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THE IMPACT OF CHANGING FLOW REGIMES ON RIPARIAN VEGETATION AND THE RIPARIAN SPECIES *MIMULUS GUTTATUS*

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Abstract. Alteration of riparian stream flow through the damming of rivers and streams impacts not only river morphology but also the vegetation communities that exist within the confines of a river's banks. To examine changes in vegetation community composition and structure resulting from human control of water flow, I conducted a series of surveys on dammed and undammed streams in the Eastern Sierra Nevada Mountains of California. These surveys documented that areas below dams contain increased leaf litter and grass thatch deposition, increased grass species coverage, and an altered community of existing forbs as compared to sites with naturally flowing streams. There was also an increased woody species canopy coverage as distance from the stream increased. To examine the proximal causes of damming on herbaceous plants, I set up a factorial field experiment examining the impact of grass thatch, shading, and herbivory on a common riparian species, *Mimulus guttatus*, the common monkeyflower. *M. guttatus*

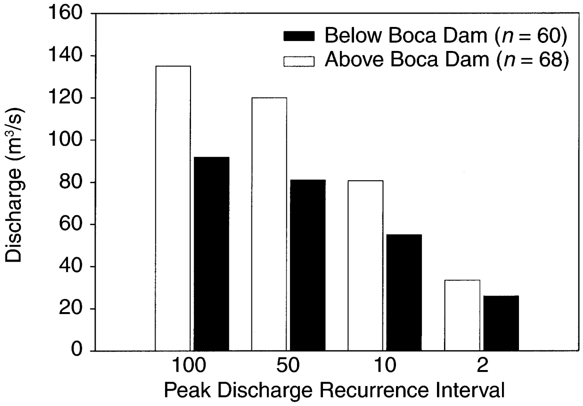


FIG. 1. Peak flow discharge recurrence intervals for a 2-year, 10-year, 50-year, and 100-year flood event on the Little

increase in shade can influence the production of antiherbivore defense mechanisms such as secondary metabolites (Iason and Hester 1993) or increase the palatability of the plant through increases in nitrogen (White 1984, Collinge and Louda 1988). Indirectly, the litter accumulated between growing seasons may also change rates of disease and herbivory by providing areas of refuge for invertebrate herbivores from their predators (Facelli 1994). Thus, increased shading and increased leaf litter deposition generated by low flows may indirectly affect performance of many riparian forbs via changes in herbivory rates.

To determine the effects of changes in river flow on riparian plant populations and its potential impacts on community structure, I conducted a set of field surveys examining community composition above dams, below dams, and in naturally flowing streams in the Eastern Sierra Nevada Mountains of California. To elucidate the mechanisms that might be responsible for overall changes in community structure, I set up a field experiment directly examining the impacts of shading, litter accumulation, and herbivory on the growth and germination of a common riparian species that is a ubiquitous part of the riparian plant community in California (Caicco 1998). Finally, to more finely gauge the impacts of shading and litter accumulation on plant performance within a controlled environment, I also conducted a parallel set of greenhouse experiments on the same riparian species.

METHODS

Field surveys

Stream surveys were conducted along 11 separate reaches of seven different rivers or streams in the Eastern Sierras of California. These streams drained into either the Truckee River or Lake Tahoe basin and areas surveyed ranged in elevation between 1800 and 2100 m. Reaches below dams were characterized by a relatively steady flow regime. Areas immediately above dams were either subjected to natural flow, or influenced by the reservoir with slow rises in water level during regular peak flow periods followed by a slow and steady decline in water level as reservoir capacity was released from the dam. Reaches along naturally flowing rivers and streams experienced peak flood periods followed by a steady decline in flow as well as periods during the nongrowing season with little or sometimes no water in the stream channel (Dunne and Leopold 1978, Jansson et al. 2000, Trush et al. 2000, Patten et al. 2001).

Of the seven streams surveyed, three of these streams (i.e., Blackwood, Sagehen, and Ward Creeks) were naturally flowing and contained no dam or other impediments to river flow within at least 15 km of the area surveyed. In order to make comparisons of vegetative community composition below dams, above dams and along undammed reaches of riparian areas, I surveyed four separate streams above and below existing dams (i.e., Boca, Martis, Prosser, and Stampede dams). Differences observed in vegetation communities above and below dams could be due to elevational differences as well as differences in flooding regime. However, for the dammed streams surveyed, the elevation difference between transects located above and below dams was always , 100 m. The lack of elevational gradient was because of the small- to midsized nature of the earthen dams on the surveyed streams, which had an average reservoir capacity of 98 3 10^6 m^3, making comparison of plots above and below the dams reasonable. For this study, all stream surveys were conducted during August 2000, two to three months after normal peak flow periods.

Areas below dams were surveyed at the beginning of the outflow point, while areas above dams were surveyed above the farthest obvious reach of the reservoir. Surveys for naturally flowing streams began at randomly selected points along the stream reach. At the start of each surveyed reach, I established a transect perpendicular to the river and placed 1-m^2 plots at distances of 0, 5, and 10 m from the stream channel along each side of the river. Each plot contained 100 sample points evenly spaced at 10-cm intervals. Within each plot, I estimated herbaceous species coverage, canopy coverage using a spherical densiometer, angle to stream channel, soil type using the ‘‘feel’’ method (Brady 1990), and litter depth. Herbaceous forb species were identified to species when flowering structures were present, and otherwise to genus. Since most grasses had no flowering structures at the time of the surveys, I classified all grasses to tribe. Litter depth was categorically classified as either 0 cm, , 2 cm, or . 2 cm. The 2-cm breakpoint corresponds to average litter depth in nonflooded meadows of Sagehen Creek, a naturally flowing stream (*unpublished data*).

A new transect segment was established every 100 m up to a distance of 500 m (except for the transect established below the Boca Dam on the Little Truckee River; approximately 250 m below the dam, the Little Truckee River flows into the Truckee River, and thus the transect was shortened to 200 m). No major tributaries flowed into the riparian areas being surveyed along each reach of the river where transects were established. In total, I surveyed 378 plots in seven different watersheds.

To examine overall herbaceous coverage between natural, above-dam plots, and below-dam plots, I conducted an analysis of variance (ANOVA) using stream type and distance from stream channel as independent variables and ranked total percentage cover as a dependent variable, since the data did not fit the assumptions of normality. I used a sequential Bonferroni correction with an adjustment for an a of 0.05 to correct for multiple tests (Rice 1989) to test for differences in percentage cover between stream types at the various distances from the stream channel. To test for differences in leaf litter and soil type at each of the three distances along the transect, a goodness of fit test was used (Sokal and Rohlf 1995). To facilitate the soil analysis, soil types were also grouped into three broad categories: sand, loam, and clay.

Differences in forb species composition between plots were first examined using a proportional similarity metric, which quantifies the overlap in community composition (Brower et al. 1990). Proportional similarity was calculated using

$$\mathrm{PS} = 1 - \frac{\sum |p_i - q_i|}{2} \qquad (1)$$

where p_i represents the proportion of species i in community p and q_i represents the proportion of species i in community q. I calculated PS for all pairwise comparisons for mean forb species coverage between different flooding regimes.

Detrended Correspondence Analysis (DCA) on individual plots, after outlier species and plots were elim-

Plots were randomly assigned to one of eight treatment combinations in which I manipulated light levels (control or 70% shade cloth), leaf litter or grass thatch (control or litter addition), and herbivory (water control or insecticide application). Three replicates of each treatment combination and one control plot to track background germination rates (i.e., no seed/plant addition) were established at each site. Levels of litter addition corresponded to those found in nonflooded sites at the meadow's edge (; 2 cm depth; *unpublished data*). For the shading treatments, I placed shade cloth on two sides of the plot and ; 1 m above the plot. The shaded sides were the side upstream and farthest from the riverbank and simulated the effects of the establishment of a woodland stand within the riparian zone (Collinge and Louda 1988). Herbivory was controlled by weekly applications of 1.25 g/L of Orthene, which controls a wide spectrum of herbivores (Doak 1992) and has no effect on *M. guttatus* germination (*unpublished data*). Plots were monitored for seedling emergence and survival on a weekly basis in 1999 and 2000 and on a monthly basis in 2001. For planted seedlings, each plant's height, number of main and side stem nodes, flower production, and percent herbivory were measured weekly for the eight weeks of the experiment. At the end of the experiment, all aboveground tissue for each surviving plant was harvested, dried for five days at a mean temperature of 58°C, and weighed. Throughout the course of the season, individual plots within sites maintained highly variable moisture due to their location next to or far from the creek or nearby seeps, as well as soil differences that affect water-holding capacity. To determine if end of the season moisture affected plant performance, I used a binary characterization (i.e., whether the soil in each plot was still moist mental data, the percentage of seeds germinating met the assumptions of ANOVA.

Field and greenhouse growth data were examined using a MANOVA. For the field experiment, the MANOVA was conducted on the height, percent herbivory, and reproductive success as dependent variables and shading, thatch, insecticide treatment, and soil moisture as independent variables. The final soil moisture char-

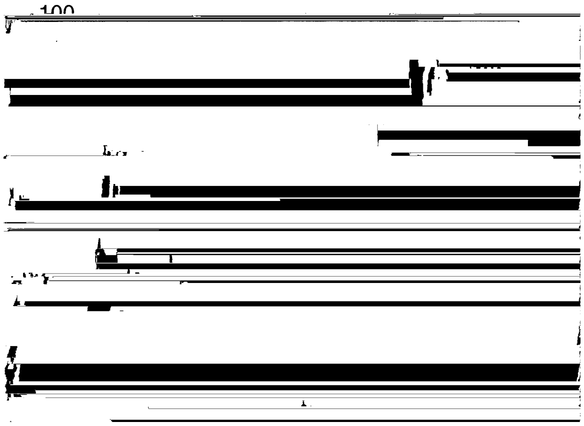


FIG. 2. Mean herbaceous coverage (11 SE) of survey plots by distance from stream (0, 5, and 10 m, respectively) and stream survey type (Above, *n* 5 48, Below, *n* 5 42, and Natural, *n* 5 36 for each distance). Differences in mean cover were only analyzed for significance within distances using a sequential Bonferroni test and a 5 0.05. Bars with the same letter within a distance are not statistically different from each other.

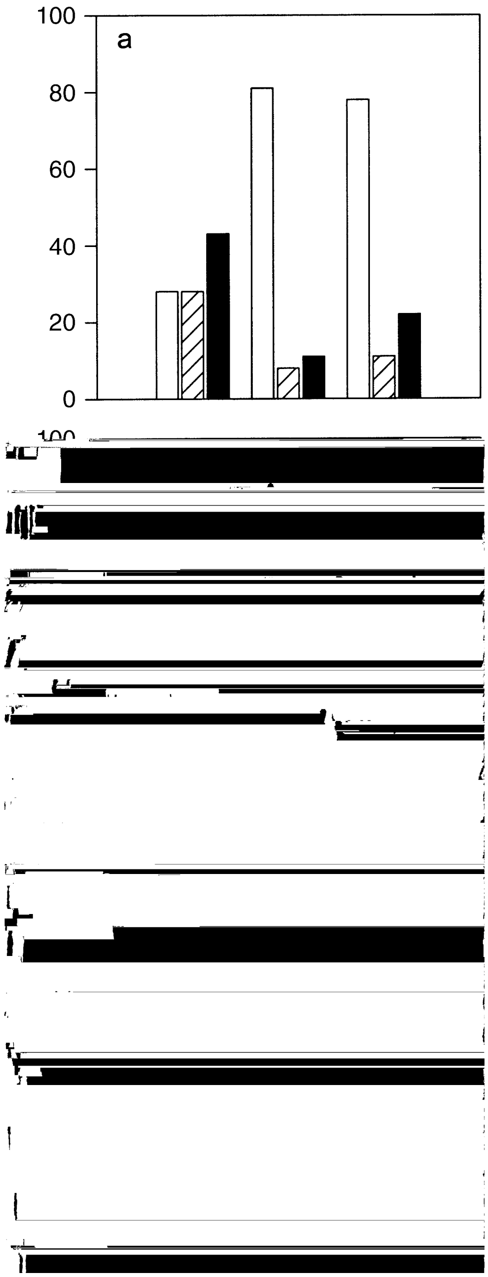


FIG. 3. Percentage of survey plots with no leaf litter, , 2 cm depth, and . 2 cm depth for (a) 0 m, (b) 5 m, and (c) 10 m from the stream channel by stream survey type (Above, *n* 5 48, Below,

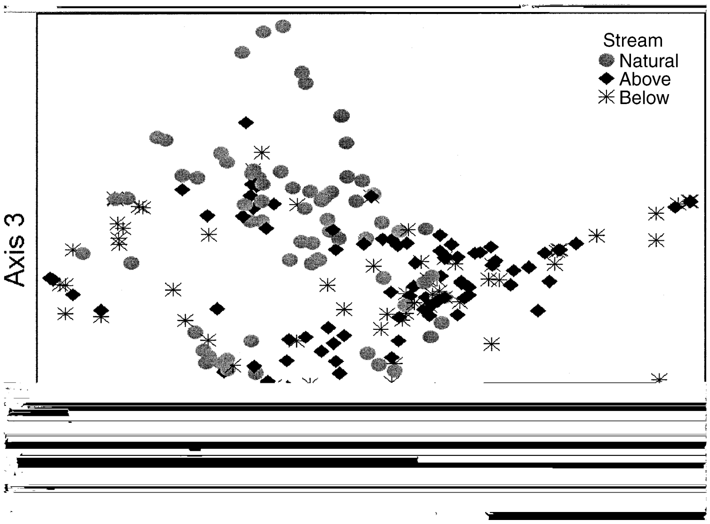


FIG. 4. Axis 1 and Axis 3 from the Detrended Correspondence Analysis (DCA) analyzing differences in forb species composition between stream survey plot types (n 5 292). Plots marked with a gray circle are for natural stream survey plots, those marked with a black dia-

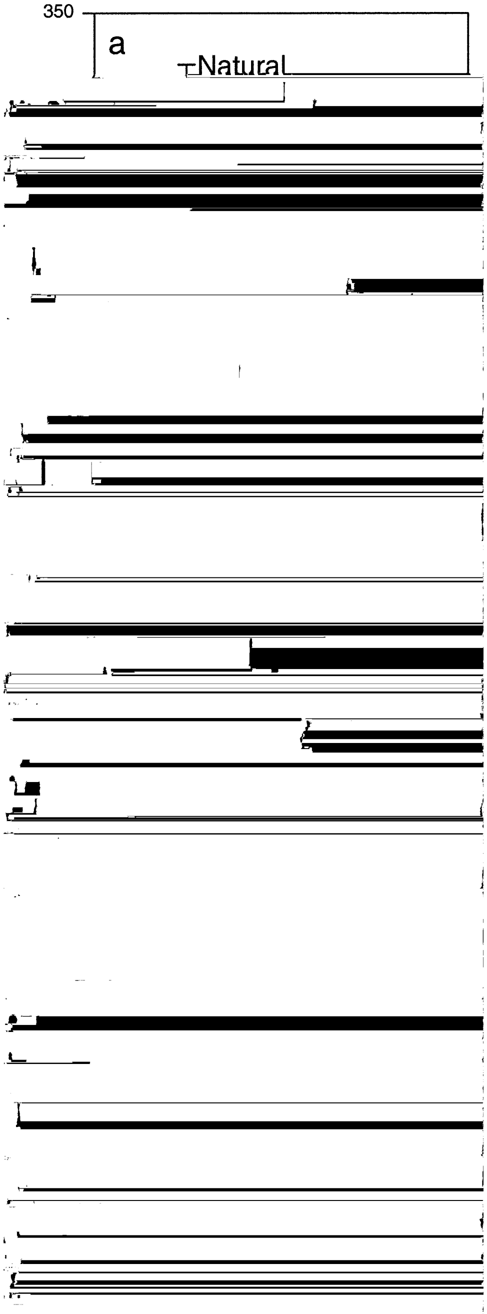


FIG. 5. Mean DCA scores for Axis 1 and Axis 3 (61 SE) of survey plots for (a) 0 m, (b) 5 m, and (c) 10 m from the stream channel with *n* 5 48 for above-dam plots, *n* 5 42 for below-dam plots, and *n* 5 36 for natural stream plots. Differences in mean coverage were only analyzed for significance within distances using a sequential Bonferroni test and a 5 0.05. Individual points with the same letter are not statistically different from each other.

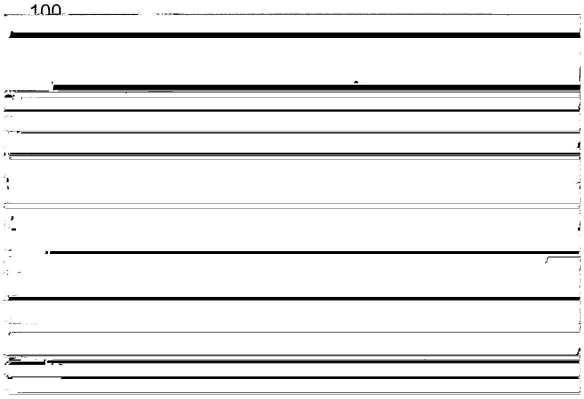


FIG. 6. Percentage of plots where germination occurred within individual treatments by year (*n* 5 216 plots).

compared to seed from mountain populations (1999, 54 6 4.1%; 2000, 56 6 3.7%). These results parallel the effects of the interaction between shading and population under 50% shading levels, with coastal populations (49 6 4.1%) faring better under shaded conditions than mountain populations (39 6 4.1%). Under 70% shading, both populations performed poorly.

When examining height and reproductive success, there were significant effects of thatch and population for both years that the experiment was conducted (Table 4). In 2000, when shading levels were increased to 70%, there was a significant effect of shading and a marginally significant interaction between thatch and population origin. In 1999, plants that were seeded in thatched pots did not differ in height (Fig. 9a) but had marginally significant greater reproduction (Fig. 9b) due to an increase in the number of side stems produced. In 2000, thatch depressed plant height and plant reproduction. Shading detrimentally impacted *M. guttatus*, but only due to the effects of the highest shading level, which decreased plant height (Fig. 9c) and also resulted in fewer side stems and numbers of flowers (Fig. 9d). When examining population origin, seeds from the Sierra Nevadas were able to grow taller (1999, mountain, 5.9 6 0.56 cm, coastal, 1.9 6 0.58 cm; 2000, mountain, 9.8 6 1.13 cm, coastal, 6.0 6 1.04 cm) and increase their reproductive success (1999, mountain, 3.4 6 0.50 structures, coastal, 1.2 6 0.26 structures; 2000, mountain, 5.2 6 0.83 structures, coastal: 3.2 6 0.32 structures) under greenhouse conditions when compared to seeds taken from coastal populations. The interaction between population origin and thatch in 2000 was due to the large difference in height of plants grown from seeds from mountain populations under

TABLE 2. Percent probability of germination in field experiments and associated results of an ANOVA examining the effects of these treatments.

Treatment	Germination (61 SE)	df	*F*	*P*
Thatch	12 6 3	1, 96	22.00	, 0.0001
Control	23 6 5			
Shade	14 6 4	1, 96	3.09	0.0821
Control	34 6 4			

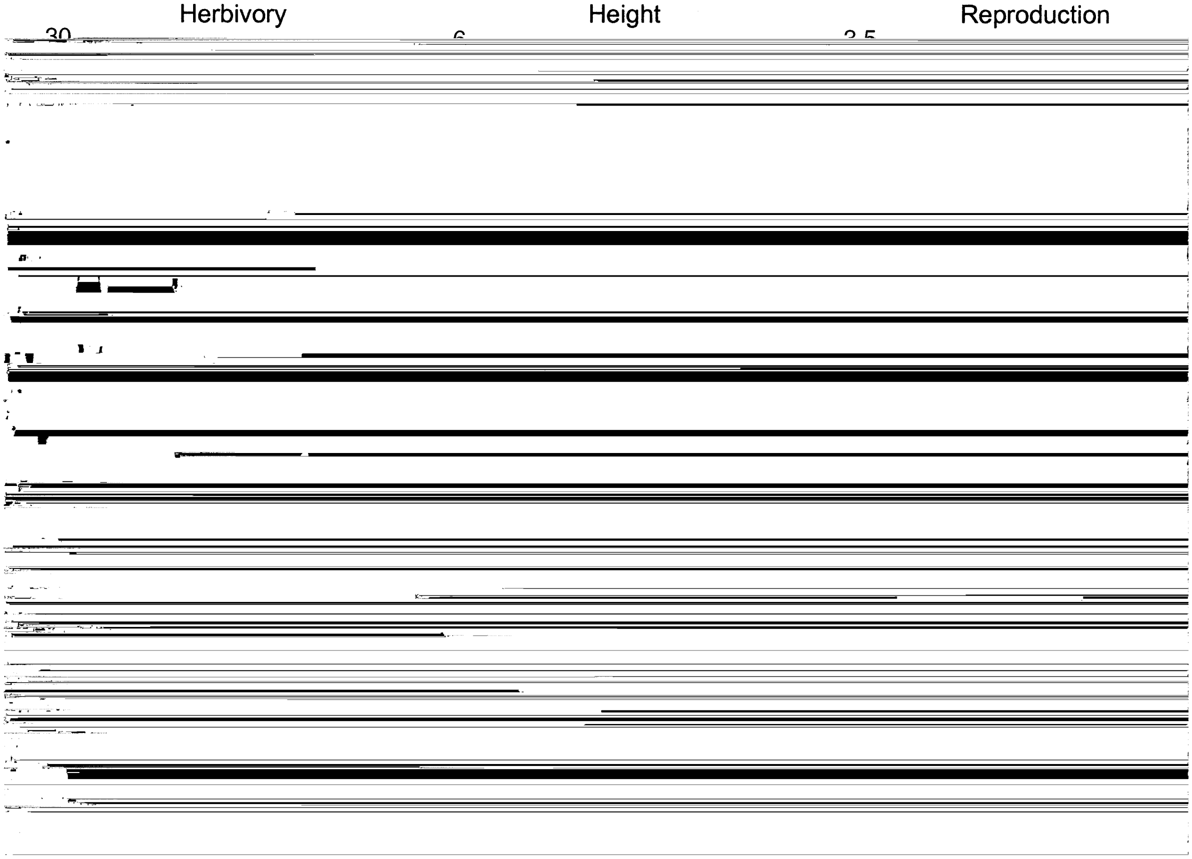
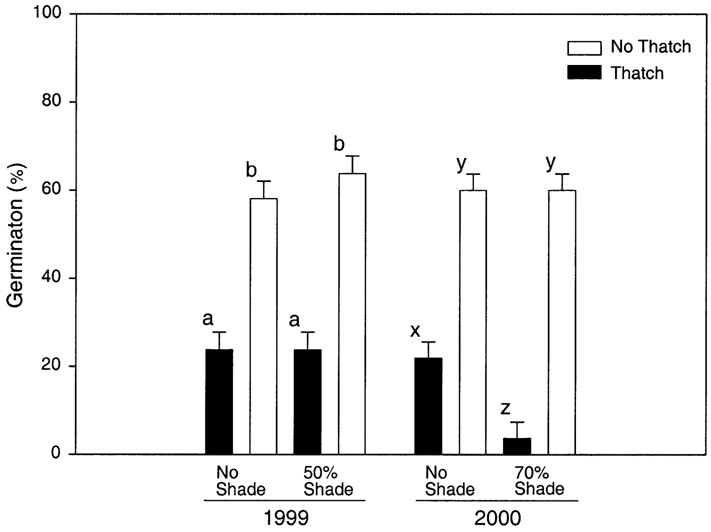


FIG. 7. Effects of thatch, shading, and insecticide treatments on *M. guttatus* herbivory (a, b, and c, respectively), height (d, e, and f, respectively), and reproduction (g, h, and i, respectively, representing numbers of flowers and side stems). Statistically significant (*P* , 0.05) differences between treatments are marked by an asterisk (*) in the upper right corner of the graph. Error bars represent 1 1 SE.

growth and reproduction due to changes in herbivory rates.

For the greenhouse study, I was able to examine the establishment and growth of a single set of seeds over the course of the experiment. These greenhouse experiments allowed me to eliminate the potential confounding effect of competition between plants in the field and herbivory in order to more finely examine the impacts of shading and grass thatch on the growth of *M. guttatus* from seed to adult plant. Within these experiments, there were again dramatic impacts of shading and grass thatch. In terms of germination, there appears to be a shading threshold effect whereby plots with high levels of shading and grass thatch experienced dramatically lower germination rates. The detrimental impact of shading and grass thatch on germination continued to follow the plant as it grew throughout the experiment. This indicates that as woody or grass species establish themselves within riparian areas, *M. guttatus*, a particularly common riparian species, may not be adversely affected by this newly developing canopy in a linear fashion. Yet as these species continue to grow, the canopies continue to close, and as litter accumulates due to increased leaf or thatch production by these species, *M. guttatus* germination declines and those individual seeds that are able to germinate are adversely affected as well. However, it is also interesting to note that *M. guttatus* may be able to compensate for adverse conditions by augmenting reproduction, as seen in the 1999 greenhouse experiments when pots with thatch increased side stem production. Changes such as these in vegetative reproduction due to site conditions have been documented before in *M. guttatus* (Vickery 1974). The impacts of shading and thatch on *M. guttatus* establishment and growth were quite broad, as they negatively affected both mountain and coastal populations. Thus, for this common riparian species, changing community structure via increased thatch or leaf litter and shading dramatically decreased the establishment of the species, which led to lasting consequences for growth and reproduction.

Overall, the ecological impacts of anthropogenic alteration of flow regimes are often dramatic, but their general patterns and mechanisms are little understood. For the most part, dams alter riparian flow regimes by


No Thatch
Thatch
Germinaton (%)
100
80
60
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a
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1999
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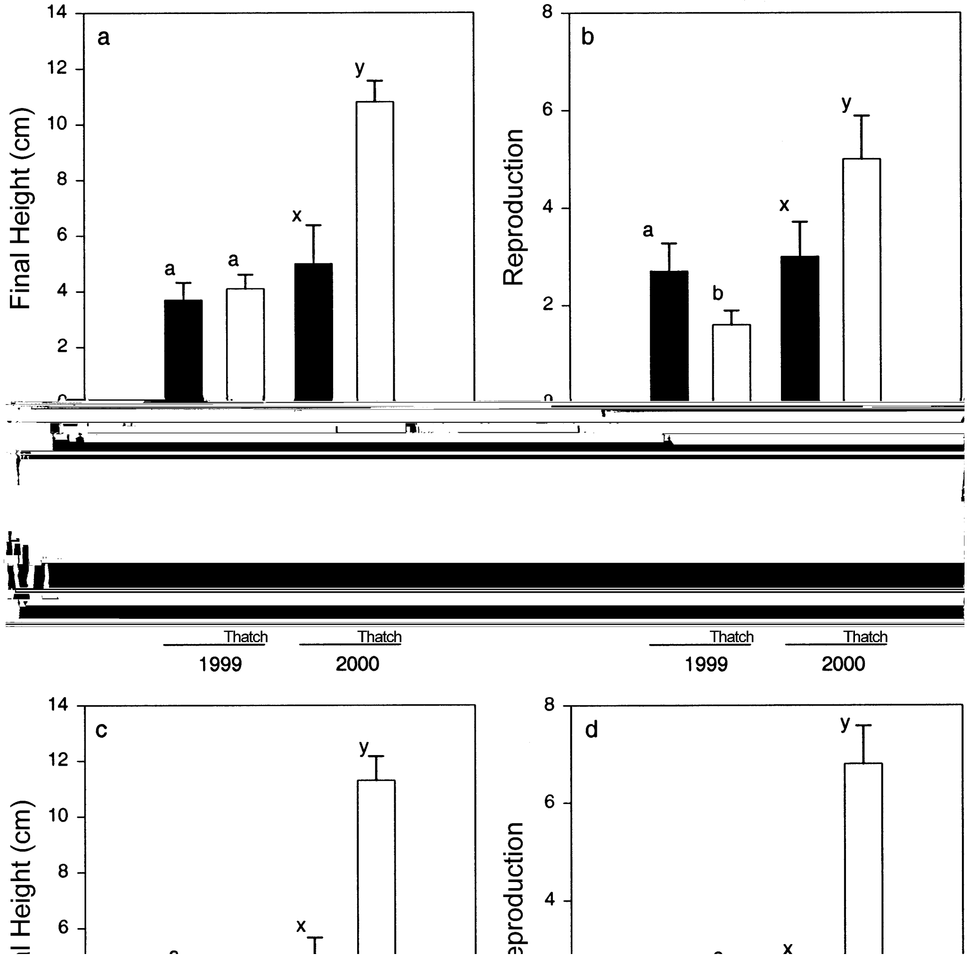

FIG. 9. Effects of thatch and shading on *M. guttatus* height (a and c, respectively) and reproduction (b and d, respectively, representing numbers of flowers and side stems) under greenhouse conditions for 1999 with 50% shading, and 2000 with 70% shading. Bars with the same letter within a year are not significantly or marginally significantly different from each other according to an analysis of least-squares means using Tukey-Kramer adjustment for multiple comparisons. Error bars represent 1 1 SE.

stream channel. These effects lessened as the distance from the stream channel increased. The riparian areas that are most frequently inundated due to high flow events are those areas next to the stream channel. During either biennial or centennial flood events areas adjacent to the channel will experience some degree of flooding and/or scouring, while areas further from the main channel in the riparian floodplain need particularly large-magnitude events to be inundated. Since most of the change in community composition occurred next to the channel, this indicates that the decline in bankfull discharge (i.e., 1.5-year flood) during the current lifetime of these dams altered overall community composition and structure, not centennial flood events. As these dams continue to age, they may also affect higher magnitude events, which would alter community composition at greater distances from the stream channel. However, the effects of altering high-magnitude events remains to be seen due to the relatively young age of these dams.

Vegetation composition of areas above dams also differ from naturally flowing streams in several ways, such as decreased herbaceous coverage and a decline in the amounts of leaf litter buildup at all distances from the stream channel. I did not expect these effects and suspect that they are due to increased reservoir retention during particularly wet years, which allows the reservoir to back up and flood these surveyed reaches of the stream. This, in combination with low-precipitation years, decreased the amount of vegetation that was able to establish a foothold in these areas due to the widely fluctuating conditions, such as the anoxic conditions created during wet years and relatively dry conditions during low-precipitation years. Thus, dams can have unforeseen impacts on riparian communities above the reaches of their reservoirs.

For *M. guttatus*, the surveys show that this species prefers areas with less thatch cover and nearer to the stream. Since plots below dams and in naturally flowing streams both fit this criteria, there is not a discernible difference in plots containing *M. guttatus*. However, in areas above dams, plots with *M. guttatus* decrease in frequency, probably due to alterations in above-dam flow regimes. Yet given the field and greenhouse experiments, it can be concluded that as community structure continues to change, *M. guttatus*, a common riparian species, would be extremely sensitive to changes brought about by decreased water flow. If other riparian-dependent forbs show similar sensitivity, the effects of reduced flooding events will result in overall changes in community composition via declines in establishment, growth, and reproduction of riparian forb species. With altered flow regimes, overall community composition and structure begin to change. This change tends to favor the species that are able to establish under decreased disturbance regimes. As these species grow in size and in number, they continue to alter community structure by increasing litter layer and shading. This, in turn, affects those riparian species that readily colonize gravel bars or other open space near the stream banks that are usually scoured by high flow events. These changes in community structure affect riparian species by decreasing successful establishment and, if establishment occurs, successful growth and reproduction. Thus these changes alter species performance at every life stage.

CONCLUSIONS

Changing river flow alters community composition and, in time, modifies community structure; these changes detrimentally affect riparian species by decreasing germination and reproduction. Thus, alterations in flow regime can be directly linked to population level impacts. Increasing peak water flows may be able to reset community structure by reducing woody and grass species establishment and leaf litter buildup. In order for this to occur, high flow events need to be simulated through controlled releases of water into the stream or river, while keeping in mind the importance of seasonal timing in order to assure proper establishment of native or desired species (Scott et al. 1997, Trush et al. 2000, Stevens et al. 2001). However, these flow events do not necessarily need to be at the same magnitude as the 100-year flood in order to restore these degraded communities. They may be able to effect change if they only exceed bankfull discharge events. Relatively small bankfull discharge events have been shown to enhance desired sediment distribution within the reaches of the Colorado River below the Glen Canyon Dam. However, these controlled releases have been less than effective at enhancing native vegetation communities, though they have limited nonnative species recruitment (Stevens et al. 2001). This lack of response may be due to the pulsed nature of this anthropogenic disturbance. Under natural conditions, bankfull discharge events occur relatively frequently, and it is likely that these disturbance events need to be replicated on a yearly or biennial basis to successfully shape riparian ecology. The importance of frequently inundating areas has been shown to alter litter dynamics within higher order streams and may set the stage for long-term restoration of riparian plant communities (Ellis et al. 1999).

Since calls for a single release of water from a dam can take considerable time and energy, calls for yearly releases of water to increase stream flow and subsequently decrease reservoir storage may be even more politically contentious. For large-scale releases on major dams (e.g., Glen Canyon Dam), it takes many years to iron out the details of these massive releases due to the involvement of multiple parties (Patten et al. 2001); thus yearly releases may be politically unfeasible. However the majority of dams, particularly within California, are not on the same scale as these large-magnitude dams, and the number of stakeholders will often be smaller than for larger projects. This makes small-scale dams more attractive for implementing yearly release strategies.

Since there is a great deal of variation in year-to-year precipitation in the West and California, the timing of releases, in terms of a particular year, should be linked to yearly precipitation trends. For instance, in above-normal years when water is more plentiful, a controlled release at bankfull discharge may not affect overall reservoir storage. During dry years, no controlled releases would be called for, since most of the water would be needed for anthropogenic uses. Not only would this be beneficial in terms of anthropogenic water needs during dry years, but it would also mimic natural climatic variation, since natural bankfull discharge events are less likely to occur during dry years and more likely to occur in wet years.

Whether or not this represents an effective strategy for restoring riparian communities could be tested by using small-scale dams as a set of replicated experiments. By conducting bankfull discharge releases on small streams, an increase in the replication of these events could be realized, adding to the statistical power and enabling more rigorous testing of the impacts of releases on riparian communities. This approach would allow for multiple study sites to be established to determine whether or not solely restoring a natural bankfull discharge regime to a riparian system effectively restores the vegetative community. However, in order for the experiment to be effective, these small-scale releases must be conducted over a long-term temporal scale due to the nature of these communities and the impacts of these relatively small disturbance events. If this procedure is followed, valuable insight into the workings and restoration of these highly important community types may be garnered.

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