IMPACT OF A FLOOD ON SOUTHERN CALIFORNIA RIPARIAN VEGETATION

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Abstract: This study assesses flood impacts on riparian vegetation in two watersheds within the Transverse Ranges. Data collected in 1993 were compared to baseline data from 1990 to measure the effect of a 1992 flood. *T*-tests were used to test for significant post-flood changes in overall vegetation characteristics, and vegetation change was regressed on drainage area to test for spatial variation in flood impacts. Results of means comparisons for the overall data set suggest that the impacts of the flood were insignificant. However, these results in part are artifacts of data agglomeration, as regression results suggest that changes in total cover and diversity are spatially varied, with profound impacts at some downstream sites. The relative cover of most species remained constant, reflecting an environment in which frequent floods help to maintain a vegetation assemblage that is not entirely flood resistant, but at least uniform across species in its degree of resistance. [Key words: riparian vegetation, floods, disturbance, equilibrium, California.]

INTRODUCTION

The biogeographic and ecological literature is replete with studies of the effects of floods on riparian vegetation (see reviews in Malanson, 1993, and Parker and Bendix, 1996). The majority of these have pursued questions that were either time independent, stressing patterns of vegetation as quasi-equilibrium responses to the distribution of flood severity (Hupp and Osterkamp, 1985; Harris, 1987; Bendix, 1994a; Birkeland, 1996), or successional, stressing post-flood seral changes in vegetation and resulting species distributions (McBride and Strahan, 1984a, 1984b; Agee, 1988; Baker and Walford, 1995). Relatively few studies have addressed the immediate impact of floods—namely, the degree and kind of difference in the vegetation in the aftermath of a flood (Stromberg et al., 1993). The reason is largely practical: since there is no way to know when a flood will occur, there is no way to plan in advance to gather baseline data shortly before a flood for comparison with the post-flood vegetation. These studies can be conducted only if a flood occurs fortuitously where the vegetation has already been surveyed. This paper results from such a coincidence: a large storm that occurred in 1992 (Raphael et al., 1994) afforded the opportunity to examine the impacts of a moderate (~10-year recurrence interval) flood on vegetation that had been previously surveyed (Bendix, 1994a) in two watersheds within the Transverse Ranges of southern California.

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Flood Impacts

On short-term time scales (i.e., ≤ 5 years), riparian vegetation may be expected to reflect the impact of a flood via two processes: (1) the destruction of pre-existing vegetation by the flood and (2) the colonization by new vegetation of substrate either cleared or deposited by the flood. Successional processes, the focus of much flood-impact research, are less likely to influence post-flood riparian vegetation over short time scales.

The fact that floods can destroy plants is central to the study of riparian vegetation, and has been well documented (e.g., Yanosky, 1982; Roberts and Ludwig, 1991). Such destruction is achieved either mechanically (through the direct impact of floodwaters and the debris they transport or through the erosion of substrate), by burial with sediment, or by oxygen depletion as a result of prolonged soil saturation (Parker and Bendix, 1996). In the arid and semiarid valleys of the southwestern United States, most floods are so short-lived that oxygen depletion is unlikely; the other means all are proportionate to flood magnitude, so that larger floods may be expected to increase the impact. Regardless of the means, the destruction is likely to be selective, as species vary in their vulnerability to these impacts (e.g., Hupp and Osterkamp, 1985). Although research directly relating species characteristics to flood survivorship is limited, there is some support for the unsurprising conclusion that flexible but deeply rooted species (e.g., *Alnus* and *Salix* spp.) have an enhanced likelihood of withstanding floods (Bendix, 1992).

If floods selectively remove some species from the valley floor, then a corollary result should be a short-term decrease in species diversity. This expectation does not contradict riparian applications of the intermediate disturbance hypothesis, whereby disturbance enhances diversity (Nilsson et al., 1989; Baker, 1990a). That hypothesis presupposes longer time scales to allow for establishment of new vegetation after a flood. The more recent the flood, the greater the probability that the species losses will not yet have been offset by the arrival of pioneer species; hence the decline of species diversity is likely to be an impermanent result, in accordance with the intermediate disturbance hypothesis. The length of time required for diversity to reach or exceed the pre-flood level will depend in part on the vagaries of colonization and in part on the measure of diversity used: richness (the number of species present) will increase as soon as seedlings of new species germinate, whereas diversity measures incorporating heterogeneity (Peet, 1974) will not increase until those pioneers have grown to represent a substantial portion of the overall vegetation present.

The establishment of pioneer species is, in itself, another flood impact. The destruction of pre-flood vegetation vacates substrate and allows for colonization, regardless of whether the new seedlings represent species already present (McBride and Strahan, 1984a, 1984b; Malanson and Butler, 1991). Under some circumstances, the stands established in this way may represent a distinctive record of a flood for decades after its actual occurrence (Baker, 1990b).

A seeming contradiction underlies much of this literature on riparian vegetation and floods. On the one hand, floods are assumed to be effective agents of change, whereas on the other it is also assumed that the vegetation already reflects the impacts of past floods—suggesting an equilibrium state that should be maintained, rather than changed, by floods. Presumably flood frequency is central to this issue. The more frequently that ecologically effective floods (i.e., those large enough to affect vegetation) occur, the less change any given flood may be expected to cause. As Malanson (1993) has discussed, equilibrium responses to flood regime may be difficult to identify in actual riparian sites. Empirical studies quantifying the impact of floods of intermediate magnitude and frequency may help to clarify this question.

Because flood magnitudes vary through watersheds, the impacts of floods may be expected to vary as well. Although the details of flow conditions and resultant impacts vary, it is at least safe to generalize that within most watersheds flood discharges increase in the downstream direction (Leopold et al., 1964). Thus, as with other aspects of riparian vegetation-environment relationships, location within a stream network may be critical to the impact of floods on vegetation (Baker, 1989; Malanson, 1993; Bendix, 1994b).

Hypotheses

The foregoing review suggests the following hypotheses regarding short-term flood impacts, which are tested in this study: (1) there will be a decrease in the total cover of vegetation; (2) there will be a decrease in the species diversity of the vegetation; (3) there will be an increase in the relative importance of species that are well-rooted and either flexible enough or large enough to avoid mechanical damage—observations in the southern California setting suggest *Alnus rhombifolia* and three local *Salix* species for the former, and *Populus fremontii* for the latter; (4) there will be colonization by seedlings of locally prominent species that have been noted in past research for their pioneer roles, such as *Salix exigua* and *Baccharis glutinosa* (Holstein, 1984) or *Salix laevigata* and *Populus fremontii* (McBride and Strahan, 1984a); (5) these effects will vary with location, with impacts increasing lower in the watershed.

STUDY AREA

Data for this study were collected in the watersheds of Piru and Sespe creeks, high-gradient mountain streams draining from the western Transverse Ranges into the Santa Clara River (Fig. 1). Drainage areas for the sites surveyed range from 12 km^2 to 510 km^2, with site elevations varying from 800 m to 1450 m above sea level. The steep, mountainous terrain of these watersheds contributes to a flashy flood regime, through orographic intensification of frontal precipitation and rapid runoff into the stream channels. Consequently these are streams in which large floods are relatively frequent occurrences (Raphael et al., 1994).

The riparian vegetation of these watersheds falls within Malanson's (1993) classification of gallery forest in a Mediterranean environment, although "forest" may be an exaggeration at some sites. Certainly the riparian vegetation forms a gallery, in which *Salix*, *Populus*, and *Alnus* dominants contrast sharply with the surrounding chaparral (Holstein, 1984; Bendix, 1994a). The study sites are located along (hydrologically) unregulated reaches of the streams, within the Los Padres National Forest.

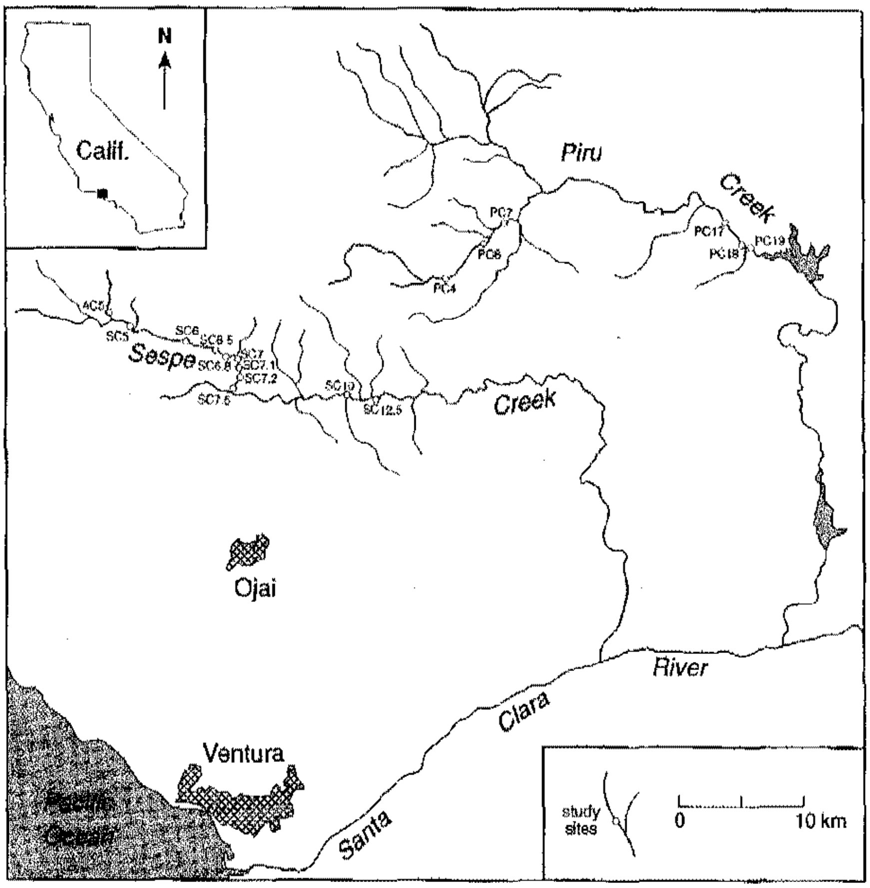

Fig. 1. Location of study sites in southern California.

Apart from floods, the only major disturbance agent here is fire, as none of the sites has been significantly affected by livestock grazing (Bendix, 1994a).

THE 1992 FLOODS

In February 1992, a series of cold fronts brought heavy precipitation to much of southern California, causing flooding through much of the region. The climatology of these storms and their hydrologic and geomorphic impacts have been described in detail by Raphael et al. (1994). They reported a recurrence interval for the peak discharge (12 February) near the mouth of Sespe Creek of 8.33 years; at an upstream site (location of site 7.1, Fig. 1) the peak discharge of 238 m^3s^{-1} had a recurrence interval of 12 years. The range of return intervals presumably reflects the local variability typical of such mountainous terrain, but it is likely that the recurrence interval throughout the watershed was on the order of 10 years. Gauge data are not available for Piru Creek, but given its proximity to Sespe Creek, and the parallel orientation of the two drainages (Fig. 1), it is probable that the recurrence interval for Piru Creek was comparable to that of Sespe. This fairly low recurrence interval does not suggest an extreme event, but Graf (1983) has demonstrated that in dryland streams floods with recurrence intervals as small as 5 years may be geomorphically effective, depending on sediment characteristics. Visible flood debris at several sites indicated that flood stages exceeded 3.5 m, presumably reflecting high-energy conditions. Certainly the analyses of Raphael et al. (1994) leave no doubt that the 1992 floods were effective in mobilizing sediment. Given the geomorphic effectiveness of these floods, it seems pertinent to examine their ecological impacts. And the high frequency of such floods here suggests that this is an environment in which short-term flood impacts may be particularly relevant.

METHODS

Baseline data for this study are from line-intercept sampling (Canfield, 1941) conducted in the summer and fall of 1990 (Bendix, 1994a, 1994b). These data include cover values for all woody species, measured along transects across the floodplain, orthogonal to the valleys' axes. Fall sampling was accomplished before deciduous species had lost their leaves, so that cover measurement was consistent. At the time each of these transects was initially surveyed, the endpoints of the transects were flagged and marked with sections of rebar pounded into the ground. Data were collected again in August 1993, approximately 18 months after the 1992 flood. While soon enough to observe the flood's impact, this interval allowed two seasons for seedling establishment, as the pioneer species here germinate in the spring or early summer (McBride and Strahan, 1984b). Resampling included only those sites for which both transect endpoints could be located, so that the transects could be exactly superimposed upon the earlier ones. This limited the data set to 17 sites, the markers for 20 other sites having been removed by floodwaters and vandalism. In addition, alluvial surfaces at each site and along most of the length of each creek between sites were examined for seedlings or small saplings that could reasonably be interpreted as having germinated since the 1992 flood.

The data from each site were used to calculate pre- and post-flood values for total cover, for the relative cover of individual species, and for the Shannon-Weaver diversity index (H'). The diversity index is calculated by the formula $H' = -\Sigma\, p_i \log p_i$, where p_i is the importance value for the ith species. Relative cover was used as the importance value. Paired *t*-tests were used to test the first three hypotheses, those relating to changes in total cover, diversity, and the relative importance of individual species. The fourth hypothesis, regarding colonization, was tested qualitatively, by observation. The fifth hypothesis, regarding spatial variation, was tested by regressing the changes in total cover, diversity, and relative cover of species on drainage area (the latter representing position within the watershed). The species for which regressions were calculated were those that accounted for ≥4% mean relative cover in the pre-flood data. The regression equations took the form $y = a + b \log D_A$, where y is the change in vegetation characteristic and D_A is drainage area measured in km^2. Examination of residuals from the regressions revealed no patterns indicative of spatial autocorrelation, and plots of residuals against drainage area showed them to be homoscedastic. However, it should be noted that the limited number of sites (n = 17 for all analyses) suggests that the statistical results, while interesting, should be interpreted with caution.

RESULTS AND DISCUSSION

Results of the paired t-test comparisons are presented in Table 1. The first hypothesis was that there would be a decrease in the total cover of riparian vegetation. This proved true on average, but the difference was not a significant one. Several of the sites actually had substantially increased cover, reflecting abundant growth since the 1990 sampling and minimal losses in the 1992 flood. Those increases may reflect increased moisture availability; the 1990 data were collected near the end of a three-year drought, and the end of that drought may have allowed accelerated growth. Whatever the reason, those increases almost balanced the flood losses at other sites, so that the mean decrease in cover was only ~1 m (down from 22.1 m in 1990).

Similarly, the slight decrease in diversity (cf. hypothesis 2) fell well short of significance. The fact that average diversity remained unchanged suggests that flood losses were not concentrated in vulnerable species, but rather were well distributed across taxa. If species vulnerability was not important in differentiating flood losses, then it is unlikely that hypothesis 3, postulating enhanced survivorship for sturdier species, would prove true either. Indeed, of the five species thought to be well adapted to resist flood damage, only two—*Populus fremontii* and *Salix laevigata*—had even slightly increased relative cover, and none experienced statistically significant changes in their relative importance within the overall riparian mix (Table 1). This apparent compositional stability was not limited to these five species. Out of 26 species present pre-flood, only *Eriogonum fasciculatum* showed a significant change in relative cover, with an increase that still left it short of 5%.

The fourth hypothesis, predicting colonization by commonly recognized pioneer species, also proved false. This was the result not of a misunderstanding of species roles, but of the complete absence of seedling establishment. Reconnaissance along several kilometers of the two creeks, in addition to examination of the study sites, revealed extensive areas of bare alluvium, but no sign of recently established individuals. There were indeed fresh stems sprouting from some flood-damaged *Alnus* and *Salix*, but such vegetative growth tended to reinforce thickets that had survived the flood, rather than re-occupy areas that had been left bare.

Successful establishment of riparian seedlings requires adequate moisture in the growing season after substrate is cleared by a flood (Baker, 1990b), and even then seedlings may be vulnerable to subsequent floods (McBride and Strahan, 1984a). In Sespe and Piru creeks, any seedlings established in the spring of 1992 probably were washed out the following winter, when another substantial flood occurred. This latter flood peaked on February 19, 1993, with a discharge of 142 m^3s^{-1} at site SC7.1. The flood had a recurrence interval of 7.8 years and presumably was large enough to uproot any small seedlings, especially given that these would have been in the sites experiencing the greatest flood impacts, floods having been the origin of the germination sites the preceding year. The absence of seedlings germinating after

Table 1. Paired *t*-Test Comparisons[a] of Vegetation Characteristics, 1990 and 1993[b]

Vegetation characteristic	1990 (mean ± SD)	1993 (mean ± SD)	*t*	*p*
Total cover (m)	22.11 ± 12.71	21.06 ± 11.45	−0.410	.69
Diversity (*H'*)	1.29 ± 0.48	1.15 ± 0.51	−0.922	.37
Relative cover (in percent)				
Salix lasiolepis	29.78 ± 28.99	27.54 ± 27.85	−0.416	.68
Populus fremontii	15.14 ± 21.80	16.54 ± 23.68	0.375	.71
Salix laevigata	9.75 ± 11.80	7.09 ± 12.20	−0.998	.33
Salix exigua	9.38 ± 16.12	7.05 ± 16.11	−1.323	.20
Alnus rhombifolia	8.12 ± 15.96	5.17 ± 15.59	−1.386	.18
Rosa californica	6.89 ± 10.56	7.40 ± 11.20	0.461	.65
Baccharis glutinosa	4.82 ± 7.14	4.43 ± 9.58	−0.306	.76
Lepidospartum squamatum	2.23 ± 8.20	1.68 ± 6.92	−1.612	.13
Ephedra viridis	1.88 ± 7.75	5.88 ± 24.25	1.000	.33
Adenostoma fasciculatum	1.84 ± 5.43	1.49 ± 4.93	−1.141	.27
Pinus ponderosa	1.73 ± 6.15	0.00	−1.160	.26
Eriogonum fasciculatum	1.29 ± 3.16	4.18 ± 6.14	2.901	.01
Eriodictyon crassifolium	0.98 ± 2.05	0.06 ± 0.27	−1.866	.08
Ceanothus leucodermis	0.84 ± 1.93	0.50 ± 2.07	−0.651	.52
Toxicodendron radicans	0.82 ± 2.93	0.57 ± 1.56	−0.359	.72
Tamarix chinensis	0.74 ± 3.06	0.00	−1.000	.33
Arctostaphylos glauca	0.56 ± 2.33	0.00	−1.000	.33
Quercus dumosa	0.55 ± 2.27	0.91 ± 3.75	1.000	.33
Rhus trilobata	0.47 ± 1.41	0.90 ± 2.57	0.647	.53
Chrysothamnus nauseosus	0.46 ± 1.33	1.24 ± 2.69	1.237	.23
Artemisia tridentata	0.42 ± 1.14	1.76 ± 4.23	1.362	.19
Prunus spp.	0.38 ± 1.58	0.15 ± 0.64	−1.000	.33
Cercocarpus betuloides	0.34 ± 1.39	0.00	−1.000	.33
Platanus racemosa	0.24 ± 0.97	1.92 ± 6.51	1.081	.30
Rubus ursinus	0.21 ± 0.86	0.76 ± 3.15	0.417	.68
Quercus chrysolepis	0.13 ± 0.56	0.30 ± 1.24	1.000	.33

[a] The *t*-test indicates whether the differences between 1990 and 1993 were significantly greater than zero.

[b] $n = 17$.

the 1993 flood remains unexplained, however; 1993 was not droughty, and even by August there were still patches of alluvium of varying texture that were visibly moist but bare of seedlings. A possible (but untestable) explanation is that abundant moisture actually prevented rather than facilitated germination, if high stream flows had not yet dropped enough to expose substrate by the time (primarily May and

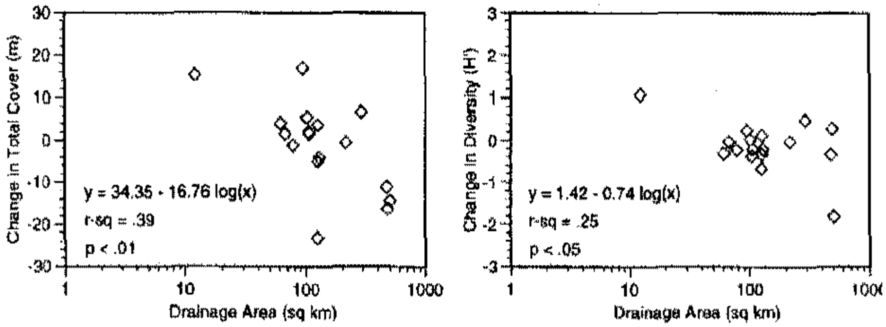

Fig. 2. Scatterplots and regression equations relating changes in total cover and the Shannon-Weaver diversity index to position in the watershed.

June) that potential pioneer species were producing seed (McBride and Strahan, 1984b).

The negative results for the first three hypotheses are at least partially explained by the findings for hypothesis 5, which related flood impacts to location. Results from the regression equations relating post-flood change to position in the watershed (Fig. 2) indicate that changes in both total cover and diversity were significantly related to position. Thirty-nine percent of the variance in cover changes was explained by drainage area. The regression coefficient was negative, reflecting a pattern in which the vegetation losses were concentrated at downstream sites, with gains at upstream sites (Figs. 3 and 4). This finding supports the hypothesis that flood impacts would be concentrated downstream, where flood discharges are highest. However, it subverts hypothesis 1, because the changes balance out in calculating average change. Changes in diversity also were significantly related to drainage area, and again the changes were greatest downstream, as hypothesized. This relationship is weaker, reflecting the fact that even where floods do destroy vegetation, they must do so selectively if they are to affect diversity.

Despite the apparent importance of downstream variability for the summary measures of cover and diversity, the changes in individual species were not well explained by drainage area (Table 2). Only *Salix exigua* had changes significantly related to watershed position, and the nature of that relationship was contrary to expectation. Although this species was expected to have good resistance to flood damage, the negative regression coefficient reflects greater losses at the high-discharge, downstream sites. One implication of this result is that substrate susceptibility to erosion may be more important than the physical characteristics of plants in determining flood losses. *Salix exigua* tends to grow in thickets on sandy and gravelly alluvium along channel margins. If this substrate is substantially reworked during floods, then the plants will be washed away, even if their flexibility has spared them breakage of stems. Excepting *Salix exigua*, the lack of significant overall changes in species' importance (Table 1) and the fact that there was no spatial variability masking changes within the overall data set (Table 2) indicate that the flood(s) had minimal impacts on the composition of the riparian vegetation in these watersheds. The spatial pattern of changes in diversity probably reflects a combina-

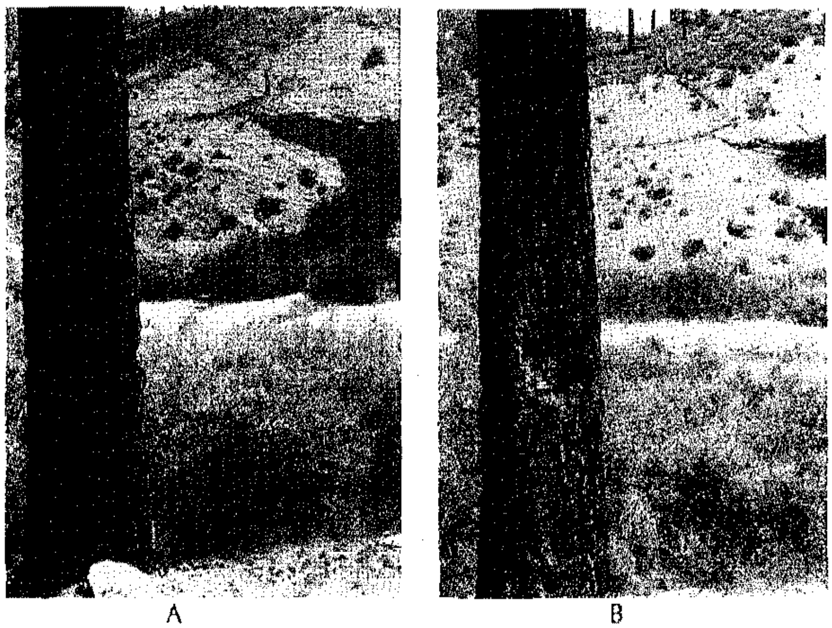

Fig. 3. Site PC4 in October 1990 (A) and August 1993 (B). This is the highest site in the Piru Creek watershed, and the cover of *Salix lasiolepis* and *Rosa californica* experienced minimal change.

tion of the pattern for *S. exigua* and much more subtle changes in the scarcer species. For example, two of the three species that disappeared entirely after the flood—*Tamarix chinensis* and *Cercocarpus betuloides* (Table 1)—had been found primarily at sites low in the watersheds (Bendix, 1994a); their loss would contribute to the decrease in diversity at those sites.

CONCLUSIONS

Two general findings in this study are of interest. The first is that, even within rather small watersheds, there is striking spatial variability in flood impacts. This spatial variability was strikingly visible in August 1993, when a surprising number of sites appeared unchanged (e.g., Fig. 3) by a flood that had left a catastrophic imprint farther downstream (Fig. 4). From a methodological perspective, this suggests that such impacts may be easily obscured, either by aggregation of data (cf. Table 1) or simply by failing to sample the watershed comprehensively. From an ecological perspective, it is a reminder of the complexity of fluvial/riparian systems. In discussion of flood impacts, emphasis frequently is placed on their recurrence interval, which often is conflated with magnitude. The distribution of impacts in the Piru and Sespe watersheds is a reminder that the spatial dimension can be as important as the temporal; recurrence interval by itself does not have ecological meaning.

Fig. 4. Site PC19 in October 1990 (A) and August 1993 (B). This is the lowest site in the Piru Creek watershed, and it experienced the greatest change. In 1990, seven species were sampled, including substantial cover of *Baccharis glutinosa*, *Tamarix chinensis*, and three *Salix* species in the thicket adjacent to the channel. In 1993 total cover and diversity were substantially reduced, as the only remaining vegetation on the sample transect was *Ephedra viridis*, well above the channel.

Table 2. Summaries for Analyses Regressing the Change in Species' Relative Cover (1990–1993) on Drainage Area (log-transformed)[a]

Species	Sign[b]	R^2	F	p
Salix lasiolepis	+	.09	1.524	.236
Populus fremontii	–	.01	0.155	.700
Salix laevigata	–	.09	1.522	.236
Salix exigua	–	.33	7.307	.016
Alnus rhombifolia	+	.00	0.009	.926
Rosa californica	–	.10	1.637	.220
Baccharis glutinosa	–	.02	0.352	.562

[a] $n = 17$.

[b] "Sign" refers to the sign of the coefficient; thus a positive sign suggests that the change was greater downstream.

The second general observation is that the flood had minimal impact on the compositional mix of species. There certainly were losses at some sites, but no important (in terms of pre-flood cover) species suffered disproportionate losses, as indicated by the stable relative-cover values. Given the fairly high frequency of this magnitude of flood, this result suggests that species that would be disproportionately vulnerable simply do not have a chance to become important components of the vegetation here. Because the species that do become important are relatively invulnerable, the resulting mix is in at least quasi-equilibrium. Such a conclusion supports the contention that riparian vegetation in at least some environments should not be considered successional (Sigafoos, 1961; Johnson et al., 1989). If that is true, frequent floods should not be regarded as agents of disturbance, in the sense of triggering a change in vegetation. Rather, they constitute an environmental characteristic, similar to temperature or moisture, that helps maintain stable vegetation by constraining the pool of species that can succeed at a site.

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BIBLIOGRAPHY

Agee, J. K. (1988) Successional dynamics in forest riparian zones. In K. J. Raedeke, ed., *Streamside Management: Riparian Wildlife and Forestry Interactions.* Seattle, WA: University of Washington Institute of Forest Resources Contribution No. 59, 31–43.

Baker, W. L. (1989) Macro- and micro-scale influences on riparian vegetation in western Colorado. *Annals of the Association of American Geographers*, Vol. 79, 65–78.

Baker, W. L. (1990a) Species richness of Colorado riparian vegetation. *Journal of Vegetation Science*, Vol. 1, 119–124.

Baker, W. L. (1990b) Climatic and hydrologic effects on the regeneration of *Populus angustifolia* James along the Animas River, Colorado. *Journal of Biogeography*, Vol. 17, 59–73.

Baker, W. L. and Walford, G. M. (1995) Multiple stable states and models of riparian vegetation succession on the Animas River, Colorado. *Annals of the Association of American Geographers*, Vol. 85, 320–338.

Bendix, J. (1992) Scale-Related Environmental Influences on Southern California Riparian Vegetation. Unpublished doctoral dissertation, University of Georgia.

Bendix, J. (1994a) Among-site variation in riparian vegetation of the Southern California Transverse Ranges. *American Midland Naturalist*, Vol. 132, 136–151.

Bendix, J. (1994b) Scale, direction and pattern in riparian vegetation–environment relationships. *Annals of the Association of American Geographers*, Vol. 84, 652–665.

Birkeland, G. H. (1996) Riparian vegetation and sandbar morphology along the lower Little Colorado River, Arizona. *Physical Geography*, Vol. 17, 534–553.

Canfield, R. H. (1941) Application of the line intercept method in sampling range vegetation. *Journal of Forestry*, Vol. 39, 388–394.

Graf, W. L. (1983) Flood-related channel change in an arid-region river. *Earth Surface Processes and Landforms*, Vol. 8, 125–139.

Harris, R. R. (1987) Occurrence of vegetation on geomorphic surfaces in the active floodplain of a California alluvial stream. *American Midland Naturalist*, Vol. 118, 393–405.

Holstein, G. (1984) California riparian forests: Deciduous islands in an evergreen sea. In R. E. Warner and K. M. Hendrix, eds., *California Riparian Systems*. Berkeley, CA: University of California Press, 2–22.

Hupp, C. R. and Osterkamp, W. R. (1985) Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology*, Vol. 66, 670–681.

Johnson, R. R., Bennett, P. S., and Haight, L. T. (1989) Southwestern woody riparian vegetation and succession: An evolutionary approach. In D. L. Abell, ed., *Proceedings of the California Riparian Systems Conference*. Berkeley, CA: USDA Forest Service General Technical Report PSW-110, 135–139.

Leopold, L. B., Wolman, M. G., and Miller, J. P. (1964) *Fluvial Processes in Geomorphology*. San Francisco: W. H. Freeman and Company.

Malanson, G. P. (1993) *Riparian Landscapes*. New York: Cambridge University Press.

Malanson, G. P. and Butler, D. R. (1991) Floristic variation among gravel bars in a subalpine river, Montana, U.S.A. *Arctic and Alpine Research*, Vol. 23, 273–278.

McBride, J. R. and Strahan, J. (1984a) Fluvial processes and woodland succession along Dry Creek, Sonoma County, California. In R. E. Warner and K. M. Hendrix, eds., *California Riparian Systems*. Berkeley, CA: University of California Press, 110–119.

McBride, J. R. and Strahan, J. (1984b) Establishment and survival of woody riparian species on gravel bars of an intermittent stream. *American Midland Naturalist*, Vol. 112, 235–245.

Nilsson, C., Grelsson, G., Johansson, M., and Sperens, U. (1989) Patterns of plant species richness along riverbanks. *Ecology*, Vol. 70, 77–84.

Parker, K. C. and Bendix, J. (1996) Landscape-scale geomorphic influences on vegetation patterns in four environments. *Physical Geography*, Vol. 17, 113–141.

Peet, R. K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, Vol. 5, 285–307.

Raphael, M., Feddema, J., Orme, A. J., and Orme, A. R. (1994) The unusual storms of February 1992 in southern California. *Physical Geography*, Vol. 15, 442–464.

Roberts, J. and Ludwig, J. A. (1991) Riparian vegetation along current-exposure gradients in floodplain wetlands of the River Murray, Australia. *Journal of Ecology*, Vol. 79, 117–127.

Sigafoos, R. S. (1961) *Vegetation in Relation to Flood Frequency near Washington, D.C.* Washington, DC: United States Geological Survey Professional Paper 424-C.

Stromberg, J. C., Richter, B. D., Patten, D. T., and Wolden, L. G. (1993) Response of a Sonoran riparian forest to a 10-year return flood. *Great Basin Naturalist,* Vol. 53, 118–130.

Yanosky, T. M. (1982) *Effects of Flooding upon Woody Vegetation along Parts of the Potomac River Flood Plain.* Washington, DC: United States Geological Survey Professional Paper 1206.