HYDROLOGIC REGIMES AND RIPARIAN FORESTS: A STRUCTURED POPULATION MODEL FOR COTTONWOOD

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Abstract. Riparian cottonwood (*Populus deltoides*) forests form the one of the most extensive deciduous forest ecosystems in arid regions of the western United States. However, cottonwood populations are threatened by flow alteration and channel degradation caused by dams, water diversions, and groundwater pumping. We developed a stochastic, density-dependent, population model to (1) consolidate information concerning cottonwood population dynamics in a conceptual and analytical framework, (2) determine whether complex forest stand dynamics can be predicted from basic cottonwood vital rates and river hydrology, and (3) aid in planning prescribed floods by projecting how altered flow regimes might affect populations. The model describes how annual variation in the hydrograph affects cottonwood mortality (via floods and droughts) and recruitment (via scouring of new habitat and seedling establishment). Using parameter values for the undammed Yampa River in Colorado, we found that abundances of seedlings and younger trees followed a boom–bust cycle driven by high flood mortalities while reproductive adult abundance followed a less erratic 5–15-yr periodicity driven by multiyear sequences of flows favorable to stand recruitment. Conversely, chance occurrences of multiple drought years eliminated cottonwood from up to 50% of available habitat, providing opportunities for competing plant species to establish. By simulating flow alterations on the Yampa ranging from channelization (many floods/droughts) to damming (few floods/droughts), the model suggested that mature cottonwood forest should be most abundant near the observed natural flow regime. Model analysis also suggested that flow regimes with high flood frequencies result in stable (albeit small) population sizes, while stable flows result in highly variable population sizes prone to local extinction.

Key words: cottonwood; crowding dependence; density dependence; disturbance; drought; flooding; hydrologic alteration; natural flow regime; Populus; *self thinning; stochastic model.*

INTRODUCTION

Riparian cottonwood (*Populus deltoides*) forests represent the most extensive and ecologically important deciduous forest ecosystems in arid parts of the western United States. Cottonwood trees are key components of river bottomland ecosystems, influencing floodplain processes such as nutrient cycling, light and water availability, rates of alluviation and river meandering, canopy structure, and habitat heterogeneity (Johnson 1992, 2000, Boggs and Weaver 1994, Busch and Smith 1995, Ellis et al. 1998). Cottonwood forest development is closely coupled with hydrologic and fluvial processes, which are responsible for the creation of new sites for cottonwood seedling establishment, for providing hydrologic conditions necessary for seedling survival, and for the process of floodplain evolution that accompanies cottonwood stand development (Scott et al. 1996). Along meandering alluvial streams, floodplain evolution—the progression of frequently flooded sand and point bars near the channel to older, less frequently flooded surfaces further from the channel—results in multiple age classes of cottonwood along a given reach of stream (Johnson et al. 1976, Stromberg et al. 1997, Merritt and Cooper 2000). However, neither rates of river meandering nor cottonwood recruitment are continuous processes. The formation of suitable habitat (bare, moist sites), the availability of seeds, the conditions necessary for seedling survival (sufficient soil moisture), and a suitable sequence of flow years following seedling establishment all must coincide in time for a given cohort to persist. The frequency at which all the necessary requirements for a stand to persist are met is determined to some degree by stochastic processes, resulting in recruitment events that have been shown to be separated by a return interval of approximately a decade (on average) along free-flowing rivers (Stromberg et al. 1991, Scott et al. 1997, Stromberg 1998).

Throughout the past several decades, many investigators have documented widespread cottonwood forest decline along rivers in western North America (Johnson et al. 1976, Bradley and Smith 1986, Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Howe and Knopf 1991, Snyder and Miller 1991, John-

son 1992). This decline has coincided with the widespread water development of rivers of the western United States and Canada through the construction of dams, flow diversions, and groundwater pumping that have directly or indirectly caused changes in the hydrologic and fluvial processes necessary for riparian forest establishment and persistence. Water development over the past century has resulted in the nearly 15 000 dams currently in operation west of the 100th meridian in the United States alone (U.S. Army Corps of Engineers 1996) and tens of thousands more diversions. Dams influence hydrologic processes and significantly alter sediment regimes along alluvial rivers. Riparian habitat submerged by reservoirs is often completely eliminated upstream from dams. Downstream from dams, reduced sediment loads and flow modifications often lead to reduced rates of meandering of alluvial rivers and changes in channel morphology (Williams and Wolman 1984, Friedman et al. 1998, Merritt and Cooper 2000). Hydrologic changes typically include decreases in the frequency and magnitude of peak flows, shifts in the timing of peak flow and changes in the rate of river stage decline, and increases in base flow (Williams and Wolman 1984, Johnson 2002, Shafroth et al. 2002). Changes in these processes have been directly linked to shifts in the population structure of cottonwood forests and to the decline of cottonwood forests on regulated streams throughout the West (Rood and Mahoney 1990); however, there are isolated examples of increased cottonwood forest extent following damming (Johnson 1994). As water resources become increasingly scarce due to increasing urban and agricultural demands throughout western North America, the negative impact of altered flow regimes on riparian cottonwood ecosystems is imminent.

While these concerns have inspired the development of models of riparian forest cover (Johnson 1992) and cottonwood forest stand dynamics (Richter and Richter 2000), to date no model has tried to capture cottonwood population dynamics by integrating fluvial processes with direct estimates of cottonwood vital rates. In this study we develop a stochastic, density-dependent, structured population model for riparian cottonwood forests. Our primary objective is to begin with the essential vital rates of cottonwood—birth and death rates, as these relate to river hydrology—and observe how more complex population dynamics arise from these fundamental quantities. We then parameterize the model using data from a free-flowing river in the Colorado Plateau to estimate how forest dynamics might change in response to human or climate-driven alterations to the natural flow regime. Sensitivity and elasticity analysis enables us to make some conclusions and speculations regarding controlled management of flows.

Cottonwood Life Cycle

Cottonwood colonizes newly created sites along river margins and is an important early-successional species along active alluvial channels in the western United States. Cottonwood seeds are dispersed over a relatively short period of time in spring and early summer, and seedlings become established upon bare, moist, freshly deposited sediment near the active stream channel (Moss 1938, Fenner et al. 1984). Cottonwood stand development is associated with the process of channel meandering along sinuous alluvial rivers, and with channel bar and island formation and channel narrowing along braided and anastomosing channels. Cottonwood stands may persist throughout succession on active stream channels and ultimately form late-successional cottonwood gallery forests on higher and older benches (Johnson et al. 1976, Stromberg et al. 1997). As a consequence, cottonwood stands spanning a range of ages may be present at any given time across a gradient from channel margin to high floodplain surfaces.

New site formation, dispersal, germination, and establishment

Cottonwood seed germination and seedling establishment are first limited by the formation of sites for germination and growth. Along alluvial channels, the rate of meandering is directly related to the extent and distribution of new site formation along channel margins (Bradley and Smith 1986, Johnson 1994). The process of meandering is driven by the erosion and sloughing of high banks on the outsides of meander bends and the subsequent deposition of transported mineral sediment on point bars. Sediment is often deposited during the receding limb of the hydrograph, resulting in bare, moist sites that are optimal for cottonwood seed germination. If conditions are suitable in subsequent years, these moist mineral deposits may serve as sites for seedling establishment and sites of eventual stand formation. Other processes that create suitable sites for cottonwood establishment, even in the absence of active channel meandering, include channel narrowing and overbank flooding (Scott et al. 1996, Friedman et al. 1996, Auble and Scott 1998).

The timing of dispersal of cottonwood seeds typically coincides with the timing of maximum availability of new sites, which suggests life-history adaptation to the flood regime (Karrenberg et al. 2002, Lytle and Poff 2004). The timing of the snowmelt peak on streams in western North America is fairly predictable, occurring in late May and early June. Cottonwood seed viability may be as high as 99% in newly released seeds (Fenner et al. 1984, Cooper et al. 1999, Sher et al. 2000), but drops off rapidly following dispersal and rarely persists for more than a few weeks. The primary resource limiting seedling survival is water, and seedlings are vulnerable to drought stress during their first season of growth. It has been suggested that, in more arid regions of the West where seedlings cannot rely upon summer precipitation, the rate of groundwater decline (which is closely tied to river
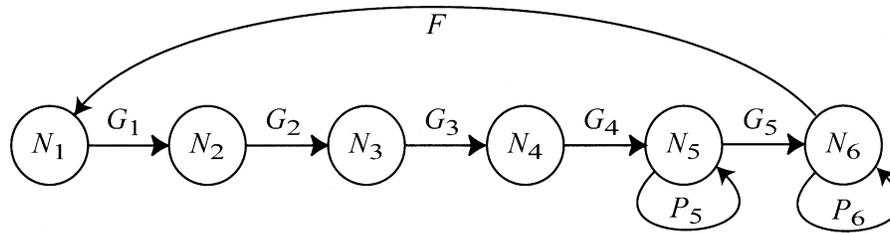
FIG. 1. Life cycle for the cottonwood model. Stage 1 represents seedlings; stages 2–4 are 2–4-yr-olds, respectively; stage 5 represents subadult trees (mostly 5–10-yr-olds); and stage 6 represents reproductive adults. N is abundance, G is the probability of transition to the next stage, P is the probability of remaining in that stage, and F is fecundity.

stage decline) must not exceed the root growth rate of cottonwood seedlings (Mahoney and Rood 1992, 1998, Segelquist et al. 1993, Shafroth et al. 2000). However, seedlings may survive in floodplain deposits that have high percentages of fines (silt and clay) by relying solely on soil water rather than phreatic water (Cooper et al. 1999). In coarse alluvial deposits, the rate of groundwater decline must be sufficiently slow ($\sim$2.5 cm/d) for elongating roots to maintain contact with the capillary fringe (Mahoney and Rood 1998, Amlin and Rood 2002). Conversely, cottonwood seedlings may experience high mortality or stunted growth rates if roots remain submerged for extended periods of time (Merritt and Cooper 2000, Amlin and Rood 2002).

The timing of seed release relative to river stage may also influence where on the floodplain seedlings become established, and the vulnerability of seedlings to desiccation and flooding in subsequent years. Seedlings resulting from seeds dispersed too early relative to the timing of peak discharge may experience drought stress and desiccation because of their locations high upon the floodplain, while those released too late relative to the peak are subject to scour from subsequent floods.

Persistence and floodplain evolution

Cottonwood seedlings that survive through the first several seasons become increasingly likely to survive the adverse conditions associated with flooding and floodplain development. Cottonwood saplings and young adults are quite resilient and have the ability to resprout vigorously following mechanical disturbance and burial, and can root adventitiously following burial during floodplain development; adults are able to survive prolonged inundation as well as short periods of drought (Braatne et al. 1996, Karrenberg et al. 2002). Although cottonwood trees are relatively short lived compared to many late-successional forest species, cottonwood forests may persist in excess of 150 years or more along western rivers if conditions permit. Older cottonwood forests continue to be vulnerable to drought and groundwater depletion, which may result in cavitation and partial canopy die back or mortality (Stromberg and Patten 1991, Tyree et al. 1994, Scott et al. 2000). The spatial position and age of cottonwood stands relative to the active river channel largely determines their susceptibility to floods and droughts. Stands of mature cottonwood may be buffered from flood mortality by their location on high benches away from the active flood channel and from drought mortality by their deep taproots. But if rates of meandering are sufficiently high, and floodplain turnover rate is shorter than the life expectancy of cottonwood ($\sim$150 years), old stands on high banks may be undercut and destroyed by flooding as a result of bank collapse. Seedlings and early year age classes are closer to the active channel and have relatively short taproots, making them more susceptible to ice scour, mechanical removal by floods, and desiccation from drought.

METHODS

Model structure

Cottonwood stands of different ages experience different growth and mortality rates, so we used a matrix model with separate stages for seedlings, second-year individuals, third-year individuals, fourth-year individuals, nonreproductive juveniles (five- to approximately 10-year-olds), and reproductive adults (Fig. 1). The model has the stochastic form $\mathbf{N}(t + 1) = \mathbf{A}(t)\mathbf{N}(t)$, where $\mathbf{N}(t)$ is a vector containing stage abundances and $\mathbf{A}(t)$ is a set of transition matrices that fluctuate according to variation in the hydrograph. The model is evaluated from an initial population $\mathbf{N}(0)$ in discrete annual time steps $t = 0, 1, 2, 3$, etc., and is written in matrix form as

$$\mathbf{N}(t + 1) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & F \\ G_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 \end{pmatrix} \cdot \begin{bmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ N_4(t) \\ N_5(t) \\ N_6(t) \end{bmatrix} \quad (1)$$

where G_i is the probability of transitioning from stage i to $i + 1$, P_i is the probability of remaining in stage i, and F is fecundity. The hydrograph affects vital rates through a flood or a drought in certain years (mortality) and by affecting the establishment of seedlings (fecundity). For elements of the $\mathbf{A}(t)$ matrices, $G_i = (1 - S_i) \times (1 - D_i) \times b_i \times a_i$, where S_i is flood mortality,
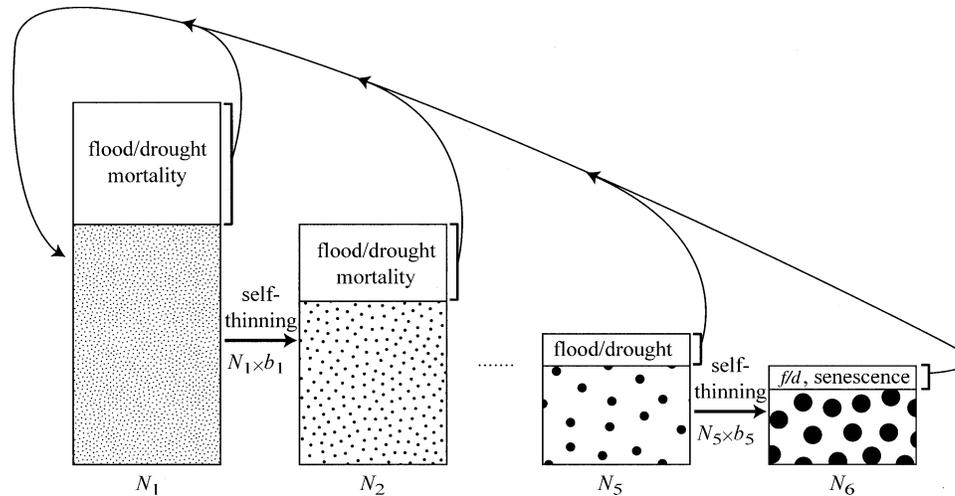
FIG. 2. Schematic showing how stand structure is represented in the cottonwood model. Every year, a fraction of each stand may be lost to flood or drought mortality. This space becomes available for colonization by new seedlings the following year (if conditions favor seedling recruitment). Within the remaining portions of stands, self-thinning occurs at rate b so that the number of individuals in a stand decreases while the space occupied by a stand remains constant.

D_i is drought mortality, b_i is a self-thinning rate, and a_i is the baseline probability of transitioning to the next stage irrespective of flood, drought, or self thinning. Similarly, $P_i = (1 - S_i) \times (1 - D_i) \times (1 - a_i)$. We assume S_i and D_i are threshold functions, such that S_i is a nonzero probability if the hydrograph exceeds a critical threshold (a flood year occurs) and is zero otherwise. Similarly, D_i is zero unless the hydrograph fails to exceed a minimum threshold (a drought year occurs). Where data are available, these threshold criteria can be relaxed to produce continuous functions for S and D that vary with flood and drought magnitude (e.g., in some systems, larger floods cause proportionately more mortality and recruitment; Friedman et al. 1996, Rood et al. 1998, Friedman and Lee 2002). In the basic form of the model, we assume that values for the annual hydrograph, and thus the $\mathbf{A}(t)$, are independent and identically distributed among years. By definition, a_1 through a_4 equal 1, $0 < a_5 < 1$ since a portion of individuals remains in stage 5 each year, and $0 < a_6 < 1$ indicating that a portion of adults senesce each year (literally, a_6 is the probability of an adult "transitioning out" of the system).

Fecundity, the number of seedlings produced, is a function of the timing, magnitude, and duration of floods. Nonzero fecundities occur only in years when the following criteria are met: (1) an above-threshold flood occurs; (2) flood recession begins before the last date of cottonwood seed set; and (3) at least one reproductive female tree is present in the population (we assume that if only one adult is present it is female). In these years, fecundity is a function of the area of bare substrates available for colonization so that:

$$F(t) = \frac{1}{N_6(t)}\left[K_T - \sum_{i=2}^{6} K_i(t+1)\right]g(h) \qquad (2)$$

where K_T is the total area available to the entire cottonwood population, $K_i(t+1)$ is the area occupied by a stage after flood mortality, and $g(h)$ is a function that describes how the duration of floods affects seedling establishment. During matrix projection, multiplication by the term $1/N_6(t)$ makes F independent of the number of reproductive adults, reflecting the fact that adult cottonwoods produce seeds well in excess of the amount of substrate available for germination (Moss 1938, Fenner et al. 1984, Cooper et al. 1999).

Although the model does not keep track of the location of individual cottonwoods, the spatial structure of cottonwood stands enters the model in several ways (Fig. 2). First, a self-thinning rule describes the relative amount of space that successive stages occupy. Stages thin at rate b_i so that $N_{i+1} = N_i \times b_i$. Thus, in the absence of flood and drought mortality, a stand of N_1 seedlings will eventually mature to $N_6 = N_1\Pi_{i=1}^5 b_i$ adults occupying the same space as the seedlings. Conversely, the area occupied by N_6 adults, expressed in seedling units (square meters could just as easily be used as the common currency), is $K_6 = N_6\Pi_{i=1}^5 1/b_i$. The inverse relationship between the population size of a stage and the space it occupies, as determined by the self-thinning rule, means that the number of individuals within a stand and stand area are related to each other by a simple conversion factor. Second, the model describes cottonwood population dynamics at the reach scale, where K_T expresses the total available habitat in terms of numbers of seedlings that could colonize the reach if it were entirely bare substrate. Because seedling establishment drops to zero as K_T is approached, cotton-

TABLE 1. Stage-specific parameter values.

Variable	Description	i					
		1	2	3	4	5	6
	density (no./m²)	350	10	1.0	0.91	0.6	0.12
b_i	self-thinning rate	0.029	0.10	0.91	0.66	0.2	
S_i	flood mortality in flood year	0.97	0.33	0.224	0.19	0.073	0.020
D_i	drought mortality in drought year	0.49	0.16	0.083	0.05	0.01	0.01
a_i	baseline transition probability	1	1	1	1	0.17	0.03
	initial area (m²)	11 816	11 816	11 144	11 144	13 819	59 605
$N_i(0)$	initial population size (no. individuals)	4.1×10^6	120 000	11 000	10 000	8300	7200

Notes: Self-thinning rates were calculated as density$_{i+1}$/density$_i$, and initial population sizes were calculated as density × initial area. All other parameters were obtained from the literature or aerial photos. Stages (i) are: 1, seedlings; 2–4, 2–4-yr-old cottonwoods; 5, subadult trees; 6, reproductive adult trees.

wood population dynamics are "crowding dependent" (Westoby 1981), which is analogous to density dependence with K_T as the maximum population size. Third, the spatial positions of stands relative to the active floodplain are implicit in the mortality rates they experience. For example, S_1 will generally be measured from field data as greater than S_5, because seedlings are closer to the active floodplain and more vulnerable to floods than juvenile stands. Because of these differences in vital rates, the stage structure of cottonwood can also influence the areal extent of floods and droughts. For example, when mature cottonwoods (low flood and drought mortality) predominate, less area would be cleared via drought mortality than if drought-vulnerable seedlings predominated. The fecundity term also assumes that space cleared by flooding and drought becomes available for seedling recruitment (Fig. 2). This is equivalent to assuming that stand generation (via succession and bench formation) is in dynamic equilibrium with stand destruction (via the erosion of established benches), an assumption that is likely met for meandering rivers. At short time scales of years to decades, it is possible for either erosional or depositional forces to predominate locally, but over longer time scales, the area of suitable cottonwood habitat along any given river must fluctuate around some average value (otherwise riparian habitat would either increase infinitely or disappear entirely). Analysis of 15 USGS gaging stations in the Yampa River watershed indicates that this quasi-equilibrium assumption is reasonable for the Yampa River at Deerlodge Park (used here as an example), as stream channel morphology is adjusted to the effective discharge at these sites (Andrews 1980). (Effective discharge is the flow that does the most geomorphic work over the course of time; Wolman and Miller 1960). Geospatial analysis of channel planform change over 60 years of aerial photographic record also indicates that the Yampa River channel is in relative equilibrium at Deerlodge Park (Merritt and Cooper 2000).

In some systems, other native or invasive riparian species may compete for cottonwood habitat, or the total amount of habitat could increase or decrease in response to changing climate; in these cases the model can be modified to allow for nonequilibrium stand dynamics (e.g., other species decrease K_T by competing for cottonwood habitat).

Model parameters

We calibrated the model using general cottonwood life history data from the literature as well as data that are specific to one focal study site, the Yampa River at Deerlodge Park in Dinosaur National Monument, Colorado (Table 1). Flood and drought mortality rates were derived from data gathered on the Green and Yampa Rivers (Cooper et al. 1999), the Platte River (Johnson 1994, 2000), and from laboratory experiments (Mahoney and Rood 1991, Segelquist et al. 1993, Amlin and Rood 2002). Hydrologic data came from 83 years of U.S. Geological Survey discharge data from the Yampa River near Maybell, Colorado gaging station (USGS gage number 09251000). In the basic form of the model, years were drawn at random with replacement. We also examined model behavior after adding autocorrelation of year types (year $i + 1$ equals year i with probability p, otherwise a new year is drawn at random), and when floods recur at regular intervals (which is possible with managed discharges from dams). Years in which the spring floods exceeded 280 m³/s were scored as flood years, and years in which floods remained below 210 m³/s were drought years. Years with peak flows between these thresholds were considered "growth years" with no flood or drought mortality. The flood threshold relates to field observations over several years that indicated that flows near 280 m³/s overtopped banks, mobilized and reworked point and sand bars, and resulted in the formation of new sites for cottonwood seedling establishment along the Yampa River in Deerlodge Park; likewise, peak flows of <210 m³/s occurred on what could be con-

sidered drought years, resulting in high seedling mortality (D. Merritt, *personal observation*, Cooper et al. 1999). This flood threshold is also close to the effective discharge (which approximates the bankfull flow) measured as 258 m^3/s at the nearest upstream gage (Andrews 1980). Mortality of seedlings and saplings from drought varies across the floodplain, as the water moisture holding capacity is often extremely spatially variable on floodplains of active rivers. Our data reflect drought mortality of seedlings measured from permanent plots at Deerlodge Park. This threshold function may be varied in the model to reflect the vulnerability of seedlings to drought for any geographic area.

Cottonwood seed dispersal typically terminates by 15 July in Deerlodge Park (Cooper et al. 1999), so recruitment was constrained to occur only in years where the hydrograph peaked before this date. The assumption is that seeds would be dispersing over at least some portion of the descending limb of the hydrograph if the peak occurred before this date. The function $g(h)$ scales fecundity from 1 (complete establishment) to 0 (complete failure) according to the rate of hydrograph stage decline h (measured in cm/d). This was obtained by fitting a lognormal function to the data of Mahoney and Rood (1991):

$$g(h) = 0.94 \times \exp\{-0.5[\ln(h/1.28)/0.99]^2\} \quad (3)$$

which has an R^2 value of 0.95. The function has a maximum near $h = 2$ cm/d, indicating that seedling establishment is highest when the post-flood stage declines at a rate neither too slow (saturation of roots) nor too fast (desiccation).

Areal coverages and densities of each cottonwood stage were quantified by digitizing relatively even-aged cottonwood stands from 1:10 000 scale aerial images of a 2 km reach of the Yampa River at Deerlodge Park. Images were first registered to known coordinates and rectified using a rubber sheeting technique in ERDAS Imagine version 8.2 (ERDAS, Inc., Atlanta, Georgia, USA). Digitizing of the aerial extent of stands of different stages was performed using ESRI ArcView version 3.2 (ESRI, Redlands, California, USA). The total area available to cottonwood along this reach was 119 300 m^2, expressed as seedling units (a convention that makes matrix projection simpler); K_T was therefore 4.176×10^7 seedlings. Densities of older stands were measured from aerial photographs taken in 1973 and in 1994 and thinning rate through time was calculated. Estimates of stem density for younger stands at Deerlodge Park were taken from measured stem densities of similar-aged cottonwood stands from other studies (J. C. Stromberg, *unpublished data*, Cooper et al. 1999). Both of these studies were on the same species of cottonwood (*Populus fremontii* synon. with *P. deltoides* subsp. *wislizenii*) and took place in the arid western United States. Because these values have been measured from field data, the thinning rates integrate mor-

tality from geomorphic change at the sites, beaver activity, insects, disease, soil salinity, and grazing.

Iterated sensitivity and elasticity

We used iterated sensitivity and elasticity analysis to quantify how changes in underlying parameter values affect predictions of the model. Because density dependence eventually limits population growth rate to $\lambda = 1$, we focused instead on the sensitivity and elasticity of adult population size, N_6 (Grant and Benton 2000). Sensitivities describe how absolute changes in parameter magnitude affect population size, while elasticities describe the effects of proportional changes (Caswell 2001). The parameter of interest was allowed to vary in the region of the observed value (± 0.1, bounded between 0 and 1) in increments of 0.01. The model was projected forward 200 years, which was sufficient time for population size to reach quasi-equilibrium, and N_6 was averaged over the last 50 years of the run. This was replicated 1000 or 10 000 times (more replicates were required for less-sensitive parameters) at each increment, and the average value of N_6 recorded. Sensitivity is the regression slope of N_6 vs. the iterated parameter values, while elasticity is the log-log regression slope. Most of these regressions were very close to linear, with R^2 always above 0.85 (and typically above 0.95). When a regression departed from linearity, the analysis was repeated using a narrower range of parameter values to better approximate the local slope, which often required more replicates to overcome noise due to model stochasticity. Essentially, iterated sensitivity (or elasticity) analysis uses numerical methods to mimic taking the partial derivative of N_6 with respect to the parameter of interest, which is not analytically feasible with our stochastic model.

Altered flow regimes

Dams moderate flow extremes by reducing flood and drought frequency, whereas groundwater depletion may produce more frequent and severe droughts. Channelization throughout a watershed may produce more frequent and severe flooding along reaches downstream of such channel modifications. We simulated these scenarios by varying flood and drought frequency and observing the effects on adult population size and variability. This was repeated for floods alone, droughts alone, and floods and droughts together. Frequency was varied from 0 (no years experience an event) to 100% (all years have an event), and adult population size was recorded at year 200. This was replicated 1000 times at increments of 1%.

RESULTS

At flood and drought frequencies representing the natural flow regime, population dynamics were characterized by extreme variation in seedling abundance and establishment, but fluctuations were more regular in the older stage classes (Fig. 3). Whereas seedling
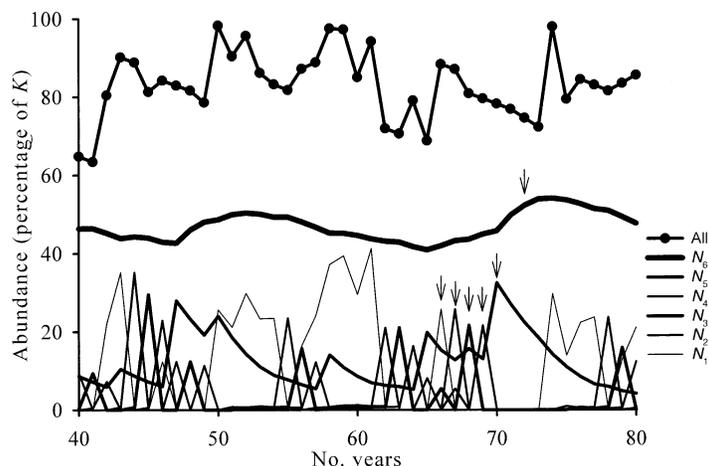
FIG. 3. Example of a projection of the model, using the vital rates in Table 1 and natural flow regime conditions. Abundances are expressed as a percentage of K_T, the total area suitable for cottonwood. Seedlings (N_1) and younger trees (N_2–N_5) show boom–bust dynamics, while the area covered by mature trees (N_6) fluctuates more moderately. Flood years, where seedling establishment occurs, can be identified by nonzero values for N_1. Significant recruitment of mature trees occurs when a flood causes high seedling recruitment, and then no floods or droughts occur for several more years (arrows point to an example of this). Self-thinning, flood mortality, and drought mortality leave a substantial amount of suitable cottonwood habitat unoccupied in some years (the total habitat occupied by cottonwood, "All," is often <100%).

abundance was constrained by the model to vary closely with the hydrograph, the magnitude of interannual population fluctuation decreased with increasing stand age. Adult populations were the most stable, varying around an average value of 7150 individuals, which covered about 50% of available cottonwood habitat (K_T). This quasi-equilibrium population size is nearly identical to the observed current population size of 7200 adults in the study reach. Quasi-equilibrium around this mean was typically reached within 100 years of model projection, even when starting populations were changed by orders of magnitude, which indicates that the model is ergodic with respect to initial population size. Even under natural flow regime conditions, as much as 45% of available cottonwood habitat remained unoccupied in certain years (Fig. 3). These low-occupancy events occurred when, by chance, the population experienced multiple drought years and no intervening flood years for recruitment.

Adult population size experienced cycles of increase and decrease every five to 15 years, although this did not occur with a regular periodicity. This was driven by the chance occurrence of year-type sequences favorable to stand recruitment: a flood year (recruitment) followed by at least two growth years (no flood or drought) would produce a strong cohort that eventually matured into the adult stage (Fig. 3). These older individuals escaped the boom–bust dynamics driven by high mortality that characterized younger stages.

Adult population size, hence the area covered in mature forest, was most sensitive to parameters affecting vital rates of seedlings, 5–10 yr olds, and adults, and was relatively insensitive to parameters affecting other stages (Table 2). Adult population size was most sen-

sitive to a_6, the senescence rate of adults apart from flood or drought mortality. Increasing a_6 by only 0.01 would decrease N_6 by over 1000 individuals. For all stages, adult population size was about twice as sensitive to flood mortality as it was to drought mortality. Because vital rates for adults and seedlings are very different in magnitude (i.e., a ±0.01 change in flood mortality would halve adult survivorship but amounts to no more than roundoff error for seedling survivorship), it may be more convenient to compare rates using the proportional scale of elasticities rather than the absolute scale of sensitivities. The largest elasticities were associated with parameters affecting seedling and adult survivorship, with flood mortality of seedlings being the greatest in magnitude. Decreasing seedling mortality by 10% would increase adult population size by 3.3%. Across all stages, elasticity values for flood mortality were greater than those for drought mortality.

Adult population size was greatest when floods occurred in only 30% of years on average, although populations were not substantially lower at the observed natural flood frequency of 53% (Fig. 4). Reducing flood frequency below 30% resulted in a significant decrease in population size, however, coupled with a sharp increase in interannual population variability. This high variability and low average population size led to reach-wide extinction in some simulation runs. Increasing flood frequency above 30% also decreased population size, but in contrast to flow regulation, increased flood frequency resulted in more stable population sizes that rarely went extinct. Drought frequency had a smaller effect on adult population size relative to flood frequency. Reducing droughts below the natural frequency of 22% increased population size by only 12%

TABLE 2. Sensitivity and elasticity of adult population size (N_6) to flood mortality (S), drought mortality (D), and transition/senescence rate (a).

Parameter	Sensitivity	Elasticity
S_1	−2406	−0.326
S_2	−1321	−0.059
S_3	−1410	−0.041
S_4	−1442	−0.035
S_5	−7684	−0.078
S_6	−41 251	−0.107
D_1	−1336	−0.090
D_2	−708	−0.014
D_3	−652	−0.007
D_4	−775	−0.007
D_5	−3563	−0.015
D_6	−15 122	−0.093
a_1	1528	0.205
a_2	553	0.074
a_3	332	0.044
a_4	345	0.046
a_5	10 266	0.240
a_6	−109 726	−0.247

Notes: Units are absolute (sensitivity) and proportional (elasticity) change in N_6 due to an incremental change in the vital rate. Stages 1–6 are defined in Table 1.

(at 0% drought frequency), and increasing droughts reduced population size by 32% (at 100% frequency). The interannual variability in population size remained nearly constant over this range, fluctuating around 600, or 5% of K_T. Because of the relatively minor effects of droughts, varying flood and drought frequency simultaneously changed the results for floods only (Fig. 4) very slightly, by increasing population size slightly at low frequencies and depressing them at high frequencies.

Adding autocorrelation to year types reduced adult population size, and the reduction was proportionately more severe at higher degrees of autocorrelation (for example, increasing autocorrelation from 0 to 0.1 reduced N_6 by 2%, but a change from 0.7 to 0.8 reduced N_6 by 13%). This occurred because the probably that a flood year is followed by several growth-favorable years decreases as autocorrelation among years increases. Forcing floods to recur at regular intervals produced results similar to those in Fig. 4, but populations were higher than those values if intervening years were growth years. The largest adult population size possible given the vital rates used, 9430 adults or 66% of available habitat covered in mature cottonwood on average, occurred with floods every five years followed by four growth years.

DISCUSSION

The primary objective of this model was to begin with the fundamental vital rates of cottonwood populations—stage-specific births and deaths, and how these relate to river hydrology—and ask to what degree these describe the complex patterns observed in natural cottonwood forest seres. The model recovered several emergent properties of cottonwood populations that were not explicitly modeled. First, the cottonwood vital rates measured from field and lab experiments predicted a quasi-equilibrium population very close to the actual population size measured from aerial photos (±1%). This was not constrained by the model to be the case, as most vital rates were not obtained from data specific to this study site, and quasi-equilibrium population sizes were ergodic with respect to starting population size (i.e., starting size does not dictate quasi-equilibrium population size). In addition, sensitivity and elasticity analysis show that even small changes in vital rates may result in quasi-equilibria that are much higher or lower (e.g., a decrease in self-thinning rate of only 0.01 would have increased adult population size from 7200 to 8200). This result suggests that although vital rates derived from field studies can produce realistic model dynamics, model sensitivity makes accurate vital rate estimation essential. Second, the boom–bust dynamics of seedling abundance observed in the model is similar to the dynamics seen in natural populations. Seedling establishment is often observed to be high following scouring floods (Fenner et al. 1984, Scott et al. 1997), but mortality from subsequent floods will often limit recruitment into older stages. Third, the ~5–15 yr return interval of peaks in mature cottonwood populations that are observed in the model is similar to the dynamics observed in natural cottonwood stands (Scott et al. 1997, Stromberg 1998, Cooper et al. 2003). Sequences of years exhibiting specific hydrologic characteristics have been shown to be more important than single year events (such as flood magnitude on a given year) on the Missouri River, in the United States. (Scott et al. 1997, Auble and Scott 1998). Taken together, these emergent model properties suggest that many of the complexities of cottonwood population dynamics—boom/bust seedling abundances, frequency of mature cottonwood stand recruitment, and fluctuation around a quasi-equilibrium population size—arise simply from the interaction of vital rates and hydrograph variability. These results suggest that simple population models that are neither spatially explicit nor individual based may capture many of the important dynamics of cottonwood populations. This also provides support for the idea of river hydrology as a "master variable" that controls other key mechanical, chemical, and ecological processes on floodplains. Many variables associated with flooding, such as channel meandering rate, floodplain geochemistry (which is related to frequency and duration of inundation and hydraulic conductivity of floodplain strata), and other important fluvial geomorphic processes are incorporated into hydrologically based models such as ours because such processes are driven by river hydrology.

The sensitivity and elasticity of adult population size to different sources of mortality could be useful for managing cottonwood forests because they identify where small changes in a mortality rate can have large
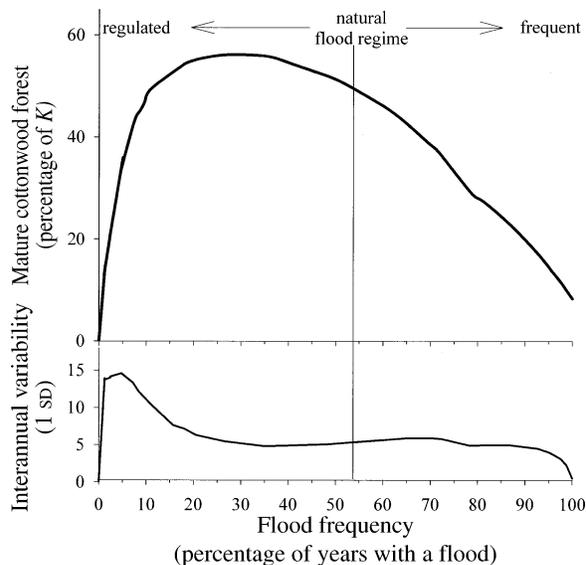
FIG. 4. Effect of altered flood regime on mature cottonwood populations. Flood frequency varies from frequent (a scouring flood every year) to highly regulated (no floods). Top panel: mature cottonwood forest is most abundant when floods are slightly less frequent than the natural flood regime. Bottom panel: interannual variability in coverage is lowest at intermediate and high flood frequencies, while low flood frequencies result in variable populations that sometimes disappear locally from reaches.

effects on population dynamics. Conversely, they identify the cottonwood life stages that matter least for overall population dynamics. Elasticity to both flood and drought mortality followed the same general pattern, with the highest values for stages 1 and 6, and elasticity to adult senescence rate (apart from flood or drought mortality) was also high. Thus, if a management goal is to increase the amount of mature cottonwood forest over the long term, management tactics that increase survivorship of seedlings and adults should yield the highest return on investment, while managing for increased survivorship of the middle stages would accomplish less. The fact that adult population size was about twice as sensitive to changes in flood mortality vs. drought mortality emphasizes the importance of flooding for cottonwood population dynamics on rivers such as the Yampa. The difference was driven in part because flood years occur twice as frequently as drought years on this river (53% vs. 22%). The relative importance of floods versus droughts could differ on rivers that experience these in other proportions.

The high sensitivity of adult population size to adult senescence rate, a_6, suggests that forces affecting this rate should have large consequences for long-term population dynamics. Increased mortality from fires (Davis et al. 2002), disease outbreaks (Andersen 2002), or beaver activity (Johnson and Naiman 1990, Andersen and Cooper 2000) would likely alter a_6. Although adult

population sizes should reflect changes in a_6, the assumption of quasi-equilibrium stand dynamics might not hold in these instances. For example, mixed cottonwood–tamarisk (*Tamarix* spp.) stands destroyed by fire or disease might be succeeded by pure stands of tamarisk. Tamarisk has the ability to resprout rapidly following fire, but most species of cottonwood do not (the exception being *Populus angustifolia* which may resprout following low intensity fire; Gom and Rood 1999).

The model also shows that, even under natural flow regime conditions, opportunities for invasion by competitors might occur when large areas of cottonwood habitat are temporarily unoccupied. In this single-species model unoccupied areas eventually become available for cottonwood recruitment, but these ''windows for invasion'' might represent critical times for interspecific competition. In this kind of non-equilibrium case, the model could be adjusted to allow K_T to decrease as cottonwood habitat is lost to competing vegetation.

An unexpected outcome of the model simulations of highly regulated flow regimes is that such regimes result in variable populations prone to local extinction, whereas frequent floods result in small but stable populations. This results from the fundamental tradeoff between floods as mortality-causing vs. recruitment-enabling events. When floods are frequent, recruitment occurs almost every year but population sizes are suppressed by high flood mortality, resulting in small but stable populations. When floods are rare, adult stands senesce over the course of decades and are then suddenly replenished when a scouring flood occurs, resulting in high year-to-year population variability and occasional extinction when return intervals of floods are long. This result underscores the importance of floods and flood-generated processes for the maintenance of viable cottonwood habitat (Scott et al. 1996). Because this single-species model assumes that space freed by senescing adults remains available for seedling recruitment elsewhere on the floodplain (rather than transitioning to another forest type), seedling recruitment may be overestimated when recruitment-generating floods are rare. This is another case where the assumption of quasi-equilibrium could be relaxed to accommodate other species interactions.

The exercise of using a model to synthesize data on cottonwood vital rates with the current understanding of riparian processes supports many established ideas and generates some new ones. The population fluctuations, dynamics of adults vs. seedlings, and quasi-equilibrium population sizes observed in the model results were similar to natural populations, yet none of these were included explicitly in the model. Despite congruence with known population dynamics, the model omits processes that undoubtedly affect specific cottonwood forests. In many cases these processes could be incorporated by changing the vital rates for certain

stages (fire, disease, insect, beaver damage, ice scour) or by relaxing a simplifying assumption (competition with other species). Ultimately, however, this model is intended to provide a framework for understanding cottonwood populations that can be tailored to specific cottonwood forests or conservation objectives.

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