Prescribing Flood Regimes to Sustain Riparian Ecosystems along Meandering Rivers

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Abstract: *The composition and structure of native riverine ecosystems are tightly linked to natural hydrologic variability. By managing river flows for water supplies and power generation, water management agencies have inadvertently caused considerable degradation of riverine ecosystems and associated biodiversity. New approaches for meeting human needs for water while conserving the ecological integrity of riverine ecosystems are greatly needed. We describe an approach for identifying the natural flooding characteristics that must be protected or restored to maintain riparian (floodplain) ecosystems along meandering rivers. We developed a computer model to simulate flood-driven changes in the relative abundance of riparian patch types along the Yampa River in Colorado (U.S.A.). The model is based on research suggesting that the duration of flooding at or above 209 m³ per second (125% of bankfull discharge) is particularly important in driving lateral channel migration, which is responsible for initiating ecological succession in the Yampa's riparian forest. Other hydrologic variables, such as the magnitude of annual peak flows, were not as strongly correlated with lateral channel migration rates. Model simulations enabled us to tentatively identify a threshold of alteration of flood duration that could lead to substantial changes in the abundance of forest patch types over time should river flows be regulated by future water projects. Based on this analysis, we suggest an ecologically compatible water management approach that avoids crossing flood alteration thresholds and provides opportunity to use a portion of flood waters for human purposes. Recommended improvements to the Yampa model include obtaining additional low-elevation aerial photographs of the river corridor to enable better estimation of channel migration rates and vegetation changes. These additional data should greatly improve the model's accuracy and predictive capabilities and therefore its management value.*

Prescripción de Regímenes de Inundación para Mantener Ecosistemas Riparios a lo Largo de Ríos Sinuosos

Resumen: *La composición y estructura de ecosistemas ribereños están fuertemente ligadas a la variabilidad hidrológica natural. Al manejar el flujo de ríos para abastecer agua y generar energía, las agencias de manejo de agua han causado inadvertidamente una degradación considerable de los ecosistemas ribereños y la biodiversidad asociada a ellos. Se necesitan nuevas estrategias para satisfacer las necesidades humanas de agua al mismo tiempo que se conserva la integridad de los ecosistemas ribereños. Describimos una estrategia para identificar las características de inundaciones naturales que deben ser protegidas o restauradas para mantener ecosistemas riparios (planicies de inundación) a lo largo de ríos sinuosos. Desarrollamos un modelo de computadora para simular los cambios causados por inundaciones en la abundancia relativa de tipos de parche ripario a lo largo del río Yampa, en Colorado (Estados Unidos de Norteamérica). Este modelo se basa en investigación que sugiere que la duración de la inundación a, o mayor a, 209 m³ por segundo (125% de descarga del banco lleno a su capacidad) es particularmente importante en la conducción de la migración de canales laterales, lo cual es responsable de la iniciación de la sucesión ecológica en el bosque ripario del río Yampa. Otras variables hidrológicas, como lo es la magnitud del pico de los flujos anuales no estuvieron tan fuertemente correlacionadas con las tasas de migración lateral de canales. Las simulaciones del modelo nos permitieron identificar límites tentativos de alteración de la duración de la inundación que*

podrían conducir a cambios sustanciales en la abundancia de tipos de parches forestales en el tiempo si los flujos de los ríos son regulados en proyectos de agua futuros. En base a este análisis, sugerimos una estrategia de manejo de agua ecológicamente compatible que evita sobrepasar los límites de alteración de las inundaciones y provee la oportunidad de usar una porción del agua de las inundaciones para fines humanos. Las recomendaciones de mejoras al modelo del río Yampa incluyen la necesidad de obtener fotografías aéreas de baja elevación adicionales del corredor del río, que permitan una mejor estimación de las tasas de migración de los canales y los cambios en la vegetación. Estos datos adicionales deberán mejorar en gran medida la precisión del modelo y sus capacidades predictivas y, por lo tanto, su valor de manejo.

Introduction

Natural streamflow variability is a primary organizing force within native riverine ecosystems. Flow regimes structure both aquatic and riparian communities by shaping key environmental conditions and their variation within particular habitats, driving patch dynamics within aquatic and riparian mosaics and influencing the movements of organisms between habitats (Poff et al. 1997). Successfully conserving riverine biodiversity and a river's natural ecosystem functions is therefore strongly dependent on the ability to protect or restore some semblance of natural flow regimes (Stanford et al. 1996; Poff et al. 1997; Richter et al. 1997b).

Natural streamflows have been substantially altered by human activities such as damming, irrigation diversion, and groundwater pumping in most rivers of developed nations (Dynesius & Nilsson 1994; Graf 1999), but growing knowledge of the ecological consequences of flow alteration is stimulating interest in restoring natural flow conditions (Stanford et al. 1996; Poff et al. 1997; Richter et al. 1997a, 1997b; Arthington 1998; Williams et al. 1999). Increasingly, water resource managers are being asked to modify management practices such as dam operations to accommodate biodiversity conservation objectives. The experimental flood releases from Glen Canyon Dam in the Grand Canyon of the Colorado River in 1996 garnered worldwide media attention, but this was just one of numerous places where flows have recently been modified for the benefit of native species or riverine ecosystems (Poff et al. 1997; Arthington 1998). The adaptive management experiments underway at the Grand Canyon (Schmidt et al. 1998), on the Kissimmee River in Florida (Toth et al. 1998), and at dozens of other sites around the world represent significant departures from long-held, narrow perceptions about the range of flows needed to sustain riverine biota.

Historical Approaches to Instream Flow Protection

Since the early 1970s, instream flow management objectives have focused largely on prescribing the *minimum* amount of water to be left in the river channel for the purpose of sustaining some particular species or environmental condition, such as an endangered species, a recreational fishery, or suitable conditions for whitewater rafting (Gillilan & Brown 1997). For instance, many states within the United States continue to base their regulatory policies on simplistic rule-of-thumb methods, such as maintaining low flow conditions above some minimum threshold (e.g., 10% of the mean annual flow level; Gillilan & Brown 1997). More progressive instream flow policies and technologically sophisticated approaches have centered around use of habitat simulation models (e.g., "PHABSIM"; Bovee 1982). These models have been applied extensively in recent decades for the purpose of evaluating flow-related habitat conditions for target species, usually fish. These habitat models have been criticized, however, for their simplistic species-based focus and reductionist or deficient treatment of complex ecosystem processes and interactions (Mathur et al. 1985; Orth 1987; Gore & Nestler 1988; Arthington & Pusey 1993; Stanford 1994; Castleberry et al. 1996; Williams 1996; Richter et al. 1997b).

Recognizing the limitations of habitat simulation models, many river managers are turning toward "channel maintenance approaches" (Barinaga 1996; Petts & Maddock 1996; Gillilan & Brown 1997). Rather than attempting to predict the specific flow needs of individual species, a channel maintenance approach conserves the fluvial geomorphic processes that maintain a dynamic channel form presumably capable of supporting all native aquatic species. This approach builds upon a long-standing concept in fluvial geomorphology, supported by much empirical evidence, that a meandering river's shape is governed primarily by an "effective discharge" level (Wolman & Miller 1960; Williams 1978; Andrews 1980; Leopold 1994; Rosgen 1996). Stated simply, the effective discharge is the flow level responsible for transporting the bulk of sediment over time, which thereby shapes the channel through erosion and sedimentation. Because low flows transport little sediment and high flows occur infrequently, empirical studies have shown that this effective discharge level commonly corresponds to intermediate-level floods (Leopold 1994; Rosgen 1996). The effective discharge has also been shown commonly to approximate the flow level that fills the main channel and thus is often referred to as the "bankfull discharge."

Floods and Riparian Ecosystems

By definition, the channel-maintenance approach stops at the riverbank without considering the fuller range and characteristics of flood flows needed to maintain the composition and structure of riparian ecosystems. Our objective was to suggest a means of prescribing a fuller range of flooding characteristics that drive fluvial geomorphic processes and thereby sustain the riparian patch types of the floodplain mosaics.
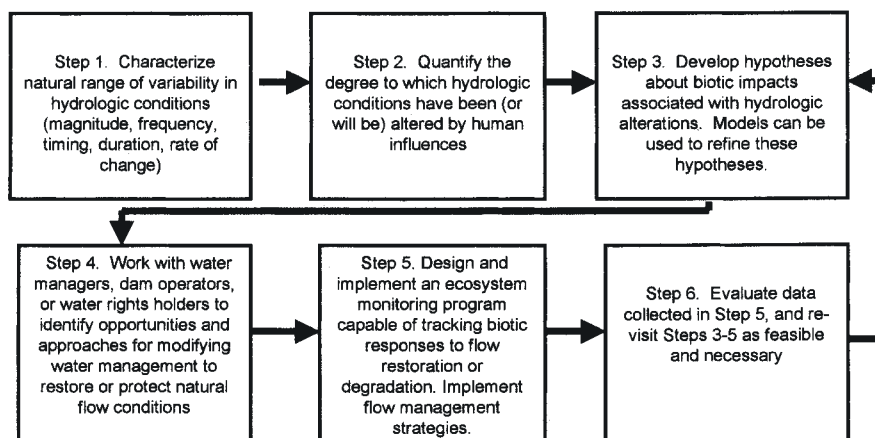
Flood regimes influence riparian ecosystems both directly and indirectly. When floods inundate floodplain soils, for example, the oxygen available to plant roots is depleted quickly. Different plant species have specific tolerances for oxygen stress (Kozlowski 1984). The duration of oxygen stress associated with the duration of flooding or "hydroperiod" can thus directly influence the composition and productivity of riparian vegetation species and communities.

Floods indirectly shape riparian ecosystems on meandering rivers through their influence on sediment erosion and deposition. Floods build and reshape floodplains by driving the lateral migration of river channels, effecting cutoffs of meander bends, and eroding and depositing sediments on the floodplain surface (Stromberg et al. 1991; Shankman 1993; Scott et al. 1996). These geomorphic changes have significant implications for the successional dynamics of riparian ecosystems (Pautou & Decamps 1985; Bravard et al. 1986; Amoros et al. 1987; Medley 1992; Malanson 1993). Therefore, human-induced changes in flooding regimes from damming and other water development can have large consequences for the ecological integrity of riparian ecosystems (Poff et al. 1997; Richter et al. 1997*a*).

Even the largest natural floods cause important ecological disturbances that shape riparian successional dynamics (Hughes 1994; Johnson 1994; Scott et al. 1996; Palik et al. 1998; Rood et al. 1998; U.S. Geological Survey 1998). For example, large floods rejuvenate secondary channels and create ponded features that help maintain local plant and animal diversity on floodplains (Sparks 1995). We recognize that restoration of large floods on dammed rivers may be socially unacceptable and economically infeasible on many developed river systems. Thus, our approach focuses on determining the adequate magnitude, duration, or frequency of floods which must be maintained or restored to sustain the composition and structure of riparian ecosystems within their natural ranges of variability. Specifically, our approach centers on the relative abundance (represented as a percentage of the total floodplain area) of patch types that comprise a riparian mosaic as indicators of ecosystem integrity. We used numerical model simulations of patch dynamics to evaluate the range of variation in the abundance expected under natural flood regimes for each patch type. We then contrasted these natural ranges with those obtained under varying degrees of flood alteration as a means for assessing the ecological consequences of such alteration. These evaluations of changes in patch-type abundance associated with alternate flood-management schemes can be used to prescribe or protect flood-regime characteristics that maintain natural riparian dynamics and associated biodiversity.

Conserving flood phenomena is only one necessary component of flow regime protection, and maintaining adequate flow regimes is only one part of river ecosystem management. Our recommendations for assessing and prescribing flood regimes follow the "range of variability approach" (RVA) outlined by Richter et al. (1997*b*; Fig. 1). The RVA represents an adaptive management approach in which quantitative flow-management targets are adopted and refined through ecosystem research and monitoring. The modeling we describe is an example of a research tool that can be used to develop or refine hypotheses about the range of flood conditions necessary to sustain riparian ecosystems within their natural ranges of variation (step 3 in Fig. 1). We illustrate the utility of this method by applying it to a case study of the Yampa River in Colorado.

Step 1. Characterize natural range of variability in hydrologic conditions (magnitude, frequency, timing, duration, rate of change)	Step 2. Quantify the degree to which hydrologic conditions have been (or will be) altered by human influences	Step 3. Develop hypotheses about biotic impacts associated with hydrologic alterations. Models can be used to refine these hypotheses.
Step 4. Work with water managers, dam operators, or water rights holders to identify opportunities and approaches for modifying water management to restore or protect natural flow conditions	Step 5. Design and implement an ecosystem monitoring program capable of tracking biotic responses to flow restoration or degradation. Implement flow management strategies.	Step 6. Evaluate data collected in Step 5, and re-visit Steps 3-5 as feasible and necessary

*Figure 1. The six steps in the range-of-variability approach adapted from Richter et al. (1997*b*). The research described in this paper helped refine our hypotheses (step 3) on the linkage between alteration in flooding regimes and consequences for riparian ecosystem dynamics.*

Methods

Study Site

The Yampa River flows from headwaters originating at approximately 3400 m above sea level in the Park and Gore ranges of northwestern Colorado (U.S.A.), through the ski resort town of Steamboat Springs, and downstream through broad, gently sloping valleys occasionally interrupted by narrow bedrock canyons. Just upstream of the Town of Hayden, Colorado, the river enters a broad alluvial valley and assumes a wide floodplain. River processes in this area support a diverse riparian mosaic of several patch types. Our case study focuses on the dynamics of this riparian ecosystem along a 20-km segment of the river upstream of Hayden.

Average annual precipitation at Hayden is only about 40 cm, but precipitation exceeds 150 cm at the watershed's divide; it falls mostly as snow during October through May. The river's flow is strongly dictated by snowmelt runoff, which produces floods in late May commonly exceeding 140 m^3/second. By late summer, flows typically drop to 5–25 m^3/second.

Presently, the Yampa's flows are only minimally impaired by headwater dams and municipal and agricultural water uses (Richter et al. 1995). Additional water development in the Yampa River watershed is likely, and numerous new dams have been proposed. The threat of increased hydrologic alteration from damming and flood control motivated us to evaluate the potential ecological consequences associated with future water development in the watershed.

Ecological Model Formulation

Ecological models span a range of complexity, from simple conceptual models to highly detailed and complex quantitative simulations using thousands of mathematical equations. Simplicity and robustness, however, are desirable attributes of any model to be used in an applied management context (Starfield & Beloch 1986). Conceptual riparian models presented as simple state and transition diagrams (Fig. 2) are particularly useful in communicating important aspects of riparian ecosystem dynamics to resource managers or nonscientists. The Yampa River model illustrates the dynamics of biotic patterns (patch types) expected under the influence of flood-driven geomorphic processes and natural biotic succession. The influence of other potentially important factors, such as flood hydroperiods or surface-ground water interactions that maintain riparian water table levels, were not represented in the Yampa model. Our study focused on the potential ecological effects associated with changes in fluvial geomorphic processes driven by flooding and assumed that other factors remain unchanged.

Riparian models (e.g., Fig. 2) are attractively simple and useful for a number of reasons: (1) riparian patch types are recognized easily in the field (for other examples see Bravard et al. 1986; Salo et al. 1986; Richter 1992; Malanson 1993; Stromberg et al. 1997); (2) most riparian ecosystems can be represented adequately with a small number of patch types, thereby minimizing model complexity; and (3) the reproduction and persistence of most riparian species within the active floodplain are adequately addressed by considering the pri-
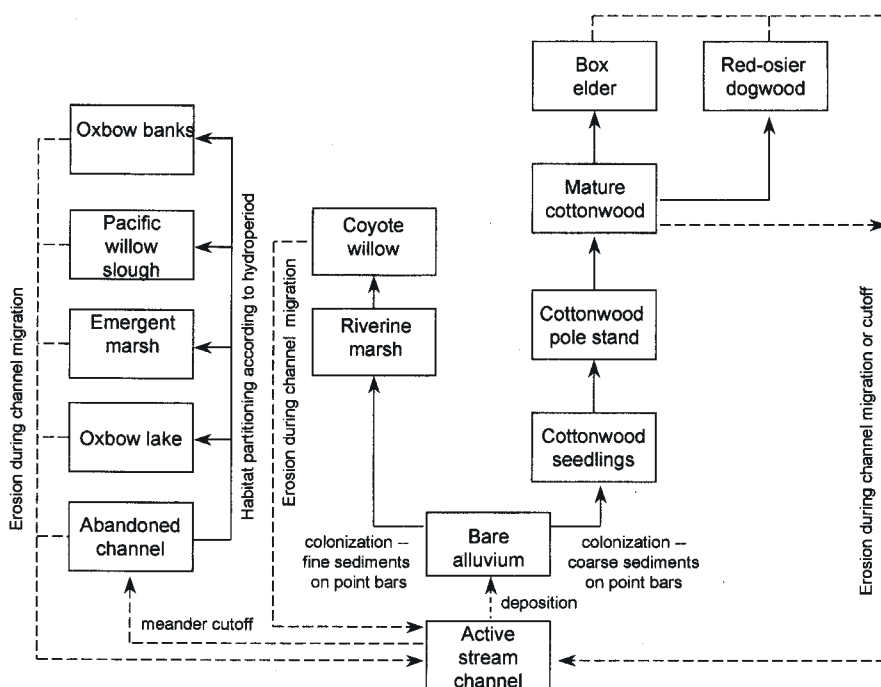

Figure 2. Yampa River conceptual ecological model. Boxes represent various patch types that comprise the riparian mosaic. Dashed lines represent changes driven by fluvial geomorphic processes. Solid lines represent changes related to biotic succession.

mary processes that create, sustain, and destroy patch types (Bravard et al. 1986). We successfully applied the basic template of the model portrayed in Fig. 2 (with minor variations) for meandering river-floodplain systems in such diverse settings as the mid-Atlantic coastal plain, the Rocky Mountains, and the Sonoran Desert of Arizona (Richter 1992, 1999; Richter & Richter 1992). Modified versions of the same type of model can be used to portray expected changes in patch type influenced by water table changes, hydroperiods, or other changes.

Two types of fluvial processes commonly dominate floodplain development and associated patch dynamics along meandering rivers such as the Yampa (Fig. 3). Lateral channel migration forms point bars (from sediment deposits) on the inside of meander bends and erodes floodplain sediments on the outside of bends. Meander cutoff results when a channel meander becomes too sinuous and the river cuts off the bend, forming a secondary channel and oxbow lake.

Many riparian plant species have strong affinities for particular fluvial landforms and their associated habitat attributes, such as depth to water table or duration of flood inundation (Fig. 4). After initial formation of landforms, colonization and succession by a fairly predictable suite of plant species greatly facilitates recognition and delineation of riparian patch types (Pautou & Decamps 1985; Salo et al. 1986).

For instance, in the Yampa River ecological model (Fig. 2), point bars formed by lateral channel migration are colonized by cottonwood seedlings (Fig. 4a). These seedlings develop into cottonwood pole stands and then form mature forest stands dominated by narrowleaf cottonwood (*Populus angustifolia*), box elder (*Acer negundo*), and red-osier dogwood (*Cornus sericea*). Box elder and red-osier dogwood are late-successional species that eventually become dominant in most of these forest stands. Because biotic succession is a relatively continuous process, a modeler must decide how to break up the successional sequence into discrete phases. In the Yampa model, for example, we distinguished among cottonwood seedlings, young cottonwoods (pole stands), mature cottonwood, and later seral types such as box-elder forests and red-osier dogwood shrublands which comprise the riparian forest successional trajectory.

The left side of the Yampa River ecological model represents patch types formed by meander cutoff (Figs. 2 & 3). Different patch types become established once the river abandons its old channel, partitioned according to a hydroperiod (flood inundation) gradient (Fig. 2). In deeper water, oxbow lakes form where no emergent vegetation can establish, but in shallow water, cattails (*Typha latifolia*) or rushes (*Scirpus* spp.) form emergent marshes (Fig. 4b). On moist, sandy channel banks or in shallow channel bottoms, stands of Pacific willow (*Salix lasiandra*) establish. At higher elevations with fine-textured channel banks, a diverse assemblage of plant species form the "oxbow lake bank" patch type. Thus,
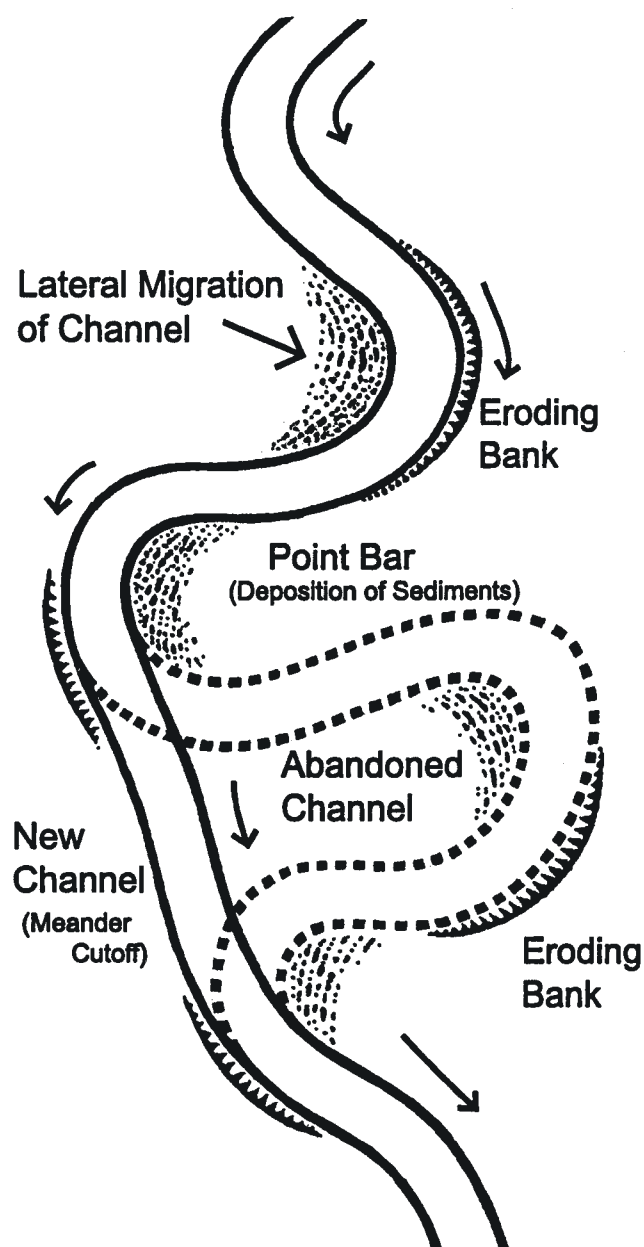

Figure 3. Illustration (plan view) of lateral channel migration and meander cutoff processes on a typical meandering river.

the biological states in a riparian ecological model and their successional relationships can usually be described easily by a riparian ecologist. Collaboration with a fluvial geomorphologist can greatly facilitate an understanding of the processes that create and destroy various geomorphic landforms and their associated patch types, thus aiding the formulation of conceptual riparian models.

Quantifying the Riparian Model

To convert the conceptual riparian model (Fig. 2) to a numerical simulation model, the causes and rates of

(a)

| Box Elder | Mature Cottonwood | Cottonwood Pole Stand | Cottonwood Seedlings | Lateral Migration of Channel → | Mature Cottonwood and Box Elder |

(b)

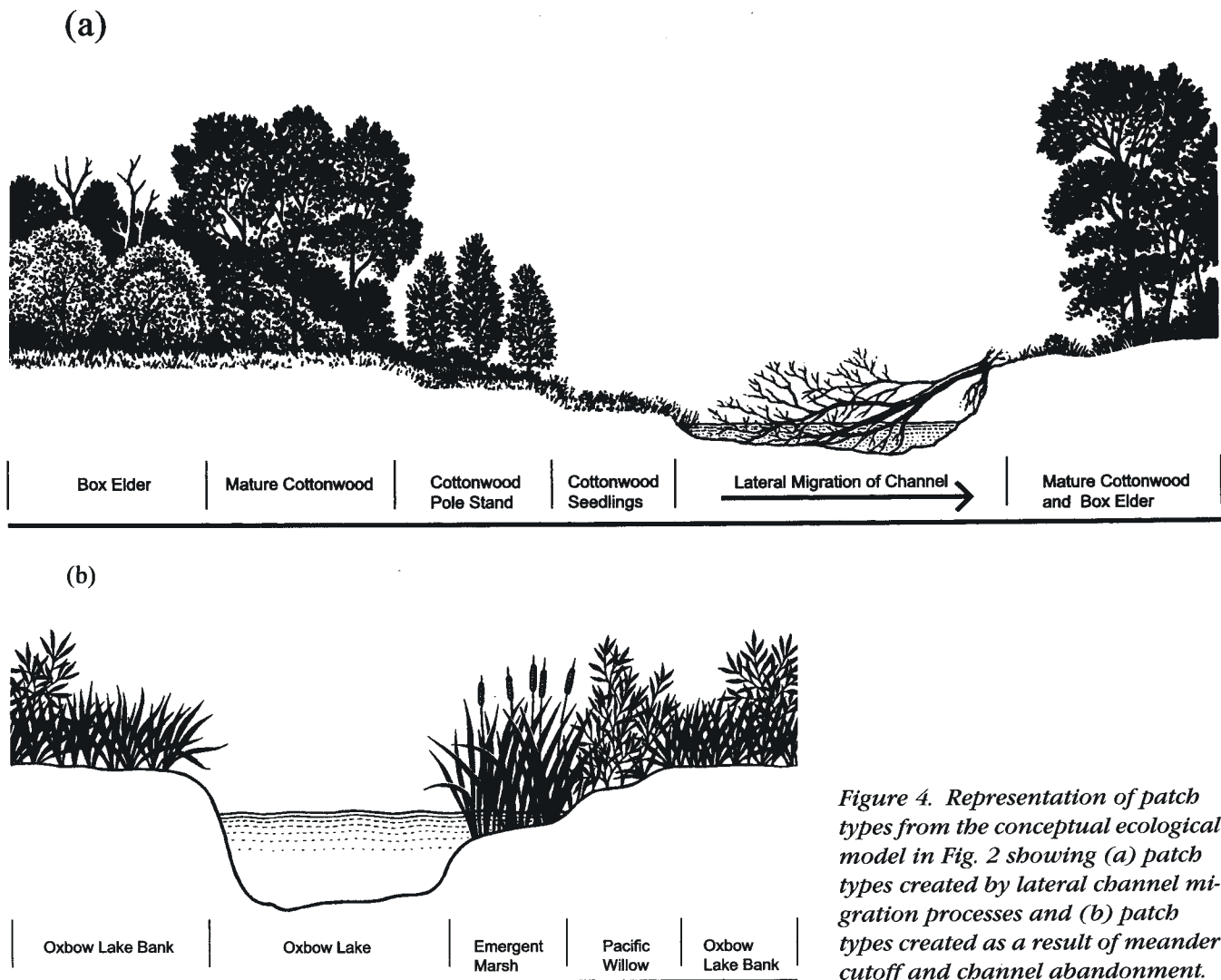| Oxbow Lake Bank | Oxbow Lake | Emergent Marsh | Pacific Willow | Oxbow Lake Bank |

Figure 4. Representation of patch types from the conceptual ecological model in Fig. 2 showing (a) patch types created by lateral channel migration processes and (b) patch types created as a result of meander cutoff and channel abandonment.

change from one patch type to another needed to be defined. We used tree age dating and vegetation measurements (diameter at breast height for trees, species composition of patches) to characterize patch types and determine biotic succession rates between patch types. The estimated mean stand ages helped us determine the approximate amount of time required for successional changes to occur from one type to the next; this was particularly useful in estimating biotic succession rates on the right side of our model (Fig. 5). We used a temporal sequence of five different aerial photographs (1938, 1954, 1969, 1980, and 1989) to estimate rates of patch creation and destruction on the Yampa River floodplain by the geomorphic processes of lateral channel migration and meander cutoff (Fig. 5). In addition, transition matrices constructed from geographic information system vegetation layers (derived from the historic aerial photograph sequence) also helped verify which transitions occurred between patch types and their associated rates of change.

We estimated rates of lateral channel migration and meander cutoff by digitizing traces of the river channel from aerial photo sets and then measuring the area of floodplain created or destroyed by each of these geomorphic processes for each sequential pair of aerial photos. Because these geomorphic process rates vary primarily as a function of flooding, we used regression analyses to test the relationship between geomorphic process (lateral migration and meander cutoff) rates and flooding variables, including annual maximum flood peak magnitudes and duration of flooding above different thresholds (Richter 1999). We computed daily mean streamflow values for our study site during 1938–1989, as described by Richter and Powell (1996), using in our regression equations U.S. Geological Survey data from streamflow gauges located both upstream and downstream of our site.

The rates of change between each of the patch types represented in Fig. 5 were incorporated into a computer simulation model using FORTRAN programming lan-
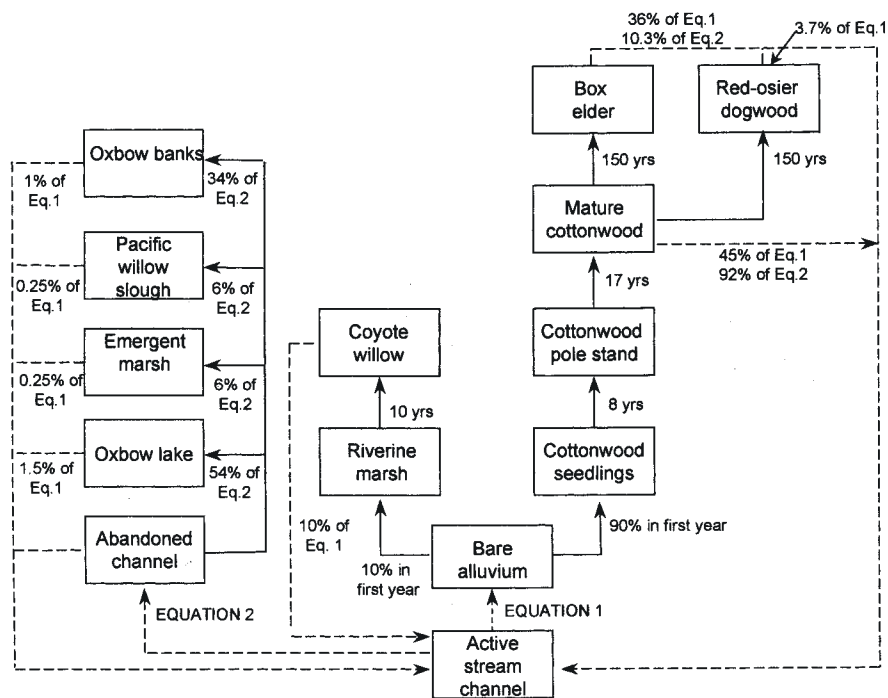
Figure 5. Quantified rates of patch succession in the Yampa River ecological model. Equation 1 is 0.000978 + 00.444 (FLO-DAYS). FLO-DAYS equals the number of days each year when flows are ≥209 m³/second. Equation 2 is a constant rate of floodplain conversion per year = 0.2%.

guage. The simulation model tracks the abundance (percentage of floodplain area) of each patch type over time. Rates of lateral channel migration during periods between aerial photo dates were best explained by the cumulative duration (days) that flood levels were ≥209 m³/second, which corresponded to 125% of bankfull discharge (Andrews 1980). Thus, the primary input variable driving lateral channel migration rates in our model—and hence rates at which patch types were created and destroyed on the right side of the model—was the annual number of days each year during which streamflow was ≥209 m³/second (i.e., FLO-DAYS; equation 1; Fig. 5: 0.000978 + 00.444 [FLO-DAYS]).

Because of the stochastic and episodic nature of channel avulsion events, we were unable to develop an adequate statistical relationship between meander cutoff rates and the flood variables tested. Therefore, we estimated that, over the full period analyzed, meander cutoff affects about 0.2% of the floodplain area per year on average (Fig. 5) based on the number and area of cutoffs documented in our aerial photo series. We used this constant rate in the model to predict the formation of newly abandoned channels.

Model Calibration and Simulation

We measured the abundance (percentage of floodplain area) of each patch type using five sets of sequential aerial photos along with field verification of current patch-type distributions. The estimated abundance of patch types at successive time periods was first used to calibrate the rates of change between patch types in the

simulation model, but the model was later calibrated to also produce a long-term dynamic equilibrium for the abundance of patch types under a natural flooding regime (for similar assumptions and approaches, see Johnson 1992). In calibrating the model, we apportioned the amount of each patch type that would be destroyed by lateral channel migration or channel cutoffs. We also calibrated the slope of equation 1, which computes lateral migration rates associated with flood duration (Fig. 5). Estimates of mature cottonwood abundance from aerial photos ranged from 38% to 43% of total floodplain area during 1938–1989 (Richter 1999); after calibration, our model predicted abundance ranging from 32% to 43% for the same period.

Using random selection (with replacement) of actual FLO-DAYS values observed between 1938 and 1989, we then randomly generated 1000 different annual series of 500 years length for the FLO-DAYS variable. We ran the model 1000 times and computed mean annual values and 90% confidence intervals for each patch-type abundance for each of the 500 simulation years. We used this approach for three reasons. First, because of the long lag times in system response associated with the relatively long persistence of cottonwood stands (average of 150 years on the Yampa), we needed to explore trends in patch dynamics over multiple centuries. For example, even if all cottonwood recruitment terminated today, it would take nearly two centuries for all cottonwood-dominated patch types to become box elder or red-osier dogwood types. These changes would be difficult to detect if the length of the model run was limited to the 52 years for which streamflow and aerial photo data are

available. Thus, we needed to extend our data so that we could examine ecosystem trends over much longer time periods. Second, by using randomization of the 52 years of measured flood values, we avoided the need to make assumptions about the probable sequence or pattern of flood variability into the future. Third, we were interested in computing confidence intervals around our model results, and by running the model 1000 times we were able to draw confidence bands that encompassed 900 of the 1000 computed values for each year (e.g., 90% confidence intervals).

Because the Yampa River's flood regime was only slightly altered by dams and diversions during the 1938–1989 period (Richter et al. 1995), the 1000 annual series of measured FLO-DAYS values were used to estimate the possible natural range of variability in patch-type abundance. To design an ecologically compatible flood-management regime using our modeling approach, we adopted a goal of maintaining riparian forest patch types within the 90% confidence limits determined from our natural flood-regime simulations. To evaluate the potential ecological consequences of future flood-management approaches, we experimentally reduced the maximum value that FLO-DAYS could assume (e.g., we set hypothetical maximums for FLO-DAYS such as 20 days, 10 days, etc.). In doing so, we assumed that cumulative flood durations (annual number of days exceeding 209 m^3/second) would most likely be altered by controlling floods in years when they would have lasted the longest, rather than simply reducing the duration of all floods.

Results

The simulation of a natural flood regime produced fairly stable abundances for each of the riparian forest patch types over the 500-year period simulated (Fig. 6). For instance, the mean abundance of mature cottonwoods (generated from 1000 simulation runs) varied between 40-43% of the floodplain area over the 500-year simulation period, with 90% confidence limits ranging from a low of 33.3% to a high of 48.6%. By experimentally reducing the maximum value of FLO-DAYS in our model runs, we were able to identify a threshold of flood alteration at which the riparian patch mosaic changed substantially over the 500-year simulation period. When FLO-DAYS values were limited to 14 days or less, the mean abundance of key patch types such as mature cottonwoods began to deviate outside the 90% confidence limits of our natural regime simulations. In the most extreme case of flood alteration, in which no floods >209 m^3/second occur, the abundance of the mature cottonwood patch type declines to zero within the length of the simulation period (Fig. 6).

Because the FLO-DAYS variable was experimentally reduced in our model simulations, a larger proportion of

the Yampa floodplain became occupied by box elder forest and red-osier dogwood. The increase in these patch types can be explained by successional trends. When flood-induced cottonwood reproduction is incapable of maintaining cottonwood forest abundance, cottonwood stands eventually become self-regenerating box elder or red-osier dogwood stands that are likely to persist without subsequent flood disturbance (Fig. 2).

Discussion

When applying the range-of-variability approach of Richter et al. (1997b), ecological research, modeling tools, or real-world experimentation can be used to adaptively identify ranges of hydrologic variation that will lead to ecosystem recovery or, conversely, the thresholds of hydrologic alteration that could lead to ecosystem degradation. Our modeling results for the Yampa River suggest that patch-level diversity in this ecosystem is vulnerable to reductions in the annual cumulative duration of flood flows (≥209 m^3/second) that drive lateral channel migration and patch dynamics associated with the riparian forest. In fact, severe reductions in the cumulative duration of flooding could push this riparian ecosystem into a new, artificially maintained stable state composed primarily of box elder and red-osier dogwood stands.

Additional research and ecological modeling efforts are needed to assess the flood-regime requirements of patch types associated with channel cutoff processes (oxbow lakes, emergent marshes, Pacific willow sloughs, oxbow banks). A different hydrologic variable (other than the annual number of days in which a flow of 209 m^3/second was equaled or exceeded) will likely be identified as the best predictor of channel cutoff processes.

Management Hypothesis and Testing

Our modeling results enabled us to formulate a hypothesis (Fig. 1, step 3) about the response of riparian forest patch types to flood alteration on the Yampa: if annual floods (≥209 m^3/second) with cumulative durations of 15 days or less are preserved, and if floods that would have naturally lasted more than 15 days are not shortened to less than 15 days, riparian forest patch types are likely to persist within their natural ranges of abundance.

A conceptual management approach for testing such a hypothesis can be described for 1984 (Fig. 7). On 11 May, river flows reached 209 m^3/second and equaled or exceeded this level for 46 days (FLO-DAYS = 46). Water managers would have been able to store all "excess" flows above 209 m^3/second for 15 days and all additional flood waters occurring after the initial 15 days. In 1983 the duration of flooding could not have been shortened (FLO-DAYS = 12), but flows in excess of 209
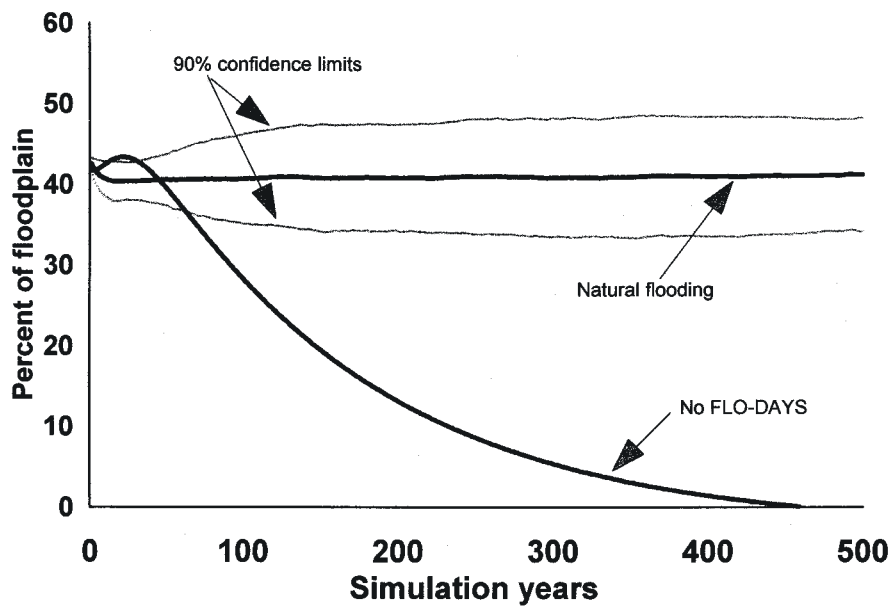
Figure 6. Model simulation results depicting abundance of mature cottonwood patches under "natural" and altered flood regimes (e.g., FLO-DAYS set to 0 days). Measured FLO-DAYS values from a 52-year flow record on the Yampa River were randomized to produce simulations of 500 years. Solid-line values for each simulation year represent an average from 1000 model runs. Lines representing 90% confidence limits are from natural flooding simulation.

m^3/second could be captured for human use. In 1980 no flood volume would have been available for human use because flows never reached 209 m^3/second. Water managers could work with ecologists to identify ways to operate water management structures to enable this management approach (Fig. 1, step 4). By instituting a rigorous ecosystem monitoring and evaluation program as part of this water management approach, our hypothesis could be tested (Fig. 1, steps 5 & 6).

Applying this management approach to the entire period of 1938–1989, the duration of flood days ($\geq$209 m^3/second) would have been constrained during only 4 of 52 years (8%), when cumulative flood durations would have naturally exceeded 15 days (Fig. 8). Because river flow levels exceeded 209 m^3/second in 25 of 52 years

(48%), however, some flood storage presumably would have been available in nearly half the years. Water supply demands in excess of the volume available from flood storage might be partially or wholly met by carefully extracting water from other parts of the annual hydrograph in a way that minimally impairs the natural flow regime. For example, some degree of hydrograph "shaving" during the rising or falling limb of the flood pulse, on days during which flows would not have naturally exceeded 209 m^3/second, might be possible.

The ecological consequences of extracting water during nonflood periods needs to be better understood before such a water management plan is pursued. We also recognize that aspects of the flood regime other than the duration of flows $\geq$209 m^3/second are likely to be
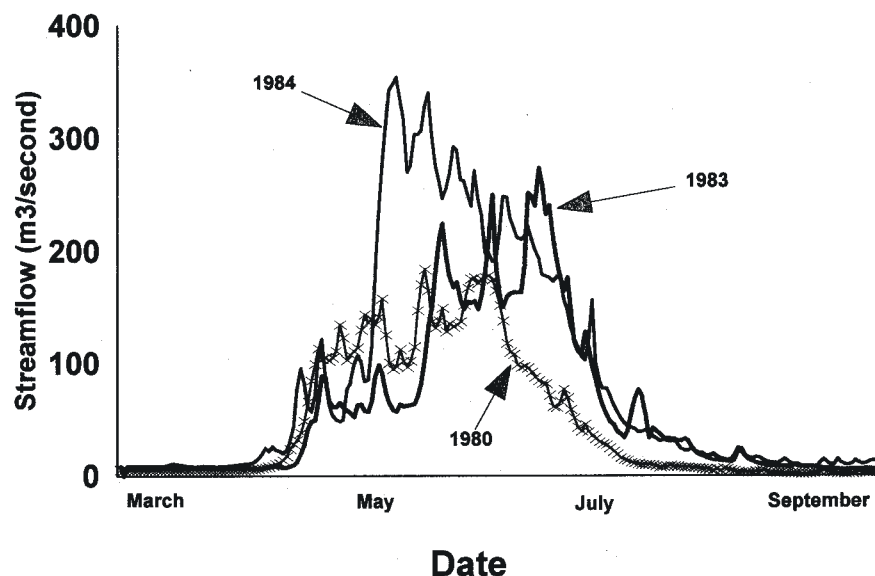

Figure 7. Variable FLO-DAYS in the simulation model represents the number of days in the year during which river flows are $\geq$209 m^3/second. In 1980, Yampa River flows never exceeded 209 m^3/second. In 1983 and 1984, flows exceeded 209 m^3/second on 12 days and 46 days, respectively. The accumulation of FLO-DAYS values need not be continuous within each year.
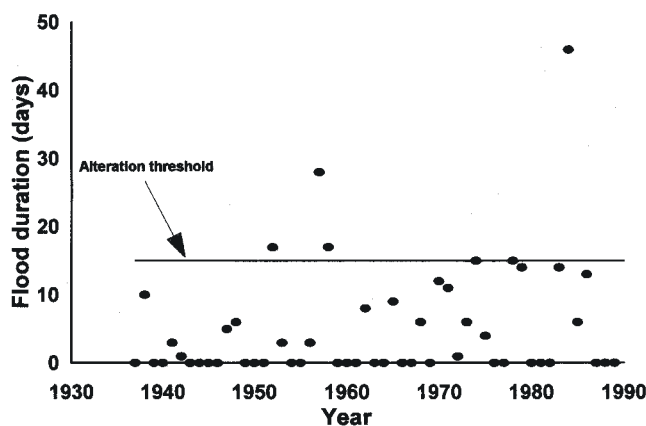
Figure 8. Natural variability in cumulative flood duration (FLO-DAYS) for each year of record on the Yampa River. During 1938–1989, FLO-DAYS exceeded 15 days during 4 years.

ecologically important. For example, we suspect that rare, large flood peaks may be instrumental in effecting meander cutoffs, even though we were not able to establish a statistically significant causal relationship. The timing of flood events is also critical to recruitment of cottonwoods and other plant and animal species (Stromberg et al. 1991; Merigliano 1996; Scott et al. 1996, 1997); the management prescription we describe intentionally preserves the timing of all flood events. Other nonflood aspects of the flow regime affect the recruitment, productivity, and mortality of riverine species (Poff et al. 1997; Richter et al. 1997*b*).

Recommended Model Improvements

We have many reasons for discouraging attempts to make precise forecasts of quantitative changes in the Yampa River ecosystem based on our current model. We recommend making some important model improvements before moving into real-world experimentation with water management on the Yampa (e.g., step 3 of Fig. 1 needs further work before moving to step 4). The weakest aspect of the current model relates to the fact that the driving geomorphic process of lateral channel migration was statistically modeled through use of only four data points. This is represented as equation 1 (Fig. 5), relating rates of point-bar formation to flood duration. Because only five sets of historical aerial photos exist, we could measure rates of lateral channel migration for only four time intervals. To create a regression equation that drives *annual* changes in patch abundances in our model, we had to assume that a statistical relationship derived from multiyear observations was applicable to an annual time frame. Our model results are quite sensitive to changes in the slope of equation 1. For instance, a 10% reduction or increase in the slope of this relationship causes the mean abundance of mature cot-

tonwoods to range from 11% to 50% at the end of our 500-year simulations. Also, during our model calibration efforts we realized that the way we apportioned the effects of erosion from lateral channel migration to each of the patch types can also significantly influence model results. These rates need to be further evaluated after more data are collected.

The reliability of our model can be improved greatly by obtaining additional low-elevation aerial photographs on an annual basis. Further calibration of the model with new aerial photo–based measurements of patch type abundance, channel migration rates, and the associated amount of erosion of each patch type would go a long way toward increasing its predictive capabilities. After the model has been improved with additional data, we recommend conducting a formal sensitivity analysis to better understand the sensitivity of model results to potential inaccuracies in all parameter estimates.

Another source of uncertainty is associated with the fact that geomorphic processes and the associated landform creation and destruction rates in river systems are affected not just by the flow of water but also by the transport of sediment. Future dam construction or substantial changes in land-use practices could alter the rate of sediment delivery to and transport in the Yampa River. The likely interactions between modified river flows and sediment deliveries are extremely difficult to predict (Williams & Wolman 1984; Church 1995; Ligon et al. 1995; Gillespie & Giardino 1997; Friedman et al. 1998). Our model necessarily assumes that the geomorphic process equations (e.g., equation 1, Fig. 5) developed from historical observations will remain stable as flood regimes are modified and that they do not change significantly over long periods of time (e.g., 500 years in our model simulations).

Richter (1999) discusses other possible sources of instability in lateral channel-migration rates for the Yampa River. Her analysis identified reaches of the Yampa that appear to be shifting from a meandering to a braided channel form, which is likely influenced by three factors acting independently or in concert: (1) approximately 25% of the streambanks have been cleared of native woody vegetation and are dominated by exotic pasture grasses, leading to a decrease in streambank stability, a common trigger for channel braiding; (2) floodpeak variability has increased consistently in recent decades; and (3) the channel slope and bankfull discharge values for the Yampa suggest that the river may be intrinsically predisposed to channel pattern changes (e.g., Leopold et al. 1964). Each of these factors can diminish the accuracy or long-term applicability of equation 1, emphasizing the need for on-going calibration of the model.

New Research Directions

Our model simulations have enabled us to explore the changing dynamics of the Yampa's riparian ecosystem

under varying degrees of flood-regime alteration. Simulation models such as ours are excellent exploratory tools for examining the potential sensitivity of natural systems to changes in their driving environmental forces, particularly alterations in disturbance regimes (Starfield & Beloch 1986). Ecological simulation models can also reveal important emergent properties of ecological systems and unveil shortcomings in our understanding of their dynamics (Starfield & Beloch 1986).

For example, our statistical evaluation of flooding variables (magnitude of flood peak, duration of bankfull flow, etc.) suggests that cumulative annual duration of flooding may be more important than the magnitude of the flood's instantaneous peak in driving lateral channel migration and associated patch dynamics. Such a relationship has been hypothesized by fluvial geomorphologists such as Wolman and Miller (1960), Knighton (1984), and Costa and O'Connor (1995). This is generally consistent with the effective discharge theory we discussed earlier that suggests low- to medium-sized floods move the greatest volume of sediment in meandering rivers over time, thereby providing the primary influence on normal channel form. The same range of floods that shapes the channel through erosion and deposition is likely responsible for driving lateral channel migration and hence the formation of bare alluvial surfaces essential for cottonwood seedling recruitment as well. The longer these geomorphically effective floods last, the greater the channel migration and availability of cottonwood seed beds.

The significance of flood duration, however, has not been adequately investigated in riparian research efforts in the western United States. Riparian studies have focused instead on the peak magnitudes of floods as the primary causal agent influencing cottonwood recruitment (e.g., Stromberg et al. 1991; Merigliano 1996; Scott et al. 1996, 1997). Furthermore, a connection between upstream damming and altered channel migration rates have been documented by various authors, including Friedman et al. (1998), but the causative hydrologic influences have not been well studied. The hydrologic processes driving channel migration in meandering rivers deserve much greater attention, which should advance general understanding of the flood characteristics of greatest importance in sustaining riparian ecosystems.

Assessment of the flood characteristics needed to simply recruit cottonwoods or other early-successional tree species is not likely to be adequate for evaluating the long-term maintenance of the whole riparian ecosystem. Colonization rates must be compared to the rates at which successional changes occur and patch abundance is reduced by erosional processes. In our model results, cottonwood recruitment appeared little affected by minor reductions in cumulative flood duration. Nevertheless, when these recruitment rates are unable to keep pace with destruction of mature cottonwood stands by the river's lateral migration, combined with the succes-

sion of cottonwoods into other patch types, the abundance of mature cottonwoods declines outside of their natural range of variability (Fig. 6).

Refinements of our ecological model, supplemented with other ecological research designed to improve understanding of biotic dependencies on the Yampa's flow variability, will increase our ability to manage this river ecosystem adaptively and wisely. Our modeling approach should also be useful in identifying the degree and nature of flood restoration necessary to conserve riparian ecosystems on rivers that have experienced greater degrees of flow alteration. Ultimately, the utility of this type of research depends entirely on society's willingness to explore ways to conserve natural river ecosystems while controlling water use at an ecologically sustainable level.

Acknowledgments

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