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* germination was decreased in the thatch augmentation plots and under artificial shading. For seedlings, shading increased final plant height and thatch increased herbivory. In plots where herbivory was not controlled by insecticide, *M. guttatus* plants grew smaller and had lower reproduction. I also repeated this experiment in a more controlled greenhouse environment using two seed sources and two levels of shading coverage. Results from this experiment largely confirm patterns seen in the field, but also revealed a strong interaction between shading and thatch treatments for both germination and growth. Overall, my results suggest that altering riparian stream flow may impact plant performance through a cascading set of biotic interactions, and that controlled releases from dams that mimic bankfull or greater discharge events may be required to restore these important and diverse communities by resetting disturbance rates.

Key words: dammed vs. undammed streams; disturbance; flooding; herbivory; leaf litter; Mimulus guttatus; *riparian vegetation; shading; Sierra Nevada Mountains, California (USA); stream flow; thatch.*

INTRODUCTION

Disturbance has been recognized as an important determinant of the mosaic of community types that exist across most landscapes (Sousa 1979, Carroll and Highsmith 1996, Wootton et al. 1996, D'Antonio et al. 1999). Although disturbance is now widely accepted as an important force for the maintenance of community structure and diversity, it is still unclear exactly how and why disturbance events exert their effects on communities (Levin and Paine 1974, White and Pickett 1985, Kinsolving and Bain 1993, Moloney and Levin 1996, Warren and Spencer 1996). This is particularly true for disturbances such as flooding that may have a multitude of interacting consequences.

However, due to the adverse economic and social impacts of flooding, as well as the desirability to store water for future uses, humanity has often sought to control flooding by controlling water flow regimes

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(Jackson et al. 2001, Patten et al. 2001). Nowhere have the effects of this control been more prevalent than within the riparian areas of the western United States and, in particular, California. Within the state of California, there are over 1200 nonfederal dams, 181 federal dams, and >8000 km of levees whose purpose is to control river flow (Mount 1995). These structures insure that in times of high water flow, urban and rural areas in the riparian floodplain will not become inundated, and that in times of low water flow, there will be plenty of water stored in the reservoirs behind dams to assure water supplies during drought periods.

This control of water flow has altered the hydrological regime of California's rivers and streams by assuring a steady base flow in riparian channels throughout the year and by decreasing peak flow, which determines disturbance rates. Steady base flow in rivers and streams has led to increased channelization and a loss of river sinuosity (Dunne and Leopold 1978, Born et al. 1998, Trush et al. 2000, Patten et al. 2001). By changing peak flow, there has also been a dramatic shift in peak discharge (i.e., the maximum rate of water flow through an area) when comparing flow rates before and after dam construction, or above and below dams over the same period (Fig. 1; Mount 1995, Trush et al. 2000).
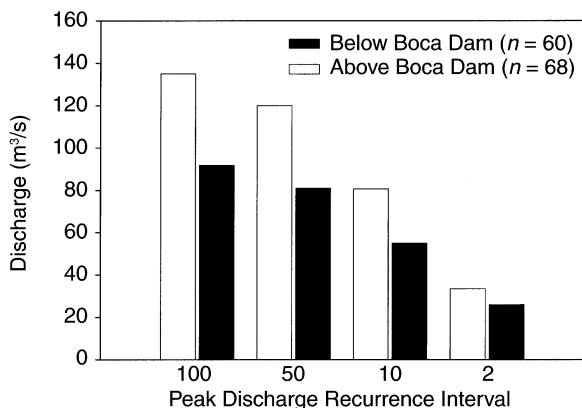
FIG. 1. Peak flow discharge recurrence intervals for a 2-year, 10-year, 50-year, and 100-year flood event on the Little Truckee River above and below the Boca Dam. Data were taken from the USGS gauging stations above and below the current site of the Boca Dam and included all available observations from 1904 to 2000 for the above-dam station and from 1940 to 2000 for the below-dam station.

Though there are dramatic declines in the mean 100-year discharge amount, there are also declines in the biennial discharge amount. While the 100-year flood (i.e., the peak discharge occurring with a 0.01 probability for each year) is often the focus of planning for major levee and dam construction (Brooks 1991), geomorphologists consider the bankfull or 1.5-year discharge amount to be the most important for determining a river's shape and function (Thrush et al. 1996). Bankfull discharge events overtop the current riparian bank and allow for flooding to occur within and across the riparian floodplain. The amount of area flooded depends upon the magnitude of the event. For instance, a 100-year flood will inundate a much greater area than the 10-year flood.

Just as high flow events are important for geomorphology, they may also be important determinants of riparian community structure (Townsend 2001). Natural variation in the frequency and intensity of flooding creates different successional cycles within these communities (Power et al. 1995). In general, varying levels of disturbance within a riparian community result in greater diversity of plants and other taxonomic groups such as arthropods (Day et al. 1988, Nilsson and Grelsson 1990, Wilcox and Meeker 1991), and appear necessary to prevent major shifts in community structure (Hemphill and Cooper 1983, Power and Stewart 1987). Altogether, there are well-documented differences in community structure between areas that experience high flow events along free-flowing rivers as compared to regulated or dammed rivers (Lind et al. 1996, Nilsson et al. 1997, Jansson et al. 2000, Shafroth et al. 2002).

In spite of clear responses of riparian communities to flooding regimes, predicting and altering the effects of changes in flooding regimes due to anthropogenic manipulation requires an understanding of the causal links between flooding and its ecological impacts. Three possible routes by which flooding may control riparian plant populations and communities are particularly compelling: (1) decreased competition (Menges 1990, Busch and Smith 1995, Molles et al. 1998, Levine 1999); (2) changes in structural elements of a community including the removal of dead plant material (Menges and Waller 1983, Busch and Smith 1995, Ellis et al. 1999, Shafroth et al. 2002); and (3) alteration of herbivore pressure (Andersen and Cooper 2000, Levine 2000).

In areas that have not been heavily disturbed by flooding for a substantial period of time (i.e., more than a decade), woody species begin to establish along riverbanks (Junk et al. 1989, Lind et al. 1996). The effects of increased shading on forb establishment and growth have been documented in other disturbance-mediated systems (Collins et al. 1985, Guariguata 1990, Bowles and McBride 1998), and shown to affect composition of species along a successional gradient (Horn 1981, Canham and Marks 1985, Runkle 1985, Jacobson et al. 1991). Woody species will easily overtop most of the forbs associated with riparian habitats, many of which are not well adapted to growing and/or establishing under shady conditions (Menges and Waller 1983, Pabst and Spies 1998). Thus, high flow events can retard the establishment of woody species by washing away recently emerged woody seedlings and damaging shoots (Scott et al. 1997, Pabst and Spies 1998) and indirectly benefit riparian forbs species through decreases in shading.

Lack of flooding can also influence plant performance through increased accumulation of dead plant material. In the absence of high flow events, the previous seasons' vegetative growth accumulates as leaf litter or grass thatch. Litter interferes with both seed germination and seedling establishment by depriving seeds and seedlings of light, shown to be a limiting factor in other systems (Facelli and Pickett 1991, Facelli and Facelli 1993, Facelli 1994, Bosy and Reader 1995). Changes in establishment rate, subsequent growth, and reproduction due to litter accumulation have also been shown to affect overall community composition (Tilman 1993). Thus, flooding may moderate not only within-season plant competition, but also what has been referred to as between-season competition as a result of litter accumulation (Bergelson 1990).

The taller and denser plant communities typically found in riparian areas following flooding control (Johnson et al. 1996, Lind et al. 1996, Toner and Keddy 1997) may also influence some riparian plant species indirectly through altered herbivory rates. Foraging rates of many phytophagous insects are limited by temperature (Strong et al. 1984, Schmitz et al. 1997). Increased shade may allow herbivores to expand their foraging efforts into the hotter period of the day, resulting in increased levels of damage. Additionally, an

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 98×10^6 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 α 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 differ-

ences 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

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

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 eliminated from the analysis, was used to further clarify forb composition differences between sites experiencing different flooding regimes (Gauch 1982). In total, 292 plots were examined in the DCA analysis using PC-Ord Version 4.0 (McCune and Mefford 1999). Eighty-six plots were not used in the analysis since they either contained no species coverage or only outlier species. I also evaluated links between environmental and species coverage variables, evaluating ranked correlations (Kendall's τ), due to the nonnormality of the data tested, between DCA axis scores and plot-specific variables (e.g., canopy coverage). To examine whether differences in mean axis score between the plot types were statistically significant, I conducted a Multiple Analysis of Variance (MANOVA) using the two axes that explained the most variation in the DCA. Separate contrasts were used to analyze whether the differences between stream types were significant at each individual distance using a sequential Bonferroni. All data analyses other than the computation of DCA axis scores were conducted in SAS Version 8 (SAS Institute 1999).

Experimental study site and species

The field experiments were conducted along Sagehen Creek (one of the creeks included in the stream surveys) at the University of California at Berkeley's Sagehen Creek Field Station (latitude 39°25′ N, longitude 120°14′ W) located 14 km north of Truckee, California, at an elevation of 1920 m. Sagehen Creek receives most of its precipitation in the winter months in the form of snow, which melts during the spring and translates directly into increased stream flow. Thus, during the late spring and early summer, areas surrounding Sagehen Creek are scoured and inundated with water. The degree to which these areas are flooded depends upon two factors: snow depth and the rate of

snow melt-off. Additional sources of water in the Sagehen basin include the numerous snowmelt-fed springs located within the creek's extensive meadow system, which can continually supply water to areas of Sagehen Creek throughout the summer (Savage 1973).

The 30-year average precipitation for Sagehen from 1966 to 1996 was 89.9 cm with a standard deviation of 33.5 cm, and an average winter snow depth of 527.8 cm with a standard deviation of 201 cm (Western Research Climate Center 2002). From 1999 to 2001, when the field experiments were conducted, precipitation and snow records were not available for Sagehen basin. However, records were available for the Truckee Ranger Station, which has similar precipitation patterns but on average receives 7 cm less in precipitation. The Truckee Ranger Station received 80.4 cm and 72.9 cm of precipitation during 1999 and 2000, respectively. During 2001, the area only received 56.4 cm of precipitation, indicating that 2001 was a particularly dry year for the region.

The field experiments outlined below were designed to study the impact of shading and litter accumulation on a common riparian plant species. For this work, I chose *Mimulus guttatus* DC, the common monkeyflower. *M. guttatus*, a perennial species in the Sierra Nevada Mountains of California, occurs throughout the Western United States from Alaska to Baja California and from the Pacific Coast to the Rocky Mountains (Vickery 1978). This species has widely scattered populations that occur in moist meadows and along streams (Grant 1924, Lindsay 1964). It is a colonizing plant that often invades recently disturbed habitats (Vickery 1978) and is extremely common along the reaches of rivers throughout California (Hickman 1993). Additionally, *M. guttatus* has been documented as a more prevalent component of the herbaceous community along the upper reaches of California rivers, rather than lower reaches where dams are more common (Caicco 1998). Therefore, it is ideal for studying quantitative responses to flooding effects, such as shading and litter accumulation.

Field experiments

In 1999, 2000, and 2001, at each of three randomly chosen inundated sites along Sagehen Creek, I established 25 1 × 1 m plots spaced 1 m apart. I placed 10 *M. guttatus* seeds within the center 0.25 m^2 of each plot. In 1999, I was unable to measure growth and herbivory rates due to low seedling establishment in some of the treatments, in particular the shade and thatch treatments. Thus in 2000 and 2001, I expanded the experiment by planting three *M. guttatus* seedlings evenly spaced along the outside of the 0.25-m^2 germination plots. Seeds and seedlings were placed out after peak snow melt-off had occurred and standing water had dissipated. This led to a later experimental start date of 10 July in 1999 as compared to 20 June and 19 June for 2000 and 2001, respectively.

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 or completely dry at the end of the 2000 and 2001 field season) as a covariate in subsequent growth and reproduction analyses for planted seedlings.

Greenhouse experiments

To further elucidate how differences in shading and litter cover directly affect *M. guttatus* without the potentially confounding effects of herbivores, competing plants, and between-site variation, I conducted a series of greenhouse experiments during the spring of 1999 and 2000. To broaden the generality of this study, I used *M. guttatus* seeds collected in two distinct geographic areas: California's Central Coast and the Eastern Sierra Mountains. Both areas contain extensive populations of *M. guttatus* along riverbanks and seeps. However, the yearly river flow cycles are vastly different. Although both areas are characterized by periods of high flow and low flow during the year, the Central Coast's yearly flow regime consists of drought-like conditions during the summer and fall, while much of the yearly precipitation falls during the winter months. This precipitation is directly translated into overland runoff after the soil has been saturated

(Brooks 1991) and in turn, directly increases the coastal river's flow rate. Thus, peak flow and its associated flooding of riparian floodplains occur during the winter months. In the Eastern Sierras, the peak flow of streams occurs during the early summer months when snowmelt takes place. These differences in flow regime as well as basic climate may or may not select for different population responses to factors such as shading and litter.

In each year, I planted 10 seeds of *M. guttatus* collected from at least eight coastal and eight mountain populations during the 1998 and 1999 field seasons in each of 64 10-cm pots. Each pot received one of eight treatments in which I manipulated seed origin (i.e., coastal or mountain seeds), shading (i.e., shading or no shading), and litter levels (i.e., litter or no litter). For pots that received shading treatments, shading structures were constructed with shade cloth placed on the top, the western, and the southern side of each pot. The shading structures were 10 cm tall, and pots were placed at least 20 cm apart so that individual shading structures would not shade neighboring pots. In 1999, 50% shade cloth was used; in 2000, 70% shade cloth was used. The litter treatment consisted of placing 2 cm of homogenized grass thatch on top of the potting soil after seeds had been added to the pot. Each greenhouse experiment contained eight replicates per treatment and used a Latin squares design to control for any environmental light gradients within the greenhouse (Potvin 1993). At the end of two weeks, each pot was thinned to three individuals if more than three seeds germinated. Pots were examined weekly for germination for a total of six weeks. Growth measurements such as height, number of nodes, longest leaf, number of side stems, and number of flowers were recorded on a weekly basis from week three to week six. At the end of six weeks, the plants were harvested, dried for five days at a mean temperature of 58°C, and weighed.

Statistical analysis of field and greenhouse experiments

Germination data for the field experiment were examined in a two-step process. First, data were analyzed using a logistic regression with individual plots classified as 1 or 0 based upon any or no germination occurring. For plots where germination did occur, I then used ANOVA to quantify the treatment effects on germination success. Field data were corrected by subtracting the average background germination rate for a given year from each plot where germination occurred, which averaged 0.33 seedlings per control plot over the three years of the experiment, and were arcsine square-root transformed to meet the assumptions of normality. Germination results from the greenhouse data were analyzed using an ANOVA with the location of the pot (i.e., row and column) included as main effects to account for greenhouse microclimatic differences (Potvin 1993). For the greenhouse experi-

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 characteristic for the field experiments (as previously described) was used as a main factor in the analysis to control for additional micro-site effects on overall plant performance. Height was deemed an appropriate growth measure since it was highly correlated with other measures such as final dry mass ($r = 0.64$, $P < 0.0001$, $n = 133$) and largest leaf ($r = 0.69$, $P < 0.0001$, $n = 133$). Additionally, prior to flowering, *M. guttatus* increases in height by adding to the number of nodes and leaves it produces (Grant 1924; *personal observation*). The MANOVA for the greenhouse experiment examined the impacts of shading, thatch, and population origin on height and reproductive success at the end of the experiment. For both of these experiments, total reproductive success was measured as the number of flowers and side stems produced by the plant, since *M. guttatus* can reproduce both vegetatively via side stems and sexually via flowers (Vickery 1974). If treatment effects were significant, a univariate ANOVA was conducted on each of the dependent factors in the MANOVA to determine degree of significance.

For the field experiments, the natural logarithm of the main stem height and the arcsine square-root transformation for herbivory were used in the analysis, whereas for the greenhouse data, reproductive success needed to be log-transformed (Sokal and Rohlf 1995). For the greenhouse experiments, each year was analyzed separately due to differences in shading treatments between years (i.e., 50% in 1999 and 70% in 2000). Analyzing both years of data together would have confounded year and shading interactions.

For both experiments, all treatment interactions were originally tested. If the *P* value for the interaction was >0.25, the data were reanalyzed by pooling the sum of squares from the highly nonsignificant interaction term (Underwood 1997). All analyses were conducted on the mean measurements for individual plots or pots. Analysis factors were considered fixed and type III sums of squares used. Post hoc multiple comparisons were conducted using a Tukey-Kramer adjustment. All the analyses above were conducted in SAS version 8.0 (SAS Institute 1999).

RESULTS

Field surveys

There were significant differences in overall herbaceous species coverage across flooding regimes ($F_{2, 369} = 25.67$, $P < 0.0001$) as well as an interaction between distance from stream and flooding regime ($F_{4, 369} =$
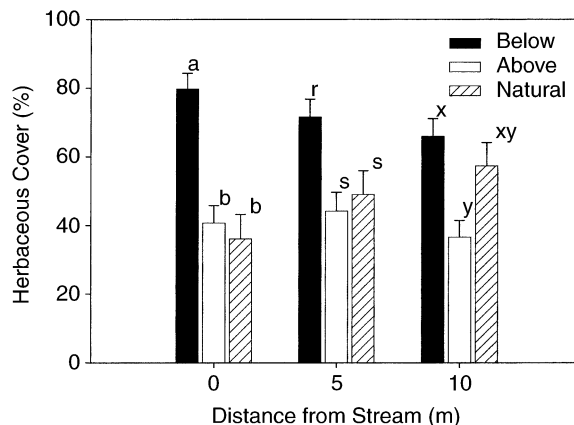

FIG. 2. Mean herbaceous coverage (+1 SE) of survey plots by distance from stream (0, 5, and 10 m, respectively) and stream survey type (Above, $n = 48$, Below, $n = 42$, and Natural, $n = 36$ for each distance). Differences in mean cover were only analyzed for significance within distances using a sequential Bonferroni test and $\alpha = 0.05$. Bars with the same letter within a distance are not statistically different from each other.

2.57, $P = 0.0376$). Herbaceous species coverage increased below dams (Fig. 2), driven largely by increased grass species coverage below dams as compared to above dams and in natural flowing streams ($F_{2, 369} = 23.98$, $P < 0.0001$; below dams: $43 \pm 3.2\%$ coverage (mean $\pm$ 1 SE), above dams: $17.6 \pm 2.5\%$ coverage, natural: $21 \pm 3.0\%$ coverage).

Results in percentage of cover were paralleled by differences in leaf litter coverage. At a distance of 0 m from the stream, most plots above dams and in natural flowing streams contained little or no litter, whereas litter tended to accumulate in 0-m plots below dams. There were also statistically significant differences at 5 m and 10 m from the stream channel, which was driven by the lack of litter accumulation above dams (Fig. 3; Table 1). Soil differences were only statistically significant for plots located 0 m from the stream channel ($G_4 = 29.62$, $P < 0.0001$) with soils above dams and in natural flowing streams composed mostly of sand particles, and soils below dams composed of clay. At distances of 5 m and 10 m, there were no differences in soil type (5 m, $G_4 = 2.28$, $P = 0.6847$; 10 m, $G_4 = 7.26$, $P = 0.1229$) with the majority of plots containing sandy soil in all survey types.

There were also significant effects of flooding regime ($F_{2, 369} = 30.24$, $P < 0.0001$) and distance ($F_{2, 369} = 9.07$, $P = 0.0001$) on canopy coverage. Naturally flowing streams, contrary to expectations, had significantly greater canopy coverage ($38 \pm 3.8\%$) than streams above dams ($13 \pm 2.5\%$; $P < 0.0001$) and below dams ($17 \pm 2.9\%$; $P < 0.0001$), but coverage did not differ between above- and below-dam sites. Not surprisingly, plots next to the stream channel at 0 m had significantly less canopy coverage ($13 \pm 2.5\%$) than plots occurring at 5 m ($23 \pm 3.2\%$; $P = 0.0071$) and 10 m ($29 \pm 3.5\%$;
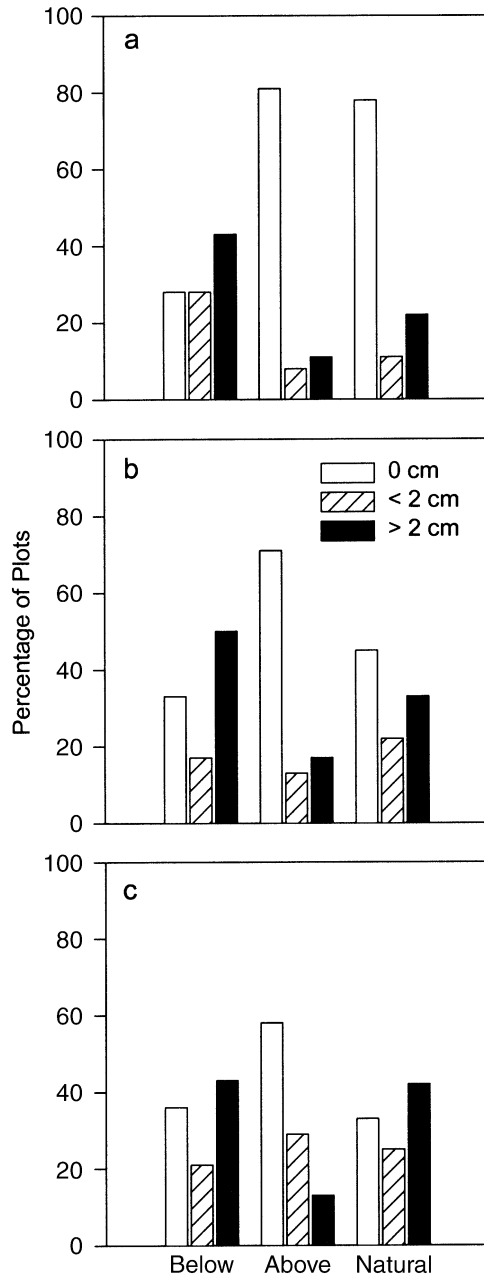
FIG. 3. Percentage of survey plots with no leaf litter, <2 cm depth, and >2 cm depth for (a) 0 m, (b) 5 m, and (c) 10 m from the stream channel by stream survey type (Above, n = 48, Below, n = 42, and Natural, n = 36 for each distance).

$P < 0.0001$), while 5-m coverage did not differ from 10-m canopy coverage.

The differences in overall herbaceous coverage, leaf litter, and soil type are paralleled by differences in forb species composition. The proportional similarity between sites suggests that plant communities along natural flowing streams have less in common with those below dams (i.e., 36% similarity index), as compared to above dams, where similarity between these sites

and below dams as well as natural flowing sites are higher (i.e., 44% and 41%, respectively). When examining forb composition using the results of the DCA, DCA Axis 1 and DCA Axis 3 each explained 10.4% of the variation seen in forb species coverage differences, while DCA Axis 2 explained 6.7% of variation based on a recommended relative Euclidean distance correlation metric (McCune and Mefford 1999). All subsequent analyses were conducted on Axes 1 and 3, since these two axes combined explained a substantial amount of the variation in the ordination data (Fig. 4).

Axis 1 separated the more riparian species from upland species. For instance, *M. guttatus* was negatively correlated with Axis 1 ($\tau = -0.22$, $P < 0.0001$, n = 292), whereas the upland species *Artemisia tridentata* was positively correlated with Axis 1 ($\tau = 0.41$, $P < 0.0001$, n = 292). Axis 3 separated species with mesic requirements from the xeric species occurring in naturally flowing streams. For Axis 3, *Solidago canadensis* was positively associated with the axis ($\tau = 0.20$, $P < 0.0001$, n = 292). However, *M. guttatus* was negatively correlated with Axis 3 ($\tau = -0.15$, $P = 0.0018$, n = 292). With respect to environmental variables, angle to the stream was positively correlated with Axis 1 ($\tau = 0.21$, $P < 0.0001$, n = 292) and 3 ($\tau = 0.15$, $P = 0.0004$, n = 292). Canopy coverage was not correlated with Axis 1 ($\tau = -0.05$, $P = 0.22$, n = 292), but was positively correlated with Axis 3 ($\tau = 0.25$, $P < 0.0001$, n = 292).

Using a MANOVA to look for differences between plots surveyed in different flooding regimes, I found a significant interaction between flooding regime (i.e., natural, above dam, and below dam) and distance from the stream channel (i.e., 0, 5, and 10 m) (Wilk's $\lambda_{8, 564}$ = 3.18, $P = 0.0016$). When comparing plots placed 0 m from the stream using a sequential Bonferroni, sites above dams, below dams, and along naturally flowing streams were significantly different from each other (Fig. 5a). At a distance of 5 m, natural streams were significantly different from below-dam and above-dam streams. However, there was no significant difference between below-dam and above-dam stream plots (Fig. 5b). This same pattern held true for those plots 10 m from the stream channel (Fig. 5c).

According to the DCA analysis, *M. guttatus* favored more mesic sites where there was little canopy coverage. Plots where *M. guttatus* occurred were closer to

TABLE 1. Goodness of fit tests for percentage of plots with no leaf litter, <2 cm depth, and >2 cm depth.

Distance (m)	df	G	P
0	4	27.07	<0.0001
5	4	15.43	0.0039
10	4	12.92	0.0117

Notes: Tests are conducted separately between flooding regimes for each distance from stream channel. Sample sizes for below dams, above dams, and natural flowing streams are 42, 48, and 36 plots for each distance, respectively.

FIG. 4. Axis 1 and Axis 3 from the Detrended Correspondence Analysis (DCA) analyzing differences in forb species composition between stream survey plot types ($n = 292$). Plots marked with a gray circle are for natural stream survey plots, those marked with a black diamond are above-dam survey plots, and those marked with an asterisk are for below-dam survey plots.
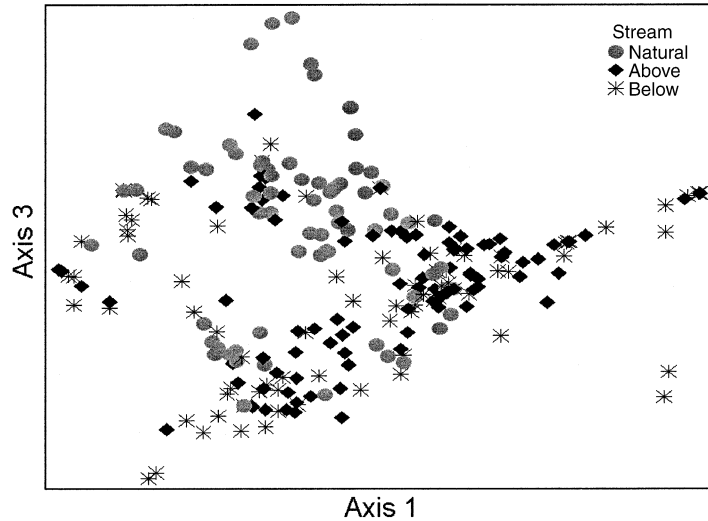
the stream ($\chi^2_2 = 26.80$, $P < 0.0001$), with 74.3% of the plots that contained *M. guttatus* located 0 m from the stream channel. Dams also affected the distribution of *M. guttatus* ($G_2 = 6.02$, $P = 0.0493$), with 4.9% of the survey plots containing *M. guttatus* above dams as compared to 11.1% for below-dam survey plots and 13.0% for natural stream survey plots.

Field experiments

Both year and site affected germination rates seen in experimental plots (year: Wald $\chi^2_2 = 46.14$, $P < 0.0001$; site: Wald $\chi^2_2 = 11.42$, $P = 0.0033$). The year 2001 was particularly dry for these sites and dramatically affected the probability of germination. The occurrence of germination was significantly affected by thatch augmentation (Fig. 6; Wald $\chi^2_2 = 29.45$, $P < 0.0001$). In fact, there was a threefold greater chance of germinating in plots without thatch than in plots with thatch across years. There were no significant effects of shading (Wald $\chi^2_2 = 2.59$, $P = 0.1077$), orthene (Wald $\chi^2_2 = 0.53$, $P = 0.4665$), or a shading thatch interaction (Wald $\chi^2_2 = 2.59$, $P = 0.1077$) on probability of a germination event occurring. I next examined rates of germination in plots where at least one seed germinated. Again, there were significant effects of site ($F_{2,96} = 5.65$, $P = 0.0048$) and year ($F_{2,96} = 4.11$, $P = 0.0193$). Additionally, I found a significant decline in percent germination in plots with thatch and a marginally significant decrease of germination rates due to shading (Table 2). Throughout the course of the experiment, there was little background germination at the field sites. A total of three seedlings were counted in control plots over the three-year course of the experiment.

For the MANOVA analyzing plant height, reproduction, and herbivory, plant performance differed between years (Table 3); plants in 2001 (i.e., the drier year) were shorter, less fecund, and had increased her-

bivory. Although there was no effect of site, there was an effect of within-site soil moisture. The lack of end of the season soil moisture adversely impacted plant performance due largely to its effects on overall plant height. Thatch resulted in a marginally significant decline in plant performance, while shading had a significant impact on plant performance (Fig. 7). The marginally significant difference in thatch treatments was due to an increase in herbivory in thatched plots (Fig. 7a). The effects of the shading treatments were due to an increase in overall height for shaded plants vs. nonshaded plants (Fig. 7e). Overall, insecticide treatments had a more dramatic impact than other main effects. Plants in plots not treated with insecticide experienced a significant increase in herbivory (Fig. 7c), a marginally significant decrease in height (Fig. 7f), and a significant decrease in reproduction (Fig. 7i).

Greenhouse experiments

Thatch strongly depressed germination in both years (Fig. 8; 1999, $F_{1,43} = 79.43$, $P < 0.0001$; 2000, $F_{1,43} = 160.33$, $P < 0.0001$). In 1999, 50% shading had no effect on germination rates ($F_{1,43} = 0.45$, $P = 0.5041$), and the interaction between shading and thatch was also not significant ($F_{1,43} = 0.45$, $P = 0.5041$). In 2000, 70% shading led to a decline in germination rates ($F_{1,43} = 5.91$, $P = 0.0193$), and these rates were further depressed by the interaction between shading and thatch ($F_{1,43} = 5.91$, $P = 0.0193$). There were also strong interactions between thatch and population origin (1999, $F_{1,43} = 8.52$, $P = 0.0056$; 2000, $F_{1,43} = 4.39$, $P = 0.0421$) as well as marginally significant interaction between shading and population when shade levels were at 50% (1999, $F_{1,43} = 3.50$, $P = 0.0681$; 2000, $F_{1,43} = 0.18$, $P = 0.6771$). The significance of the thatch and population interaction was driven by improved germination of coastal population seed under a no-thatch treatment (1999, $68 \pm 4.1\%$; 2000, $64 \pm 3.7\%$) as
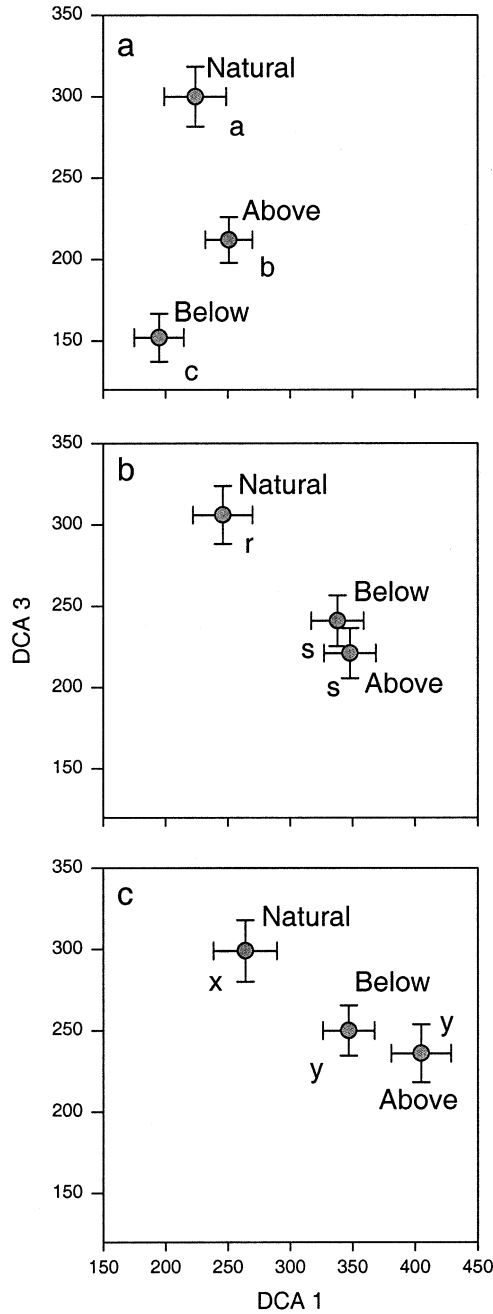
FIG. 5. Mean DCA scores for Axis 1 and Axis 3 (±1 SE) of survey plots for (a) 0 m, (b) 5 m, and (c) 10 m from the stream channel with $n = 48$ for above-dam plots, $n = 42$ for below-dam plots, and $n = 36$ for natural stream plots. Differences in mean coverage were only analyzed for significance within distances using a sequential Bonferroni test and $\alpha = 0.05$. Individual points with the same letter are not statistically different from each other.

compared to seed from mountain populations (1999, 54 ± 4.1%; 2000, 56 ± 3.7%). These results parallel the effects of the interaction between shading and population under 50% shading levels, with coastal popu-
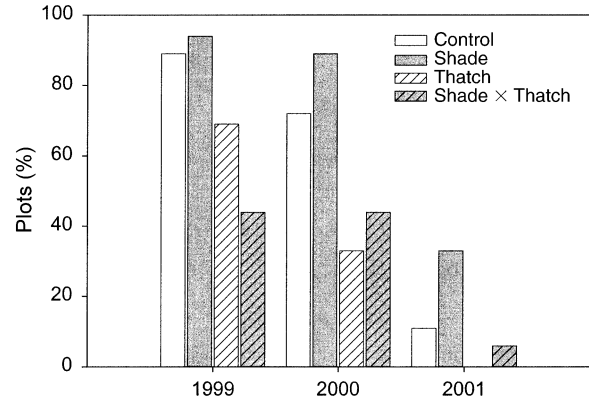

FIG. 6. Percentage of plots where germination occurred within individual treatments by year ($n = 216$ plots).

lations (49 ± 4.1%) faring better under shaded conditions than mountain populations (39 ± 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 ± 0.56 cm, coastal, 1.9 ± 0.58 cm; 2000, mountain, 9.8 ± 1.13 cm, coastal, 6.0 ± 1.04 cm) and increase their reproductive success (1999, mountain, 3.4 ± 0.50 structures, coastal, 1.2 ± 0.26 structures; 2000, mountain, 5.2 ± 0.83 structures, coastal: 3.2 ± 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 (±1 SE)	df	F	P
Thatch	12 ± 3	1, 96	22.00	<0.0001
Control	23 ± 5			
Shade	14 ± 4	1, 96	3.09	0.0821
Control	34 ± 4			

TABLE 3. MANOVA and subsequent ANOVA results if MANOVA effect is significant for field experiments. Field experiments analysis used height, reproduction, and herbivory as response variables.

Effect	Response variable	df	Wilks' lambda	F	P
Site		6, 200	0.97	0.50	0.8108
Year		3, 100	0.30	79.26	<0.0001
	height	1, 102		237.01	<0.0001
	reproduction	1, 102		5.90	0.0169
	herbivory	1, 102		10.57	0.0016
Shade		3, 100	0.89	4.06	0.0091
	height	1, 102		11.74	0.0009
	reproduction	1, 102		0.01	0.9059
	herbivory	1, 102		0.09	0.7700
Thatch		3, 100	0.93	2.33	0.0788
	height	1, 102		0.63	0.4301
	reproduction	1, 102		0.87	0.3541
	herbivory	1, 102		4.72	0.0321
Insecticide		3, 100	0.52	30.59	<0.0001
	height	1, 102		3.62	0.0598
	reproduction	1, 102		5.69	0.0189
	herbivory	1, 102		83.34	<0.0001
Soil moisture		3, 100	0.09	5.57	0.0014
	height	1, 102		13.81	0.0003
	reproduction	1, 102		1.02	0.3141
	herbivory	1, 102		2.34	0.1289

nonthatch conditions as compared to all other treatments.

DISCUSSION

The effects of alteration of stream flow on riparian plant communities and plant species comprised a varied set of responses. When comparing plant communities within natural flowing streams and areas adjacent to dams, a notable set of differences appeared. Areas below dams contained increased herbaceous species coverage, possibly due to an increase in grass coverage and accumulation of leaf litter or grass thatch. These differences extended to the forb communities occurring along dammed and undammed streams, particularly when examining community composition nearest to the main channel (Fig. 5). In terms of canopy coverage, streams without dams contained increased canopy coverage, perhaps due to the lower order of natural streams compared to dammed streams; canopy coverage increased as distance from the stream channel increased. As shown in the DCA analysis, areas nearest to the stream were associated with more mesic riparian-dependent species and decreased canopy coverage. These changes in species composition reflect the importance of the relationship between water availability and plant community structure within riparian areas (Stromberg et al. 1996). Although these surveys were only conducted on relatively small streams, they serve as a broader indication of the ecological effects of changes in flood regimes and agree with other surveys conducted in much larger basins (Nilsson et al. 1997, Molles et al. 1998).

Changes in herbaceous species communities could be driven by multiple factors including those investigated in this study (i.e., leaf litter or grass thatch accumulation and increased canopy coverage). For *M. guttatus*, a common herbaceous species in riparian communities, both grass thatch and shading affected species establishment and could potentially alter growth and reproduction. An increase in leaf litter or grass thatch dramatically decreased the probability of any germination occurring within a plot. If germination did occur, both grass thatch and increased shading (i.e., 70%) decreased germination rate. For adult plants, shading increased height by increasing internode length, not the number of leaves or nodes produced, which signals that the plant may be exhibiting a shade-avoidance response (Donohue et al. 2000). Grass thatch also impacted herbivory rates, perhaps by providing refuge from potential predators in the form of an enemy-free space (Murdoch et al. 1989). However, in my experiments, this increase in herbivory was not large enough to decrease overall plant reproduction. Yet if in natural circumstances herbivory rates continue to increase during the season, there are likely to be detrimental impacts on plant performance, as I saw in the comparison between insecticide-treated and untreated plots. Both year and site differences were also an important component of *M. guttatus*' establishment and growth due to interannual differences in rainfall and differences in water retention and soil type within sites. Overall these potential changes in riparian areas affected *M. guttatus* performance by decreasing the probability of germination, and could potentially alter
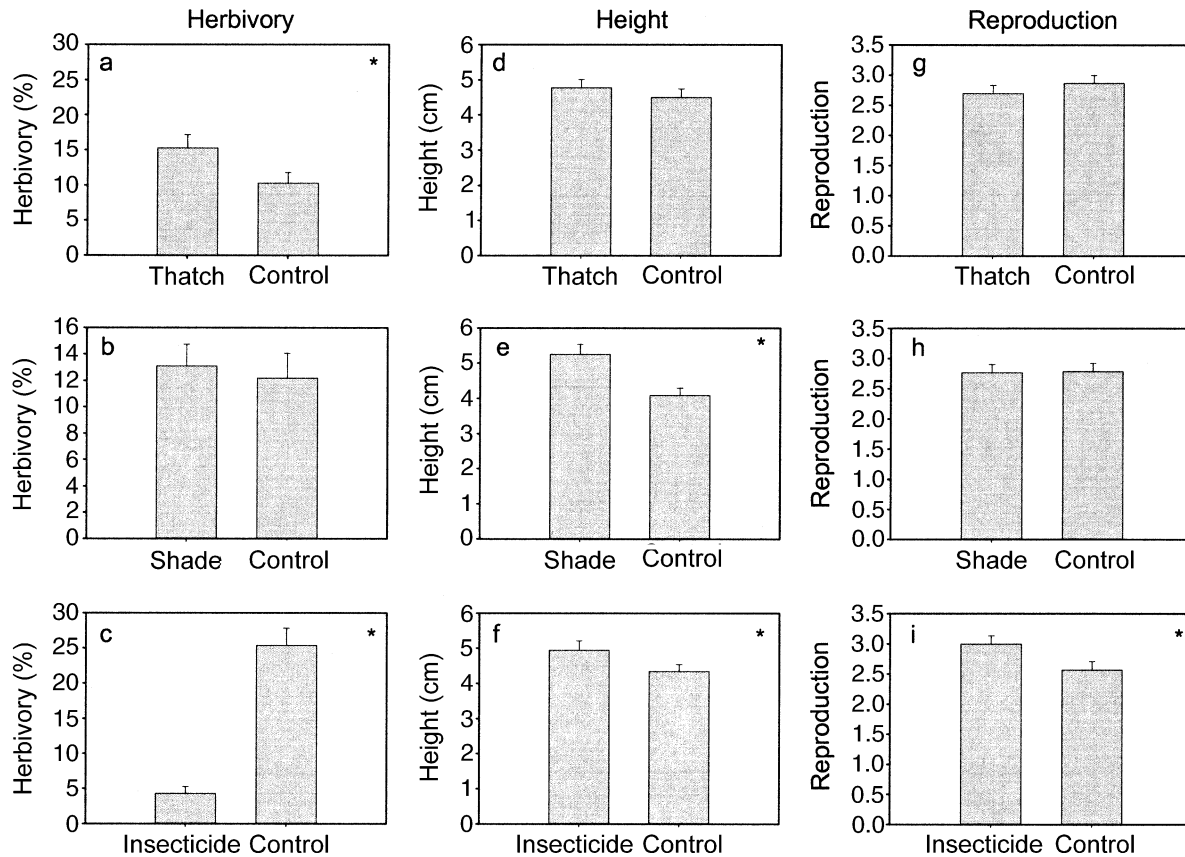
FIG. 7. Effects of thatch, shading, and insecticide treatments on *M. guttatus* herbivory (a, b, and c, respectively), height (d, e, and f, respectively), and reproduction (g, h, and i, respectively, representing numbers of flowers and side stems). Statistically significant ($P < 0.05$) differences between treatments are marked by an asterisk (*) in the upper right corner of the graph. Error bars represent +1 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

FIG. 8. Effects of thatch and shading treatments on *M. guttatus* germination under greenhouse conditions for 1999 with 50% shading, and 2000 with 70% shading. Bars with the same letter within a year are not statistically different from each other according to an analysis of least squares means using Tukey-Kramer adjustment for multiple comparisons. Error bars represent +1 SE.
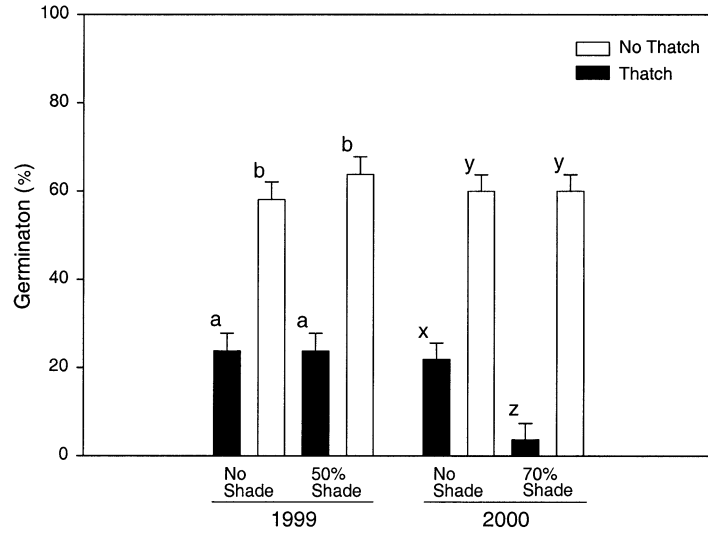
decreasing peak discharge flows. Although large flow events can only be controlled by relatively large dams with greater reservoir capacity, small flow events such as biennial floods are decreased by dams of all sizes (Mount 1995). Given that most dams and reservoirs are not of the same magnitude as the well-known Hoover or Shasta dams, these common peak flow events are the ones most dramatically altered throughout the West. As my field surveys show, these changes in flow regime result in greater amounts of fine-particle sediment, an increase in nonriparian herbaceous coverage, and an increase in amount of leaf litter or grass thatch seen below dams as compared to areas above dams and areas surrounding naturally flowing streams.

Most of the changes due to dams that I document occurred below dams and immediately adjacent to the

TABLE 4. MANOVA and subsequent ANOVA results if MANOVA effect is significant for greenhouse experiments. Greenhouse experiments used height and reproduction as response variables.

| Year and effect	Response variable	df	Wilks' lambda	F	P
1999					
50% shade		2, 35	0.98	0.28	0.7585
Thatch		2, 35	0.77	5.02	0.0121
	height	1, 36		0.23	0.6313
	reproduction	1, 36		4.32	0.0448
Population		2, 35	0.57	12.95	<0.0001
	height	1, 36		24.64	<0.0001
	reproduction	1, 36		18.78	0.0001
Thatch × population		2, 35	0.95	0.88	0.4252
Row		14, 70	0.61	1.36	0.1945
Column		14, 70	0.73	0.85	0.6184
2000					
70% shade		2, 25	0.40	18.34	<0.0001
	height	1, 26		24.00	<0.0001
	reproduction			35.43	<0.0001
Thatch		2, 25	0.66	6.54	0.0052
	height	1, 26		13.26	0.0012
	reproduction			7.09	0.0131
Population		2, 25	0.76	3.87	0.0344
	height	1, 26		6.01	0.0212
	reproduction	1, 26		6.84	0.0147
Thatch × population		2, 25	0.79	3.38	0.0502
	height	1, 26		5.19	0.0311
	reproduction			6.02	0.0211
Row		14, 50	0.51	1.42	0.1808
Column		14, 50	0.80	0.42	0.9604
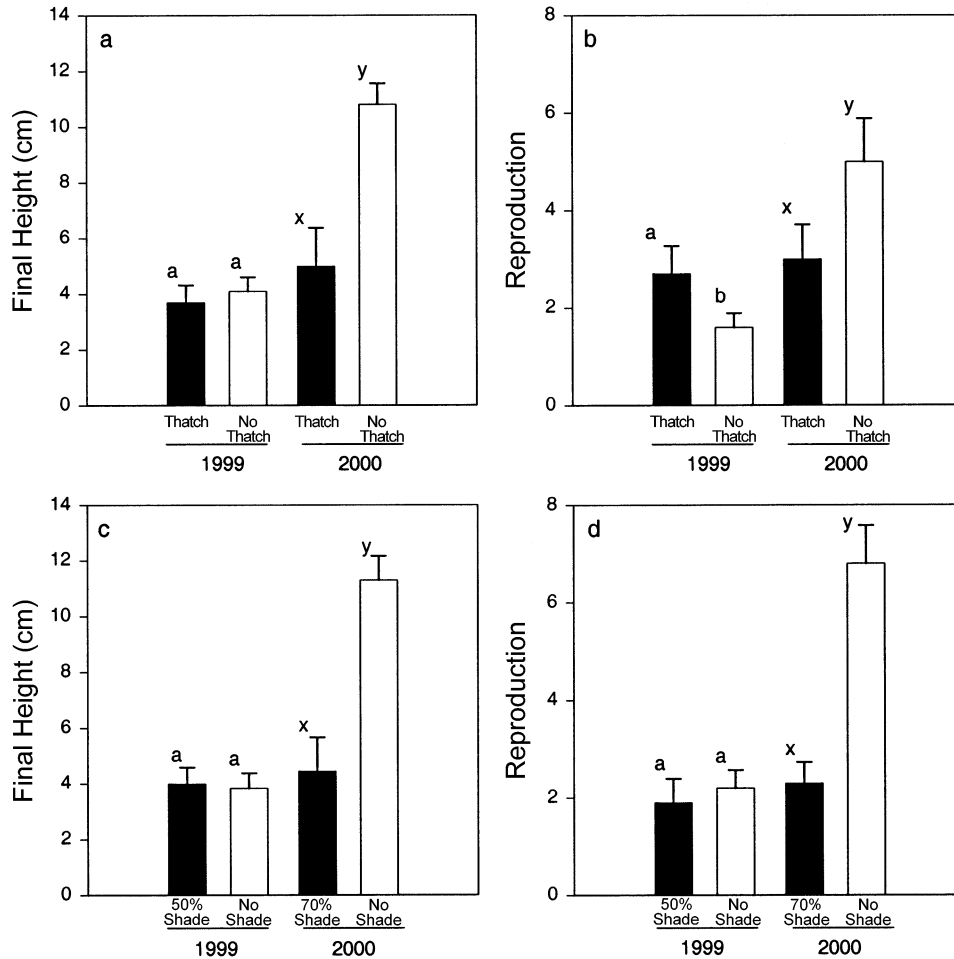
FIG. 9. Effects of thatch and shading on *M. guttatus* height (a and c, respectively) and reproduction (b and d, respectively, representing numbers of flowers and side stems) under greenhouse conditions for 1999 with 50% shading, and 2000 with 70% shading. Bars with the same letter within a year are 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 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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