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РЕАКЦИЯ РАСТИТЕЛЬНОСТИ НА СПУСК ВОДОХРАНИЛИЩ

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В прошедшие два десятилетия в Соединенных Штатах Америки были разрушены более 500 дамб (U.S.A.; Stanley, Doyle, 2003). Это произошло прежде всего потому, что большая часть из них не соответствует цели, ради которых они были созданы, существование других стало опасным. Зачастую стоимость восстановления дамбы или потенциальных затрат, связанных с ее неисправностью, превышает выгоды от сохранения дамбы на месте. В то время как разрушение дамб производилось прежде всего в целях безопасности, в некоторых случаях еще одной целью было восстановление окружающей среды (Heinz Center, 2002). Большая часть дамб, которые были разрушены - относительно небольшие (< 5 м высотой) и они расположены, главным образом, во влажных районах на востоке США. Разрушение дамб в засушливых районах менее типичное явление.

Возрастание числа разрушенных дамб привело к увеличению научных исследований реакции экосистем на изменения как в нижнем, так и в верхнем бьефе. Этому посвящен специальный выпуск журнала BioScience (2002, vol. 52, по. 8). В опубликованных там работах показано, что обусловленное разрушением дамб изменение химизма среды и транспортируемых наносов, которые отложились за дамбой могут оказать существенное воздействие на экосистемы нижнего бьефа. В некоторых случаях пойменные отложения содержали токсины, которые транспортировались от места попадания, и концентрация загрязнений в донных отложениях после удаления дамбы приводила к возникновению проблем загрязнения (Heinz Center, 2002). Места накопления и перераспределения загрязнений во времени достаточно сложны и пока не поддаются прогнозированию (Pizutto, 2002). Загрязнения донных отложений оказывают воздействие и на водную биоту и прибрежную растительность, и передаются по пищевым цепям (Bednarek, 2001; Stanley et al., 2002). Спуск водохранилищ устраняет барьер в перемещении рыбы, хотя это явление пока не прослежено (Stanley, Doyle, 2003). На водную и пойменную биоту оказывает также воздействие изменение режима речного стока после удаления дамбы. Имеется несколько публикаций, касающихся исследований ответных реакций растительности па спуск водохранилищ (Shafroth et al., 2002).

В данной статье дан обзор относительно скудной информации, документирующей ответную реакцию наземной растительности на спуск водохранилищ и возможность сукцессионных процессов, приводящих к восстановлению растительности до состояния, предшествующего созданию плотины. Кроме того, излагаются данные собственных исследований по процессам трансформации природных комплексов при создании дамб и их восстановлении после спуска водохранилищ. В работе использованы публикации и экспериментальные данные авторов, выполненные в Северной Америке.

Авторы рассматривают различные стратегии удаления дамб и сосредотачивают внимание на процессах зарастания дна бывшего приплотинного водоема и возможные приемы его ускорения.

Учитывая более длительную историю существования дамб в Европе и Азии, обзоры подобных процессов спуска водохранилищ были бы очень полезными для науки и

практики. Эти исследования смогли бы объяснить возможные долгосрочные ответы экосистем на спуск водохранилищ в различных природно-климатических зонах и обеспечить важную проблему прогнозирования для будущих случаев при необходимости разрушения дамб в Северной Америке и в других регионах.

VEGETATION RESPONSES TO DAM REMOVAL

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Introduction

In the past two decades, there have been more than 500 dams removed in the United States of America (U.S.A; Stanley, Doyle, 2003). The increase in dam removal has occurred primarily because many dams either no longer serve the purposes for which they were constructed, or they have become unsafe. Often, the cost of repairing or updating a dam exceeds the likely benefits, and the dam is removed instead. When dams are removed, there are various potential effects on ecosystems both upstream and downstream. However, there are very few studies documenting the biological and physical responses to dam removal. In this paper, we focus on potential vegetation responses to common changes to hydrology and geomorphology associated with dam removal. We review the scant information documenting responses of terrestrial vegetation to dam removal and derive expected responses both up- and downstream of the former dam based on empirical and theoretical relationships between vegetation, stream hydrology, and fluvial processes. We focus on vegetation associated with river banks and flood plains, commonly referred to in the North American literature as "riparian" vegetation.

In this paper we review the scant information documenting responses of vegetation to dam removal and derive expected responses both up- and downstream of the former dam based on empirical and theoretical relationships between riparian plants, stream hydrology, and fluvial processes. We evaluate case studies of planned or completed dam removals, natural analogs of dam removal, and alternative strategies of releasing and exposing water and sediment. We consider transient and equilibrium responses, and the effects of different dam removal strategies on native vs. exotic plants. We focus on natural establishment of vegetation following dam removal, although we also discuss active measures such as planting.

Vegetation responses

Vegetation response to dam removal is highly dependent on changes to physical environmental conditions. Vegetation at the interface between a water body and the surrounding uplands is dominantly structured by the hydrologic gradient. Sites along this gradient differ in the duration, frequency, and timing of inundation (generally referred to as hydroperiod). Species differences in hydroperiod tolerances and requirements produce zonation and pattern in species composition and general cover types along the hydrologic gradient (Figure 1). Dam removal may change aspects of the hydrological regime that structure riparian vegetation, including flood and low flow regimes, and associated water table dynamics. Further, dam removal will generally result in the creation of two classes of bare sediment that can be colonized by riparian plants: 1) downstream deposits transported from the former reservoir pool and upstream sources; and 2) surfaces within the former reservoir pool (Figure 1).

The distribution of new bare substrates and the character of the new flow regime will vary tremendously across sites. Removal of small dams in systems with low sediment transport may result in few downstream changes and relatively simple upstream changes associated with vegetation colonization and succession on the former lake bottom. Removal of dams that have trapped large quantities of sediment could result in erosion of those deposits and transport of sediment downstream. Deep, fine-textured, and nutrient-rich deposits in the former reservoir or downstream may provide novel site conditions for plants. On rivers with multiple dams, a dam removal may result in only spatially limited or

partial restoration of natural flows. Along rivers where reservoir capacity has been severely reduced by sedimentation, flow regimes may no longer be substantially different from natural flows, and dam removal will have little effect on the downstream flow regime.

Riparian plant communities are often part of primary successions, with colonizing plants becoming established on bare, moist alluvial sediments, like those expected to be present following dam removal. Life history characteristics of plants can have an important effect on the trajectory of a riparian primary succession (Walker et al. 1986). Initial colonization of bare sediment in riparian environments is primarily accomplished through a combination of wind and water dispersal, although animal dispersal may bring a more diverse set of propagules to a site over time (Kalliola et al. 1991, Galatowitsch et al. 1999). Dam removal should increase the efficiency of long distance transport of seeds by water (Jansson et al. 2000), which may enhance riparian restoration efforts. The timing of viable seed dispersal (Walker et al. 1986), substrate characteristics (Krasny et al. 1988), and soil moisture influence which species are able to successfully colonize a site. Soil seed banks contribute to vegetation dynamics along lake or reservoir shorelines and along margins of confined rivers (Keddy and Reznicek 1986) and, following dam removal, would be expected to play an important role in primary succession on newly exposed sediments upstream of the dam. Seeds of some wetland species buried by sediment and submerged in water have been estimated to remain viable for between 45 and 400 years (Leck 1989). Vegetative reproduction can also be an important strategy for expansion of pre-existing or founder populations (Krasny et al. 1988, Kalliola et al. 1991).

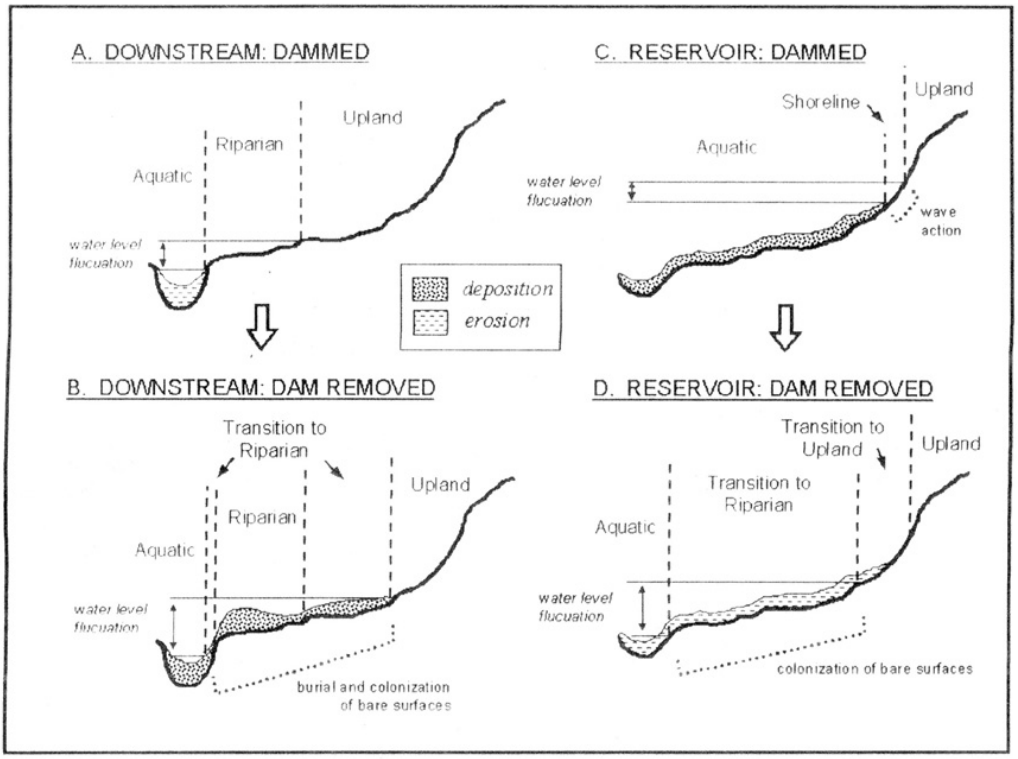

Fig. 1. General changes to key physical environmental factors and vegetation following dam removal: a) during the dammed period, the downstream river may experience some channel degradation, a decrease in flow variability (depicted as water level fluctuation), and a narrowed riparian zone; b) following dam removal, transport of upstream river sediment and sediment trapped in the reservoir may lead to a pulse of sediment deposition, which combined with increased flooding may both stress existing vegetation and create sites for the colonization and establishment of new vegetation; c) during the dammed period, vegetation along the reservoir shoreline is often confined to a narrow band and its composition is driven largely by fluctuations in the reservoir water level and wave action; d) following dam removal, large areas of former reservoir bottom are exposed and may be colonized by riparian or upland plants. Trapped sediments behind the dam may be subject to erosion. **Рис. 1.** Основные изменения факторов среды и растительности, которые обусловлены спуском водохранилищ: а) за период существования плотины участок реки в нижнем бьефе изменяется из-за зарегулирования стока (указаны изменения уровня воды в реке и прибрежная зона); б) последствия разрушения дамбы, переотложение наносов в верхнем бьефе является одной из причин различий в зарастании донных отложений; с) в зарегулированный период структура и состав растительности на побережье искусственного водоема обусловлена колебаниями уровня и воздействием волн; d) после разрушения плотины обширные площади бывшего ложа водохранилища колонизуются растительностью, которая может внедряться из верховий. Отложения позади дамбы подвергаются эрозии.

Downstream responses

Effects of a downstream sediment pulse. Dams generally trap and store sediment, often depleting reaches downstream (Williams and Wolman 1984). Dam removal may result in the downstream transport of stored sediment, which is usually seen as a potential problem (Simons and Simons 1991, Hotchkiss et al. 2001). For example, the sediment may kill fish, clog spawning gravels, or cause damage to neighboring property. However, this transient pulse of sediment provides an opportunity for channel change and the creation of new surfaces suitable for the reproduction of riparian pioneer species (Figure 1, Figure 2a). Such surfaces may have been scarce following dam construction; thus, from the perspective of riparian vegetation, sediment released upon dam removal may be a benefit (Semmens and Osterkamp 2001).

Most dam removals so far have involved small reservoirs with small amounts of sediment, and there are little data available concerning the effects of the downstream pulses of sediment on channel morphology and vegetation (Hotchkiss et al. 2001). There are, however, better described cases of sediment pulses resulting from other causes including hydraulic mining (Gilbert 1917, James 1989), timber cutting (Madej and Ozaki 1996), volcanic eruption (Major et al. 2000), large floods (Jarrett and Costa 1993), and dam maintenance (Wohl and Cenderelli 2000). Several generalizations may be drawn from this literature. The sediment pulse travels downstream as a wave whose amplitude decreases and wavelength increases over time (i.e., Gilbert 1917, Simons and Simons 1991, Pizutto 2002). At a point along the stream, the wave may be observed as an increase in bed elevation or in the rate of sediment transport. Because finer particles are transported more easily than coarser particles the sediment pulse may be sorted over time, with finer particles moving downstream more rapidly. The trailing limb of this pulse can take the form of exponential decay, and it may take decades or longer for sediment loads to return to pre-pulse conditions (James 1989, Simons and Simons 1991). The sediment pulse may partially or completely fill channels resulting in temporary or permanent channel avulsion. Avulsion and fluctuations in bed elevation often leave behind terrace deposits (James 1989) that may persist for centuries or more. Vegetation may colonize these terrace deposits, as with some valley oak (Quercus lobata) forests in California's central valley. Other surfaces associated with temporally and spatially variable aggradation and degradation of the sediment pulse will be colonized by vegetation, as has been described for mudflows associated with volcanic eruption (Halpern and Harmon 1983).

In addition to creating new alluvial surfaces, sediment deposition downstream of a removed dam could bury existing vegetation (Figure 2b). Riparian species vary in their tolerance of high sedimentation rates (Hupp 1988). If vegetation downstream of dams has succeeded to late seral stages (e.g., Johnson 1992), then dominant species in these communities are likely to be less tolerant of burial by sediment than pioneering species. In 1982, a dam breach in Rocky Mountain National Park resulted in a large flood that deposited a 0.18 km2 alluvial fan that was up to 13.4 m thick (average thickness was 1.6 m; Jarrett and Costa 1993). Some vegetation died immediately due to complete burial (Kiegley 1993), while many trees succumbed over a period of years likely due to the effects of anoxic soils and accumulations of toxic levels of micronutrients (Barrick and Noble 1993; Figure 2b).

Effects of a naturalized downstream flow regime. Along rivers, the hydrologic regime interacts strongly with the geomorphic setting to influence establishment and growth of riparian plants. Dam removal could restore natural hydrologic regimes, which can contribute to the rehabilitation of native plant communities (Poff et al. 1997, Taylor et al. 1999). Regulated flow regimes are generally less variable than unregulated flows, and some vegetation downstream of dams is more competitive under relatively homogenous flow regimes. The timing, magnitude and duration of flood and base flows exert strong influence on riparian vegetation (Friedman and Auble 2000, Nilsson and Berggren 2000). For example, cottonwood (Populus spp.), willow (Salix spp.) and many other riparian species native to North America are pioneers that colonize bare sites produced by flood disturbance. By reducing flood magnitude and frequency, dams decrease establishment opportunities for such species (Johnson 1992) and can improve the competitive ability of shade-tolerant exotic species that do not depend upon disturbance, such as Russian-olive (Elaeagnus angustifolia; Katz 2001). However, even if dam removal reduces available habitat for seedlings of exotic species, established adults may persist for decades until they are killed by a flood, drought, age-related factors, or some other agent. Persistence of large woody plants established under the former regulated flow regime could indefinitely impede the resumption of channel movement after dam removal due to their stabilizing influence on channel banks.

Upstream responses

Upstream of the dam, dam removal exposes areas of bare ground that were formerly underwater and river discharge (rather than reservoir storage) controls water stages. This will generally produce shifts from the always inundated aquatic zone to mostly inundated and occasionally inundated wetland and riparian vegetation zones and from inundated or groundwater affected zones to upland vegetation (Fig. 1). Thus, dam removal may lead to mortality of vegetation along the former reservoir margin, especially if it is sensitive to water table declines associated with the drawdown. The distribution and location of changes in hydroperiods will depend on the topography and stage-discharge relations that develop following dam removal. In many cases, accumulation of sediment behind the reservoir will have altered the topography. If the new stream channel down cuts to near its previous elevation faster than the overall area erodes, then the overall distribution of hydroperiods in the reservoir pool may be drier following dam removal than before the dam was constructed (Lenhart 2000). On the other hand, partial dam removals where a lowered control structure is left in place will yield a new storage capacity and effective stage-volume relation and could produce a new set of hydroperiods that may be wetter than the pre-dam river.

Initially, vegetation is unlikely to be in equilibrium with the new distribution of hydroperiods. Rather, there will be a transition phase involving colonization of extensive bare areas or mud flats uncovered as water stages decline with the draining of the reservoir (Fig. 2).

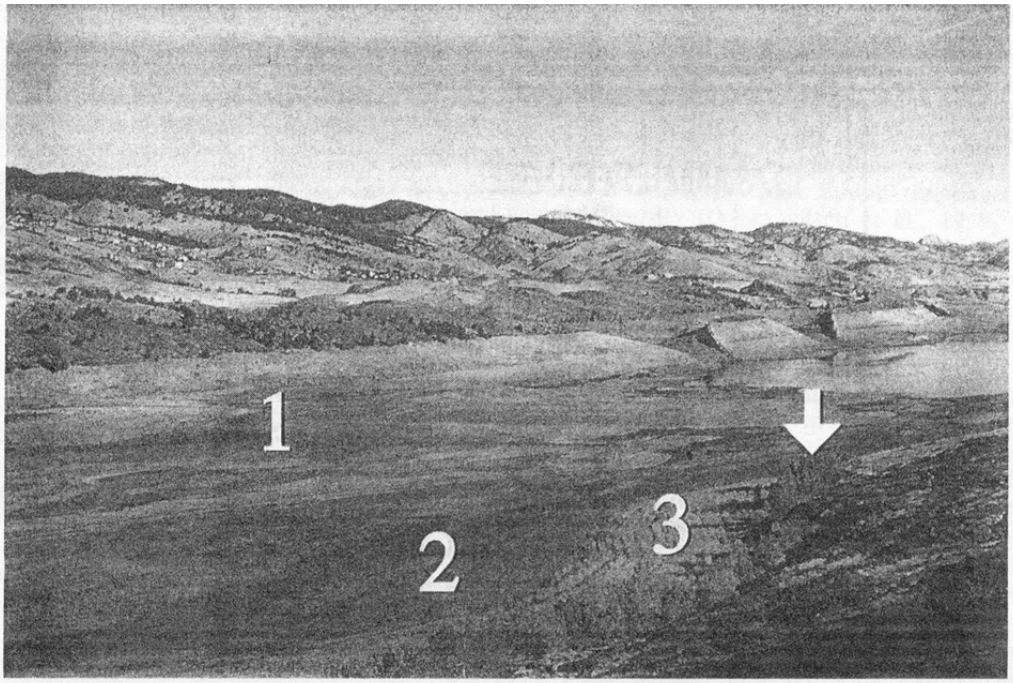

Fig. 2. Vegetation colonization on the exposed bottom of Horsetooth Reservoir, Colorado, USA. Between january 2000 and october 2001, water was drawn down 32 m to enable dam repairs, reducing the water surface area from 621 to 77 ha. Numbers refer to bands of vegetation dominated by the following non-native species: 1) goosefoot (*Chenopodium glaucum*); 2) smartweed (*Polygonum lapathifolium* and *P. persicaria*); 3) sweet clover (*Melilotus* spp.). The arrow points to mature cottonwood trees (*Populus deltoides*) that approximate the high water line. (Photo by PB Shafroth). **Рис. 2.** Зарастание обсохшего ложа спущенного водохранилища Зубы Лошади в Колорадо, США, между январем 2000 г. и октябрем 2001 г. Уровень воды был опущен на 32 м, водная поверхность сократилась с 621 до 77 га. Вокруг новой береговой линии сформировались следующие пояса растительности из не местных видов. Стрелками указаны места произрастания тополя, которые маркируют положение прежней береговой линии.

Dense, natural revegetation of these areas during the growing season has been observed within weeks in humid regions (FOE et al. 1999), while vegetation cover can take years to recover in less productive settings such as subalpine reservoir margins in the Rocky Mountains (Mansfield 1993). Propagules of early colonizing plants may be present in seedbanks or may be dispersed from adjacent areas. The initial colonizing plants can have a substantial long-term influence on plant composition through the persistence of long-lived individuals, vegetative reproduction, relatively higher seed production of those species, and

alterations of the physical environment (Mansfield 1993). Initial plant colonists of sites characteristic of former reservoir bottoms (bare, moist, nutrient-rich, with a depauperate seed bank), will tend to be weedy plants with typical ruderal traits such as rapid growth, high levels of seed production, and effective dispersal mechanisms. This group of plants may include a relatively high fraction of invasive, non-native species (Galatowitsch et al., 1999; Lenhart, 2000).

C.F. Lenhart (2000) performed a retrospective analysis of natural vegetation recolonization in five former impoundments in Wisconsin. Two sites represented long-term (>40 years) recovery periods, whereas three sites had recovered from 3-5 years. Across all sites, high-nutrient sediments, ranging in depth from 25 to 200 cm, had been deposited over pre-dam soils. Vegetation at the three younger sites had low species diversity and were dominated by large, monotypic stands of pioneer species like stinging nettle (Urtica dioica), reed canary grass (Phalaris arundinacea), and rice-cut grass (Leersia oryzoides). The plant communities observed on the younger sites did not resemble any native communities. Young sites tended to be composed of a high fraction of wetland plants, whereas older sites were dominated by drier site species. The two older sites had higher species diversity but included a higher percentage of non-native species.

Management considerations

Dam removal should not be expected to restore riparian ecosystems to their pre-dam condition (Fig. 3). Dam removal should not be expected to restore riparian ecosystems to their pre-dam condition (Fig. 3). There are likely a spectrum of possible outcomes, given the variability in pre-dam conditions, the responses of the system to the dam, and the responses to dam removal (Zedler 1999). Ecological systems frequently exhibit hysteresis and time-lagged responses, the details of which are not clear with respect to riparian vegetation, although a transient phase of 50-100 years has been observed when systems respond to dam construction and operation (Johnson 1998, Petts 1987).

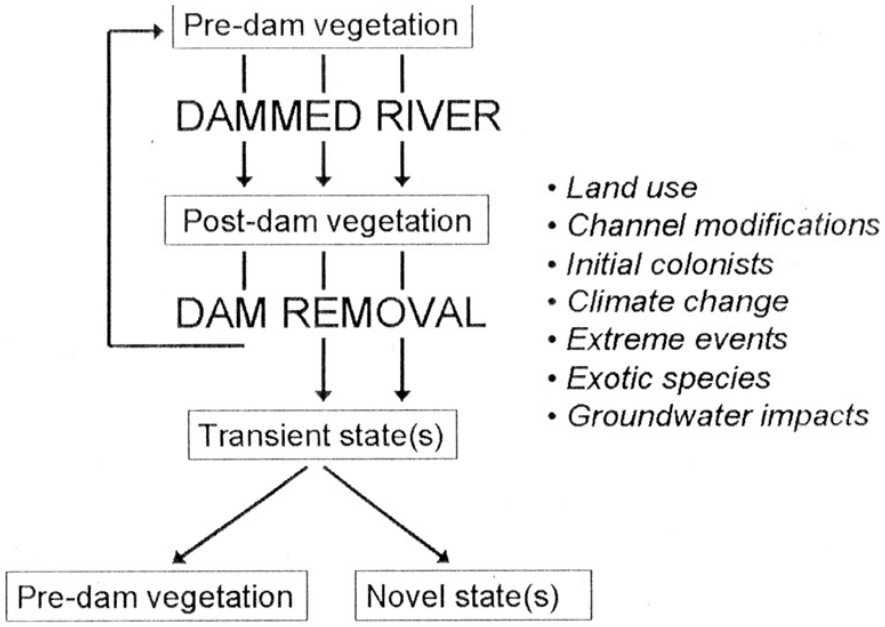

Fig. 3. Multiple pathways of riparian vegetation change from unregulated conditions through post-dam removal states. Riparian vegetation may respond to dam construction and operation in various ways, and multiple trajectories are also possible following dam removal, depending on initial conditions and the nature of hydrologic and geomorphic change. Other factors, including those listed next to the flow diagram also influence riparian vegetation response. As a result, in many cases, riparian vegetation is unlikely to quickly return to its pre-dam condition. **Рис.3.** Направления сукцессионных сингенетических сукцессий после спуска водохранилища. Основными дифференцирующими факторами выступают: характер бывшего водоема, его гидрологический режим, геоморфология. Предполагается, что в конечном итоге сукцессия приведет к состоянию, предшествующему строительству дамбы.

Legacies of flow regulation such as altered channel morphology, species composition, and age

structure may result in a delayed response of the system to naturalized flows. Even if dam removal restored the natural flow regime, effects of dam removal would vary regionally with factors such as climate, flood regime, geology, and the fluvial processes associated with riparian vegetation establishment (Friedman and Auble 2000). Other anthropogenic impacts to a river system such as adjacent groundwater pumping, channel stabilization, agricultural and residential development, could prevent a return to pre-dam conditions (Fig. 3). Effects of extreme events that occurred before but not during the dammed period (Katz 2001) or climate differences in the pre-dam and post-dam removal periods could also influence the response.

Despite these possible limitations, dam removal has the potential to restore valuable components of riparian ecosystems, and some management actions could enhance this potential. In some dam removal situations, relatively small pulses of sediment could promote enough channel change to create surfaces suitable for the establishment of riparian forest without greatly damaging other resources. Upstream of the dam the timing and pattern of drawdown heavily influences the species composition of bare, moist areas by exposing sites at times that do or do not match the life history characteristics of various species with respect to germination and early seedling establishment requirements. Much practical experience with manipulating drawdowns to achieve desired mixes of herbaceous species is embodied in the wildlife management strategy of “moist soil management” (Fredricksen and Taylor 1982). Many refuges and waterfowl management areas actively manipulate drawdowns in shallow constructed impoundments or moist soil units to grow specific species with desired food and cover values for wildlife. Similar approaches have been effectively employed in riparian restoration efforts to encourage natural establishment of desired native trees and shrubs (Roelle and Gladwin 1999). In arid and semi-arid landscapes where seedling establishment requirements for native riparian trees are often much wetter than the conditions they require as adults, the plants established during the transition or drawdown phase may persist and dominate the drier post-dam regime for many decades.

Although dam removals represent a significant opportunity for riparian habitat restoration, they also provide opportunities for invasion of undesirable, non-native species (Figure 4; Galatowitsch et al. 1999, Lenhart 2000). High levels of physical disturbance result in significant proportions of exotic species in many riparian floras (Planty-Tabacchi et al. 1996, Tickner et al. 2001). The extensive, bare, nutrient rich sediments of the former impoundment provide a substrate that may favor weedy, non-native plants. Once established, non-native weeds may inhibit the establishment of native species, thus reducing species diversity and habitat value (Galatowitsch et al. 1999, Middleton 1999) and influencing succession (Hobbs and Mooney 1993). Where the risk of establishment of non-native vegetation is high, a more managed approach to vegetation establishment following dam removal may be warranted.

Revegetation approaches

Dam removal plans may include broadcast seeding or limited tree planting aimed at precluding the establishment of undesirable non-native species or stabilizing sediments in the former reservoir pool (Figure 6; ASCE 1997, FOE et al. 1999). Additional reasons for active revegetation following dam removal include the creation of habitat diversity and improving recreational use. Secondary mitigation techniques such as bank stabilizing structures to slow or reduce bank erosion, fenced exclosures to manage livestock, and special planting techniques, including multi-year irrigation to allow phreatophytes to make root contact with the water table, have been necessary elements of revegetation efforts in arid and semiarid regions of the US (Briggs 1996). Active revegetation of riparian shrubs and trees in the western US have often failed due to an insufficient understanding of establishment and survival requirements of native species and continued livestock grazing following planting (Briggs 1996, Kauffman et al. 1995).

Plantings of early successional native species with relatively high rates of growth may be an effective means of minimizing the establishment of exotic plant species and initiating natural successional processes. Dense stands of native woody plants, such as cottonwood (Populus spp.) and willow (Salix spp.) can effectively shade out and thus exclude many exotic herbaceous annual and perennial plants. In contrast, planting of slow growing, late-successional or climax species following dam removal may provide exotic weeds with an initial advantage. In the Midwestern US, plants such as smartweeds (Polygonum spp.), rice-cut grass (Leersia oryzoides), barnyard grass (Echinochloa crus-galli), and sod-forming sedges (Carex spp.) often naturally recolonize disturbed prairie wetlands. Other species, which may effectively compete with aggressive weeds, have been suggested for planting as potential native cover crops. These include late-season grasses such as Spartina pectinata and forbs, such as Coreopsis

spp. and Ratibida spp. (Galatowitsch and van der Valk 1994). Cover crops may quickly occupy sites, stabilizing the soil surface and usurping positions that might otherwise be taken by less desirable, but persistent, species (Figure 6). In subsequent years more slowly growing species may gradually replace the annuals. In the southwestern US, attempts to actively restore native riparian understory species by planting, removal of non-natives, and use of commercial soil-amendments was ineffective largely because of the rapid re-growth or establishment of non-native species already on site (Wolden and Stromberg 1997). Recommendations for future efforts suggested that: 1) seeding should be done over several years to accommodate climatic and hydrologic variability; 2) seed mixes should include species reflecting a diversity of life-history traits so species can sort out across the range of fine-scale environmental conditions that may exist at the restoration site; and 3) some weedy native annuals may compete well initially with non-natives. The assumption that a diverse set of species will naturally disperse to and become established on a site following the planting of a few of the dominant species is not always valid and has produced stands of relatively low diversity in reforested bottomland hardwood forests (Allen? 1997). Experimentation can make seed selection more efficient by helping to determine which species will recruit well naturally vs. which need to be planted, and which and how many species are necessary to develop ecosystem functions (Zedler et al., 2001).

Conclusion

There is a strong need for more quantitative studies of the response of vegetation to dam removal. This may include rigorous monitoring of new or recent dam removals, or retrospective analyses of older sites. Long-term studies will be necessary to elucidate potentially complex pathways of vegetation change. The potential for the generation of novel plant communities associated with the unusual physical conditions that may follow dam removal represents an intriguing topic of ecological research. Manipulative experiments could be used to test different management techniques, including controlled drawdowns and various planting approaches. Given the well-documented importance of fluvial geomorphic and hydrologic conditions in structuring riparian vegetation, botanists and plant ecologists should seek collaborations with physical scientists and couple plant response models to models used to estimate water and sediment dynamics following dam removal.

Given the longer history of dam building in Europe and Asia, there are likely examples of dam removals or dam failures from these continents that would provide opportunity for retrospective study. This work can elucidate possible long-term responses of ecosystems to dam removal. Collaborative studies of dam removals from similar climatic, physiographic and biogeographic settings in Eurasia and North America could provide important insights for future dam removals in North America and elsewhere.

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