SOUTHWESTERN WOODY RIPARIAN VEGETATION AND SUCCESSION: AN EVOLUTIONARY APPROACH[1]

R. Roy Johnson, Peter S. Bennett, and Lois T. Haight [2]

Abstract: Interrelationships between flooding and climax woody vegetation in riparian ecosystems of the desert Southwest are discussed. The lack of succession in woody desert upland and desert riparian plant communities results from opposite stresses, the former from aridity, the latter from flooding. Today's "wet riparian big five" are northern tree species of hydroriparian and mesoriparian (wet riparian) ecosystems; remnants of the Arcto-Tertiary Geoflora. The "dry riparian big five" are tree or subtree constituents of xeroriparian ecosystems occurring as Madro-Tertiary remnants at the northern extremes of their ranges. Human activities have interrupted normal flood regimes of Southwest rivers, resulting in desertification and endangering native riverine ecosystems.

Changes in the diagnostic vegetative structure of a given riparian ecosystem is an early warning of broader problems. Closer examination invariably shows triggering processes—soil erosion or deposition, dewatering of the system resulting in the changing of perennial or intermittent streams to ephemeral watercourses, and other signs of riparian and aquatic degradation.

In order to better interpret and understand the full implications of such historic and continuing changes one must understand the driving forces of riparian ecosystems. The interrelationships of flooding, succession (or lack thereof) and different woody plant regimes—Arcto-Tertiary vs. Madro-Tertiary Geofloras—need to be fully understood.

Woody Riparian Vegetation

Trees and shrubs are major components of riparian ecosystems. Their elevated woody structure forms the characteristic landscape feature which visually distinguishes riparian ecosystems from their surroundings, especially in the Southwest deserts. It is also this structure which provides habitat for the highest concentrations of birds in North America; provides shade for recreationists, fish, and cattle; and forms the biomass of the basic trophic level in these productive riparian ecosystems (Johnson and Carothers 1982).

Riparian Big Five

Lowe (1961, 1964) developed the concept of the riparian "big-five" in reference to five widespread riparian trees in the Arizona lowlands: cottonwood (*Populus fremontii*), willow (*Salix bonplandiana*) and others, e.g. (*S. gooddingii*), sycamore (*Platanus racemosa wrightii*), ash (*Fraxinus velutina*), and walnut (*Juglans microcarpa major*). Other riparian species of the desert Southwest show more limited geographic and elevational distributions (fig. 1). These or closely related species also occur throughout the California and Southwest desert lowlands in general (table 1).

Table 1 — Lowe's (1961, 1964) "wet riparian big five" or Arcto-Tertiary Geoflora riparian species of the desert Southwest with California (Holstein 1984) and eastern United States analogs (Little 1980).

Common Name	Southwest	California	Eastern United States
Ash	*Fraxinus velutina* [*F. v.* subsp. *pennsylvanica*]	*F. latifolia*	*F. pennsylvanica*
Cottonwood	*Populus fremontii*	*P. f.*	*P. sargetii*
	[*P. deltoides* & subsp. *P. palmeri, P. wislizenii*]		*P. d.*
Sycamore	*Platanus racemosa* var. *wrightii*	*P. racemosa*	*P. occidentalis*
Walnut	*Juglans microcarpa* var. *major*	*J. hindsii*	*J. nigra*
Willow	*Salix goodingii* [*S. nigra* subsp. *goodingii*]	*S. g.*	*S. n.*

[1]Presented at the California Riparian Systems Symposium; September 22-24, 1988; Davis, California.

[2] Senior Research Scientist, Research Scientist, and Research Assistant, respectively; Cooperative National Park Resources Studies unit, University of Arizona, Tucson.

ran Desert of the United States and Mexico but is too frost-tender to live in either of the colder Mohave or Chihuahuan deserts. Carothers and others (1974) were the first to quantify the importance of the wet riparian big five to avian populations. Parallel wildlife importance has been recently discussed for xeroriparian ecosystems, of which the dry riparian big five are major components (Johnson and Haight 1985).

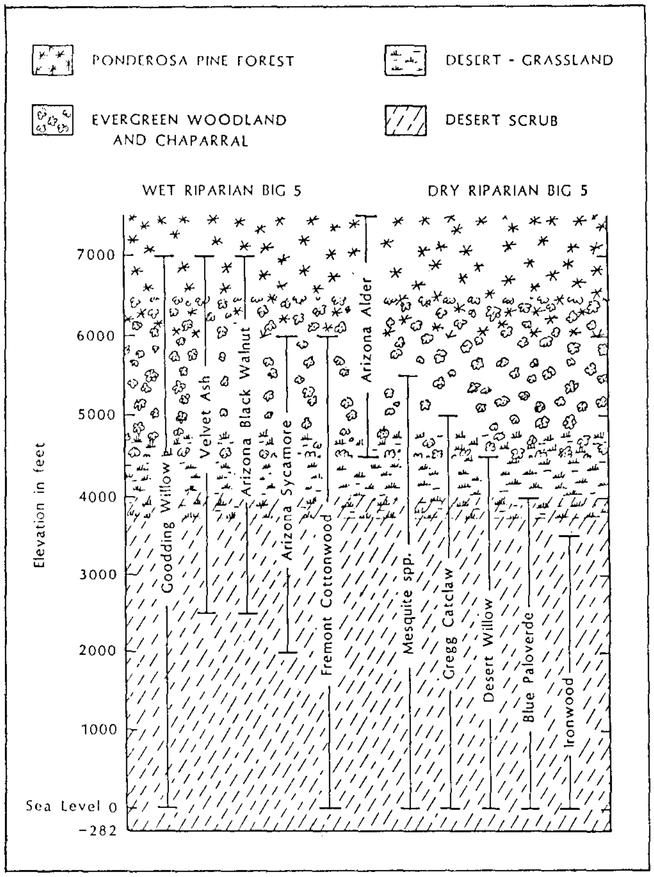

Figure 1 – Elevational and ecological amplitudes (spans) for the "wet riparian big five" and "dry riparian big five" in the desert Southwest. Other species, e.g. Arizona alder (*Alnus oblongifolia*) were excluded from these categories by Lowe (1961, 1964) and Johnson and Lowe (1985) due to their narrow amplitudes (after Benson and Darrow 1981; Kearney and Peebles 1969; Little 1980).

These generally occur as dominant woody species of hydroriparian (perennial) and mesoriparian (intermittent) ecosystems (Johnson and Lowe 1985) along lowland watercourses. A more technical paleobotanical term is "Arcto-Tertiary riparian big five." Using the same criteria for xeroriparian systems along desert washes Johnson and Lowe (1985) listed the "dry riparian big four" – mesquite (*Prosopis* spp.), catclaw acacia (*Acacia greggii*), ironwood (*Olneya tesota*), and blue paloverde (*Cercidium floridum*); we here add a fifth species, desert willow (*Chilopsis linearis*), to complete the "dry-tropic riparian big five." These five species occur in the Lower Colorado subdivision of the Sonoran Desert of southern California. As with the "wet riparian big five," these or closely related species are widely distributed in the Southwest deserts. The one exception is Olneya, which is widespread throughout the Sonoran Desert of the United States and Mexico but is too frost-tender to live in either of the colder Mohave or Chihuahuan deserts.

Plant Succession

Plant succession is the replacement of a plant community on a given site by other plant communities on the same site over a period of time, usually occurring in a predictable order. Although European botanists were the first to record the processes, two mid-western botanists, Fredrick E. Clements (1916) and his student, J.E. Weaver (Weaver and Clements 1938), further developed the concept while working in the eastern United States. Odum (1969) identified three general characteristics of plant succession. It is an orderly, predictable process with one natural community modifying the environment and thereby allowing for the establishment of subsequent communities (seres). This culminates in a stabilized, energy-optimizing ecosystem (climax community).

Absence of Desert Riparian and Upland Succession

The development of plant communities in Southwest deserts differs markedly in several ways from that in classical, mesic vegetation. Clementsian succession, so well studied and documented in the eastern United States, does not occur either in desert upland or riparian communities. This was discussed at length by Lowe (1959) and for upland systems first pointed out by Shreve (1951) who wrote:

> "It is not possible to use the term 'climax' with reference to desert vegetation ...If a particular community is destroyed without change in the soil, the earliest stage in the return of vegetation will be the appearance of young plants of the former dominants. Not only do the same species reappear at the outset, but their first individuals ultimately constitute the restored community."

Shreve (1951) did not differentiate between upland and riparian habitats in his writings about desert vegetation. Lowe (1964) was the first to specifically address riparian succession in the Southwest, finding a lack of succession for Southwest desert riparian ecosystems where cottonwoods and willows are both "pioneer" and "climax" riparian species (in Clementsian terms). Further, the same individual plant is both a pioneer and a member of the climax vegetation.

Although succession does not occur in either riparian or upland ecosystems of the desert Southwest two different, opposite stresses are involved. In riparian ecosystems flooding ("too much" water) is the driving function behind plant community development. In upland systems aridity ("too little" water) limits community development, excluding succession.

Interestingly, Lowe (1964) also points out the lack of succession in a high elevation spruce-fir forest in northern Arizona. Here the stressful environment results from water occurring only as ice much of the year, thus being unavailable for uptake by plants. Consequently plant communities at high elevation and/or high latitude may demonstrate some of the same xeric characteristics of desert upland plant communities, including abbreviated or non-existent successional stages.

In a paper on "riparian succession" Campbell and Green (1968) suggested "mosaics of various seral stages" but did not demonstrate succession for Southwest riparian vegetation. They stated, "The channel vegetation probably never reaches a climax hierarchy due to periodic flood disturbances such as erosion, inundation, and deposition."

Reichenbacher (1984) likewise discussed riparian succession in the Southwest without substantiating it. He also considered the establishment of different riparian species under different physical conditions at different microsites as successional—stating, "On the convex bank early seres are initiated by seedling establishment while mature vegetation on the concave bank is undercut." Rather than succession, he was discussing the aforementioned vegetational mosaic mentioned by Campbell and Green (1968) characteristic of riparian vegetation. This patchiness in riparian vegetation is largely a result of shifting channels and abandoned meanders. Riparian communities are composed of species as they occur along a moisture gradient. Reichenbacher (1984) and Campbell and Green (1968) actually made a better case for the continuum concept, a concept especially discussed by Whittaker (1975). A continuum is "a gradient of environmental characteristics or of change in the composition of communities" (Ricklefs 1979). This concept postulates that plant communities are composed of a collection of species, each with a specific gradient and coexisting not because of biological affinities for one another but because of common environmental needs. The continuum concept has been discussed for other areas; e.g. for riverine aquatic ecosystems and their physical and biological parameters as expressed by headwater to mouth gradients (Vannote and others 1980). Similarly, riparian continua have been discussed along drier to wetter moisture gradients both for headwater to mouth (intrariparian) and upland to deepwater (transriparian) gradients (Johnson and Lowe 1985).

Mechanisms preventing either riparian or upland succession in the southwest have not been thoroughly examined, but for riparian ecosystems there are contributing factors. Competition is an important factor in plant succession (Odum 1971; Ricklefs 1979). Shreve (1951) pointed out that in the southwestern deserts the struggle is with the environment rather than inter- or intraspecific competition with other plants, and "the frequency on the desert of extensive communities which are simple in composition is not due to the poverty of the perennial flora so much as to the severity of the physical conditions."

Compared to desert upland systems, Southwest riparian ecosystems are much more mesic and thus might be expected to show a closer similarity to eastern deciduous hardwood forests in respect to competition and succession. This, however, is not the case. The different plant communities occurring along a river that are interpreted by some as different seral stages occur side by side in different physical habitats. For example, mesquite bosques often occur on higher terraces or alluvial fans while adjacent floodplain bottomlands are vegetated by cottonwood-willow forests. Mesquites, because of their long tap roots, can secure water from deeper water tables than cottonwoods and willows. Therefore, because of differing abilities to obtain water, the two communities occur side by side at the same time rather than one community following the other on same site.

Two related processes to consider in the lack of riparian succession in the Southwest are catastrophic floods and the long period of time required for successional stages (seres) to evolve into a climax community. Our examination of historic photos show flooding as a major reason for riparian plant communities in the Southwest not reaching more than 100 years in age before being greatly disrupted or destroyed. These photos, taken at chronological intervals along southwest rivers, show groves of mature cottonwoods and mesquite bosques at different sites along a river from one decade to the next. Periodic floods scour the substratum and destroy attendant groves at a given locality. Subsiding flood waters then create conditions for a seedbed, allowing germination of a new stand of young cottonwoods either in the same spot or elsewhere (Brady and others 1985). Thus, the relatively short intervals between catastrophic floods in the Southwest deserts does not allow sufficient time for succession. Factors that have changed flow regimes along southwest lowland streams, greatly affecting development of riparian plant communities, are discussed later under *floods*.

Although individual sandbars, terraces, or riparian plants may be short-lived, the riparian ecosystem is stable. The most pertinent statement in literature is by Lowe (1964:62):

> The southwestern riparian woodland formation is characterized by a complex of trees, and their plant and animal associates, restricted to the major drainageways that transgress the landscape of desert upward into forest. It is incorrect to regard this biotic formation as merely a temporary unstable, seral community. It is an evolutionary entity with an enduring stability equivalent to that of the landscape drainageways which form its physical habitat. That is, it is a distinctive climax biotic community.

Desertification of Southwest Riparian Ecosystems

Many historically recorded Southwest perennial and intermittent streams are now ephemeral watercourses. Analyses of factors involved in the disastrous conversions of these watercourses have been conducted by investigators such as Hastings (1959), Hastings and Turner (1965), Cooke and Reeves (1976), Dobyns (1981), and Betancourt and Turner (1988). In many cases there has been an almost total loss of both the aquatic and riparian resources that originally attracted European settlers to these linear desert oases.

Before the North American import of Old World cattle and the invention of the steel plow, most of the soils of the United States were largely covered by vegetation. The root-filled sod served as a sponge, allowing water to run off slowly toward drainages and clean water to percolate into the watertable. Runoff water from the uplands was partially cleansed by riparian processing (biological and physico-chemical processes of riparian ecosystems) before entering branching, meandering networks of drainages and flowing slowly downstream. When floods overtopped the riverbanks, rich alluvial soils were deposited, increasing the fertility and productivity of riparian ecosystems. Today these channels are carrying increased volumes of debris and silt-laden water from tributaries that have been greatly altered by humans, e.g. storm drains and gullies, from uplands denuded of absorptive vegetation and topsoil through misuse of the land by livestock and humans. Many of these channels have been heavily silted-in or, more often at lower desert elevations, have become incised and denuded, allowing increasingly serious environmental degradation (Betencourt 1988; Cooke and Reeves 1976; Dobyns 1981; Rea 1983; and Turner 1988). Other human activities that have interfered with flow regimes, especially water storage and diversion projects, are discussed by Johnson and Carothers (1982). Overgrazing and consequent desertification has also greatly affected natural riparian community development (Brown and others. 1977; Dobyns 1981; Glinski 1977; Johnson and Simpson 1988; Reichenbacker 1984). Without concentrated efforts to reverse many of these disastrous, often unnecessary, activities, desertification of riparian and aquatic ecosystems of the Southwest will irreversibly proceed, thereby destroying some of our most valuable natural resources.

Acknowledgements

We thank Dr. Charles H. Lowe, University of Arizona; Dr. Steven W. Carothers, SWCA, Inc, Environmental Consultants; and Mr. James M. Simpson, Phoenix, Arizona, for numerous discussions about the contents of this paper. Mrs. Donna Marchant assisted with the typing and technical writing aspects.

References

Benson, L.; Darrow, R.A. 1981. Trees and shrubs of the Southwestern Deserts. Tucson: Univ. of Ariz. Press; 416 p.

Betancourt, J.L.; Turner, R.M. 1988. Historic arroyo-cutting and subsequent channel changes at the Congress Street Crossing, Santa Cruz River, Tucson, Arizona. In: Whitehead, E.E.; Hutchinson, C.F.; Timmermann, B.M.; Varady, R.G., eds. Arid lands: today and tomorrow. Boulder, Colo: Westview Press; 1353-1372.

Brady, W.; Patton, D.R.; Paxson, J. 1985. The development of Southwestern riparian gallery forests. In: Johnson, R.R.; Ziebell, C.D.; Patton, D.R.; Ffolloitt, P.F.; Hamre, R.H., tech. coords. Riparian ecosystems and their management: reconciling conflicting uses. Ft. Collins, Colo: USDA For. Serv. Gen. Tech. Rep. RM-120; 39-43.

Brown, D.E.; Lowe, C.H.; Hausler, J.F. 1977. Southwestern riparian communities: their biotic importance and management in Arizona. In: Johnson, R.R.; Jones, D.A., tech. coords. Importance, preservation and management of riparian habitat: a symposium. Ft. Collins, Colo: USDA For. Serv. Gen. Tech. Rep. RM-43.; 201-211

Campbell, C.J.; Green, W. 1968. Perpetual succession of stream-channel vegetation in a semiarid region. J. Ariz. Acad. Sci. 5:86-98.

Carothers, S.W.; Johnson, R.R.; Aitchison, S.W. 1974. Population structure and social organization in southwestern riparian birds. Amer. Zool. 14:97-108.

Clements, F.E. 1916. Plant succession: analysis of the development of vegetation. Washington: Publ. Carnegie

Inst.; 242:1-512.

Cooke, R.U.; Reeves, R.W. 1976. Arroyos and environmental change in the American Southwest. Oxford, England: Oxford Res. Stud. in Geog., Clarendon Press; 213 p.

Dobyns, H.F. 1981. From fire to flood: historic human destruction of Sonoran Desert riverine oases. Ballena Press Anthro. Pap. No. 20. San Rafael, CA: Ballena Press; 222 p. [out of print]

Glinski, R.L. 1977. Regeneration and distribution of sycamore and cottonwood trees along Sonoita Creek, Santa Cruz County, Arizona. In: Johnson, R.R.; Jones, D.A., tech. coords. Importance, preservation and management of riparian habitat: a symposium. Ft. Collins, Colo: USDA For. Serv. Gen. Tech. Rep. RM-43.; 116-123.

Hastings, J.R. 1959. Vegetation change and arroyo cutting in southeastern Arizona. J. of the Ariz. Aca. of Sci. I:60-67.

Hastings, J.R.; Turner, R.M. 1965. The changing mile. Tucson: Univ. of Ariz. Press; 317 p.

Holstein, G. 1984. California riparian forests: deciduous islands in an evergreen sea. In: Warner, R.E.; Hendrix, K.M., eds. California riparian systems. Berkeley: Univ. of Calif. Press; 2-22.

Johnson, R.R.; Haight, L.T. 1985. Avian use of xeroriparian ecosystems in the North American warm deserts. In: Johnson, R.R.; Ziebell, C.D.; Patton, D.R.; Ffolloitt, P.F.; Hamre, R.H., tech. coords. Riparian ecosystems and their management: reconciling conflicting uses. Ft. Collins, Colo: USDA For. Serv. Gen. Tech. Rep. RM-120; 156-160.

Johnson, R.R.; Lowe, C.H. 1985. On the development of riparian ecology. In: Johnson, R.R.; Ziebell, C.D.; Patton, D.R.; Ffolloitt, P.F.; Hamre, R.H., tech. coords. Riparian ecosystems and their management: reconciling conflicting uses. Ft. Collins, Colo: USDA For. Serv. Gen. Tech. Rep. RM-120; 112-116.

Johnson, R.R.; Simpson, J.M. 1988. Desertification of wet riparian ecosystems in arid regions of the North American Southwest. In: Whitehead, E.E.; Hutchinson, C.F.; Timmermann, B.M.; Varady, R.G., eds. Arid lands: today and tomorrow. Boulder, Colo: Westview Press; 1383-1393.

Johnson, R.R.; Carothers, S.W. 1982. Riparian habitat and recreation: interrelationships and impacts in the Southwest and Rocky Mountain region. Eisenhower Consortium Bull. 12. Ft. Collins, Colo: Rocky Mt. For. and Range Exper. Sta., USDA For. Serv.: 31 p.

Kearney, T.H.; Peebles, R.H. 1969. Arizona flora. Berkeley and Los Angeles: Univ. of Calif. Press; 1085 p.

Little, E.L. 1981. The Audubon Society field guide to North American trees: eastern region. New York: Alfred A. Knopf; 714 p.

Lowe, C.H. 1959. Contemporary biota of the Sonoran Desert: problems. In: Univ. of Ariz., Arid Lands colloquia, 1958-1959:54-74.

Lowe, C.H. 1961. Biotic communities in the sub-Mogollon region of the inland Southwest. J. Ariz. Acad. Sci. 2(1):40-49.

Lowe, C.H. 1964. Arizona's natural environment. Tucson: Univ. of Ariz. Press; 136 p.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164:262- 270.

Odum, E.P. 1971. Fundamentals of ecology. 3rd ed. Philadelphia, Pa.: W.B. Saunders Co. 574 p.

Rea, A.M. 1983. Once a river: bird life and habitat changes on the middle Gila. Tucson: Univ. of Ariz. Press; 285 p.

Reichenbacher, R.W. 1984. Ecology and evolution of southwestern riparian plant communities. In: Desert Plants 6(1):1-62.

Ricklefs, R.E. 1979. Ecology. 2nd ed. New York: Chiron Press, Inc.; 966 p.

Shreve, R. 1951. Vegetation and flora of the Sonoran Desert: vol. I, vegetation. Carnegie Inst. Washington Publ. 591:1-192.

Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Weaver, J.E.; Clements, F.E. 1938. Plant ecology. New York: McGraw-Hill Book Co.

Whittaker, R.H. 1975. Communities and ecosystems. 2nd ed. New York: MacMillan Publ.; 385 p.