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of these systems, either increasing or decreasing dis-

EXPERIMENTS AND FIELD SURVEYS

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-m^2 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 w14.9(ept 33()-100(–27 J)3 than-fl904ey.1492servec76 Tw [(g)]y rbi w 14.9(e)0(r)12.9(v)13.9(e 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:

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

where $_t$ is a vector of population stage abundances at time *t* and **A** is a standard population projection matrix composed of two seasonal matrices, which project the population through winter, **W**, and sumg2(i.6467 TD ( )

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

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 (± 0.37 SE) side stems in flooded areas and 0.9 (± 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 a single factor linear model, consisted of the linear equation:

eqn 3

where $\lambda^{\cdot\cdot\cdot\cdot}$ is the dominant eigenvalue for the overall mean matrix, $\mathbf{A}^{\cdot\cdot\cdot\cdot}$, of all treatments, α^{i}, β^{j} and γ^{k} represent the 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), $^{1}/_{2}(\mathbf{A}^{i\cdots} + \mathbf{A}^{\cdots\cdot})$ is actually composed of vital rates and takes the form of $^{1}/_{2}(\ ^{i\cdots} + \ ^{\cdots\cdot})$, where 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 treatments 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:

(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:

(eqn 14)

where the numerator represents the variance of the log

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 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

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