basin. The degree or magnitude of the flood will depend upon the previous season's snowpack and the length of the snowmelt period.

The focal species, *M. guttatus*, occurs throughout western North America (Vickery 1978). *M. guttatus* can be a facultative annual or perennial depending upon water availability and can reproduce either sexually or vegetatively (Hickman 1993). Within Sagehen Basin, *M. guttatus* is a perennial species (Elderd, personal observation). This species has widely scattered populations that occur in moist meadows and along streams (Grant 1924). It is a colonizing plant that readily invades recently disturbed riparian habitats (Vickery 1978) and is extremely common along riparian areas in California (Caicco 1998).

Flooding along Sagehen Creek strongly shifts the composition of the arthropod community, with the herbivorous insect and predator guilds dominated by leafhoppers and wolf spiders in flooded areas, and by grasshoppers and ants in non-flooded areas, respectively (Elderd 2005). The main vegetative difference between flooded and non-flooded sites is due to changes in dominant graminoid species and not overall cover. Flooded sites are dominated by *Carex nebraskansis* and non-flooded sites contain mostly *Poa* spp. (Elderd, unpublished data).

To test the contributions of both flooding regime and insect herbivores on *M. guttatus* population growth, we established experimental *M. guttatus* populations in flooded and non-flooded areas and manipulated trophic structure during 2000 and 2001. We randomly choose three 5×5 m naturally flooded and three 5×5 m non-flooded sites prior to the 2000 field season (Elderd 2005). Flooded sites were at least 200 m apart, whereas non-flooded sites were located at least 100 m apart. Although flooded sites experienced annual inundation, none was impacted by flood scouring. Within each site, we established a grid of nine 1-m² plots, each separated by 1 m from adjacent plots and transplanted three *M. guttatus* seedlings into each plot. Seedlings were spaced 50 cm apart within the plots.

Seedlings were derived from seed capsules that were collected during September 1999 and 2000 from seven distinct populations spread throughout the Truckee and Lake Tahoe Basins. Once collected, capsules were stored for 1 week at 0 °C to kill any herbivore larvae present. Seeds were separated from individual capsules and pooled within each population. An equal number of seeds from each population was randomly selected and combined to create a seed pool representing all populations. The following spring, seeds were germinated and grown under glasshouse conditions for 2 weeks before being transferred to Sagehen Creek Field Station. Seedlings were maintained in plug trays at Sagehen Creek for 3 weeks before planting to ensure acclimatization to local conditions.

Each plot randomly received one of three manipulations: exclusion of non-flying predators; exclusion of both predators and herbivores; or control. In 2001, we added three cage control plots, consisting of predator/herbivore barriers with 10-cm openings along two sides, at each site. For the current analysis, we used only data from the control and predator/herbivore-exclusion plots, referred to hereafter as herbivore-exclusion plots. To exclude non-flying predators, we surrounded plots with a 10-cm-tall tanglefoot- (The Tanglefoot Company, Grand Rapids, MI, USA) covered aluminium barrier. To exclude herbivores, we applied a 1.25 g L⁻¹ solution of Orthene® (Valent USA, Walnut Creek, CA, USA) each week to individual plants. Orthene protects plants from a wide spectrum of herbivores (Doak 1992) and does not affect *M. guttatus* growth (Elderd, unpublished data). All plots that did not receive the Orthene treatment received a water control treatment. To remove errant arthropods from herbivore control treatments, plots were swept with a modified leaf vacuum weekly. In order to control for the impacts of vacuuming on the overall arthropod community within each plot, we also swept each control plot on the same schedule; thus, the measured effects of herbivory are probably conservative due to the need for herbivores to re-establish in these plots on a weekly basis. Because non-flooded sites are far more water-limited than sites that experience annual flooding within Sagehen Basin, we also partially alleviated water stress by daily watering of all sites, again making our estimate of treatment effects conservative.

Experiments were initiated on 26–27 June 2000 and 28 June 2001. They were conducted for 7 weeks during which survival, growth and flowering of transplanted *M. guttatus* were recorded weekly. In a previous analysis of the experimental treatment on plot-level mean rates of survival, results showed that flooded herbivore-exclusion plots were not significantly different from control plots, whereas there were significant effects of treatments at non-flooded sites that varied between years (Elderd 2005). However, these data had been analysed by year due to differences in levels of exclusion treatments across years. A simpler analysis, which pooled across years and life-history stages of seedling and adult survival (see Estimating parameters), showed that the main effects of flooding, herbivore exclusion, the nested effect of site within flooding and the interaction between flooding and herbivore exclusion were all significant (Year: $F_{1,48} = 0.04$, $P = 0.8495$; Flood: $F_{1,4} = 12.99$, $P = 0.0227$; Exclusion: $F_{1,48} = 40.42$, $P < 0.0001$; Flood × Exclusion: $F_{1,4} = 18.93$, $P = 0.0122$; Site(Flood): $F_{4,48} = 5.18$, $P = 0.0015$), with varying effects on the contrast between herbivore exclusion and control plots. No other higher order interactions were significant. From these experiments, we also derived field germination rates by placing 50 *M. guttatus* seeds in control and experimental plots at the end of the field season and resurveying these plots the following spring. Overall, these experiments provided estimates for germination, oversummer survival and growth measurements (Table 1).

Field surveys provided data for overwintering survival, fruit production and seed number per fruit (Table 2). For these surveys, individual *M. guttatus* plants were followed for up to 3 years. In August 2000 after seed set had occurred, 90 individual plants were marked along a 2.5-km stretch of Sagehen Creek. An individual was selected if it was a clearly defined individual (i.e. there were no apparent connections to mother or daughter plants). Each plant was then identified as either a rosette or a flowering individual. The number of fruits on each surveyed flowering plant was also recorded. In June 2001, we resurveyed the plants to determine overwinter survival. In August 2001, we marked an additional 81 plants and resurveyed the original individuals. In June 2002, we resurveyed the entire marked population. Because there was no appreciable difference in rosette and flowering plant survival, these data were pooled to estimate overwintering survival. Estimates of seeds per fruit were obtained by counting the seeds contained within 50 seed capsules taken from multiple populations throughout Sagehen Basin.

Because seed banks can contribute to population growth, especially for species that inhabit environmentally variable areas (e.g. Kalisz & McPeek 1993), we

Table 1 Variable vital rates used in LTRE calculations for flooding and herbivore-exclusion treatments and stochastic calculations of population growth rate (λ) that were derived from field experiments. Experimental sites were either flooded or non-flooded and herbivores were either allowed access (Control) or denied access (Exclusion) to plots. Note that germination rates were calculated by pooling across herbivore exclusion treatments and years. The sample size for seedling survival, growth of seedlings, oversummer survival was constant across treatments ($n = 18$ plots) except for Non-Flood Control sites where limited survival decreased sample sizes for growth of seedling ($n = 9$ plots) and oversummer survival ($n = 6$ plots). The sample size for germination estimates across years and treatments was 6 plots

| Parameter | Description | Experimental Treatments | | | | | | | |
| | | Flood Control | | Flood Exclusion | | Non-Flood Control | | Non-Flood Exclusion | |
		Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance
G	Germination rate	0.229	0.0994	0.229	0.0994	0.010	0.0002	0.010	0.0002
S_N	Survival of seedlings	0.944	0.0163	1.000	0.0000	0.315	0.1500	0.889	0.0523
G_N	Growth of a seedling to a flowering adult	0.019	0.0062	0.0074	0.0203	0.000	0.0000	0.018	0.0062
S_S	Oversummer survival of adult plants	0.963	0.0116	1.000	0.0000	0.556	0.2222	0.815	0.1206

Table 2 Variable vital rates used in all matrices to calculate LTRE effect size and stochastic population growth rate (λ) that were derived from field surveys (S_W, G_R, S_T, F_R and D) and glasshouse experiments (S_D). Field survey rates were calculated by marking 90 individual plants in 2000 and 81 plants in 2001. For glasshouse experiments, sample size was 15

Parameter	Description	Mean	Variance
S_D	Annual survival of seeds in the seed bank	0.534	0.0064
S_W	Overwinter survival	0.479	0.0216
G_R	Growth of a rosette to a flowering adult	0.416	0.0112
S_T	Probability of staying a flowering adult	0.834	0.0370
F_R	Number of fruits produced	11.2	176.89
D	Number of seeds produced	258.8	47921.24

© 2006 The Authors
Journal compilation
© 2006 British
Ecological Society,
Journal of Ecology,
94, 656–669

obtained seed bank viability estimates from a glasshouse experiment using stored *M. guttatus* seeds (Table 2), which do not have prolonged dormancy (Waser *et al.* 1982), collected from multiple populations throughout the Sierra Nevada from 1998 to 2000. Seeds for each year were collected from separate populations, pooled and mixed according to the same methodology used in the field experiment. For each individual year from 1998 to 2000, we set up five Petri dishes with Whatman® filter paper (Whatman Inc., Clifton, NJ, USA) and placed 50 seeds in each dish. The dishes were kept moist, and we recorded the number of seeds germinated for 5 weeks. Because estimating long-term viability of the seed bank from stored seeds may over- or underestimate seed viability *in situ* depending upon the length of time stored (Baskin & Baskin 1998), we also examined the impact of changes in the estimate of seed-bank longevity on population growth.

THE POPULATION PROJECTION MODELS

To delineate the abiotic and biotic contributions of flooding to changes in *M. guttatus* population growth, we constructed a set of matrix models, which depended upon year, site, flooding treatment and herbivore exclusion and took the general form of:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t \qquad \text{eqn 1}$$

where $\mathbf{n}_t$ is a vector of population stage abundances at time t and $\mathbf{A}$ is a standard population projection matrix composed of two seasonal matrices, which project the population through winter, $\mathbf{W}$, and summer, $\mathbf{S}$, seasons, such that:

$$\mathbf{A} = \mathbf{S}\mathbf{W}. \qquad \text{eqn 2}$$

Both seasonal matrices are composed of three stages (seeds, rosettes and flowering plants) and together encompass 11 vital rates (Tables 1 & 2) over a single-year time step.

The winter projection matrix, $\mathbf{W}$, is composed of the overwintering survival rates for seeds and adult plants (see Table 2 for an explanation of vital rate terms) and takes the form of:

$$\begin{pmatrix} S_D & 0 & 0 \\ 0 & S_W & 0 \\ 0 & 0 & S_W \end{pmatrix}.$$

The summer projection matrix, $\mathbf{S}$, is composed of the summer survival rates, probabilities for growing or shrinking into the adjacent stage class depending on

the stage and flowering plant fertility (see Tables 1 & 2 for an explanation of vital rate terms), i.e.

$$\begin{pmatrix} 1-G & 0 & S_S F_R D R_D \\ G S_N S_S (1-G_N) & S_S(1-G_R) & S_S(1-S_T) \\ G S_N S_S G_N & S_S G_R & S_S S_T \end{pmatrix}.$$

where R_D represents the percentage of seeds retained at the site. For our analysis, we used a density-independent model, which was a reasonable assumption for this system, given that disturbance is likely to limit the impacts of density dependence.

In constructing these models, we made three further simplifications due to limited data. First, although *M. guttatus* can reproduce vegetatively via side stems, we did not quantify vegetative reproduction in the matrix model. In control sites, each plant produced, on average, 2.0 ($\pm$ 0.37 SE) side stems in flooded areas and 0.9 ($\pm$ 0.66 SE) side stems in non-flooded areas over the summer (Elderd, unpublished data). However, converting these estimates into number of individuals would have involved some conjecture about overwinter survival, summer survival and growth. Because the goal of the analysis was to estimate differences between treatments in population growth rate, not including vegetative reproduction represented an underestimation of growth rate for flooded areas. Second, we had no estimate of the rate of seed loss due to dispersal away from suitable sites. *M. guttatus* seeds are extremely small and readily disperse via wind and water (Waser *et al.* 1982). We included seed dispersal in the fertility transition portion of the matrix and used the flooded control treatment matrix as a base matrix, setting seed dispersal rate to 98%. This is equivalent to a seed retention rate of 2%, which reflected a moderately growing population for flooded control areas (i.e. flooded sites where herbivores were allowed access to the plots) under the stochastic analysis. Seed retention rate was set at the same constant in all other matrices constructed, although we did investigate the impacts on our analysis of increasing or decreasing this rate. Third, we also assumed no seed immigration to a site. In general, these assumptions represent a relatively conservative estimate of the contributions of flooding.

ESTIMATING PARAMETERS

Estimates for the vital rates used in the analysis came from experimental treatments (Table 1) as well as field surveys and glasshouse experiments (Table 2). Estimates for germination rate, seedling survival, growth from seedling to adult and summer survival were derived from experimental data by calculating means and variances across experimental sites using the overall plot means within a site (Table 1). Seedling survival was defined as the probability of surviving the first 2 weeks after transplanting. For the analysis, germination was calculated as the mean germination rate for flooded and non-flooded areas across herbivore treatments as

no germination occurred in non-flooded control plots and the effects of the herbivore-exclusion treatment probably had a limited effect on germination rate. We also pooled across sites to increase sample size for the mean and variance estimates. To obtain an estimate of annual survival of seeds in the seed bank, we used the same approach as Gross *et al.* (1998), regressing percentage germination in the glasshouse experiment by year of seed collection and calculating the point in time where seeds had a low probability of germinating (i.e. 0.001). This resulted in an annual survival rate of 0.534 (Table 2) and corresponded to 11-year viability for the seed bank. We also examined the impact of decreasing seed-bank viability to 2 years and increasing viability to 20 years. Variance for this vital rate was calculated by using the mean squared error of the regression with respect to time. All other vital rate estimates for the analysis were taken from the survey data by calculating the mean and variance across survey years. Additionally, the mean and the variance for the survey data and field germination rates were corrected for potential sampling variation using Kendall's method (Kendall 1998). Without this correction, we could have overestimated the variance associated with each of these vital rates and may have also obtained a biased estimate of the mean.

SENSITIVITY AND ELASTICITY ANALYSIS

For each of the matrices, we conducted a basic sensitivity and elasticity analysis (Caswell 2001; Morris & Doak 2002). Sensitivity analysis quantifies the impacts of changes in a particular matrix element, a_{mn}, or vital rate, v_p, on the matrix's dominant eigenvalue, λ, where m and n represent the row and column of the matrix, respectively, and p serves as an index of vital rates. The dominant eigenvalue is defined as the long-term population growth rate for the matrix once a stable age or stage distribution has been reached. Given that we estimated vital rate sensitivity using the full matrix, **A**, rather than calculating matrix element sensitivity, we did not need to use standard periodic methodology (Caswell & Trevisan 1994; Lesnoff *et al.* 2003) but rather relied on lower-level parameter or vital rate analysis (Caswell 2001; Morris & Doak 2002). Elasticity analysis reweights the sensitivity of the matrix element or vital rate to changes in λ to allow comparison across both fertility rates and survival probabilities. Here, we present only elasticity values.

LTRE ANALYSIS

LTRE analysis allows for a direct retrospective examination of the contributions of individual experimental treatments on λ (Caswell 2000). For this analysis, in which experimental sites were nested within flooding, we used a fixed effect nested design model to calculate response factors properly. The LTRE nested design, elaborating on Caswell's notation (Caswell 2001) for

a single factor linear model, consisted of the linear equation:

$$\lambda^{ijkl} = \lambda^{\cdots} + \alpha^i + \beta^j + \alpha\beta^{ij} + \gamma^k + \theta^{l(i)} \qquad \text{eqn 3}$$

where $\lambda^{\cdots}$ is the dominant eigenvalue for the overall mean matrix, $\mathbf{A}^{\cdots}$, of all treatments, α^i, β^j and γ^k represent the main effects of flooding i, herbivore exclusion j and year k, respectively. $\alpha\beta^{ij}$ denotes the interaction between flooding and herbivore exclusion ij, and $\theta^{l(i)}$ corresponds to the nested effects of site l within flooding treatment i. Because no higher-order interactions were significant in an analysis of survival, we did not include them in our LTRE analysis (eqn 3). The above equation can be rearranged to provide an estimate of the contributions of each effect to changes in population growth rate. These subsequent equations can be given by:

$$\hat{\alpha}^i = \lambda^{i\cdots} - \lambda^{\cdots} \qquad \text{eqn 4}$$

$$\widehat{\alpha\beta}^{ij} = \lambda^{ij\cdot\cdot} - \hat{\alpha}^i - \beta^j - \lambda^{\cdots} \qquad \text{eqn 5}$$

$$\hat{\theta}^{l(i)} = \lambda^{i.l} - \lambda^{i\cdots} \qquad \text{eqn 6}$$

where eqn (4) represents the main effect of flooding, eqn (5) describes the interaction between flooding and herbivore exclusion, and eqn (6) calculates the nested effect of site within flooding. In eqs (4) and (6), $\lambda^{i\cdots}$ is the dominant eigenvalue of a matrix constructed of mean values over all other factors, given flooding i; λ^{ij} and $\lambda^{i.l}$ are defined similarly. Note that eqn (4) can be considered a general main effect equation and β^j and γ^k, along with the corresponding λs, could be easily substituted for α^i. In general for eqns (4)–(6), the greater the treatment's contribution, the greater the change in λ will be, which, in turn corresponds to a greater impact on population growth rate.

Just as λ for a single matrix can be decomposed into the impacts of particular matrix elements or vital rates on λ via either sensitivity or elasticity analysis, the same is true for LTRE analysis. The contribution of a particular factor to changes in λ can be calculated as the sum of the impacts of individual matrix elements on λ:

$$\tilde{\alpha}^i = \sum_{m,n} (a_{mn}^{i\cdots} - a_{mn}^{\cdots}) \frac{\partial\lambda}{\partial a_{mn}} \bigg|_{\frac{1}{2}(\mathbf{A}^{i\cdots} + \mathbf{A}^{\cdots})} \qquad \text{eqn 7}$$

$$\widetilde{\alpha\beta}^{ij} = \sum_{m,n} (a_{mn}^{ij\cdots} - a_{mn}^{\cdots}) \frac{\partial\lambda}{\partial a_{mn}} \bigg|_{\frac{1}{2}(\mathbf{A}^{ij\cdots} + \mathbf{A}^{\cdots})} - \tilde{\alpha}^i - \tilde{\beta}^j \qquad \text{eqn 8}$$

$$\tilde{\theta}^{l(i)} = \sum_{m,n} (a_{mn}^{i.l} - a_{mn}^{i\cdots}) \frac{\partial\lambda}{\partial a_{mn}} \bigg|_{\frac{1}{2}(\mathbf{A}^{i.l} + \mathbf{A}^{i\cdots})} \qquad \text{eqn 9}$$

where the main effects such as $\tilde{\alpha}^i$ are evaluated at the mid-point between the mean matrix for treatment $\mathbf{A}^{i\cdots}$ and the overall mean matrix $\mathbf{A}^{\cdots}$. Note that similar to eqn (4), β^j and γ^k, along with the corresponding matrix elements and mean matrices, could be easily substituted

for α^i in eqn (7). The interaction, $\alpha\beta^{ij}$, is evaluated at the midpoint between the interaction matrix $\mathbf{A}^{ij\cdots}$ and the mean matrix $\mathbf{A}^{\cdots}$ minus the main effects of the flooding and herbivore-exclusion treatments. The nested effect is evaluated at the midpoint of the matrix for each site $\mathbf{A}^{i.l}$ and the mean matrix for flooding $\mathbf{A}^{i\cdots}$. For $\tilde{\alpha}^i$, $a_{mn}^{i\cdots}$ is defined as the mean matrix element for flooded or non-flooded areas across herbivore-exclusion treatments, year and site and $a_{mn}^{\cdots}$ is the mean matrix element across all factors. For $\alpha\beta^{ij}$, we need to only define $a_{mn}^{ij\cdots}$, which is the matrix element for the interaction between herbivore-exclusion treatment and either the flooded or non-flooded effect. For $\theta^{l(i)}$, $a_{mn}^{i.l}$ is the mean matrix element for site l nested within flooding. Equation (9) is a modified version of the formula presented by Caswell (2001, section 10.1.2) that accounts for the nested design of the experiment. The above equations are basically composed of two parts – the difference in the matrix elements between the treatment matrix and the mean matrix and the sensitivity of the matrix element as evaluated at the midpoint between the two reference matrices.

Equations (7)–(9) can be further decomposed into the sum of impacts of a particular vital rate on λ:

$$\tilde{\alpha}^i = \sum_{m,n} \sum_p (v_p^{i\cdots} - v_p^{\cdots}) \frac{\partial\lambda}{\partial a_{mn}} \frac{\partial a_{mn}}{\partial v_p} \bigg|_{\frac{1}{2}(\mathbf{A}^{i\cdots} + \mathbf{A}^{\cdots})} \qquad \text{eqn 10}$$

$$\widetilde{\alpha\beta}^{ij} = \sum_{m,n} \sum_p (v_p^{ij\cdot\cdot} - v_p^{\cdots}) \frac{\partial\lambda}{\partial a_{mn}} \frac{\partial a_{mn}}{\partial v_p} \bigg|_{\frac{1}{2}(\mathbf{A}^{ij\cdot\cdot} + \mathbf{A}^{\cdots})} - \tilde{\alpha}^i - \tilde{\beta}^j \qquad \text{eqn 11}$$

$$\tilde{\theta}^{l(i)} = \sum_{m,n} \sum_p (v_p^{i.l} - v_p^{i\cdots}) \frac{\partial\lambda}{\partial a_{mn}} \frac{\partial a_{mn}}{\partial v_p} \bigg|_{\frac{1}{2}(\mathbf{A}^{i.l} + \mathbf{A}^{i\cdots})} \qquad \text{eqn 12}$$

where $\tilde{\alpha}^i$, $\widetilde{\alpha\beta}^{ij}$ and $\tilde{\theta}^{l(i)}$ are now evaluated with respect to the vital rates instead of the matrix elements. For eqn (10), $v_p^{i\cdots}$ is defined as the mean vital rate for flooded or non-flooded effects across herbivore-exclusion treatments and $v_p^{\cdots}$ is the mean vital rate across all treatments. For eqn (11), $v_p^{ij\cdot\cdot}$ is defined as the vital rate for the interaction between the flooding and the herbivore-exclusion treatment and in eqn (12), $v_p^{i.l}$ is the mean vital rate for an individual site nested within either the flooded or the non-flooded effects. Note again that eqn (10) can be considered a general main effect equation and β^j and γ^k along with the corresponding vital rates and mean matrices could be easily substituted for α^i. Thus, eqns (10)–(12) can be used to calculate the individual contributions of a particular vital rate to changes in λ given the difference in vital rates between the mean and experimental matrix and the sensitivity of the weighted matrices to changes in that vital rate.

Cooch *et al.* (2001) point out that decomposition of λ with respect to vital rates using the mean matrix estimates of sensitivity can either overestimate or underestimate the contributions of a treatment due to Jensen's inequality. To guard against these potential

problems, we evaluated the sensitivity matrix for each LTRE contribution using the mean vital rates rather than the mean of the matrix elements. Thus, for this study, we present the vital rate element analysis such that all sensitivities are evaluated at the mid-point between vital rate estimates. For example, in eqn (7), $\frac{1}{2}(\mathbf{A}^{i\cdots} + \mathbf{A}^{\cdots})$ is actually composed of vital rates and takes the form of $\frac{1}{2}(\mathbf{v}^{i\cdots} + \mathbf{v}^{\cdots})$, where $\mathbf{v}$ represents a vector of vital rates. However, we also calculated the contributions of vital rates to changes in λ using the mean matrix approach and found that there was no appreciable difference. This suggests that using a matrix composed of mean elements would also provide a good first-order approximation of the impacts of treatments.

STOCHASTIC SIMULATION MODELS

We simulated environmental stochasticity by means of random draws from the distribution of each vital rate. Variability in all survival, growth and germination probabilities was modelled using beta distributions with estimated means and variances, while the number of fruits produced per flowering plant was modelled with a log-normal distribution. The number of seeds per fruit was simulated with a stretched-beta distribution to enforce realistic constraints on maximum values (Morris & Doak 2002).

In creating each annual matrix, we also included the covariance structure of the vital rates (Morris & Doak 2002: chapter 8). Because our surveys and experiments were limited to two intervals, we could not estimate this temporal correlation structure directly. Instead, emulating the previous sins of others and of ourselves (e.g. Doak *et al*. 1994; Gross *et al*. 1998), we used the observed spatial correlation structure across field experiment sites to estimate temporal correlations. However, perennial plants have been shown to differ in their response to spatial and temporal variation (Jongejans & de Kroon 2005). Therefore, this assumed equivalency between spatial and temporal covariance patterns should not be regarded lightly. The spatial correlation structure between vital rates was only estimated for parameters derived from field experiments. All other correlations were set to 0. We also ran the projection matrices with no correlation structure, and the results did not appreciably change.

In order to estimate the impacts of herbivores on population growth rate in a variable environment, we constructed two sets of simulations that took advantage of the data from the experimental treatments. One set of simulations used the data from the flooded and non-flooded herbivore-exclusion plots and the other used data from the flooded and non-flooded control plots, where herbivores were allowed access. For each of these simulations, we pooled our data across years and varied the probability of flooding. For example, if the probability of flooding was equal to 1 and we were simulating the control matrices, stochastic matrices would be constructed from the flooded control treat-

ments only. However, if the probability of flooding was 0.5, we would randomly draw a number from a uniform distribution and construct a matrix from the flooded control treatments if the number was < 0.5 otherwise we would construct a matrix from the non-flooded control treatments. For these simulations, the probability of flooding could take on a value of 1.0, 0.9, 0.7, 0.5, 0.3, 0.1 or 0.0.

We began each simulation with a stable stage distribution. This distribution was derived from either the mean control or mean exclusion matrix depending upon the simulation. We ran each simulation for 50 000 years and calculated population growth rate and 95% confidence intervals by using the mean and variance of adjacent simulated years. The equation for calculating the estimated mean of the stochastic population growth rate (Caswell 2001, section 14.3.6) takes the form:

$$\widehat{\log \lambda_s} = \frac{1}{T} \sum_{t=0}^{T-1} \log(N_{t+1}/N_t) \qquad \text{(eqn 13)}$$

where λ_S represents stochastic population growth rate, T denotes the maximum number of years simulated and N_t corresponds to the population at time t. In order to estimate the 95% confidence intervals, we used:

$$\widehat{\log \lambda_s} \pm 1.96 \sqrt{\frac{\sum_{t=0}^{T-1}(\log(N_{t+1}/N_t) - \widehat{\log \lambda_s})^2/(T-1)}{T}}$$

$$\text{(eqn 14)}$$

where the numerator represents the variance of the log of the population growth rate (Caswell 2001, section 14.3.6). All of the above simulations and analyses were conducted in MATLAB version 5.1 (Math Works, Natick, MA, USA).

Results

ELASTICITIES

Across both herbivore treatments, flooding substantially increased λ (Fig. 1). The vital rate element with the highest elasticity was summer survival, S_S, for both flooded matrices and for the non-flooded exclusion matrix (Fig. 1a–c). The non-flooded exclusion matrix (Fig. 1c) also showed a slight increase in the elasticity for seed-bank survival, S_D, and a decrease in all other vital rates as compared with the flooded sites. Exclusion had little effect in flooded plots but elasticities changed dramatically (Fig. 1d) in the non-flooded control plots, compared with the other three treatments. This was emphasized by the increase in the elasticity for seed-bank viability, S_D, which was 20-fold higher than any other vital rate. The same pattern held true if seed-bank viability was increased from 11 to 20 years. If the seed-bank estimate was decreased to 2 years, only the elasticity for non-flooded sites changed appreciably, with overwinter and summer survival becoming paramount. As we increased seed retention rate, R_D, there
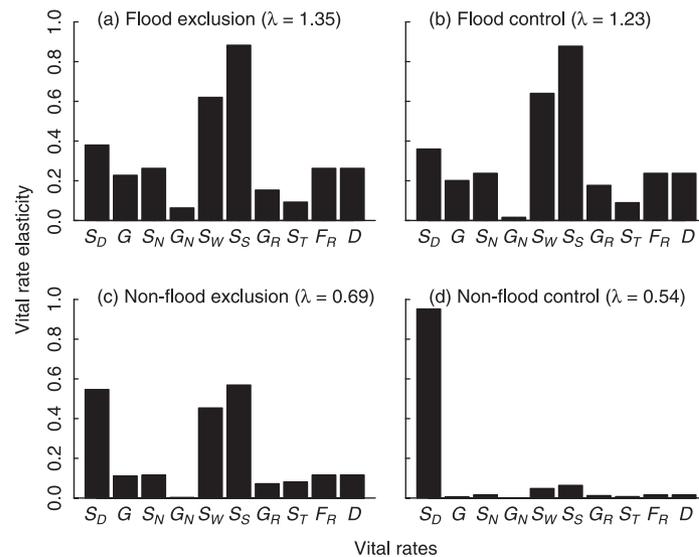
Fig. 1 Elasticity values for vital rates in the matrix model for treatments where a) herbivores were excluded from flooded plots (Flood exclusion), b) herbivores were allowed access to flooded plots (Flood control), c) herbivores were excluded from non-flooded plots (Non-flood exclusion), and d) herbivores were allowed access to non-flooded plots (Non-flood control) with their corresponding dominant eigenvalues (λ). Terms on the x-axis represent seed bank survival (S_D), germination rate (G), seedling survival (S_N), seedling growth to a flowering adult (G_N), overwinter survival (S_W), oversummer survival (S_S), rosette growth to a flowering adult (G_R), staying a flowering adult (S_T), number of fruits produced (F_R), and number of seeds produced (D).

was an appreciable increase in the elasticity of summer survival, S_S, for both flooded treatments and non-flooded herbivore-exclusion treatments; for non-flooded control treatments, the elasticity of summer survival, S_S, also increased, but the elasticity of seed bank survival, S_D, was always larger. Elasticity patterns for year, which are not presented, were similar to the flooded matrices, with summer and winter survival (S_S and S_W, respectively) dominating. Elasticities for site (also not shown) reflected a mixture of exclusion and control matrices nested within flooding. In general, a combination of no flooding and insect herbivory resulted in seed bank survival, S_D, dominating elasticity values, as opposed to larger values for summer and winter survival elasticities in all other treatments.
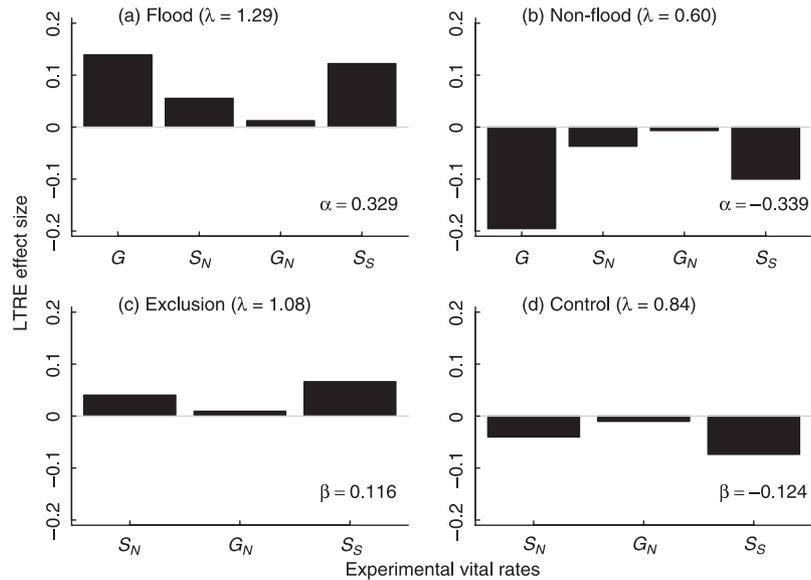
LTRE

Most of the increase in population growth rate between flooded and non-flooded sites arose from the positive contributions of flooding on summer survival and germination rates (Fig. 2a & b). Of an overall difference in the average λ of flooded and non-flooded matrices of 0.69, 32% was accounted for by the difference in summer survival, S_S. This large contribution to changes in population growth occurred in spite of our watering individual plants on a daily basis, which controlled for some of the abiotic factors associated with flooding. A further 48% of the difference in average λ was due to greater germination rates in flooded plots, but no other vital rates had much impact on population growth. In general, flooding positively impacted population growth through recruitment of new individuals and through adult survival.

The abiotic contributions of flooding had a greater impact on λ than did the biotic impacts of herbivores (Fig. 2). However, regardless of flooding, there were positive contributions to changes in λ due to excluding herbivores. Increased summer survival had the largest impact, with a large and positive contribution in exclusion treatments (Fig. 2c), and a large negative contribution in control treatments (Fig. 2d), reflecting the negative impacts of herbivory on plant survival. Across herbivore treatments, 58% of the change in average λ was accounted for by changes in summer survival, S_S, showing that this element was largely responsible for increased population growth rates due to both flooding treatment and insect exclusion.

To gauge the accuracy of these main effects in describing the overall change in λ due to experimental treatments, we summed the absolute value of the individual contributions (Fig. 2) across vital rates and compared these estimates with differences in the observed population growth rate. The observed difference in λ between flooded and non-flooded sites was 0.69 while the sum of all LTRE contributions due to flooding was 0.67. For herbivore exclusion, the observed difference was 0.24 and the sum of the LTRE contributions was also 0.24. Therefore, the main effects of flooding and herbivore exclusion provide excellent approximations to the changes in λ brought about by the experimental treatments and, overall, these two main effects are additive, with no need to account for their interaction.

LTRE analysis of the two other effects, site and year, illustrated differences in spatial and temporal dynamics during the study period. Sites in flooded areas (Fig. 3) were generally similar except for an increase in the importance of seedling growth to flowering adult at a
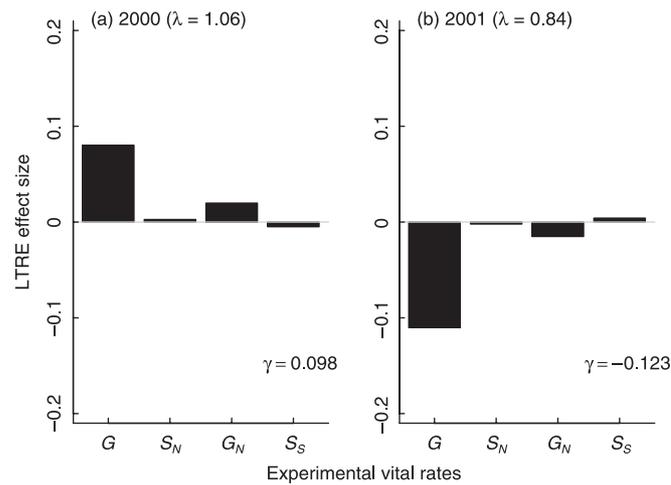
Fig. 2 Life Table Response Experiment (LTRE) analysis for the main experimental treatments of a) flooding, b) non-flooding, c) herbivore exclusion, and d) control treatments where herbivores were allowed access with their corresponding dominant eigenvalue (λ) and total contribution for individual treatments (α and β). Terms on the x-axis represent germination rate (G), seedling survival (S_N), seedling growth to a flowering adult (G_N) and oversummer survival (S_S). All other vital rates were derived from field and glasshouse measurements and did not vary across treatments. Note that germination rate was pooled across exclusion and control treatments and, thus, no contribution due to germination is presented in c and d.
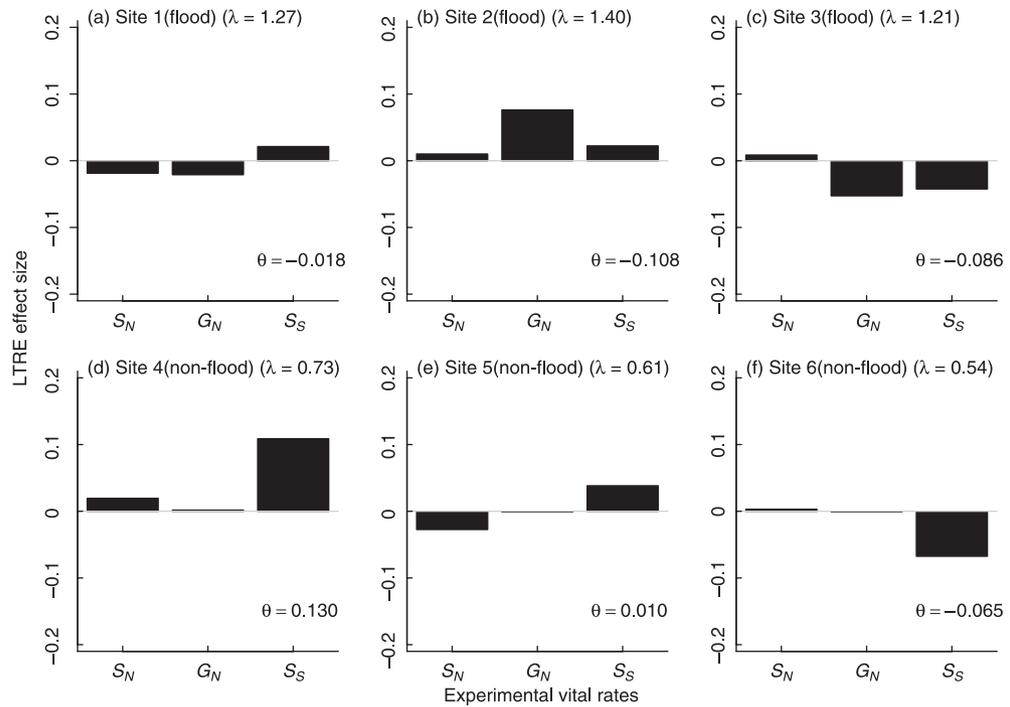

Fig. 3 Life Table Response Experiment (LTRE) analysis for site nested within flooding treatment and their corresponding dominant eigenvalue (λ) and total contribution for individual sites (θ). Sites 1 through 3 (a–c) experienced annual flooding (flood) whereas sites 4 through 6 (d–f) experienced no flooding (non-flood). Terms on the x-axis represent seedling survival (S_N), seedling growth to a flowering adult (G_N) and oversummer survival (S_S). All other vital rates were derived from field and glasshouse measurements and did not vary across treatments.

© 2006 The Authors
Journal compilation
© 2006 British
Ecological Society,
Journal of Ecology,
94, 656–669

single site. For non-flooded sites, site 4 showed a much larger positive contribution of summer survival than did the other two sites (Fig. 3d vs. Fig. 3e & f). The only substantial overall contribution to between-year differences in λ was due to a large increase in germina-

tion rate in 2000 as compared with 2001 (Fig. 4). Comparing the magnitudes of spatial and temporal variation, the overall size of the contributions due to site (Fig. 3) was generally larger than those contributing to annual differences (Fig. 4).

Fig. 4 Life Table Response Experiment (LTRE) analysis by year for a) 2000 and b) 2001 with their corresponding dominant eigenvalue (λ) and total contribution for individual years (γ). Terms on the x-axis represent germination rate (G), seedling survival (S_N), seedling growth to a flowering adult (G_N) and oversummer survival (S_S). All other vital rates were derived from field and glasshouse measurements and did not vary across treatments.
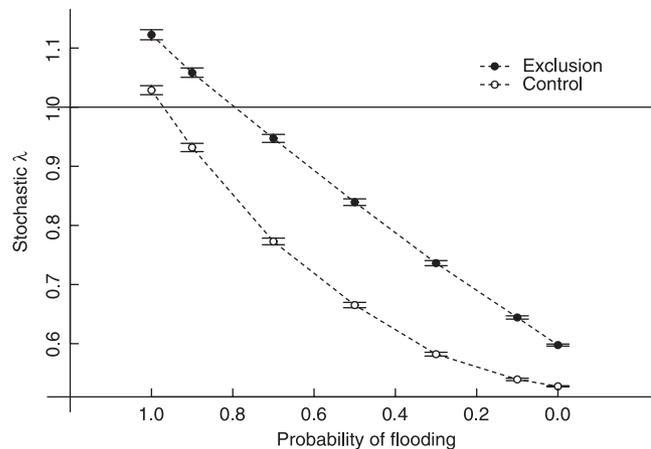
Fig. 5 Stochastic estimates of population growth rate (λ) along with their 95% confidence interval for plots where herbivores were excluded (Exclusion) or allowed access (Control) while varying the probability of flooding. The solid horizontal line represents λ equal to one.

As with the elasticity analysis, our LTRE results are quite robust to changes in seed bank survival, S_D, and seed retention rate, R_D. If we either increased seed bank survival to 20 years or decreased seed retention rate, we saw little change in the size of the LTRE contributions. If we decreased seed bank survival to 2 years, the contribution attributed to germination rate declined and summer survival increased in importance. When we increased seed retention rate, R_D, there was an increase in the overall contribution to changes in λ due to summer survival. Thus, our estimates of both seed bank survival and seed retention rate are relatively conservative with respect to the magnitude of the potential contributions of summer survival to population growth.

STOCHASTIC GROWTH RATES

For both herbivore control and exclusion treatments with flooding, stochastic λ estimates are dramatically lower than the deterministic estimates shown in Fig. 1, due to the high variability in number of fruits and seeds produced. The difference also represents the impact of stochasticity in vital rates derived from field surveys (e.g. overwinter survival, S_W), which were not directly related to experimental treatments. As the probability of flooding decreased, stochastic λ-values decreased and there was also a decline in the variance of λ (Fig. 5). For all probabilities of flooding, the 95% confidence intervals were non-overlapping. The difference between treatments was similar at very high and very low probabilities of flooding, even though the impact of the two main herbivores (i.e. leafhoppers and grasshoppers) on survival was dramatically different (Table 1). However, at intermediate flooding probabilities, the difference between treatments in terms of population growth increased from around 10% with probability of flooding set to 0.0 or 1.0 to greater than 20%, showing a substantial interaction between flooding and herbivore exclusion. Besides the obvious effect of raising or lowering λ depending on whether the seed-bank estimate

itself was raised or lowered, changes in seed-bank transmission rates did not alter the overall pattern seen. Decreasing seed retention rate did not change the overall pattern, while increasing seed retention rate accentuated the negative impact of intermediate levels of disturbance when herbivores were present. Overall, these results emphasize that although abiotic effects were extremely important for riparian species, biotic interactions, in particular with herbivores, also play an important role.

Discussion

Within riparian areas, both abiotic and biotic factors affect population growth rates. The degree to which these factors impact various species will be determined by individual life history. For *Mimulus guttatus*, abiotic factors play a driving role in determining population growth. However, the biotic factors associated with herbivory also impact population growth. This is particularly surprising for flooded sites because the impact of herbivores on survival in flooded areas was not particularly large, especially as compared with differences in non-flooded sites (Table 1). Nonetheless, as these results show, differences in plant survival that are quite small and, at times, may be difficult to detect (i.e. a 3.8% increase in summer survival due to herbivore exclusion at flooded sites compared with a 46.6% increase in summer survival in non-flooded sites) may have a greater biological impact than much larger changes in other demographic rates. This is due to the fact that the impact of changes in survival on population growth rate are a combination of two factors (eqns 10–12) – the difference between vital rates in experimental and control plots as compared with the mean matrix and the sensitivity of the species to changes in a particular vital rate. Only by analysing these data within a life-history context can the overall effects of abiotic and biotic impacts be adequately quantified and thus disentangled.

Few demographic studies have examined the interactions between abiotic and biotic effects of disturbance on population dynamics (but see McEvoy & Coombs 1999). Instead, most studies have focused on either the impacts of disturbance (Silva *et al*. 1990), the effects of a single biotic factor (Garcia & Ehrlén 2002; Gotelli & Ellison 2002; Ehrlén 2003), or the combined effects of disturbance and biotic interactions on separate components of a species' life history (Tyler 1996), without extending the analysis to population-level impacts. Additionally, because disturbances often occur on large scales, have multiple effects and are often hard to implement experimentally in a full factorial design, there is an important need to extend LTRE analysis to nested effects in order to examine potential interactions between disturbance, its biotic impacts and potential site variability. Attention to the interplay between abiotic and biotic factors may often be needed to gain insights into species interactions and their population-level impacts (Dunson & Travis 1991; Collins 2000; Bertness & Ewanchuk 2002).

STOCHASTIC ANALYSIS

The stochastic analysis also showed that in a highly variable environment (i.e. with intermediate probabilities of flooding), herbivory on *M. guttatus* has greater negative effects than it does in more constant areas. This magnification of herbivory effects can be understood by the greater sensitivity of a mean matrix, composed of flooded and non-flooded control treatments, to summer survival as compared with the non-flooded control treatment alone. Thus, with frequent occurrence of both flooded and non-flooded years, the impact of grasshoppers on summer survival rates in non-flooded years is effectively decreasing a more sensitive vital rate than when flooded years are rare (Table 1). Thus, the stochastic analysis demonstrated that rapidly switching between two life-history strategies, in this instance the importance of seed-bank survival and adult survival, may have increased detrimental effects.

ABIOTIC FACTORS

The degree to which abiotic factors play a role in determining population growth rate is not particularly surprising for *M. guttatus*, given similar results for other riparian species (Menges 1990; Rood *et al*. 1998; Smith *et al*. 2005). Yet, the magnitude of the difference we find is much greater than expected, given that we watered each plant on a daily basis (Figs 2 & 5). These differences between flooded and non-flooded control treatments could be due in part to biotic differences (e.g. changes in species composition). In fact, the main habitat difference between sites is a change in the dominant graminoid species in flooded vs. non-flooded areas (see Materials and methods). This longer-term consequence of flooding plus other abiotic differences in addition to water availability (e.g. soil characteristics and differing effects of early summer frost on plant survival; Elderd 2002) are together the probable cause of the majority of the contribution of flooding in our current study. Thus, the abiotic indirect contributions measured by changes in λ between flooded and non-flooded areas also reflect the potential impact of other abiotic differences.

BIOTIC FACTORS

Herbivores also decreased population growth rate across flooded and non-flooded sites. Although leafhoppers (the most abundant herbivore in flooded areas) did not greatly affect plant survival (Table 1), their observed contributions to changes in λ when incorporated into a life-history analysis are much greater than expected due to the high sensitivity and elasticity of summer survival in flooded sites (Fig. 1a). When this is combined with small changes in the flooding regime, it could

potentially alter population growth from a population that is increasing in numbers to one that is declining. Within non-flooded sites, herbivores (i.e. grasshoppers) have a dramatic negative effect on adult survival (Table 1). However, the contributions of grasshopper herbivory to changes in population growth are mediated by a shift in sensitivities and elasticities (Fig. 1d). In flooded control sites, adult survival has the largest elasticity; whereas within non-flooded sites, the elasticity for seed-bank viability increases and that for adult survival decreases. The differences in population growth rate (Fig. 5) and the magnitude of the LTRE contributions (Fig. 2c & d) would have been much greater had this shift not occurred. The importance of the seed bank for population growth reflects similar changes in elasticities in more ephemeral plants (Kalisz & McPeek 1992) that depend on potentially irregular flood events to germinate. These types of shifts between life-history stages are also seen when conducting interspecific comparisons in plants (Silvertown *et al*. 1996) as well as vertebrates (Heppell *et al*. 2000) and have been documented in other riparian plant species (Smith *et al*. 2005). For *M. guttatus*, this shift in elasticities can lend insight into changes in life-history dynamics when comparing perennial and annual populations and suggests that the seed bank provides a key environmental buffer (Doak *et al*. 2002). Although sensitivities and elasticities are local characteristics of a matrix (Caswell 2001), our results are generally robust to uncertainties in our estimates of seed bank longevity and seed retention rate. In fact, the relatively low seed retention rate that we set may have underestimated the much larger contribution to changes in λ that summer survival could be responsible for if we had directly estimated seed retention. Overall, the LTRE analysis and the stochastic simulations provide insight into the importance of considering the effects of biotic and abiotic factors on population dynamics and potential shifts in life-history dynamics.

SPATIAL AND TEMPORAL DYNAMICS

Spatial dynamics had a greater impact on λ than did temporal dynamics (Figs 3 & 4), as has also been demonstrated to varying degrees in other species (Jongejans & de Kroon 2005). These differences may either be due to greater variation across sites in general or to the limited temporal window of the study. The impact of spatial variation across sites was often limited to a single vital rate at a particular site (e.g. summer survival, S_S, at site 4). In terms of the limited impact of temporal dynamics, the daily watering of the experimental plants may have lessened the differences between survival and growth rates in 2000 and 2001, especially so because 2001 was a relatively dry year for Sagehen Basin (Elderd 2003). Indeed, the potential negative impact of a low precipitation year is highlighted by the differences in the contributions of germination rate across years (Fig. 4). In general, spatial and temporal

variation affected different vital rates (Figs 3 & 4). This suggests that the correlation structure for the stochastic model, which was estimated spatially, had little effect on those vital rates that varied temporally. However, it appears that spatial variation may be much greater than temporal variation across years.

As is true of most demographic analyses, our data were not a complete description of the life history of our study species. Ideally, we would like to estimate the correlation structure across all 11 vital rates, which should be explored in order to examine additional trade-offs among vital rates. Additionally, our model should also include asexual reproduction. However, this would only magnify the pattern seen in the results because asexual reproduction for *M. guttatus* almost exclusively occurs in non-water-limited sites (Galloway 1995; Elderd, personal observation). Furthermore, it is unclear how adding vegetative reproduction would affect the stochastic estimates of population growth, and in particular how it might buffer population growth rates. This should be an avenue of further investigation. The model also does not test for the effect of flooding magnitude on *M. guttatus* population growth rate, only flooding frequency. Yet it does provide a reasonable estimate of mean survival during flooding events of different magnitudes because data for overwinter survival are from *M. guttatus* within the stream channel. Thus, the relative magnitude of the flooding event is incorporated into the mean and variance of overwinter survival. Although only two years of survey data were used, they reflect a normal and dry year based on rainfall data (Elderd 2003), although not a high-magnitude flooding event. Thus, the above analyses, although not being quantitatively exact, probably represent the general pattern of environmental variation in this system.

Conclusions

For *Mimulus guttatus*, in particular, and riparian plant species in general, both abiotic and biotic factors limit the colonization of new populations and the viability of established ones. The degree to which these factors impact individual populations and species will vary. However, much of the emphasis in disturbance ecology has been focused on the importance of abiotic factors in determining both community composition and population dynamics, with little explicit attention given to the indirect effects of disturbance that are generated through community interactions. By examining the impacts of both of these factors within the context of a life-history analysis, the importance of these effects on population dynamics can be better elucidated and the overall ecological dynamics of disturbance-driven systems can be better understood.

© 2006 The Authors
Journal compilation
© 2006 British
Ecological Society,
Journal of Ecology,
94, 656–669

References

Baskin, C. & Baskin, J. (1998) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.

Bertness, M.D. & Ewanchuk, P.J. (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia*, **132**, 392–401.

Caicco, S.L. (1998) Current status, structure, and plant species composition of the riparian vegetation of the Truckee River, California and Nevada. *Madroño*, **45**, 17–30.

Caswell, H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**, 619–627.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Inc, Sunderland, MA.

Caswell, H. & Trevisan, M.C. (1994) Sensitivity analysis of periodic matrix models. *Ecology*, **75**, 1299–1303.

Collins, S.L. (2000) Disturbance frequency and community stability in native tallgrass prairie. *American Naturalist*, **155**, 311–325.

Cooch, E., Rockwell, R.F. & Brault, S. (2001) Retrospective analysis of demographic responses to environmental change: a Lesser Snow Goose example. *Ecological Monographs*, **71**, 377–400.

Dempster, J.P. (1963) The population dynamics of grasshoppers and locusts. *Biological Reviews of the Cambridge Philosophical Society*, **38**, 490–529.

Doak, D.F. (1992) Lifetime impacts of herbivory for a perennial plant. *Ecology*, **73**, 2086–2099.

Doak, D.F., Kareiva, P. & Klepetka, B. (1994) Modeling population viability for the desert tortoise in the Mojave Desert. *Ecological Applications*, **4**, 446–460.

Doak, D.F., Thomson, D. & Jules, E.S. (2002) Population viability analysis for plants: understanding the demographic consequences of seed banks for population health. *Population Viability Analysis* (eds S.R. Beissinger & D.R. Mc Cullough), pp. 312–337. University of Chicago Press, Chicago, IL.

Dunson, W.A. & Travis, J. (1991) The role of abiotic factors in community organization. *American Naturalist*, **138**, 1067–1091.

Ehrlén, J. (2003) Fitness components versus total demographic effects: evaluating herbivore impacts on a perennial herb. *American Naturalist*, **162**, 796–810.

Elderd, B.D. (2002) *Changing rivers and streams: the effects of anthropogenic alteration of riparian systems on* Mimulus guttatus. PhD thesis, University of California at Santa Cruz, Santa Cruz, CA.

Elderd, B.D. (2003) Changing flow regimes: its impacts on riparian vegetation and a common riparian species, *Mimulus guttatus*. *Ecological Applications*, **13**, 1610–1625.

Elderd, B.D. (2005) Disturbance–mediated trophic interactions and plant performance. *Oecologia*, doi: 10.1007/s00442-005-0267-1.

Galloway, L.F. (1995) Response to natural environmental heterogeneity: maternal effects and selection on life-history characters and plasticities in *Mimulus guttatus*. *Evolution*, **49**, 1095–1107.

Garcia, M.B. & Ehrlén, J. (2002) Reproductive effort and herbivory timing in a perennial herb: fitness components at the individual and population levels. *American Journal of Botany*, **89**, 1295–1302.

Gotelli, N.J. & Ellison, A.M. (2002) Nitrogen deposition and extinction risk in the northern pitcher plant, *Sarracenia purpurea*. *Ecology*, **83**, 2758–2765.

Grant, A.L. (1924) A monograph of the genus *Mimulus*. *Annals of the Missouri Botanical Garden*, **11**, 99–389.

Gross, K., Lockwood, J.R., Frost, C.C. & Morris, W.F. (1998) Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. *Conservation Biology*, **12**, 1291–1301.

Heppell, S.S., Caswell, H. & Crowder, L.B. (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, **81**, 654–665.

Hickman, J.C. (ed.) (1993) *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley, CA.

Hobbs, R.J. & Mooney, H.A. (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology*, **72**, 59–68.

Jongejans, E. & de Kroon, H. (2005) Space versus time variation in the population dynamics of three co-occurring perennial herbs. *Journal of Ecology*, **93**, 681–692.

Kalisz, S. & McPeek, M.A. (1992) Demography of an age-structured annual – Resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology*, **73**, 1082–1093.

Kalisz, S. & McPeek, M.A. (1993) Extinction dynamics, population growth and seed banks. *Oecologia*, **95**, 314–320.

Kendall, B.E. (1998) Estimating the magnitude of environmental stochasticity in survivorship data. *Ecological Applications*, **8**, 184–193.

Lesnoff, M., Ezanno, P. & Caswell, H. (2003) Sensitivity analysis in periodic matrix models: a postscript to Caswell and Trevisan. *Mathematical and Computer Modeling*, **37**, 945–948.

McEvoy, P.B. & Coombs, E.M. (1999) Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications*, **9**, 387–401.

Menges, E.S. (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 52–62.

Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer Associates, Inc, Sunderland, MA.

Paine, R.T. & Levin, S.A. (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs*, **51**, 145–178.

Pascarella, J.B. & Horvitz, C.C. (1998) Hurricane disturbance and the population dynamics of a tropical understory shrub: Megamatrix elasticity analysis. *Ecology*, **79**, 547–563.

Ritchie, M.E. (2000) Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology*, **81**, 1601–1612.

Rood, S.B., Kalischuk, A.R. & Mahoney, J.M. (1998) Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands*, **18**, 557–570.

Shafroth, P.B., Stromberg, J.C. & Patten, D.T. (2002) Riparian vegetation response to altered disturbance and stress regimes. *Ecological Applications*, **12**, 107–123.

Silva, J.F., Raventos, J., Caswell, H. & Trevisan, M.C. (1990) Population responses to fire in a tropical savanna grass, *Andropogon semiberbis*: a matrix model approach. *Journal of Ecology*, **79**, 345–356.

Silvertown, J., Franco, M. & Menges, E. (1996) Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology*, **10**, 591–597.

Smith, M., Caswell, H. & Mettler-Cherry, P. (2005) Stochastic flood and precipitation regimes and the population dynamics of a threatened floodplain plant. *Ecological Applications*, **15**, 1036–1052.

Sousa, W. (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, **60**, 1225–1239.

Tyler, C.M. (1996) Relative importance of factors contributing to postfire seedling establishment in maritime chaparral. *Ecology*, **77**, 2182–2195.

Vickery, R.K. Jr (1978) Case studies in the evolution of species complexes in *Mimulus*. *Evolutionary Biology*, **11**, 405–506.

Waser, N.M., Vickery, R.K., Jr & Price, M.V. (1982) Patterns of seed dispersal and population differentiation in *Mimulus guttatus*. *Evolution*, **36**, 753–761.

White, P.S. & Pickett, S.T.A. (eds) (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego, CA.

Wootton, J.T., Parker, M.S. & Power, M.E. (1996) Effects of disturbance on river food webs. *Science*, **273**, 1558–1561.