A Synthesis of Information on the Relationship of Stream Regulation to Riparian and Wetland Ecosystems

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FINAL REPORT

Submitted by

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ABSTRACT

This review on the impact of dams on riparian vegetation considered more than 50 studies conducted around the world.

1. Studies determined that upstream (reservoir) effects of dams on vegetation are largely negative, resulting in a loss of vegetation cover and often species, and substantial changes in plant species composition. This is due to a loss of colonizable habitat due to inundation. However, extensive riparian vegetation often becomes established when deltas form where tributaries meet reservoirs and sediments are deposited. The same patterns of loss of cover and species hold for impounded bottomland hardwood forests and swamps.

2. Effects of dams on downstream vegetation are more complex and strongly influenced by channel type (whether rivers occurred in constrained or alluvial basins), and regulation type (whether or not dammed rivers are diverted). Vegetation cover increased along dammed, undiverted rivers regardless of whether they occurred in constrained or alluvial drainages. Vegetation cover typically decreased downstream of diverted rivers.

3. Small dams, such as check and crib dams, that are a common feature of small drainages in the western United States, support extensive stands of riparian vegetation, due

to rapid accumulation of sediments and conversion of ephemeral streams into perennial streams.

4. Where studied, nearly all studies found changes in species composition in riparian plant communities in response to impoundment.

5. Vegetation responses to impoundment are highly complex, due in part to variable responses of different plant species. When multiple plant species were studied, some species responded positively and others negatively to impoundment. Many studies considered only one species or pooled all species into one measured response, with both techniques resulting in an incomplete understanding of vegetation responses to impoundment.

Details of research on dam impacts on riparian vegetation, including study design, methods, and techniques are reviewed in this report.

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I. INTRODUCTION

A. Importance of Riparian Vegetation

Riparian habitats are among the most productive of all terrestrial habitats, and support diverse plant species assemblages (Gregory et al. 1992). These plant communities provide critical resources for numerous aquatic and terrestrial animal species, making them regions of high levels of biodiversity, particularly in arid regions (Knopf et al. 1988, Brown et al. 1977, Stevens et al. 1977, Johnson 1991). Riparian habitat in Arizona, U.S.A., comprises less than 0.05 percent of the landscape (Simcox and Zube 1985), but supports more than 50 percent of the species in those landscapes (Brown et al. 1977, Knopf et al. 1988). Riparian vegetation contributes significant quantities of nutrients to rivers (e.g., Edwards and Meyer 1987, Anderson and Day 1986), and may play an important role in maintaining bank stability.

Large proportions of riparian and wetland habitats in the United States are being lost due to flow modifications, land development and land management policies. Dahl (1990) reported that the United States originally supported 392 million acres of wetlands in the coterminous 48 states. Wetlands comprised 5 percent of the pre-settlement land surface. In the 1980's, only 104 million acres of wetlands remained in the lower 48 states, reflecting a loss of 53 percent of the wetlands there. Wetland losses have varied among states, with largely undeveloped western states losing from 30 percent (Utah) to 56 percent (Idaho), while highly urbanized and agricultural states such as California have lost more than 90 percent of their original wetland area.

B. The Extent of Dams

According to the World Register of Dams (International Commission on Large Dams 1973), more than 12,000 dams larger than 15 m tall had been constructed worldwide by 1971. Most dams were constructed after 1945, with dams now occurring on nearly all major rivers of the world (Petts 1984). In North America alone more than 200 dams per year were built between 1962 and 1968 (Beaumont 1978). While Beaumont (1978) concluded that on a world-wide scale the peak of dam-building has passed, dam construction has actually increased in a number of countries since 1970, including Brazil, Argentina, Canada, India, Japan, Turkey, Spain and the People's Republic of China (Mermel 1981, Petts 1984). Large numbers of dams are under construction in Central and South America and southern Asia (Petts 1984). The frequency of impoundment and loss of riparian habitat underscore a need to understand the effects of dams on riparian ecology.

C. Scope and objectives

This review summarizes available literature on dam impacts on riparian vegetation occurring upstream and downstream from flow regulation sites along rivers and nonriverine bodies of water, including swamps and man-made lakes. The review emphasizes freshwater lotic systems.

Studies reported changes in vegetation cover, density, growth, recruitment, diversity and species composition in response to river regulation. Factors contributing to changes in riparian plant community dynamics, including the type and size of dam and geomorphic and hydrologic conditions, are also reviewed.

Many studies included management recommendations designed to benefit riparian vegetation. These recommendations, along with patterns that emerged from this review, are incorporated into a discussion on some of the problems encountered in this area of research, how to conduct research to effectively measure dam effects on riparian vegetation, and how to manage dam operations and flow regimes to the benefit of riparian vegetation and habitats. A bibliography and library of the literature used in this review are provided to the Bureau of Reclamation.

II. BACKGROUND

A. The Ecology of Riparian Vegetation

Riparian Vegetation Although its Latin root, riparius, means river, riparian vegetation has been more broadly defined as that which lies in close proximity to a water source. Riparian vegetation consists of woody and herbaceous phreatophytes, and of opportunistic mesic and xeric species from the surrounding terrain (Brown et al. 1977; Reichenbacher 1984). Phreatophytes are riparian plants that "...absorb water from a permanent water table"(Lincoln et al. 1982: 191). Riparian vegetation "may be composed either of constituents peculiar to the riparian situation, or an extension of a higher, climax association fingering downward into the drainageway"; the latter has been termed "pseudo-riparian" (Campbell and Green 1968) to distinguish its facultative nature from the obligate nature of purely riparian species (Brown et al. 1977: 201). Therefore, characteristics distinguishing 'riparian' from 'wetland' vegetation appear vague.

Classification of Riparian Plant Communities Several classification systems have been developed for characterizing riparian vegetation communities (Brown and Lowe 1974; Pase and Layser 1977; Dick-Peddie and Hubbard 1977; Cowardin et al. 1979; Brown 1982). Among the most widely used classifications, that of Cowardin et al. (1979) emphasizes the geomorphic setting of habitats as the primary determinant of plant community type. In this classification, riparian communities are divided into systems (marine, estuarine, riverine, lacustrine and palustrine), and subsystems (e.g., riverine, tidal, lower perennial, upper perennial, intermittent), with classes further subdivided based on substrata such as rock, unconsolidated, or vegetation type (Cowardin et al. 1979). Modifiers of water regime, water chemistry, soil, etc., also influence community classifications.

Another widely used classification scheme (Brown 1982) emphasizes plant species composition in defining riparian plant communities. Brown (1982) distinguishes riparian plant communities of the southwestern United States on the basis of 'extensive categories' (vegetation development, formation and climate), within 'intensive categories' of floristic provinces (biomes). This classification scheme subdivides biomes into communities (series), associations, subassociations, and then by composition, structure and phase. Such an approach yields mappable descriptions of regional plant communities that are based on species assemblages. This classification system is under review for possible adoption by the U.S. National Park Service (J. Spence, personal communication, 1993).

Factors Affecting Riparian Vegetation Riparian vegetation development is influenced by hydrology, geomorphology, soils and climate, and complex interactions among them (Table 1). Plant life history strategies and the biogeographic history of the drainage basin also influence the composition of riparian vegetation communities.

a. Hydrologic characteristics that directly influence riparian vegetation include the frequency, magnitude, duration and seasonal timing of flooding (Sousa 1984; Kozlowski 1984), patterns of sedimentation (Schmidt and Graf 1990), and to a lesser extent, variables such as water quality and temperature. A robust literature on fluvial geomorphology and flow dynamics is relevant to this area (e.g., Hupp 1988).

Several studies describe zonation of riparian environments on the basis of flooding frequency and/or vegetation assemblages. Carothers et al. (1979) defined four zones of riparian vegetation along the dam-controlled Colorado river in the Grand Canyon. Zone I was composed of Sonoran/Mohave Desert and upland vegetation; Zone II was a pre-dam vegetation belt consisting of mesquite and acacia; Zone III was a largely uncolonized belt of habitat lying

Table 1. Factors affecting the structure of riparian plant communities.

- -Hydrologic conditions, including frequency, magnitude, duration and timing of flooding, and water quality and temperature
- -Geomorphic conditions, including channel geology
- -Climatic conditions, including long-term and short-term drought and flood events
- -Biogeographic patterns, including available plant species within the region and patch dynamics
- -Plant life history traits, including reproductive phenology, seed production and dispersal, germination and allocation, and environmental tolerance

elevationally lower than Zone II; and Zone IV, the lowest, consisted of a belt of exotic and native shrubs, herbs and grasses. Zone IV developed following impoundment by Glen Canyon Dam.

Nilsson (1984) developed a generalized description of riparian habitat zonation including upper, middle and lower geolittoral and aquatic hydrolittoral zones. This classification recognized both flood frequency and vegetation assemblages as descriptors of riparian zonation; however the term geolittoral is essentially equivalent to riparian. Therefore, in this review we use the terms upper, middle and lower and hydro-riparian zones to describe the zones of vegetation along rivers and lakes.

Several major kinds of stream channels have been identified, and their relation to dam effects on vegetation are considered in this review. We use Jackson and Beschta's (1992) distinction between constrained channels(structurally controlled) and unconstrained or alluvial channels. In constrained channels, geologic structure (e.g., parent rock hardness, faults or fractures, and the frequency of channel constriction) controls channel geometry (Webb et al. 1987; Hupp 1988; Schmidt and Graf 1990). Such geologic controls typically operate in lower order streams, but may also influence higher order streams in topographically diverse landscapes, such as the Colorado River in the Grand Canyon (Schmidt and Graf 1990). In contrast, unconstrained or alluvial channels cut through softer bed materials and are less confined by incised channels or local geomorphology. Low gradient, unconstrained rivers characteristically meander, and examples include North American prairie rivers, such as the lower Platte and Missouri rivers, and coastal deltaic rivers. Low gradient fluvial environments and palustrine habitats produce swamps, marshes, bogs and estuaries. These unique riparian habitats form as a result of local geologic and geomorphic controls.

Riparian soils often consist of fluvial deposits derived from parent rock and modified by weathering, hydraulic reworking and vegetation. Flooding prevents or interrupts pedogenesis along rivers by disrupting the weathering and scouring organic matter. Riparian soils in arid land drainages, such as the American Southwest, are typically young, unweathered entisols, inceptisols and, rarely, mollisols that have been described as torrifluvents or, when containing more organic matter, as haplustolls (Brock 1985). Under more mesic climates, such as in continental grassland temperate forest biomes, riparian soils may include mollisols. Research on riparian soil classification and geochemistry has been relatively recent (Gerrard 1987). In a study of geolittoral soil chemistry along the Colorado River in Grand Canyon National Park, Arizona, Scala (1984) found that upper riparian zone, pre-dam sediments contained considerably more silt than did post-dam sediments in the lower geolittoral zones. Exchangeable base cation concentrations that are important to colonizing plants, were negatively correlated with particle size there.

Stevens and Waring (1988) described the lower riparian zone soils in this system as young, unweathered xerifluvents. Dam-induced coarsening of riparian soil texture reduced plant germination by decreasing soil water holding capacity and nutrient concentrations, thereby shifting dominance from seed-reproducing species towards dominance by clonal phreatophytes on Grand Canyon sand bars (Stevens 1989a).

b. Climate influences riparian vegetation through both flooding and drought. Climate is the major determinant of flooding, which opens patches of habitat and creates suitable germination environments for plants that establish by seed. Post-dam flooding in the Colorado River downstream from Glen Canyon Dam following record runoff in the Rocky Mountains in 1983 resulted in extensive vegetation loss and stimulated germination throughout the river corridor (Stevens and Waring 1985). Plant mortality during the flood resulted from drowning, severe thrashing and scouring. Flooding also affects germination success in Populus spp. (Fenner et al. 1984; Baker 1990), Tamarix ramosissima (Stevens 1989a,b); and many other riparian species (e.g., Stromberg and Patten 1991).

Riparian vegetation is highly susceptible to water deficits as riparian plants are poorly adapted for water conservation (Fenner et al. 1984; Stevens 1989a; Sacchi and Price 1992). Drought reduces growth rates, reproduction, and recruitment and alters species composition among riparian plants (Stromberg and Patten 1992, Sacchi and Price 1992). Many phreatophytes, however, may be more drought tolerant due to contact with the water table.

Long-term effects of climate on flow regime have been established with dendrochronological and hydrological techniques (Hupp 1988). Hereford (1984) described sedimentation patterns in the Little Colorado River basin using, in part, excavated trunks of the exotic woody phreatophyte, Tamarix chinensis. Sediment transport from that basin was high prior to about 1940, whereas sediment storage occurred in the floodplain from 1940 to 1980. Hereford (1984) attributed these changes to shifts in climate, a finding supported by Graf et al. (1992) in the nearby Paria River drainage.

B. Applications of Ecological Theory

A robust, general literature on plant biogeography, patch dynamics, ecological disturbance, and life history strategies is relevant to riparian vegetation dynamics. An introduction to these theoretical issues offers insights as to how disruption of fluvial ecosystems by dams affects riparian vegetation.

a. Biogeography The structure of riparian plant communities is determined by numerous ecological interactions over time. Vegetation patterns result from propagule dispersal, patch shape, degree of isolation, and disturbance frequency. River systems, particularly those in deep canyons, can serve as a barrier or a refuge for some species, while gene flow in highly vagile species may not be affected (Stevens 1983). Propagules are generally dispersed downstream, and hydrochory is a common form of dispersal for riparian vegetation (Nilsson et al. 1991). Riparian zones also passively sample propagules dispersed by wind, gravity or animals.

Riparian vegetation is organized in long, thin zones that are comprised of adjacent belts of plant groups running parallel to the channel. This pattern of zonation has been attributed to flood frequency (Campbell and Green 1968, Turner and Karpiscak 1980, Hupp 1988), soil moisture, nutrient status and texture in combination with flood frequency (Stevens 1989), herbivory by animals such as beaver and cattle (Glinski 1977, McGinley and Whitham 1985), and interactions between disturbance, productivity and competition (Connell 1978, Huston 1979, Stevens 1989a).

Riparian plant communities are structured in part by floristic interchanges over geologic time. Based on paleontological data, Axelrod and Raven (1985) concluded that present day flora of California, USA, is the result of a mingling of boreal Arcto-tertiary and southern Madero-tertiary assemblages through several million years of changing climates.

b. Patch dynamics studies emphasize the importance of ecological scale in disturbed landscapes (White 1979, Pickett and White 1985). In the case of riparian habitats, a variety of geographic scales influence local biological processes, such as the distribution of safe germination sites (Grubb 1977, Sacchi and Price 1992), and antecedent hydrological events that affect the rate and direction of temporal geomorphic changes (White 1979, Schmidt and Graf 1990).

c. Ecological disturbance theory emphasizes how interactions among disturbance, productivity, competition and time affect species diversity (Connell 1978, White 1979, Grime 1979, Huston 1979, Sousa 1984). Odum (1981) proposed that disturbance resets communities to earlier stages along their successional trajectories and that recovery of a community from disturbance was a function of time, productivity and competitive interactions. Tests of these models generally support the immediate disturbance and dynamic equilibrium models (e.g., Sousa 1979, Resh et al. 1988). Riparian vegetation has rarely been used to test these models. However, studies by Nilsson (1984), Day et al. (1988) and Stevens (1989a) report strong interactions between diversity and productivity, providing little support for intermediate disturbance hypotheses.

Impoundment provides an opportunity to understand the effects of flooding disturbance on vegetation. Nilsson (1984) found that riparian vegetation responded differently to different discharge strategies on regulated rivers. Nilsson et al. (1988) reported characteristic zonation of most species, but no predictable distribution patterns of rare species in response to reduced flooding following impoundment. The rapidly growing literature on impoundment effects will improve dam management strategies relative to riparian processes, and contribute to theoretical aspects of disturbance ecology.

Riparian habitats experience numerous forms of natural disturbance (e.g., fire, wind throw, and herbivory) and numerous forms of anthropogenic disturbances, including grazing, logging, road construction, urbanization and agricultural development. It can be difficult to distinguish regulation effects from these other human impacts.

d. Life history strategies determine plant survival and succession along both natural and regulated rivers (Horton et al. 1960, Hosner 1960, Fenner et al. 1984, Stevens 1989a, Siegel and Brock 1990). Plant life history characteristics include reproductive phenology, seed production, dispersal and longevity, germination and establishment requirements, growth and allocation strategies, physiological tolerance limits for environmental parameters, resistance to herbivory and disease, and competitive abilities. Differential success of life history traits may direct succession in riparian habitats (Stevens 1989a).

e. The River Continuum Concept (Vannote et al. 1980) proposes that river hydrology, water quality and biotic assemblages change predictably as stream order increases from the headwaters to the mouth of a river. A recent review of river regulation effects on aquatic ecology suggests that dams interrupt the continuity of these fluvial processes and reset rivers to conditions similar to lower stream orders (Ward and Stanford 1983). This concept has yet to be applied to riparian vegetation.

Floristic succession is defined as a change in plant species composition through time. Riparian vegetation in unregulated river basins may be held in a state of perpetual succession by flooding disturbance (Campbell and Green 1968). The degree to which an assemblage has proceeded through its successional trajectory depends on the interval since the last significant flooding event. Although succession in riparian plant communities is not well studied, several studies have documented vegetation change in regulated rivers where flooding disturbance has been disrupted (Nielsen 1984, Turner and Karpiscak 1980).

C. Regulation of Rivers

Today, most of the large rivers on earth are impounded or diverted, and some, such as the Mississippi, Columbia and Colorado rivers in the United States, are completely regulated (Petts 1984). Stream regulation ranks with water pollution as a primary human influence on rivers, and its effects are extensive.

River regulation is analogous to fire suppression as an anthropogenic habitat disturbance that overshadows the intensity of other disturbance factors (Stevens and Ayers 1993). Decreased frequency of either form of disturbance may alter interactions among plant species and result in new successional pathways. By stabilizing floodplains impoundment may result in the co-occurrence of species that were formerly separated, with novel ecological and evolutionary outcomes. Large dams may stand for centuries and affect plant phenology and species interactions on an evolutionary scale (e.g., Kinnaird 1992). Unlike fire suppression, prolonged flood control does not inevitably increase the intensity of the next disturbance event. Armitage (1984) and Petts (1984) review forms of stream regulation, including impoundment, diversion, groundwater flow alteration, and land drainage. Ward (1976) discussed four major kinds of flow alteration resulting from stream regulation, including reduced flow, increased flow, seasonally constant flow and short-term (daily, weekly) flow fluctuation. Prolonged flooding also affects riparian habitats along regulated streams (Stevens and Waring 1985). Water temperature may also change with regulation; summer cold (hypolimnial release) or winter warm (thermal effluent) releases may affect riparian vegetation.

Riparian habitats and vegetation may change dramatically following flow alteration (Turner and Karpiscak 1980, Lillehammer and Saltveit 1984, Petts 1984, Johnson 1991). Vegetation along the Platte River increased below the Garrick Dam, because the dam converted the Platte River into a perennial river (Nagel and Dart 1980). Flood control may result in a proliferation of riparian vegetation in newly stabilized streamside habitats (e.g. Turner and Karpiscak 1980), or riparian vegetation may deteriorate if the river bed is dewatered through diversion (e.g., Stromberg and Patten 1992). Impoundments used for hydroelectric power generation or irrigation may produce, ecologically anomalous flow fluctuations (Johnson 1991). Impoundment may also lead to changes in riparian soil chemistry and nutrient availability (Stevens 1989a).

Sedimentation is a predictable, and often problematic, feature of reservoirs on regulated rivers (Goldman 1979, Bhowmik et al. 1986, Pearce 1991, Mahmood 1988). Sediments in rivers are derived from rock weathering and erosion, and by less predictable events such as landslides due to earthquakes or mudslides due to volcanoes (Pearce 1991). Tropical Asian and Latin American rivers produce

Table 2. Abiotic effects of impoundment on riparian habitat

-Modified flow regime, including flood control

-Altered water temperature and chemistry

-Sedimentation upstream, sediment loss downstream disproportionate amounts of sediments, due to exposure of young rocks in Asia and due to deforestation in Latin America (Pearce 1991). The reservoir behind the Sanmenxia Dam on the Yellow River, China, was completely filled with silt and disabled within four years of construction (Pearce 1991). Reservoir fluctuations in response to hydroelectric demands can encourage landslides that increase siltation rates of reservoirs (Pearce 1991).

Concern over the increasing frequency of stream regulation through impoundment and diversion has stimulated scientific research on the effects of regulation, particularly in arid lands where water use planning and development has stimulated intensive analysis of water supplies and associated biological resources. Similar concerns are being expressed throughout the world, for boreal, temperate and tropical rivers, and in mesic as well as arid regions. In the United States, mismanagement of riparian habitat has stimulated several recent symposia on habitat management, and state and federal habitat protection programs (e.g., Johnson and Jones 1977, Johnson and McCormick 1978, Johnson et al. 1985, Warner and Hendrix 1985, Tillman 1993). This concern has prompted major federal (e.g., the National Wetlands Protection Act) and state legislation to protect wetlands in the United States. International symposia on regulated rivers have also been convened (Ward and Stanford 1979, Lillehammer and Saltveit 1984), and several journals have been created specifically to address riparian habitats and river regulation impacts (e.g., Wetlands, Rivers, and Regulated Rivers).

III. Methods

1. Data Acquisition Literature for this review was acquired through a computerized search of international data bases, library searches and interviews with numerous scientists working in the field of riparian ecology. This search produced a body of literature of global proportions with most major continents were represented, as well as studies of rivers in mesic and xeric habitats and at high and low latitudes.

A computerized literature search was conducted at Northern Arizona University's library, using the BIOSIS international index of biological literature, which catalogues research published between 1969 and the present. This search produced more than 300 titles and abstracts. Approximately 160 were acquired and 68 were used in the data portion of this review (Appendix I). More than 60% of these studies were conducted in the United States, followed by comparable numbers of studies from Africa, Australia and Tasmania, Scandinavia, continental Europe and Canada (Table 3).

2. Data Organization and Interpretation The collected studies were read in entirety and results were organized into primary categories including upstream and downstream effects, riverine versus nonriverine systems (including swamps, bottomland hardwood forests and man-made lakes), and dam size (large versus small dams). Upstream studies examined vegetation along reservoirs that formed due to damming. Downstream studies examined the impacts of both damming and stream diversion on riparian vegetation. Constrained rivers (rivers in canyons) were compared with unconstrained rivers (alluvial, floodplain rivers). The responses of vegetation to flow regulation within each of these categories were compared.

a. Methods Used in Regulation Studies A large array of study designs, techniques and methods was used among the various studies was enormous, ranging from highly detailed, quantitative findings to more qualitative observations (Appendix I). Studies compared vegetation on unregulated and regulated rivers, upstream and downstream of dams, before and after regulation and/or over a distance from dams. The two most commonly used techniques for measuring vegetation responses were measuring changes in cover on aerial photographs with time series, with comparisons of cover before and after impoundment or upstream and downstream from dams; and the use of study plots for measuring responses of vegetation to regulation.

b. Vegetation Responses Vegetation response variables included measurements of canopy cover, stem density, growth rates and productivity, germination and recruitment (establishment and development of individuals), species composition and species diversity.

In this review, vegetation responses to regulation were scored as positive (+), negative (-) or no response (=). A positive response implied an increase in at least one of these vegetation variables, such as an increase in percent cover. In tabulating responses, one response per regulated reach per study was counted. Measurements of

Overall responses to river regulation were tabulated according to upstream versus downstream conditions, riverine versus nonriverine conditions, etc. and presented in a matrix. Methods used for assessing impacts of dams on vegetation, including aerial photography, field surveys and experiments, are reviewed below. Recommendations for managing and preserving riparian plant communities are also discussed.

IV. Results and Discussion

A. The Review

The list of rivers discussed here indicates the breadth of the review (Table 3, Appendix I). Studies on more than 50 rivers worldwide were compiled. Studies from South America and Asia are particularly lacking in the literature, while there is a better representation of studies from North America, Europe and Africa (Table 3). Intensive construction of large dams has begun only recently in South America and Asia, in response to rapid population growth and an increased demand for power.

B. Impacts of Dams on Upstream Riparian Vegetation

There are initial and subsequent, longer-term effects of impoundment on upstream or reservoir vegetation (Table 4). Initial impoundment of rivers results in extensive plant mortality through inundation and drowning of existing vegetation during reservoir filling. This is such a predictable effect that it is often noted only anecdotally and is rarely measured.

Secondary impacts of impoundment on vegetation result from water level fluctuations that occur after the initial filling of a reservoir. The nature of such fluctuations

Table 3. A demographic breakdown of studies used in this review impoundment effects on riparian vegetation.

Country	No. of Studies
UPSTREAM EFFECTS:	
USA	19
Guyana	1
Egypt	1
Tasmania	1
Sweden	2
Poland	1
DOWNSTREAM EFFECTS:	
USA	20
Australia	5
Canada	3
Germany	1
France	1
Norway	1
Sweden	4
Zimbabwe	1

Table 4. Impoundment effects on upstream vegetation due to reservoir filling, in both riverine and nonriverine riparian areas.

I. Primary effects (during reservoir filling):

- -Inundation leads to reduced plant productivity and/or extensive plant mortality
- -Altered water chemistry, due to decomposing vegetation
- -Loss of colonizable shoreline and substrates for plants
- -Loss of faunal productivity and/or diversity

II. Secondary effects (during reservoir operation):

- -Limited recolonization and productivity of vegetation along new shorelines, due to limited germination substrates, and to altered patterns of water level fluctuations
- -Altered plant species composition, often towards more weedy species
- -Reduced plant species diversity, due to loss of species

will determine colonization patterns of vegetation along the new reservoir shoreline. Fluctuation patterns will determine what types of species colonize shorelines, and an understanding of their effects may require a long-term consideration of shoreline vegetation development (Waring 1993, Nilsson et al. 1991).

1. Riverine Impoundments

The literature reviewed describes initial upstream drowning events as rivers are regulated, and the subsequent colonization of new shorelines are reservoirs are filled. Various studies describe how fluctuations of reservoir levels and the geomorphology of the basin determine what species will colonize the new shorelines and what the structure of these new communities will be.

The 25 studies that evaluated dam impacts on upstream vegetation involved rivers in six countries on five continents (Table 3, Appendix I).

a. Initial Impoundment Effects on Riparian Vegetation Ten studies that discussed initial impoundment effects on existing vegetation reported extensive loss of vegetation (Table 5, Appendix I). In these cases, pre-existing vegetation in the filling reservoir basin drowned and died.

Table 5. A matrix summarizing impoundment effects on upstream vegetation cover, productivity and species composition (+ = increase, - = decrease, = = no change).

	CHANGES IN:						
	Cover/ density			Growth/ productivity			Plant species composition
	(+)	(-)	(=)	(+)	(-)	(=)	
RIVERINE:							
Primary effects	-	11	-	-	2	-	5
Secondary effects	4	6	1	-	2	1	13
NONRIVERINE:	2	8	1	2	1	-	10

These initial drowning events, along with the environmental conditions that result from transforming a river into a reservoir, can have long-term or even permanent effects on the type of vegetation that will become established along the new shoreline. Nilsson et al. (1991) found that post-impoundment plant communities along new shorelines (bordering deep reservoirs) were significantly 'floristically dissimilar' to communities of a nearby unregulated river in Sweden, while communities along old shorelines (bordering shallow reservoirs) were more floristically similar to those of unregulated rivers. When shoreline vegetation is not entirely eliminated through inundation, such as along reservoir headwaters, it may become re-established relatively quickly along reservoirs.

Inundated vegetation can affect the water chemistry and navigability of reservoirs (Goldman 1979, Bonetto et al. 1987, Potter and Drake 1988). In tropical South American rivers, decaying vegetation promotes the spread of disease and creates eutrophic, deoxygenated conditions (Barrow 1987, Leentvaar 1985, Goldman 1979). Decaying vegetation in the reservoir behind Siranumum Dam in Papua New Guinea produced hydrogen-sulfide-rich water, which is highly corrosive to metal (Goldman 1979). Decaying, submerged vegetation in

Lake Powell produced adequate resources to support a sports fishery for a brief period, following the initial filling of the lake; this productivity was only short-lived, however (Potter and Drake 1989).

b. Development of Reservoir Shoreline Vegetation Five studies reported establishment of vegetation along new reservoir shorelines (Schmidly and Ditton 1978, Peck and Smart 1986, Springuel et al. 1991, Nilsson et al. 1991, Waring 1993; Table 5, Appendix I). While these 'positive' responses indicate that vegetation becomes established along reservoir shorelines, vegetation development was reduced relative to that which occurred prior to impoundment. Even long-term studies (Peck and Smart 1986, Nilsson et al. 1991, Waring 1993) determined that reservoir vegetation was still more sparse than that occurring on the pre-impoundment shoreline. Species composition of upstream communities is strongly altered by impoundment. In all studies, species composition of these riparian plant communities was changed, often with increased representation of annual, weedy species over woody plants (Appendix I). Some annual plant species, termed 'annual shuttle species' (Nilsson et al. 1991), are better-adapted to exploit these modified environments, than the species that colonized them previously. Reduced and taxonomically altered shoreline plant communities also represent reduced habitat for riparian fauna (Schmidly and Ditton 1978).

Recolonization of lake shorelines by pre-existing riparian species is often limited, relative to pre-impoundment conditions (e.g., Schmidly and Ditton 1978, Waring 1993). According to Mr. Cliff Amundsen (University of Tennessee-Tennessee Valley Authority ecologist, personal communication), even after 50 years there is only limited re-establishment of riparian plant species along the impounded Tennessee River. The shoreline vegetation there today is dominated by conifers that occurred outside the riparian zone prior to impoundment. In the western United States once-common native species, such as Fremont cottonwood, have only sparsely recolonized reservoir shorelines, if at all; while exotic tamarisk (Tamarix ramosissima) and Russian thistle (Salsola iberica) have extensively colonized reservoir shorelines (e.g., Waring 1993, Turner 1974). In Egypt, native Tamarix nilotica has extensively colonized the shoreline of Lake Nasser, along with numerous annual species (Springuel et al. 1991).

Responses of vegetation to reservoir development are complex, with different species responding differently to the same conditions. Differences in plant life history strategies need to be considered when analyzing or predicting the effects of reservoir formation on vegetation.

c. Factors Affecting Vegetation Establishment Along Reservoirs Limited availability of riparian soils plays a large role in colonization of reservoir shorelines (Potter and Pattison 1976, Schmidly and Ditton 1978, Nilsson et al. 1991, Waring 1993). Deep reservoirs can eliminate much colonizable shoreline, as along Lake Powell in southern Utah, where 75% of the current shoreline is comprised of near vertical rock cliff, talus and rockslides (Potter and Drake 1989).

Despite overall reductions in colonizable shoreline along reservoirs, sedimentation occurs where tributaries meet reservoirs (see River Regulation section), and these areas have the potential to support an abundance of riparian vegetation. Sediments moving from tributaries into reservoirs settle out as water velocity slows, and deltas form. Extensive stands of vegetation are developing at the mouth of tributaries of Lake Powell on large deltas more than 70 feet deep that are forming as sediments are deposited (Waring, personal observation, Potter and Drake 1989). Along the impounded upper Mississippi River, marsh vegetation is increasing with continued sediment aggradation (Peck and Smart 1986), and this trend is expected to continue. An extensive riparian woodland developed on alluvium at the top of Isabella Reservoir on the South Fork Kern River (Fleshman and Kaufman 1984).

Fluctuating water levels in reservoirs provide challenges to plant colonization and influence community structure along shorelines. Reservoir levels may fluctuate on daily, weekly, annual and larger time scales (see River Regulation section). Fluctuations can be frequent and significant enough that only annual plant populations can successfully colonize the interpool zone (Nilsson et al. 1991, Grelsson 1988, Waring 1993). Prolonged high reservoir levels on the South Fork Kern River, California, reduced densities and growth in riparian plants that had developed along the reservoir (Fleshman and Kaufmann 1984). Significantly more Goodding's willow than Fremont cottonwood survived the prolonged flooding (Fleshman and Kaufmann 1984). Prolonged drawdown of Lake Powell during more than 7 years of regional drought left the shoreline vegetation perched nearly 30 m over the water level (Waring 1993). No new colonization and only limited growth occurred during that period (Waring 1993). Pines growing along an annually fluctuating Scandinavian reservoir showed no difference in growth rates, while those growing along a daily-weekly fluctuating reservoir showed significantly greater variation in growth rates (Grelsson 1988). Nilsson and Keddy (1988) reported that water fluctuation patterns explained 41% of variation in plant community composition along reservoir shorelines.

Reservoirs located in steep, narrow drainages may experience a greater loss of vegetation cover and species than those located along wider floodplains. Constrained reaches in deep drainages lose a higher proportion of colonizable substrata when impounded, compared with shallow alluvial reaches.

2. Nonriverine Impoundments

Nonriverine impoundments include shallow impoundments in wetland habitats such as swamps and bottomland hardwood forests, greentree reservoirs, and man-made lakes. They typically involve shallow bodies of water and smaller dams, such as levees, than those on rivers.

Although the number of studies on the impacts of dams on nonriverine riparian ecosystems is limited (Appendix), several studies reported experimental results that reveal a great deal about how riparian vegetation responds to shallow impoundments (Conner and Day 1992, Thibodeau and Nickerson 1985, Conner et al. 1981).

Bottomland forests and swamps are wetter environments than other most riparian environments. Despite this, bottomland hardwood species are remarkably variable in their tolerance of both flooding and water deficits (Kozlowski 1984). Species such as bald cypress and water tupelo exhibit the most growth in response to flooding, while other species grow more when water is drained from impoundments (Klimas et al. 1981, Whitlow and Harris 1979, Kozlowski 1984). Consequently, responses of bottomland forests to either prolonged flooding or desiccation are complex, with some species being lost while others persist or thrive, as is found along impounded rivers (see above). There are limits to flooding tolerance for even the most tolerant species (Klimas et al. 1981). Seedlings of most species do poorly when submerged (Broadfoot and Williston 1973). For example, seedlings of flood-tolerant bald cypress (Taxodium) and tupelo (Nyssa) are unable to establish in standing water (Conner and Day 1992). Therefore, some variation in water stage may be essential to permit recruitment of multiple species.

<u>a. Vegetation Responses to Impoundment</u> Eight studies reported loss of vegetation cover, densities and/or growth when nonriverine bodies of water were impounded, which

resulted in prolonged flooding, indicating a negative impact from impoundment (Appendix I).

Six of these studies reported a change in species composition in plant communities. Yeager (1949) reported total mortality in pin oak while some green ash survived impoundment in a swamp in the lower Mississippi Valley. Miller (1990) reported a loss of species diversity as seasonally-flooded bottomland hardwoods were replaced by shallow-water marsh species along an impounded reservoir along the Middle Fork-Forked Deer River, Tenn. Fredickson (1979) found the highest plant species richness on sites with the least water in an impounded swamp. Correspondingly, 3 studies reported that plant cover or species richness increased as impoundments were drained (Appendix I). Dense and more diverse riparian vegetation colonized a shrub swamp in Massachusetts within three years after it was drained, while in an adjacent impounded swamp several common species were extirpated and densities of most other species declined (Thibodeau and Nickerson 1985). These studies provide evidence that prolonged flooding can be detrimental even to swamp species.

<u>b. Factors affecting vegetation responses</u> Low dissolved oxygen concentrations in water, such as in stagnant water, affect the response of species to flooding (Kozlowski 1984).

Nyssa seedlings grew five times more in running water than in stagnant water (Hook et al. 1970). The fact that floods can stimulate growth in some bottomland hardwood trees suggests that the movement of water and high levels of oxygen are important. That suggests that long-term impoundment of swamps will typically produce negative effects on hardwoods.

Conner and Day (1992) found higher litterfall, or greater productivity, in a bottomland hardwood stand in a managed wooded crayfish pond compared to an adjacent naturally flooded swamp in Louisiana over a 5 year period. The crayfish pond was flooded in autumn and drained in summer each year, while water level fluctuations in the natural swamp were far more erratic. Other studies have found this pattern of greater productivity when forests are flooded once per year during the dormant season and then drained during the growing season (Gosselink et al. 1981). This suggests that bottomland plants probably rarely experience such a consistent flooding regime and may typically exist in suboptimal conditions. Suboptimal conditions in the form of excess flooding are expected to persist or increase as subsidence continues in southern Louisiana, due to decreased sedimentation in wetlands there

(Conner and Day 1992, Templet and Meyer-Arendt 1988).

Greentree reservoirs are levied, forested areas in the southeastern United States that are flooded in dormant winter months to provide habitat for waterfowl. This management procedure increases both the magnitude and duration of flooding compared to natural flood conditions, and often results in a shift in plant species composition towards more water tolerant species (Fredickson and Batema 1992). Benefits to vegetation, such as increased acorn production in oaks, decrease within 10 years, and longer-term effects on both wildlife and vegetation are largely negative (Fredickson and Batema 1992). Inadequate draining of these reservoirs in the spring has a particularly negative effect on vegetation, and a recent review of greentree reservoirs recommends that natural flooding regimes be emulated (Fredickson and Batema 1992).

The tolerance of bottomland species of all but the most prolonged and extreme levels of flooding or drought suggest that effective management of these habitats is within reach. Prolonged flooding, particularly involving stagnant water, can ultimately convert bottomland vegetation from diverse hardwood forests to herbaceous hydrophytic assemblages of plants (Klimas et al. 1981). The range of flooding tolerances among bottomland species and the demonstrated positive responses of some species to draining, suggests that natural seasonal flow patterns may accommodate the most different types of life histories. Alternatively, different management regimens could be implemented simultaneously, leading to a patchwork of different successional plant groups, similar to that which exists naturally in less-disturbed bottomlands (Klimas et al. 1981).

C. Downstream Effects of Dams

A total of 36 studies discussed 44 cases (either separate rivers, or different reaches of the same river) demonstrating flow regulation impacts on downstream riparian vegetation. The geographic distribution of these studies included streams in Australia, Europe, Africa and North America (Table 3, Appendix I). Stream types varied from low-order, constrained headwater streams to high-order alluvial temperate and tropical rivers. Flow regulating structures in these cases included dams and diversions of different sizes, with release patterns ranged from simple flood control to complete diversion of flow.

Cases that involved riparian vegetation changes associated with factors other than flow regulation, or that evaluated the responses of single riparian plant species were excluded from the tabulation of riparian vegetation cover changes. Four cases involved anthropogenic factors other than flow regulation that obscured the mechanisms of vegetation change (Sands and Howe 1977, Dunham 1989a,b, Dister et al. 1990, Pautou 1992). Six autecological cases documented decreasing cover of dominant species, especially Populus spp. in western North America, but other riparian cover changes were not reported (Fenner et al. 1985, Bradley and Smith 1986, Hunter et al. 1987, Snyder and Miller 1991, Stromberg and Patten 1992). Although the cover of dominant riparian phreatophytes, such as Populus may decline after flow regulation, other species' populations may expand, particularly non-native phreatophytes (e.g. Ohmart et al. 1988). If these autecological studies were included the interpretation of cover loss could increase by as much as 33%. Excluding these 10 cases reduced the tabulation to 34 cases, but the 10 cases were included in the evaluation of compositional change.

1. Effects of Regulated Flow on Riparian Vegetation

Vegetation responses to flow regulation were strongly dictated by the type of river (alluvial versus constrained), the type of flow regulation (undiverted versus diverted), the riparian zone (lower, middle or upper riparian zones) and the plant species or assemblages under study.

When the data are compiled more generally, without consideration of the above phenomena, patterns are equivocal. Fourteen of 34 cases (41%) demonstrated that flow regulation increased riparian vegetation in downstream reaches (Appendix I). The opposite pattern-the loss of riparian vegetation downstream from dams-is equally well documented in this body of literature. Eleven of 34 cases (32%) reported decreased riparian vegetation cover downstream from dams (Appendix I). Only when stream type and type of flow regulation are considered to the patterns of regulation effects on riparian vegetation become clear.

a. Plant Cover on Undiverted Regulated Rivers

In nearly all cases, riparian vegetation cover increased along undiverted regulated streams, compared with unregulated conditions. Ten of 11 cases (91%) of essentially undiverted streams reported increased cover in response to impoundment (Table 6). Although flood frequency changed, mean flows did not change greatly after regulation of the Colorado River in the Grand Canyon (Turner and Karpiscak 1980) or just below Lake Mohave (Ohmart et al. 1988), in the River Murray in Australia (Bren 1992), and regulation resulted in enhanced low flows in portions of the South Platte River (Knopf and Scott 1990). In all cases,

Table 6. A matrix summarizing impoundment effects on downstream vegetation cover, productivity and species composition (+ = increase, - = decrease, = = no change).

	CHANGES IN:						
	Cover/ density			Growth/ productivity			Plant species composition
	(+)	(-)	(=)	(+)	(-)	(=)	
ALLUVIAL RIVERS:							
Diverted	2	5	1	-	-	-	15
Undiverted	7	-	1	-	1	-	9
CONSTRAINED RIVERS:							
Diverted	2	6	7	-	2	-	6
Undiverted	3	-	-	-	-	-	3

riparian vegetation cover increased. Increases occurred in both constrained and alluvial or unconstrained basins.

The frequency of riparian vegetation cover increases following regulation were equally high in both alluvial and constrained, undiverted rivers. Seven of 8 cases (88%) of alluvial regulated undiverted rivers reported vegetation increases, whereas 3 of 3 (100%) cases of constrained regulated undiverted rivers reported vegetation increases (Table 6, Appendix I).

b. Plant Cover on Diverted Regulated Rivers Flow diversion resulted in loss or no change in riparian vegetation cover. Of the 23 total cases of flow diversion, only 4 cases (17%) reported increased riparian vegetation cover. Flow diversion on alluvial rivers was associated with loss of riparian vegetation in 5 of 8 cases (63%, Table 6), including Nilsson's (1981) examples of Swedish "rivers laid dry" and McDonald and Sidle (1992) studies of diverted portions of the South Platte River in the western United States. Established phreatophytes growing along diverted alluvial rivers may persist as long as the water table does not decrease in elevation. In some cases, alluvial channels may receive flow from both stream and groundwater sources (Loeltz and Leek 1983).

Flow diversion in geologically constrained streams rarely resulted in increased riparian vegetation cover. In only 2 (12%) of 17 cases of diverted, constrained rivers did riparian vegetation cover increase after flow regulation; riparian vegetation typically decreased or remained unchanged (Table 6, Appendix I). Harris et al. (1987) found that 5 of 14 diverted, constrained streams lost vegetation and Stromberg and Patton (1992) reported loss of cottonwoods along Rush and Bishop Creeks in the Sierra Nevada Range. Odland et al.'s (1991) study of mist zone regulation on Norway's Aurland River is another example of loss of vegetation in a diverted, constrained river. Diversion of flow from constrained, bedrock streams reduces water availability, increasing drought-related stress.

c. Effects of Flow Regulation on Community Composition

Plant species composition in riparian communities is strongly affected by flow regulation. Thirty-seven of the 44 studies (84%) reported compositional changes associated with flow regulation (Table 6). Shorelines protected by flow regulation from high flows were often colonized by upland (e.g., Nilsson 1979a,b) or by native and non-native phreatophytic species (Turner 1974, Turner and Karpiscak 1980). Only the 7 streams examined by Harris et al. (1987)

that did not differ from their upstream, unregulated reaches were considered not to have changed compositionally following regulation.

The compositional changes that follow regulation can lead to new vegetation associations, including unusual combinations of upland and non-native phreatophytes. Johnson et al. (1976) reported that original cottonwood cover in the upper riparian zone along the Missouri River was gradually replaced by upland species, including ash and elm (Johnson et al. 1976). Nilsson (1979b) examined riparian communities along regulated versus unregulated rivers in Sweden and reported that the cover of species and associations characteristic of unregulated rivers were rare on regulated rivers, although cover increased for other species along regulated rivers. Roberts and Ludwig (1991) developed a conceptual model of wetland assemblages to predict changes in species composition following impoundment.

<u>d. Regulation Effects on Different Plant Zones</u>

Stabilized lower riparian terraces generally undergo rapid initial colonization and 10 of 13 cases (77 percent) of the cases in which elevation-related changes were documented reported increased vegetation in the low riparian zone following impoundment. For example, Turner and Karpiscak

(1980) and Pucherelli (1988) used photographic evidence to document increased low riparian zone vegetation (primarily non-native saltcedar) in the Grand Canyon, Arizona following flow regulation by Glen Canyon Dam. However, upper riparian zone vegetation cover tends to change little and slowly following impoundment. Pucherelli (1988) reported only a slight, non-significant decreases in upper riparian zone cover after more than 2 decades of flow regulation in the Grand Canyon.

2. Other Factors Affecting Vegetation along Regulated Rivers

Other factors besides, or loosely associated with, flow regulation may alter riparian vegetation, including climate, non-native species invasions, latitude, post-dam flooding, zonation, and other anthropogenic influences.

The effects of phenomena such as climate and non-native species invasions on vegetation cover, may be mistakenly attributed to regulation. Williams and Wolman (1984) cautioned that vegetation increases downstream from dams may result from climatic changes rather than flow regulation. Repeated measurement of the same transects or study sites upstream versus downstream of impoundments, coupled with analysis of climatic and flow data, provide a reliable method for detecting and understanding the extent of climate-induced vegetation changes. Harris et al. (1987) reported increased riparian vegetation downstream of 2 diverted Sierra Nevadan streams in California by comparing vegetation upstream and downstream of impoundments, thereby controlling for other influences such as climate. Cases of rapid riparian vegetation change immediately after flow regulation (e.g. Turner and Karpiscak 1980) support the contention that flow regulation is usually a more important factor than climate change for riparian vegetation along regulated streams.

Several studies, particularly in the American West, discuss the spread of non-native plant species in regulated riparian habitats. Turner (1974) reported increased cover of exotic saltcedar (Tamarix pentandra) a long the Gila River in Arizona, and following both upstream diversions and downstream construction of dams. Turner and Karpiscak (1980) and Ohmart et al. (1988) documented extensive invasion of saltcedar in the Grand Canyon and lower Colorado River following flow regulation. Knopf and Scott (1990) and McDonald and Sidle (1992) discuss the rapid invasion of Russian olive (Elaeagnus angustifolia) that occurred contemporaneously with flow regulation in the upper Platte River drainage. In all of these cases, it is not clear that flow regulation was responsible for increased cover of non-native vegetation. Certainly both of these exotic, opportunistic species proliferate on the headwater deltas of western reservoirs (e.g. Warren and Turner 1975), but they were apparently simply present at a time when flow regulation protected, for the first time, shoreline habitats throughout the rivers of the West.

Ice scour is a latitudinal factor that affects vegetation downstream from boreal river dams. Ice formation on regulated rivers in high latitude settings scours shorelines (Nilsson 1981, Day et al. 1988), sometimes entirely removing riparian vegetation. Nilsson (1981) attributed increased severity of ice scour to freezing of discharge that repeatedly ran across the surface of the already frozen Vojman River. Ice formation does not occur along low latitude, low elevation rivers.

Several studies reported that prolonged flooding in regulated rivers reduced riparian vegetation cover and survivorship, and altered species composition (Stevens and Waring 1985, Pucherelli 1988, Hunter et al. 1985). Post-dam flooding along the Colorado River in Arizona produced a significant reduction in lower riparian zone vegetation cover (Pucherelli 1988), and resulted in greater mortality of upland and nonclonal phreatophytes as compared to clonal phreatophytes (Stevens and Waring 1985). Similarly, post-dam flooding along the Bill Williams River in Arizona differentially reduced densities of Fremont cottonwood as compared to Goodding's willow (Hunter et al. 1985).

Other anthropogenic factors such as grazing, fire, and direct human use also alter vegetation patterns along regulated rivers. As much as 99 percent loss of riparian vegetation was reported along the upper Rhine River during the last two centuries by Dister et al. (1990). These losses resulted from complex interactions between flow regulation, urbanization and other anthropogenic factors. Sands and Howe (1977) reported on widespread decline of riparian vegetation following regulation of the Sacramento River, California, but agriculture and urban water use also affected the distribution of riparian vegetation. Dunham (1989a,b) reported a decrease in tree cover between 1961 and 1987 on the Zambezi River floodplain, but his data also include influences of interactions between riparian vegetation and flow regulation, reduced fire frequency and changing populations of large herbivores (antelope and elephants) and decomposers (termites).

Regulation exerts strong effects on riparian vegetation dynamics. Vegetation may increase or decrease depending on stream type and the extent to water is diverted from rivers.

These studies revealed many other factors that may influence or confound regulation effects on vegetation, including climate, exotic plant invasions, and grazing, which along with others must be accounted for in future studies on regulation impacts.

D. Small Dams and Riparian Vegetation

Smaller dams, such as check dams or crib dams, are a common feature on small drainages in the western United States (DeBano and Schmidt 1990). They are employed to restore highly erosive streams that are degraded from disturbances such as logging or overgrazing. Such disturbances can lead to severe floods that produce deeply incised channels (DeBano and Schmidt 1990). Check dams can augment baseflow in drainages (DeBano and Schmidt 1990, Ponce 1989), which is one of the reasons that they tend to encourage extensive growth of riparian vegetation (Szaro and DeBano 1985).

Of 8 studies reviewed, all reported rapid and extensive development of riparian vegetation following the construction of channel checks (Appendix I). Based on a survey of thousands of check dams throughout Los Angeles County, Ruby (1973, 1974) reported riparian vegetation development in association with such impoundments. While most studies described development of riparian vegetation upstream of small dams, 4 studies also reported development of vegetation downstream (Szaro and DeBano 1985, Hansen and Kiser 1988, DeBano and Hansen 1989, Heede 1977).

Riparian vegetation development occurs when sediments are trapped behind small dams and permit colonization and growth. Accumulated sediments store water during stormflows and release it slowly over time, resulting either in prolonged duration of intermittent stream flow or conversion of ephemeral streams to perennial streams. This phenomenon has been observed numerous locations throughout the West (Stabler 1985). Accumulated sediments and persistent water set the stage for extensive plant development.

The development of riparian vegetation upstream from small dams is analogous to vegetation development on sediments deposited where tributaries meet large reservoirs, although the rapid sedimentation of the former permits a more rapid vegetational response.

E. Methods Used for Assessing Impacts of Dams on Vegetation

A variety of methods, response variables and analyses were used to evaluate changes in riparian vegetation in response to flow regulation. These included comparing (1) vegetation along regulated and unregulated rivers (e.g., Stromberg and Patten 1992), (2) vegetation along downstream and upstream reaches of regulated rivers (e.g., Harris et al. 1987), (3) comparison of pre-regulation vegetation with post-regulation vegetation (e.g Turner and Karpiscak 1980), and (4) vegetation change over distance from the impoundment in comparable reaches (Stevens and Ayers 1993).

These comparisons involved rematching historical photographs, comparing serial aerial photogrametry, analysis of long-term study plots, and monitoring recruitment, plant growth, and/or the physiological condition, reproductive output, or other characteristics of individual plants.

Confounding factors such as exotic plant invasions and climate make it essential that regulation studies include an analysis of unregulated river sections for comparison. Comparison of vegetation patterns along rivers before and after they are regulated would not detect the effects that factors such as exotic plants and climate might be having on vegetation.

One of the most widely used techniques has been measurement of vegetation cover from series of aerial photographs. If such photographs are available and the measurements are accurately calibrated, they provide a valuable means, and often the only means, of determining historical patterns of vegetation response to regulation.

Likewise, photogrametric analysis can be useful in long-term monitoring. However, cover by itself can be misleading. Significant shifts in species composition following regulation, such as those due to invasion of exotic species or changes in understory taxa, are often not detectable from aerial photographs. Field studies are essential for accurate determination of composition.

Several authors evaluated response variables other than cover for monitoring the effects of changing flow patterns. For example, stem density and annual tree-ring growth (Reilly and Johnson 1982; Stromberg and Patten 1992), nodal growth (Anderson and Ruffner 1988; Stevens and Ayers 1993), plant water potential (Ayers and Stevens 1993), survivorship (Stevens and Waring 1985), evapotranspiration (Nagel and Dart 1980), reproductive output, and phenological shifts have been employed as response variables.

F. Recommendations for Future Studies

Based on this review, it is recommended that the following information be gathered to develop a clear understanding of vegetation responses to river regulation:

1) Identify basin characteristics, including geology, geomorphology, land use, and climate of the rivers under study. Identify the kind of river or reaches (constrained

versus unconstrained), as well as the sediment transport condition and load type of the stream.

2) Describe pre-impoundment flow conditions as accurately as possible, including flow duration, seasonal variablility, flood frequency and water quality.

3) Describe the nature of flow regulation, including seasonal variability, flood frequency, flow durations and water quality.

4) Distinguish the impacts of regulation on vegetation co-occurring in the different riparian stage zones (e.g., subaqueous, low riparian, middle riparian, upper riparian zones).

5) Identify the overall impact of regulation on the vegetation response variables of interest (cover, density, recruitment, species composition, etc.). As more variables are considered, a clearer picture of vegetation responses to regulation will develop. Vegetation cover changes provide a strong indication of response, but when coupled with measurements of responses of multiple species, an indication of the community's response will emerge. It is clear from this review that changes in these communities seem to consistently involve population increases in some species and decreases in others as environments change following regulation.

Additional recommendations are presented in Appendix II.

V. CONCLUSIONS

Dams have strong and complex effects on riparian vegetation. These effects include changes in vegetation cover, altered species composition and reductions in plant diversity. Impoundment leads to significant vegetation losses upstream, and also downstream-when rivers are diverted. There is little evidence that riparian plant communities ever fully recover from these events. Undiverted regulation of rivers can lead to increases in vegetation cover, due to flood control effects. Clearly, the negative consequences of diversion to vegetation lie in removal of water from a riparian habitat. The degree of diversion correlates strongly with degree of vegetation loss.

Vegetation loss is likely to be greatest and most rapid upstream of dams due to the inundation of extensive areas during reservoir filling, and to a loss of colonizable shoreline. If rivers are entirely diverted in constrained channels vegetation loss will be extensive, though perhaps less rapid.

Dam operations, subsequent to dam construction, also have significant effects on upstream and downstream vegetation development. Post-dam flooding can drown upstream vegetation that has established along reservoir shorelines, and remove downstream vegetation through drowning and scouring. Post-dam flooding can also alter species composition both upstream and downstream and exert erosive effects on beaches. Low flows can reduce productivity or even destroy upstream and downstream vegetation through desiccation.

Studies of bottomland hardwood forests and greentree reservoirs showed that periodic short-term flooding, similar to natural flooding events, can have a positive effect on riparian vegetation. While flooding is known to be a prerequisite for establishment of some riparian species on unregulated rivers, the positive benefits of flooding to vegetation on regulated rivers have yet to be elucidated.

Future studies of dam effects on both upstream and downstream riparian vegetation need to emphasize patterns of response at the community-level and at the level of individual species. This combined perspective is lacking in most studies, effectively limiting our understanding of large-scale effects of dams on riparian vegetation. It may be significant that most dam-building in the western United

States coincided with the recent, rapid invasion by the exotic plants tamarisk and Russian olive (Tamarix ramossissima and Elaeagnus angustifolia). These two species figure prominently in many studies and yet the influence of regulation on their distributions upstream and downstream of dams is not well understood.

Similarly, many studies in the western USA emphasized the responses of cottonwood, a relatively early successional species, to flow regulation. It may be that the decline of this species in stabilized postdam environments is accompanied by an increase in later colonists and non-native invading species, such as saltcedar.

Small dams such as check dams and crib dams consistently increase upstream vegetation development. Several studies found the same pattern for downstream vegetation. The small eroded streams on which such structures are usually employed are often initially devoid of vegetation. Sediments accumulate quickly in these small drainages, permitting rapid vegetation colonization. Such a process also takes place in larger reservoirs through the process of siltation.

This review represents a departure point for future research on dam impacts on riparian ecosystems. The techniques recommended here are widely applicable, and have produced important and reliable results. Flow regulation is now commonplace but ability to predict effects is poor. Regulation destroys the integrity of upstream fluvial ecosystems and strongly alters downstream ecology as well. This form of habitat disruption constitutes largescale landscape experimentation, which can be used to improve our understanding of how discharge affects river ecology and can provide insight into the mitigation of those impacts.

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Appendix I. Listing of all studies included in review of vegetation responses to impoundment.

LOCALITY	VEGETATION TYPE	METHOD[1]	CHANNEL[2]	COVER/ DENSITY	SPECIES COMP.	GROWTH/ PRODUCT.	RECRUIT/ GERM.	REFERENCE
I. UPSTREAM EFFECTS:								
A. RIVERINE IMPOUNDMENTS: Initial impoundment effects								
Lower Snake R., WA, USA	riparian vegetation	observ.	constr.	-				Holzwarth 1978
Lake Tapakuma, Guyana	riparian vegetation	observ.	constr.	-				Dodson 1978
Lake Gordon, Tasmania	rainforest, wet schlerophyll forest	observ.	constr.	-				Steane and Tyler 1982
Lake Powell, AZ, USA	willow/ cottonwood	observ.	constr.	-	*			Waring 1983
Isabella Reservoir, CA, USA	willow/ cottonwood	observ.	unconstr.	-				Fleshman & Kaufman 1984
Upper Miss. R., USA	forest, meadow	aerial	unconstr.	-	*			Peck & Smart 1986
Upper Miss. R., USA	marsh	aerial	unconstr.	-	*			Peck & Smart 1986
Mississippi R., USA	riparian forest	plots	unconstr.	-	*	-		Green 1947
Rio Grande R., TX, USA	willow/ Phragmites	observ.	unconstr.	-				Schmidly & Ditton 1978

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TVA reservoir, TN, USA	riparian forest	observ.	unconstr.	-	*	-		Amundsen, TVA
San Carlos Reservoir, AZ USA	cottonwood	aerials	constr.	-				Turner 1974

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Post-impoundment impacts								
Lake Nasser, Egypt	riverine species including Tamarix nilotica	plots	unconstr.	+	*			Springuel et al. 1991, Pulford et al. 1992
Rio Grande R., TX, USA	willow/ Phragmites	observ.	unconstr.	+	*			Schmidly & Ditton 1978
	annuals				*			
Lake Powell, AZ, USA	tamarisk/ annuals	plots	constr.	+	*			Waring 1993
Lake Powell, AZ, USA	tamarisk/ annuals	plots	constr.	=	*	- (low lake elevation)		Waring 1993
San Carlos Reservoir, AZ USA	tamarisk/ cottonwood	aerials	constr.	+ flooding	*			Turner 1974
Isabella Reservoir, CA, USA	willow/ cottonwood	plots	unconstr.	- flooding	*			Fleshman & Kaufman 1984
	annuals				*			
Elk Ck, IA, USA	willow/ herbaceous emergent	plots	unconstr.	- flooding	*			Weller et al. 1991
Upper Miss. R., USA	forest, meadow	aerial	unconstr.	-	*			Peck & Smart 1986
Upper Miss. R., USA	marsh	aerial	unconstr.	-	*			Peck & Smart 1986

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TVA reservoir, TN, USA	riparian forest	observ.	unconstr.	-	*	-		Amundsen, TVA
Ume R., Sweden	riparian forest	plots	constr.	-	*			Nilsson et al. 1991
Gardiken Reservoir, Sweden	Picea abies	dendro.	constr.			=	(annual fluctuations)	Grelsson 1988
Gardiken Reservoir, Sweden	Pinus sylvestris	dendro.	constr.			more variable	(daily/weekly fluctuations)	Grelsson 1988

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B. NONRIVERINE IMPOUNDMENTS:								
Lac de Allemands swamp, LA	baldcypress/ water tupelo/ ash	point quarter	unconstr.	-	*	- (permanent flooding)		Conner & Day 1992, Conner et al. 1981
Lac de Allemands swamp, LA	baldcypress/ water tupelo/ ash	point quarter	unconstr.	-	*	+ (controlled flooding)		Conner & Day 1992, Conner et al. 1981
Barr Lake, CO, USA	riparian vegetation	observ.	unconstr.		*			Lovell et al. 1985
Lake Chicot, LA, USA	cypress/ tupelo gum	plots	unconstr.	-	*			Eggler & Moore 1961
Lake Strykowskie, Poland	Phragmites/ Carex	plots	unconstr.	-				Goldyn 1992
Forked Deer R., TN, USA	bottomland hardwoods	plots, aerials	unconstr.	-	*			Miller 1990
Forked Deer R., TN, USA	bottomland marsh	plots, aerials	unconstr.	+	*			Miller 1990
Great Swamp, MA, USA	High-bush blueberry, other wetland shrubs	plots	unconstr.	+	* (drained swamp)			Thibodeau & Nickerson 1985
Great Swamp, MA, USA	High-bush blueberry, other wetland shrubs	plots	unconstr.	-	* (flooded swamp)			Thibodeau & Nickerson 1985

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Kentucky Reservoir, TN, USA	riparian forest	plots	unconstr.	-				Hall & Smith 1955
Alton Dam, ILL, USA	bottomland hardwoods	plots	unconstr. (prolonged flooding)	-	*			Yeager 1949
Shallow impoundments, MS, USA	bottomland hardwoods		unconstr.			+ (brief flooding)		Broadfoot 1967
Greentree reservoir, MS, USA	bottomland hardwoods		unconstr.	=	* (dormant season flooding)			Fredickson 1979

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II. DOWNSTREAM EFFECTS: A. DAMMED, UNDIVERTED RIVERS								
Bighorn R., WY, USA	cottonwood	dendro/ aerial	unconstr.	-	*		-	Akashi 1988
Colorado R., AZ, USA	riparian vegtation	aerial	constr.	+				Pucherelli 1988
Colorado R., AZ, USA	riparian vegetation	oblique photo	constr.	+				Turner & Karpiscak 1980
Colo. R., AZ, USA	tamarisk/ willow	trans	constr.	-				Carothers et al. 1979
S. Platte R., USA	cottonwood	observ.	constr.	+				Knopf & Scott 1990, Kircher & Karlinger 1983
River Murray, NSW Aust.	red gum	aerial	unconstr.	+				Eren 1992
River Murray, NSW Aust.	riparian vegetation	observ.	unconstr.		*			Chesterfield 1986
River Murray, NSW Aust.	red gum	review	unconstr.	-				Dexter et al. 1986
River Murray, NSW, Aust.	riparian monocots	trans.	unconstr.		*			Roberts & Ludwig 1991
Mangrove Ck., NSW, Australia	Leptospermum	aerial	unconstr.	+				Sherrard & Erskine 1991

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B. DAMMED AND DIVERTED RIVERS								
Sacramento R., CA, USA	riparian vegetation	review	unconstr.	-	*			Sands & Howe 1977
St. Mary R., Alberta, Canada	cottonwood	aerial	unconstr.	-				Rood & Heinze-Milne 1989
Waterton R., Alberta, Canada	cottonwood	aerial	unconstr.	-				Rood & Heinze-Milne 1989
S. Platte R., NE, USA	cottonwood	oblique photos	unconstr.	-				Crouch 1979
Missouri R., ND, USA	cottonwood	aerial/ dendro.		-	*	-	-	Johnson et al. 1976
Platte R., NE, USA	riparian vegetation	evapo. trans.	unconstr.	+				Nagel & Dart 1980
Missouri R., ND, USA	cottonwood	dendro.	unconstr.			-		Reilly & Johnson 1982
Milk R., Alberta, Can & MT, USA	cottonwood	trans.	unconstr.	-			-	Bradley & Smith 1986
Rhine R., France/ Germany	riparian vegetation	observ.	unconstr.	-	*		-	Dister et al. 1990
Zambezi R., Zimbabwe	riparian trees	oblique photo	unconstr.	-	*		-	Dunham 1989a,b

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Salt R., AZ, USA	cottonwood	growth studies	unconstr.				-	Fenner et al. 1985
Umealven R., Sweden	pines	trans.	unconstr.	+	*			Grelsson & Nilsson 1980
Platte R., USA	riparian vegetation	observ.	unconstr.	+				Hadley et al. 1987
Alder Ck., CA, USA	riparian herbs	trans.	constr.	+				Harris et al. 1987
Fall Ck., CA, USA	riparian shrubs	trans.	constr.	+				Harris et al. 1987
Rucker Ck., CA, USA	riparian herbs & shrubs	trans.	constr.	-				Harris et al. 1987
Texas Ck., CA, USA	riparian shrubs	trans.	constr.	-				Harris et al. 1987
Stanislaus Ck., CA, USA	riparian trees	trans.	constr.	-				Harris et al. 1987
Lee Vining Ck., CA, USA	riparian shrubs	trans.	constr.	-				Harris et al. 1987
McGee Ck., CA, USA	riparian herbs	trans.	constr.	-				Harris et al. 1987
Salt R., AZ, USA	cottonwood/ willow	observ.	unconstr.	-	*		-	Jones 1988
N. Platte R., CO,WY,NE, USA	cottonwood	observ.	constr.	+	*			Knopf & Scott 1990

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S. Platte R., Reach 5, NE, USA	riparian vegetation	aerial	unconstr.	+				McDonald & Sidle 1992
N. Platte R., NE, USA	riparian vegetation	aerial	unconstr.	+				McDonald & Sidle 1992
Umealven R., Sweden	riparian vegetation	aerial/ observ.	unconstr.	+				Nilsson 1977, 1979, 1981
Gejman R., Sweden	riparian vegetation		unconstr.	=	*			Nilsson 1979
Vojman R., Sweden	riparian vegetation	observ.	unconstr.	-			-	Nilsson 1981
Aurland R., Norway	riparian vegetation	plots	constr.	-	*			Odland et al. 1991
Rhone R., France	riparian vegetation	plots	unconstr.	-	*		+	Pautou et al. 1992
Prairie R., USA, CAN	cottonwood	review	unconstr.	-			-	Rood & Mahoney 1990
Arkansas R., CO, USA	cottonwood	aerial	unconstr.	-	*		+	Snyder & Miller 1991
S. Platte R., CO, USA	cottonwood	aerial	unconstr.	-	*		-	Snyder & Miller 1991
Rush Ck., CA, USA	cottonwood	dendro.	constr.	-		-		Stromberg & Patton 1990
Bishop Ck., CA, USA	cottonwood	dendro.	constr.	-		-		Stromberg & Patton 1992, Smith et al. 1991

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III. EFFECTS OF SMALL DAMS:								
Alkali Ck., CO, USA	willow/ sedges	observ.	constr.	+	*		+	Heede 1977, Heede & DeBano 1984
Queen Ck., AZ, USA	willow/ tamarisk	plots	constr.	+	*		+	Szaro & DeBano 1985
Monroe Canyon, CA, USA	willow/ Baccharis	observ.	constr.	+				DeBano & Schmidt 1989
Silver City watershed, NM, USA	willow	observ.	constr.	+			+	DeBano & Hansen 1989
High Clark Draw, NM, USA	marsh/ cottonwood	observ.	unconstr.	+				DeBano & Hansen 1989
Sheep Ck., UT, USA	riparian vegetation	observ.		+				Hooper et al. 1987
Trout Ck., CO, USA	riparian vegetation	observ.		+				Van Haverson 1986
Sandstone Ck., OK, USA	riparian vegetation	observ.		+				Kennon 1966

1 method = observ. = observation, aerial = aerial photograph analysis, trans. = transects, dendro. = dendrochronological measurements, evapo. trans. = evapotranspirational analysis, oblique photo = photo comparisons over time, review = literature review.

2 channel = constr. = constrained, unconstr. = unconstrained or alluvial river.

Appendix II. Management Recommendations

Numerous studies documented short term responses of riparian vegetation to river regulation, and in some cases, researchers examined up to several decades of riparian vegetation change (e.g., Turner 1974, Pucherelli 1988). However, how can managers establish monitoring programs to evaluate long-term responses of riparian habitats to river regulation? What variables should be measured, how much sampling is sufficient, how representative are study areas, and what are appropriate sampling schedules?

Management of riparian habitats cannot be separated from river management, particularly in the case of regulated rivers. Riparian habitats are directly influenced by interactions between hydrology (particularly flooding frequency) sediment transport, channel geometry and geomorphology (Gregory et al. 1991, Whittaker et al. in press). Prediction of stream regulation effects on riparian habitats requires coupling four basic kinds of analyses (Jackson and Beschta 1992):

1) Landscape Position: The geomorphic position of vegetation is influenced by stream types (constrained versus unconstrained), and hydrologic characteristics that position (e.g. susceptibility to flooding or lowering of the groundwater surface).

2) Sediment Balance: Sediment transport and balance influences many aspects of riparian habitats, including germination site availability and patch dynamics, as well as hydric soil quality, moisture retention, and site stability.

3) Channel Morphology and Hydraulic Geometry: Stream channels adjust to changing flow regimes by changing energy regimes. Erosion, aggradation, meandering and other forms of bank alteration are responses of channels to alteration of flow regimes. Riparian vegetation can play a role in bank stability, particularly in lower velocity environments (Platts et al. 1985), but the significance of this role for riparian vegetation may be over-stated for constrained reaches of large rivers (Stevens and Ayers 1993).

4) Flood-dependent River Processes: Floods are erratic events that govern much of the ecological processes that characterize rivers. Using floods to regenerate dynamic riparian and riverine processes can be a primary management strategy for fluvial ecosystems. Flood management options may be constrained by feasibility (water availability), downstream property damage and other factors; however, managing riparian habitats as sustainable ecosystems virtually requires the use of intentional flooding (Jackson and Beschta 1992).

Individual riparian plant species display wide variation in inundation tolerance (Hosner 1960; Stevens and Waring 1985; Stevens and Ayers 1993). A direct gradient analysis approach to understanding how flow regime changes influence riparian vegetation entails determining the elevational distribution of riparian plant species at sites with well defined stage-to-discharge relationships. Subsequent determination of inundation frequencies (e.g. maximum daily flow duration curve data) can then be related to plant elevational ranges to predict how vegetation will change when flow durations are altered. This approach was used by Franz and Bazzaz (1977) to estimate reservoir head vegetation responses to changing water levels in a floodplain forest at the head of a reservoir.

Several conclusions can be drawn about management of riparian vegetation in regulated river systems:

1) Predicting vegetation cover type changes in relation to flow alteration can be an effective approach when suitable time series of aerial photographs are available (e.g. Johnston 1988).

2) Knowledge of the distribution of patch types and simulation of hydrologic regimes can be used to predict safe germination and establishment site distribution (sensu Grubb 1977), and thereby patch development rates. Modelling

approaches suffer from the difficulty of including erratic flooding events, and therefore require adjustment for stochastic events.

3) At the species level, the Markovian transition matrix approach may provide a means of determining the probability of a given species' success under a specific flow regime(s) if sufficient historic and field data are available. This method uses probabilities of transition of one patch type to another through time or space to produce estimates of net system change.

4) Transpiration, or water loss patterns in plants, have been modelled to predict effects of altered moisture availability for vegetation development (Bovee et al. 1978; Davenport et al. 1978; Gay 1989). These efforts use groundwater data, experimental lysimetric approaches and physiological studies to determine the rates of transpiration of various riparian species under different groundwater regimes. *Populus* spp., *Tamarix pentandra*, *Prosopis* spp. and *Salix* spp. have been subjected to these studies in the American Southwest. Davenport et al. (1978) reported that, in general, riparian tree species transpire a mass of water equivalent to the mass of their canopy every hour on moderately warm days during the growing season. Carbon isotopes are also used to assay plant moisture stress

(Donovan and Ehleringer 1991).

5) Simons and Associates (1990) proposed an analysis of river bank stability and vegetation development following flooding. This model involves interactions among erosion, exposure, flow duration, and susceptibility of different sized individuals to flooding.

6) Day et. al. (1988) developed a model of fluvial marsh development along the Ottawa River in response to disturbance (flooding and ice scour) and fertility gradients. They used ordination techniques to define four assemblages and related development of each under flow-related gradient interactions. If this modeling approach was validated in a regulated river, it could be used to predict changes in composition resulting from alteration of the flow regime.

Stevens and Ayers (1993) used several of the above approaches to evaluate the significance of inundation regime and soil texture on fluvial marsh development along the dam-regulated Colorado River in the Grand Canyon, Arizona. They found that species composition of wet (cattail/reed) versus dry (horsetail/willow) fluvial marshes strongly depended on these two variables.