Ecology and Evolution of Southwestern Riparian Plant Communities

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Introduction

The riparian plant communities of the arid and semiarid Southwest have received much recent attention. Basic theoretical problems such as the relationship between the site distributions of riparian plants, the physical dynamics of the floodplain, ecological succession and a definition of the riparian plant community that makes ecological sense are now widely discussed matters. Public concerns over the management of riparian habitats have stimulated a great deal of attention by federal and state agencies. The National Wetlands Classification (Cowardin et al. 1979) and Inventory of the U.S. Fish and Wildlife Service in particular has made the need for a more rigorous treatment of the biology of Southwestern riparian plant communities even more apparent.

Here I report on the relationship between the distributions of plants in the floodplain and a set of physical site factors. It is clear that the plant-floodplain relationship does indeed have an important evolutionary basis, and that its understanding contributes to useful perspectives on the nature of riparian plant communities. Pertinent field data on the riparian woodland vegetation of Trout Creek, Mohave County, Arizona are provided in Reichenbacher (1980, 1981). Trout Creek is a 50 km perennial stream along which six study sites were located between 829 and 1044 m elevation, within the Fremont Cottonwood *(Populus fremontii)*—Goodding Willow *(Salix nigra)* association that dominates lower Trout Creek (Fig. 1). The Trout Creek data, obtained during 1975-1980, illustrate well the concepts discussed here.

Dynamics of the Stream

Riparian plants respond by species, site, and abundance to two critical features of their drainageway habitat: (1) an unstable substratum with (2) a greater plant-available soil moisture than in surrounding uplands.

Wolman and Leopold (1957) first demonstrated that sediment age in floodplains increases with elevation above low water. Everitt (1968) supported this with a unique method that related the reproductive biology of Plains Cottonwood *(Populus sargenti)* to channel migration and sediment deposition (Fig. 2). Migration of the stream in its floodplain means a steep gradient in substratum instability. On concave banks, established vegetation is gradually undercut by the stream's erosive forces, and on convex banks sediment is deposited (Gill 1972, Johnson et al. 1976, Irvine and West 1979 and White 1979).

A major difference in site factors influencing vegetation between humid or sub-humid and arid floodplains is that plant-available soil moisture decreases more dramatically with increasing distance from the streambank in the latter than in the former (Figs. 3 and 4). Consequently, terraces above stream-level and within the floodplain in arid regions can be nearly as harsh as the surrounding uplands (Meinzer, 1927; Gary, 1965; Davis, 1974).

Along "losing" streams, floodplain terraces are so high above the dome-shaped water table that plants are unable to utilize that moisture (Ellingson, 1979; Fig. 5). In the Southwest terraces above flat or even slightly elevated water tables (i.e., "gaining" streams) are still arid, particularly when compared to similar situations in humid or sub-humid regions.

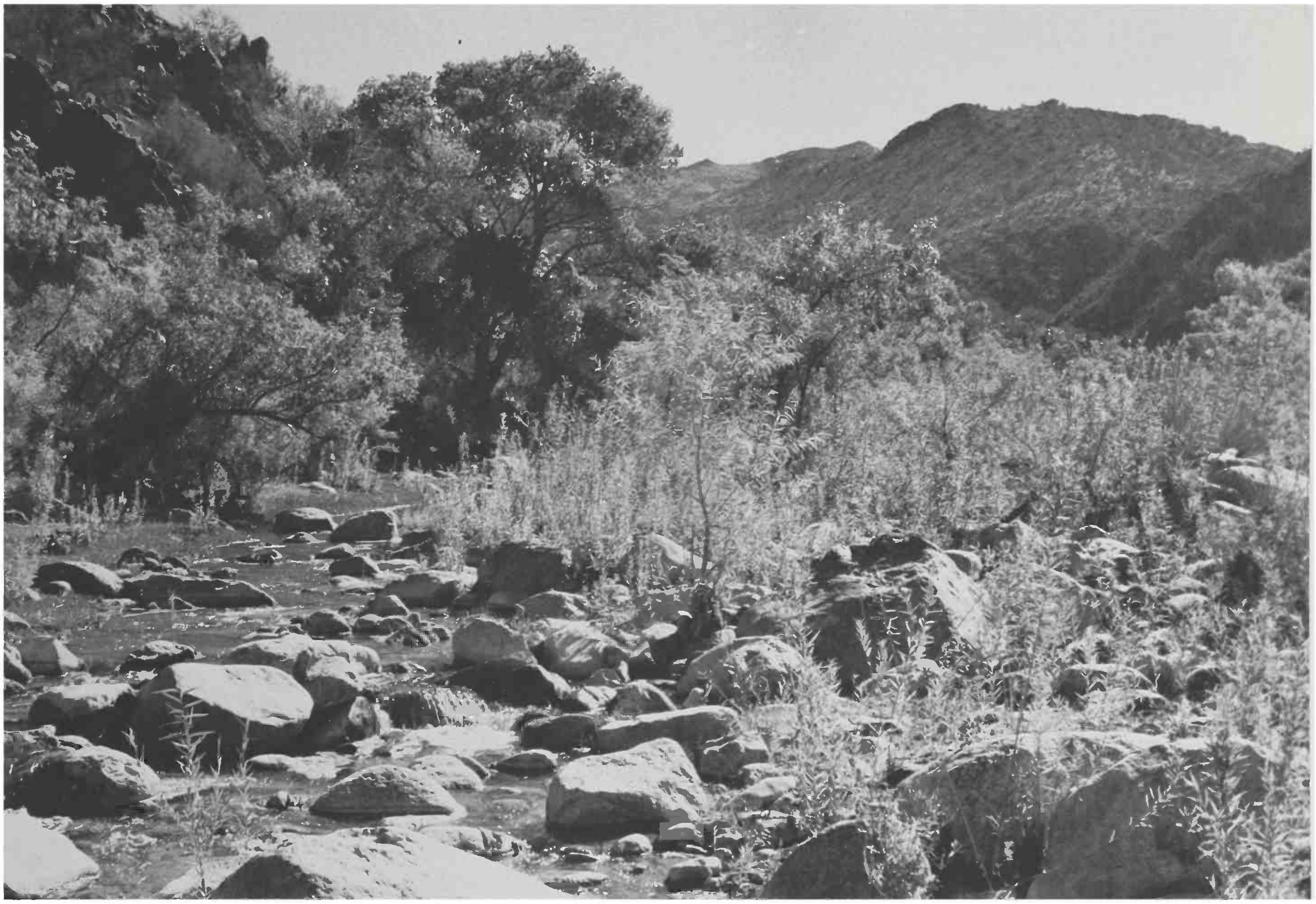


Figure 1. *Deciduous riparian woodland of Fremont Cottonwood and Goodding Willow along lower Trout Creek, Mohave County, Arizona.*

Reproductive Adaptations

Riparian plants have specialized along particular segments of the substratum stability and soil moisture gradients. Lowe (1961, 1964) recognized this when he defined a *Populus-Salix* association along the channel and streambank, and a *Prosopis-Acacia* association on upper floodplain terraces (Fig. 4).

Populus-Salix Association—Cottonwoods and willows have long been known as aggressive colonizers of disturbed sites in a wide variety of ecological situations. These include high elevation fell fields (Clausen, 1965), glacial outwash (Crocker and Major, 1955), glacial moraines (Decker, 1966), arctic tundra (Argus, 1973), burned areas in conifer forests (Braun, 1950; Argus, 1973) and sand dunes (Cowles, 1899; and Olson, 1958).

Table 1 summarizes the essential adaptations of the few floodplain salices for which reliable data are available. In general, cottonwoods and willows produce large numbers of wind and water dispersed seeds which are viable for extremely short periods of time.

These coupled with other physiologic, ontogenic, and morphologic adaptations make salices ideally adapted to the floodplain environment. Riparian salices germinate and successfully establish *only* on the fresh wet sand and gravel exposed nearly every year following spring snow melt at higher elevations and latitudes, or spring rains in sub-Mogollon Arizona (Moss, 1938; Horton et al., 1960; Hosner and Minckler, 1963; Farmer and Bonner, 1967; Everitt, 1968; Wilson, 1970; Gill, 1972; McLeod and McPherson, 1973; Johnson et al., 1976; Franz and Bazzaz, 1977; White, 1979; Noble, 1979). Salices are not as highly tolerant of flooding as many swamp trees, indicating that growth to maturity is possible only when lateral migration of the stream leaves the trees well above the level of prolonged submergence (Moss, 1938; Hosner, 1960; Hosner and Boyce, 1962; McLeod and McPherson, 1973; Pereira and Koslowski, 1977; White, 1979).

Figure 6 shows the distribution of Goodding Willow across the floodplain at a Trout Creek study site. A flood approaching the "50 year" or "100 year" magnitude had swept the canyon five months prior to collection of line intercept data. All individuals on the left side of the stream (north bank) were post-flood seedlings and all those on the right side (south bank) were flood survivors. At this site the north bank was convex and essentially barren of vegetation while the south bank was concave and thickly vegetated by mostly adult plants.

Seepwillow *(Baccharis salicifolia)* is an aggressive, weedy, streambank species which shares many of the adaptations of cottonwoods and willows. It produces many small seeds which are wind dispersed and viable for a short period of time. Germination and establishment occurs on wet sandy alluvium as flood flows recede (Horton et al., 1960; Wilken, 1972; Warren and Turner, 1975). Figure 7 shows the distribution of

Table 1. Reproductive adaptations of floodplain species in *Populus* and *Salix*.

Adaptation	**Taxon**	**Reference**
Seed Set		
25,000,000 seeds/tree/season	*Populus deltoides*	Bessey (1904)
425,000 seeds/lb.	*Populus deltoides*	Schopmeyer (1974)
2,600,000 seeds/lb.	*Salix amygdaloides*	Schopmeyer (1974)
10,000,000 seeds/lb.	*Salix exigua*	Schopmeyer (1974)
Seed Dispersal		
Wind and water dispersed by an arillate comae of trichomes	Salicaceae	Argus (1973), Dorn (1976), Warren and Turner (1975).
Seed Longevity		
1-2 weeks	*Populus deltoides, Salix nigra*	White (1979)
1-3 weeks	*Salix*	Ware and Penfound (1949), Moss (1938)
7 weeks	*Populus fremontii*	Horton et al. (1960)

Seepwillow across the floodplain at another Trout Creek study site. Seedlings were most abundant on the convex south bank 1-8 meters from the streambank. All the flood survivors were concentrated on the concave north bank. The cluster at 5-12 m represents a small clump of Seepwillow isolated by a shift in stream course. The data were collected in late June shortly before the onset of summer rains; by late August only 5-10 seedlings had survived recurrent (but minor) floods.

Prosopis-Acacia Association—Mesquites *(Prosopis juliflora)*, Acacias *(Acacia greggii)* and other upper terrace species have not been extensively studied as such. They are widespread as dominants of upland subtropical/tropical and warm temperate savannas. Their reproductive strategies are summarized in Table 2. Mesquites produce few, well-nourished seeds that may remain viable for many years, and are dispersed by frugivorous mammals. They apparently co-evolved with the now extinct Plio-Pleistocene megafauna.

The Trout Creek study sites were all located in gorges too narrow for extensive development of a *Prosopis-Acacia* association. In fact, neither Mesquite nor Catclaw were encountered on any of the intercepts. However, there are several locations in the canyon where the floodplain terrace vegetation is relatively well developed. At sites such as those included in the Trout Creek study, the floodplain, and consequently the riparian community is laterally truncated (see Fig. 4). The terraces and broad floodplains of larger, shallow gradient rivers and streams are absent in most of lower Trout Creek (Zimmermann 1969, Turner 1974, Lacey et al. 1975, and Turner and Karpiscak 1980).

Evolutionary Relations

Mesquites and acacias in the North American Southwest are derived from Neotropical floras. Their adaptations to semiarid uplands have proved preadaptive in certain riparian situations. Consequently upper floodplain terraces in the arid Southwest are dominated by microphyllous short-tree associations.

The broadleaf deciduous trees characteristic of our Southwestern riparian woodlands and forests include genera and species once a part of a widespread Early Tertiary mixed mesophytic forest. As climates became less equable in the continental United States during Middle to Late Tertiary time, this northern forest fragmented and even disappeared over wide areas (Raven and Axelrod, 1974). Upper floodplain terrace species of the Midwest are derived from it and the highly fractured distributions of obviously closely related species groups reflect that fact (e.g. *Juglans hindsii, californica, major, microphylla, nigra; Fraxinus pennsylvanica pennsylvanica, lanceolata, velutina*). *Populus-Salix* associations diversified during the Tertiary and now occupy a wide variety of regions, all of which share the common feature of running water and a shifting substratum. The distribution of closely related species (e.g. *Populus fremontii, deltoides, sargenti, wislizeni; Salix nigra, virginiana, amygdaloides, gooddingii*) reflects that ecological diversification (Reichenbacher, 1980).

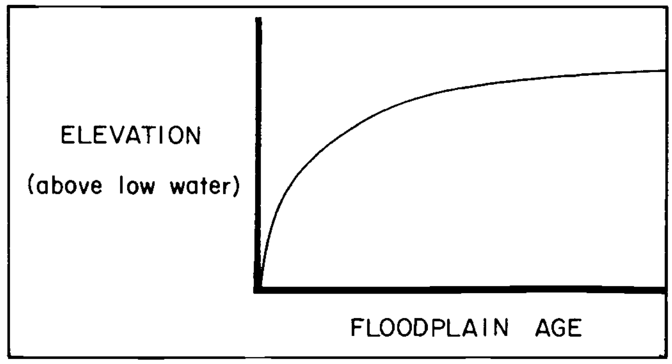


Figure 2. *Relationship between floodplain age and elevation at low water. It is this feature of riparian environments that generates successional dynamics (from Wolman and Leopold, 1957 and Everitt, 1968).*

For many years ecologists referred to such riparian broadleaf deciduous taxa in *Populus, Salix, Fraxinus, Juglans, Platanus* and others as obligate riparian species. This and other terms, including facultative riparian and pseudoriparian, have been applied to diverse "riparian" taxa (Campbell and Green, 1968; Brown, Lowe and Hausler, 1977; Dick-Peddie and Hubbard, 1977; and others). Recently the U.S. Fish and Wildlife Service adopted such nomenclature in its data base on the wetlands of the United States (see Cowardin et al., 1979): "obligate riparian" for "true riparian" and "facultative riparian" for "pseudoriparian." Although still useful for many of the utilitarian purposes for which they were originally intended, such classifications are often counterproductive, and fail to recognize the role of

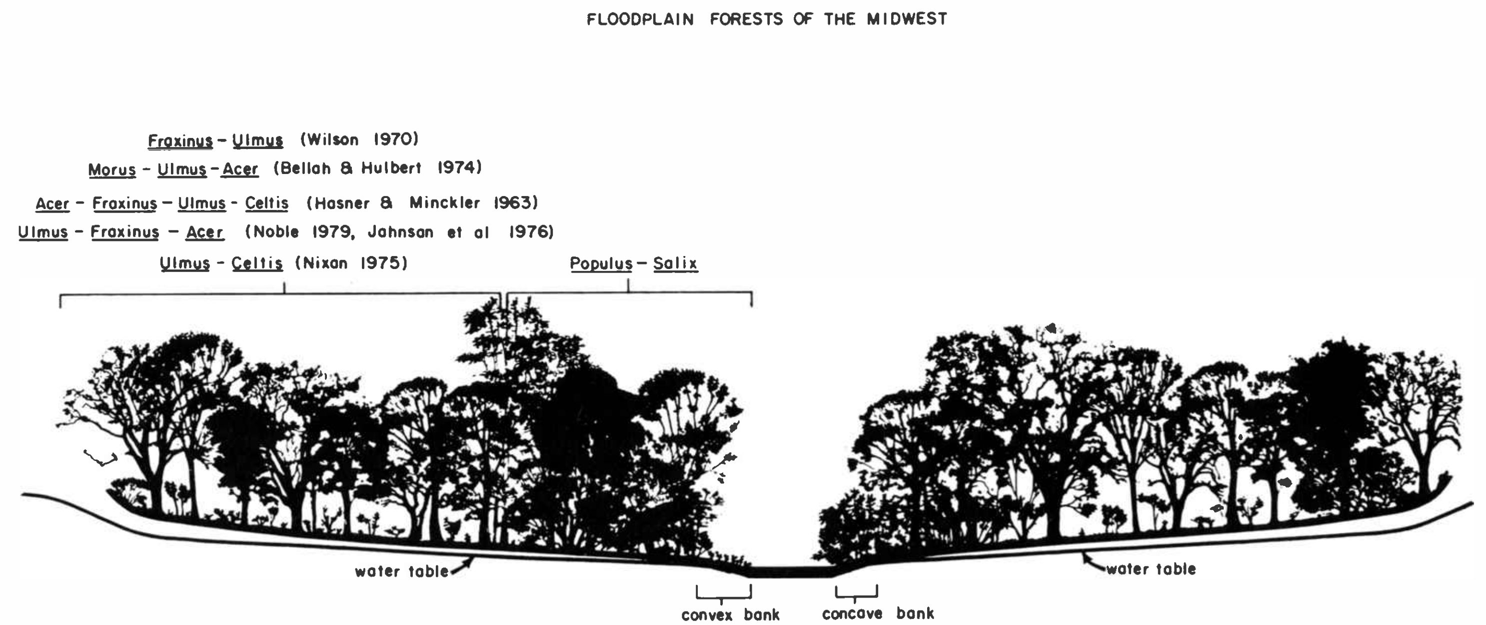


Figure 3. *Cross-section of an idealized floodplain in the midwestern United States. Upper floodplain terraces are dominated by various broadleaf tree associations while the streambank is dominated by Cottonwood-Willow associations. On the convex bank early seres are initiated by seedling establishment while mature vegetation on the concave bank is undercut.*

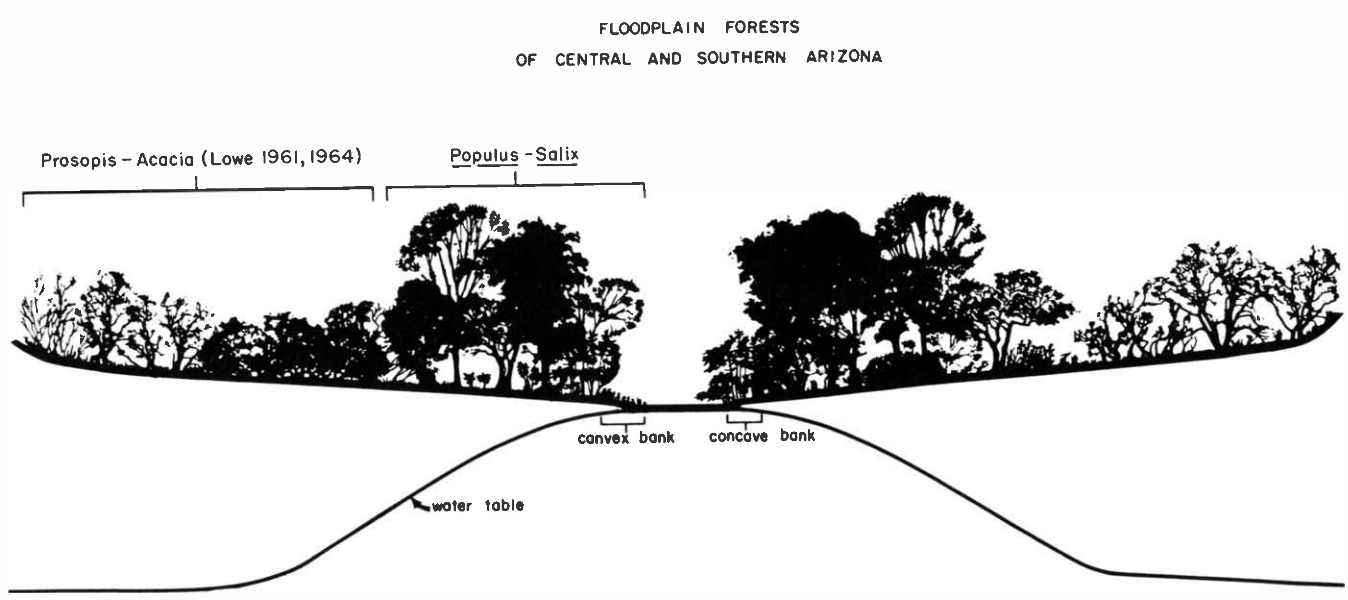


Figure 4. *Cross-section of an idealized floodplain in sub-Mogollon Arizona. Upper floodplain terraces are dominated by a microphyllous short-tree Mesquite-Catclaw association while the streambank is dominated by a broadleaf Cottonwood-Willow association. On the convex bank early seres are initiated by seedling establishment while mature vegetation on the concave bank is undercut.*

Table 2. Reproductive adaptations of floodplain species in *Prosopis.*

Adaptation	Taxon	Reference
Seed Set		
19,000 seeds/tree/season	*Prosopis chilensis*	Solbrig and Cantino (1975)
142,000 seeds/tree/season	*Prosopis velutina*	Glendening and Paulsen (1955)
13,400 seeds/lb.	*Prosopis glandulosa*	Schopmeyer (1974)
Seed Dispersal		
Frugivores	*Prosopis*	Glendening and Paulsen (1955) Mooney et al. 1977)
Seed Longevity		
2 years underground	*Prosopis velutina*	Glendening and Paulsen (1955)
10 years underground	*Prosopis velutina*	Solbrig and Cantino (1975)
50 years on herbarium sheets	*Prosopis velutina*	Solbrig and Cantino (1975)

Table 3. Coverage (percent) of selected plants at six study sites along Trout Creek, Mohave County, Arizona.

	Grazed			Ungrazed		
Site #	1	4	5	2	3	6
Shrubs and Herbs						
Baccharis salicifolia	3.46	3.26	10.79	.07	1.74	
Melilotus alba	.18	.03	.05	7.10	5.53	2.34
Tamarix chinensis		.05		.02		.01
Hymenoclea monogyra	.15	1.99	.47	.01		8.90
Bebbia juncea	1.92					
Amorpha fruticosa					1.60	
Sub-Total	5.71	5.35	11.31	7.27	8.89	11.25
Emergent Aquatics						
Scirpus americanus				19.46	5.13	
Sub-Total				19.46	5.13	
Trees						
Fraxinus pennsylvanica	1.37		8.31	.14	4.23	
Salix nigra	11.48		20.56	22.47	84.01	39.89
Populus fremontii	11.11			3.45		
Sapindus saponaria						25.84
Sub-Total	23.96		28.87	26.33	88.24	65.78
TOTAL	29.67	5.35	40.18	33.60	97.13	77.03

successional dynamics in shaping the nature of the individual species that are involved.

The most succinct and widely accepted definition of the riparian plant community has been provided by Lowe (1964). The "riparian . . . association occurs in or adjacent to drainageways and/or their floodplains and which is further characterized by species and/or life forms different from that of the immediately surrounding non-riparian climax." In light of the previous discussion, the definition of the riparian plant community may be enlarged. The riparian plant community is that group of species which participates in the successional dynamics of the floodplain vegetation. It is recognized that the successional sequence is on a habitat continuum, and that different riparian plant species are more or less attuned to particular segments of that continuum.

Livestock Grazing

At three locations on Trout Creek, masses of granite rubble have naturally prevented livestock access, an unusual situa-

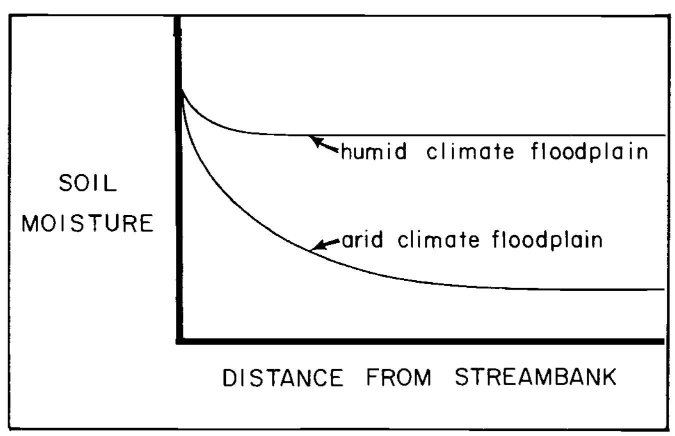


Figure 5. *Hypothetical relationship between soil moisture and distance from streambank in humid and arid climate floodplains. In humid regions upper floodplain terraces are more mesic habitats than those in arid regions.*

Table 4. Estimated densities of selected plant species at six study sites along Trout Creek, Mohave County, Arizona.

	Grazed			**Ungrazed**		
Site #	1	4	5	2	3	6
Shrubs and Herbs						
Baccharis salicifolia	12625	1944	283	102	9	
Melilotus alba	70	28	19	125	2747	79
Tamarix chinensis	172	260		46		32
Hymenoclea monogyra	9	111	23			143
Bebbia juncea		116				
Amorpha fruticosa					97	
Sub-Total	12992	2343	325	273	2853	254
Emergent Aquatics						
Scirpus americanus	1888		752	99315	24430	
Eleocharis cf. *macrostachya*	1104					
Sub-Total	2992		752	99315	24430	
Trees						
Fraxinus pennsylvanica	9			9	5	
Salix nigra	23		9	28	125	32
Populus fremontii	3			42		5
Sapindus saponaria						79
Sub-Total	35		9	79	130	116
TOTAL	16019	2343	1086	99667	27413	370

tion in the Southwest. The result is three stretches of ungrazed floodplain vegetation, each from 100-300 meters long and 20-40 m wide, along a 5.6 km reach of lower Trout Creek. Here the presence of extensive mats of American Bulrush *(Scirpus americanus)*, Cat-tail *(Typha latifolia)*, dense patches of Sweet-clover *(Melilotus alba)*, and thickets of tree saplings provide a remarkable riparian luxuriance that is nowhere seen on the *grazed* 45-odd kilometers of streamway.

The contrast between grazed and ungrazed sites, as reflected by differences in estimated coverage and density, is indeed striking. The grazed sites are characterized by a riparian woodland dominated by Fremont Cottonwood and Goodding Willow with a shrubby understory comprised almost entirely of Seep-willow. Ungrazed sites are dominated by the same trees in roughly the same proportions yet with an *herbaceous understory of bulrush and sweetclover.* Tables 3 and 4 show estimated coverage and density of plant species that occurred on more than one site or in appreciable numbers on one site. Table 4 shows estimated densities of plants per 464 m^2, the size of the smallest study site, to obtain frequencies large enough for chi-square tests.

Estimated density and coverage show both cottonwoods and willows far more prominent in ungrazed than grazed sites. This was largely due to the fact that most of the cottonwoods and willows in ungrazed sites were seedlings and saplings (DBH $\lesssim$ 2 cm). Among cottonwoods some of the juveniles appeared to have been the result of suckering.

Species diversity is consistently lower on grazed than ungrazed sites. The Shannon-Weaver maxima (Shannon and Weaver, 1963) show plant species diversity to be approximately 3X greater on ungrazed riparian sites (1.00 on grazed versus 2.83 on ungrazed sites).

Conclusions

The data on grazed versus ungrazed riparian communities on Trout Creek in Arizona, are consistent with the unanimous consensus on the impact of stock grazing in riparian woodland and forest communities elsewhere in the Southwest: grazing impact is everywhere negative, and locally disastrous.

The critical features of the floodplain environment to which riparian plants are adapted, are a relatively high plant-available soil moisture in an unstable substratum. The gradients created by the movement of the stream across its floodplain result in a dynamic successional sequence in a riparian habitat continuum.

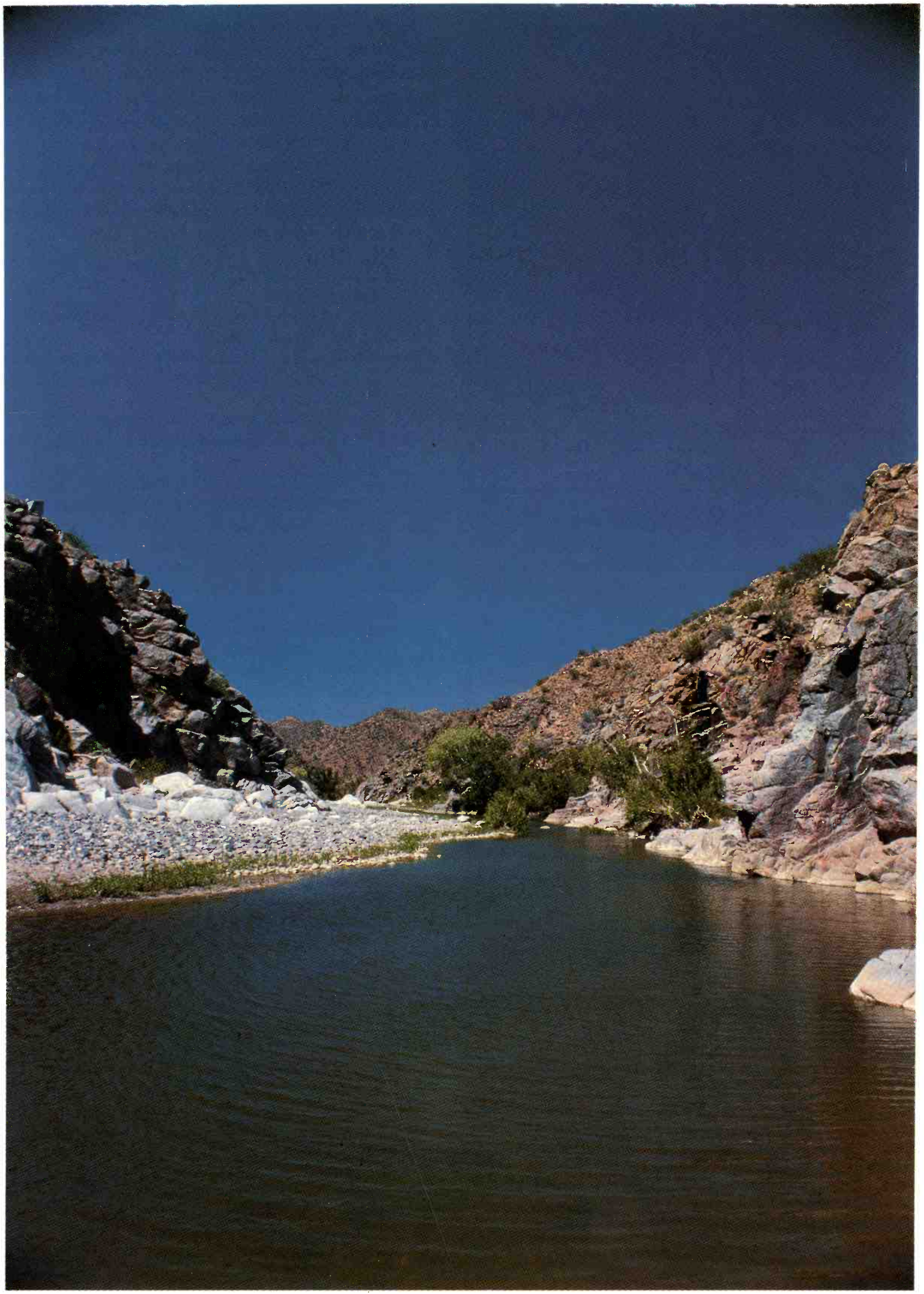
At the moist-unstable side of the continuum (near the stream channel) cottonwoods and willows are both the pioneer and climax species of a "distinctive climax biotic community" that is "an evolutionary entity with an enduring stability" (Lowe 1964) specifically adapted to this unique environment.

On the other end of the continuum, that is relatively arid and stable (floodplain terraces) locally adapted species such as mesquites and acacias form an equally distinctive community. The vegetative associations characteristic of the whole continuum are collectively termed the "riparian plant community."

The *Populus-Salix* associations of sub-Mogollon Arizona are ultimately derived from early Early Tertiary forests once covering large areas of the northern North American continent. Early on they specialized in adaptation to the peculiar requirements of the floodplain environment and have diversified in response to the climatic regionalization which fragmented the ancestral forests.

The *Prosopis-Acacia* association includes a group of locally preadapted trees and shrubs of Neotropical origin. Their ecological origins are in subtropical and tropical savannas, not floodplains.

Although useful for most of the purposes for which they were intended the terms "pseudoriparian," "obligate riparian" and "facultative riparian" do not recognize the role of successional dynamics in shaping the nature of the individual species



Trout Creek, Mohave County, Arizona. An advancing convex bank to the left is being colonized by seedlings of Fremont Cottonwood, Goodding Willow and Seepwillow. On the right is a retreating concave bank dominated by mature individuals of the same species.

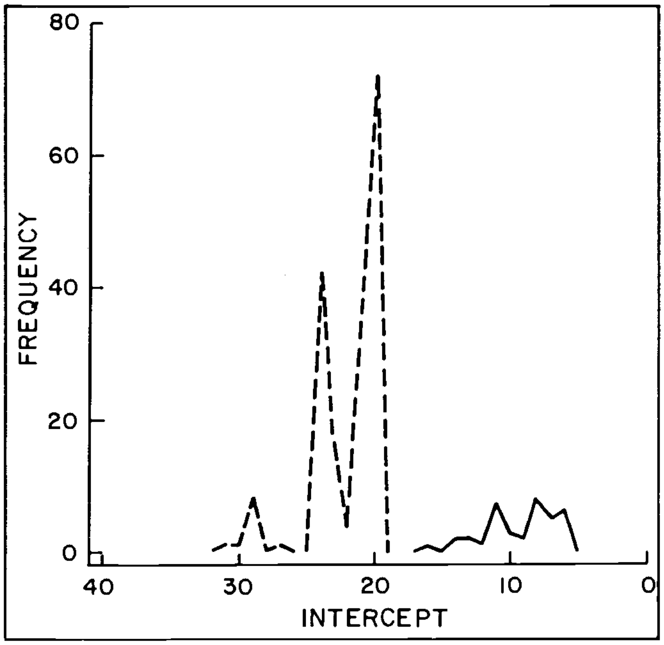


Figure 6. *Distribution of Goodding Willow across the floodplain at a Trout Creek study site. The dashed line indicates post-flood seedings on the bare alluvium of the convex north bank. The solid line represents flood survivors on the concave south bank.*

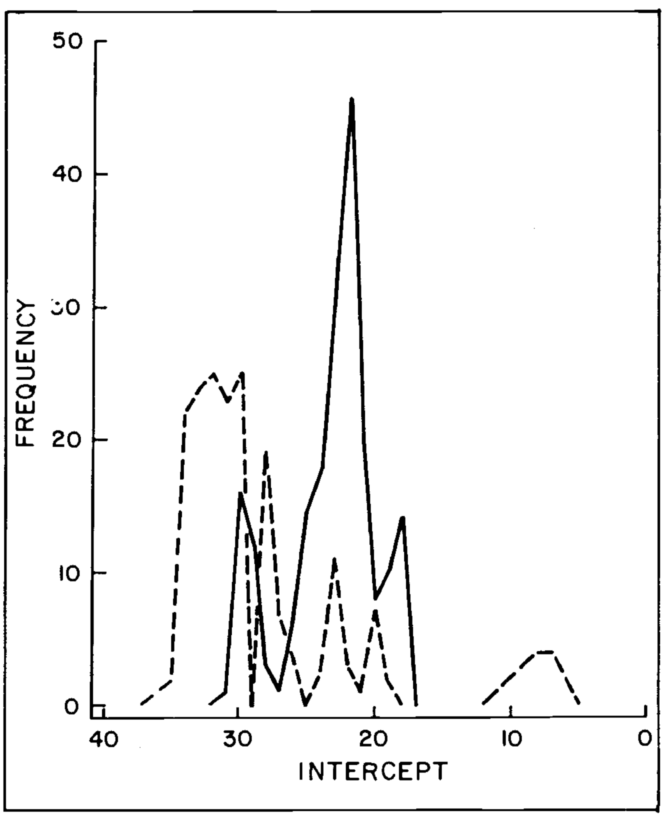


Figure 7. *Distribution of Seepwillow across the floodplain at a Trout Creek study site. The dashed line represents flood survivors and the solid line represents post-flood seedlings. The stream lay between roughly 26 and 28 m on the intercept.*

involved. They obscure the fact that numerous factors combine to make a species adapted to the floodplain environment and that a variety of species possess one or more of the necessary morphologic, physiologic and reproductive adaptations. All the plants in the floodplain participate in the successional advance and retreat of the vegetation and may all be correctly considered riparian species.

The key feature of riparian environments is successional dynamics, and it is the adaptations of riparian plants to this feature that should provide the most fruitful framework for the classification of riparian ecosystems.

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