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Abstract To enable assessment of risks of water management to riparian ecosystems at a regional scale, we developed a quantile-regression model of abundance of broadleaf cottonwoods (*Populus deltoides* and *P. fremontii*) as a function of flood flow attenuation. To test whether this model was transferrable to narrowleaf cottonwood (*Populus angustifolia*), we measured narrowleaf abundance along 39 river reaches in northwestern Colorado, USA. The model performed well for narrowleaf in all 32 reaches where reservoir storage was <75% of mean annual flow. Field data did not fit the model at four of seven reaches where reservoir storage was >90% of mean annual flow. In these four reaches, narrowleaf was abundant despite peak flow attenuation of 45–61%. Poor model performance in these four reaches may be explained in part by a pulse of narrowleaf cottonwood expansion as a response to channel narrowing and in part by differences between narrowleaf and broadleaf cottonwood response to floods and drought.

Key words cottonwood; flow alteration; streamflow management; ecological limits of hydrologic alteration (ELOHA); environmental flows; index of flow modification (IFM); *Populus*; riparian vegetation

Réponses riveraines à la réduction des débits de crue: comparaison et différences entre peupliers à feuilles larges et à feuilles étroites

Résumé Pour permettre une évaluation des risques de la gestion de l'eau dans les écosystèmes riverains à l'échelle régionale, nous avons développé un modéle de régression sur les quantiles de l'abondance de peupliers à feuilles larges (*Populus deltoides* et *P. fremontii*) en fonction de l'atténuation du débit de crue. Pour tester si ce modèle était transférable au peuplier à feuilles étroites (*Populus angustifolia*), nous avons mesuré l'abondance des peupliers à feuilles étroites le long de 39 biefs de rivières dans le Nord-Ouest du Colorado, Etats-Unis. Le modèle a donné de bons résultats pour les peupliers à feuilles étroites dans les 32 biefs où le réservoir de stockage contenait moins de 75% du débit moyen annuel. Les données de terrain ne correspondaient pas au modèle pour quatre des sept biefs où le réservoir de stockage contenait plus de 90% du débit moyen annuel. Dans ces quatre biefs, les peupliers à feuilles étroites étaient abondants malgré l'atténuation du débit de pointe de 45 à 61%. Les mauvaises performances du modèle dans ces quatre tronçons peuvent en partie s'expliquer par une poussée de peupliers à feuilles étroites en réponse à un rétrécissement de la section, et en partie par des différences de réponse aux inondations et à la sécheresse entre les peupliers à feuilles étroites et larges.

Mots clefs peuplier ; altération du débit ; gestion de l'écoulement fluvial ; limites écologiques d'altération hydrologique ; débit environnemental ; indice de modification de débit ; *Populus* ; végétation riveraine

INTRODUCTION

Rivers are becoming increasingly stressed around the globe as societies develop water for human needs (Vörösmarty *et al.* 2005). Understanding how water development and management affect river ecosystems is critical to ensuring that the values provided by these ecosystems are not lost. The modification of river flow regimes has, in many cases, altered riparian vegetation, including plant species richness (Jansson *et al.* 2000, Nilsson and Svedmark 2002), plant growth (Stromberg and Patten 1990), community composition (Merritt and Cooper 2000, Merritt and Wohl 2006) and the loss of riparian forests (Swift 1984, Rood and Mahoney 1990). Riparian vegetation supports ecosystem function in streams and rivers by providing shade, habitat and food for terrestrial and aquatic animals, stabilizing banks, intercepting and sequestering contaminants and contributing coarse woody debris that creates diversity in aquatic habitats (Gregory *et al.* 1991, Naiman and Décamps 1997, Davies-Colley and Quinn 1998, Patten 1998, Pusey and Arthington 2003, Scott *et al.* 2003). Throughout western North America, cottonwoods (*Populus* spp.) are the predominant mid- and low-elevation riparian trees and are especially dependent on the river flow regime and flow-mediated fluvial processes (Rood and Mahoney 1990, Patten 1998, Friedman and Lee 2002, Merritt *et al.* 2010).

It is critical that we understand the consequences of flow alteration for cottonwoods in the Rocky Mountain West, where water demand for human use is high and intensifying. Multiple methods exist for relating flow regime to attributes of riparian vegetation (reviewed in Merritt *et al.* 2010). These include detailed, site-specific analyses of tree growth (Stromberg and Patten 1990), population cohorts (Baker 1990) and flood-driven point bar migration (Richter and Richter 2000). However, these methods are, in isolation, not scalable to entire basins and they do not necessarily provide generalizable models. Methods based on analysis of streamflow parameters (e.g. Richter *et al.* 1996) can be applied basin-wide, but, in the absence of a quantifiable model of the relationship between streamflow dynamics and cottonwood function, species response can only be assumed based on similar species in other settings, or based on ecological principles.

Understanding the consequences of water management for ecosystem function at a watershed scale has been facilitated through development of the Ecological Limits of Hydrologic Alteration (ELOHA) framework (Poff *et al.* 2010). This framework is currently being tested and refined in many locations throughout the world (Kendy *et al.* 2012). An important step in the ELOHA approach is the formulation and verification of models that describe relationships between streamflow alteration and ecological responses (referred to as flow–ecology models). A watershed flow evaluation tool, based on the ELOHA framework, was developed for three rivers in northwestern Colorado that are major tributaries of the Colorado River, the master drainage of the intermountain western USA (Sanderson *et al.* 2011, 2012a, 2012b), and a flow–ecology model for cottonwood was developed in this context. The challenge in developing such a flow–ecology model was to include enough detail to project likely outcomes at specific locations while being sufficiently general to apply at many locations across large watersheds. The model also needed to be compatible with the hydrologic models commonly used by river managers.

Flow–ecology models for riparian cottonwood can be developed from an understanding of the mechanisms by which cottonwoods reproduce, establish and grow, as functions of elevation, hydrogeomorphic setting, sediment dynamics and multi-year flow dynamics. Among different species of cottonwoods (genus *Populus*, including species commonly referred to as "poplar"), there are both similarities and differences across these characteristics. Both narrowleaf and broadleaf cottonwood species are abundant in the headwaters of the Colorado River. Narrowleaf cottonwood refers to *Populus angustifolia* James, section *Tacamahaca*. Broadleaf cottonwood refers to *Populus deltoides* ssp. *wislizenii* (S. Watson) Ecken., section *Aigeiros* (also known as plains cottonwood and Rio Grande cottonwood). Our use of broadleaf cottonwood also encompasses other closely related taxa in the section *Aigeiros*, including *P. deltoides* Marshall subspecies *monolifera* (Aiton) Ecken. and *P. fremontii* S. Watson. The elevational range of narrowleaf cottonwood (1600–2300 m in Colorado; Carsey *et al.* 2003) is higher than broadleaf cottonwood (<2000 m), with about 400 m of overlap in elevation range. The higher elevations tend to be cooler and less arid. Narrowleaf cottonwood are found in geomorphic settings ranging from broad, low-gradient flood plains in alluvial valleys to steep (up to 4% gradient), confined mountain valleys, whereas broadleaf cottonwood is generally restricted to alluvial valleys. Narrowleaf cottonwood reproduce both sexually (Mahoney and Rood 1998, Richter and Richter

2000) and asexually through clonal processes (Mahoney and Rood 1998, Roberts 1999), whereas broadleaf cottonwood reproduces almost exclusively from seed (Rood *et al*. 2007).

The mechanisms by which cottonwoods depend upon streamflow to recruit from seed are well established (Friedman *et al*. 1995, Scott *et al*. 1996, Mahoney and Rood 1998, Cooper *et al*. 1999, Richter and Richter 2000, Karrenberg *et al*. 2002, Shafroth *et al*. 2002, Stromberg *et al*. 2007). Floods remove competing plants and deposit fresh alluvium on aggrading point bars, providing moist, mineral substrate and unshaded conditions for seed germination. The short-lived seeds travel to these surfaces by air or water and their timing must coincide with receding flows to avoid being scoured away (Fenner *et al*. 1984, Mahoney and Rood 1998). Flow recession must be gradual enough for the roots of seedlings to keep pace with dropping water levels (Mahoney and Rood 1998). It may take three years of growth before plant roots achieve reliable access to groundwater, assuming that they are not browsed, desiccated or scoured away (Auble and Scott 1998, Cooper *et al*. 1999, Polzin and Rood 2006, Rood *et al*. 2007). Given the rarity of this combination of environmental conditions, even under natural flow conditions, successful recruitment might only occur every 3–5 years in wide alluvial valleys (Scott *et al*. 1996, Rood *et al*. 2007), and the total area of mature cottonwoods along a river may be 50% or less (Lytle and Merritt 2004).

Mechanisms underlying reproduction of narrowleaf cottonwood through the clonal process are less well understood. Clonal processes, including root suckering, may be induced by flood-scarification, but can also be induced by other processes such as colluvial disturbance (Friedman *et al*. 2006). If narrowleaf cottonwood depends on peak streamflows, either for seedling recruitment or for clonal processes, then narrowleaf might show a response to peak flow attenuation similar to that observed for broadleaf cottonwood.

Due to natural variability in flows, the abundance of cottonwood at sites with minimal flood attenuation may range from 0 to 100%. Based on this understanding of flood dependence for reproduction from both seed and clonal processes, we hypothesized that flood flow attenuation would limit the maximum abundance of narrowleaf cottonwood, with increasing constraint as flood attenuation increases. We further hypothesized that the response to flood flow reduction would be similar for narrowleaf and broadleaf cottonwoods. To test these hypotheses, we: (a) developed flow–ecology models for

broadleaf cottonwood abundance as a function of flood attenuation using data from across the western and southwestern United States (Merritt and Poff 2010), and (b) collected data on narrowleaf abundance at sites across northwestern Colorado representing a range of flood attenuation and examined how well the new data fit the broadleaf model. For the few sites where the response of narrowleaf did not fit the broadleaf model, we examined characteristics of both narrowleaf cottonwood and the anomalous sites to identify factors that may explain differences in response between the two cottonwood types.

STUDY AREA

The study area for broadleaf cottonwoods included sites across four large river basins, the Great Basin (Truckee, Carson and Humboldt Rivers), the Colorado River and tributaries, the Rio Grande River and the Pecos River Basins (Merritt and Poff 2010). The total area covered by the study sites is large, with the Colorado River Basin alone covering 640 000 km^2. Site elevations are in the range 80–1990 m a.m.s.l. Mean annual precipitation across the study area is 100–420 mm, and mean temperatures are 10.4–22.5°C. Snowmelt from mountainous headwaters feeds these rivers, and flows for the southernmost sites were also influenced by monsoonal rains in summer.

The study area for narrowleaf cottonwood extended to higher elevations (<2650 m a.m.s.l.) across three basins in Colorado, including the Yampa River, White River and Upper Colorado River (above the Gunnison River confluence), with the basin area totalling 53 000 km^2. Mean annual precipitation is 280–880 mm and mean temperatures are 9.2–17.9°C. More than half the sites surveyed in Colorado could be classed as semi-arid, and the rest as moist (zero water balance threshold between 346 and 492 mm precipitation/year, depending on temperature). The snowmelt flow regime of these rivers produces predictable timing of peak flows, typically in late spring or early summer (i.e. between late April and early July).

METHODS

Developing flow–ecology models for broadleaf cottonwood

Merritt and Poff (2010) described a flow–ecology relationship for broadleaf cottonwood using data

collected at 64 reaches on 13 perennial rivers, including several rivers in Colorado. Reaches were chosen to represent varying degrees of flow alteration and therefore selection depended on adequate flow records.

To assess the abundance of adult cottonwoods (>5 years old), a 200-m-long section of river was randomly selected and, at every metre increment, adult cottonwood occurrence (presence/absence) was observed for a perpendicular transect that ran across the entire flood plain (Merritt and Poff 2010). This provided frequency of occurrence across 200 1-m-wide transects from which we calculated per cent abundance.

$$\% \text{ abundance} = [(\text{number of transects containing 1 or more adult cottonwood})/200] \times 100 \quad (1)$$

The 200 1-m sections were replicated by spacing additional sections every 0.5 km over the reach of interest. For recruitment, the presence of 2–5-year-old saplings was recorded for each 200-m-long section. Plants less than 2 years old were not included, because the mortality of young trees is high and does not yet indicate successful regeneration.

To relate broadleaf cottonwoods to flow, Merritt and Poff (2010) used a multivariate indicator of hydrologic alteration, termed the Index of Flow Modification. This index was calculated using principal component analysis of eight flow metrics, from which the axes scores were used to calculate the Euclidean distance of each site from the centroid of relatively unregulated rivers. The index performed well in representing flow alteration (accounting for 74% of variation in flow data), while dealing with collinearity among the various flow metrics.

The flow data needed to calculate Merritt and Poff's Index of Flow Modification were not available at most of our sites in Colorado, so we had to develop an alternative model that used a simpler independent variable representing flow alteration. We developed this alternative model using US Geological Survey (USGS) stream gauge data from the same sites as used by Merritt and Poff (2010), but we selected flow metrics that were compatible with StateMod (CDWR and CWCB 2009). We used the StateMod hydrologic model to estimate streamflow at ungaged sites in Colorado (see Supplementary Material, Table S1, for USGS gauges used and their periods of record).

Merritt and Poff (2010) established the statistical significance of the relationship between this cottonwood data set and flow alteration, and accounted for collinearity between flow metrics (by using principal components analysis). Our analysis used these same data to identify which StateMod compatible flow metric is the best proxy for the complex flow dynamics that explain cottonwood abundance. The flow metrics we chose to assess as alternatives to the Index of Flow Modification were selected because they are mechanistically linked to broadleaf cottonwood recruitment, including daily series of 5- and 10-year return flood; 1-, 7-, 30- and 90-day maxima; and 1-, 7-, 30- and 90-day maxima for "wet" years only, wet years being defined as 30% exceedence mean annual flow (see Bradley and Smith 1986, Scott *et al.* 1996, Mahoney and Rood 1998, Rood *et al.* 2007). The flow metrics were calculated using Indicators of Hydrologic Alteration, Version 7.1 (Richter *et al.* 1996), and subsequently converted to per cent alteration as:

$$\% \text{ alteration} = [(\text{post-alteration flow}) - (\text{pre-alteration flow})/ (\text{pre-alteration flow})] \times 100 \quad (2)$$

Quantile regression (Cade and Noon 2003) was used to describe the upper bound for broadleaf cottonwood response to flow, using Blossom statistical software (Cade and Richards 2007). The 90th percentile upper bound represents the constraint on the maximum expected abundance due to flow alteration. Under natural conditions, abundance can be expected to range from 0 to 100%; other factors outside the flow manager's control, such as grazing or fire, can also limit cottonwood abundance, keeping abundance below the upper bound (see Dunham *et al.* 2002, Cade and Noon 2003). The significance of the relationships was tested (null hypothesis: slope = 0) using a permutation rank score statistic (Cade *et al.* 2006) calculated from 5000 permutations, and the best model was identified as the one having the lowest *p*-value.

To test the robustness of the 90-day metric, we also tested how well it performed in a flow–ecology model to estimate the occurrence of juvenile broadleaf cottonwoods (see Merritt and Poff 2010). To construct this model given presence/absence data, we used a generalized linear model with a binomial distribution and logit link (logistic regression; Merritt and Poff 2010). Flow metrics were compared using

the Akaike Information Criterion (AIC), together with a *p*-value (χ^2 statistic) to confirm that the best model was statistically significant.

Data collection on narrowleaf cottonwood

To test the performance of the broadleaf cottonwood model when applied to narrowleaf cottonwood, we collected data on narrowleaf cottonwood abundance and geomorphic setting at 68 sections along 39 reaches of 21 streams in an elevation range of 1550–2650 m during July and August 2011 (Fig. 1; locations in Supplementary Material, Table S2). Sites were chosen among 223 locations for which we had modelled flow data. Potential sites were excluded if they were higher than 2650 m a.m.s.l., since cottonwoods generally do not occur above this elevation. Canyons, gorges and reaches with slope >4% were also excluded because cottonwood recruitment in these geomorphic settings was not expected to be primarily flow-mediated. Additional sites were eliminated because they were on private lands that we could not access. At least one section of stream was surveyed (200 m) at each reach. The location of the first section was randomly selected within the accessible reach, and subsequent sections were spaced every 500 m, for up to four sections (accessible reach length permitting).

Data on riparian vegetation were collected along each 200-m section mostly adhering to the methods of Merritt and Poff (2010). We differed from Merritt and Poff by recording the number of visible narrowleaf saplings (2–5 year old) for each 200-m section, up to a maximum of 50 plants. To determine the age

Fig. 1 Locations of the Colorado River Watershed in the United States, and the Yampa, White and Colorado River Watersheds in the state of Colorado.

class, we relied primarily on stem diameter (10–30 mm at ground level for 2–5 years old), having confirmed these size–age relationships from growth-ring counts at both high- and low-elevation sites. We also collected data on willow (*Salix* spp.) abundance in the same manner as for cottonwood.

The metric used in the flow–ecology relationship for broadleaf cottonwoods (wet-year 90-day maximum) was calculated with Indicators of Hydrologic Alteration software (Richter *et al.* 1996) using a daily time series for both current and natural conditions for 1975–2005 (Colorado River) and 1954–2005 (Yampa River) as modelled using StateMod. The percent alteration for this metric was then calculated as for broadleaf cottonwood (see Equation (2)).

Several physical characteristics of sites were estimated using the Geomorphic Valley Classification (Bledsoe and Carlson 2010) and the National Hydrography Dataset (NHDPlus, www.horizon-systems.com/NHDPlus). In addition, we estimated mean channel width for each site from 20 random locations on aerial photographs. Valley width was the median of three estimates: (a) valley width modelled from a digital elevation model (Bledsoe and Carlson 2010), (b) site sketches of riparian width and (c) site sketches of break points in bank slope. Only the latter two estimates were available for the White watershed, as it was not yet classified for the Geomorphic Valley Classification. Water balance (in m^3 $year^{-1}$ m^{-2}) was estimated for the study sites using an equation calibrated to a similar river in Colorado as:

$$\text{Water balance} = \text{ppt}/1000 - 0.1395\exp(\text{tmp}\times0.09182)$$
(3)

where ppt is total annual precipitation (in mm) and tmp is mean annual temperature (in ºC). A negative water balance indicates a semi-arid site with a moisture deficit and a positive water balance indicates a mesic site with a moisture surplus.

Abundance data for cottonwood were compared to the broadleaf cottonwood flow–ecology curve to test applicability of the broadleaf model to narrowleaf. Correlations between abundance of narrowleaf and physical characteristics of sites were explored to develop hypotheses that may explain why some narrowleaf sites did not fit the broadleaf model. Similar correlations were explored for willow to describe how willow-like characteristics of narrowleaf may explain the observations.
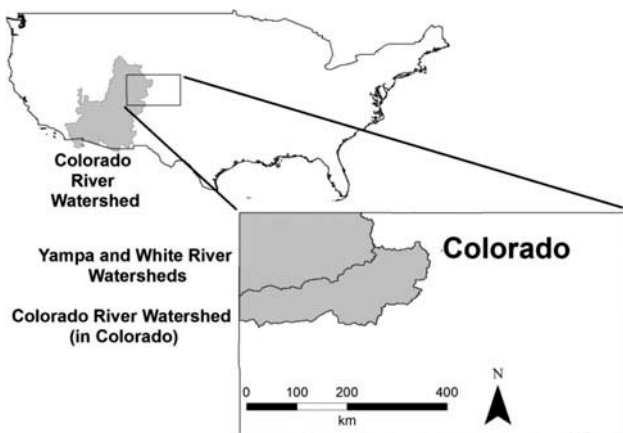
Photo interpretation of temporal changes

During our field work we observed that a portion of the study area supported extensive, multi-age-class narrowleaf cottonwood forests downstream from large dams that have reduced the wet-year 90-day flow magnitude by over 60%. Consequently, we sought to better understand patterns of riparian vegetation change over time by comparing aerial photographs taken prior to dam building (October 1938) with post-dam photographs (2005–2010) over a 39-km length of the Colorado River below the major reservoirs. Unvegetated bars were counted from 1938 images and contemporary vegetation cover was determined from recent aerial photographs (2005–2011) for each 1938 bar. Existing vegetation was categorized as: (1) cottonwood, (2) willow-dominated, (3) other vegetation, (4) partially vegetated or (5) bare (no vegetation). Images from 1947 were also inspected for a subset of locations (reflecting availability), and provided confirmation that the 1938 images were representative of prevailing conditions at that time. This process was repeated for a 2.2-km reach of the Fraser River upstream from the Colorado River confluence—a tributary with large trans-basin flow diversions but lacking large dams. For the Colorado River portion, we investigated how river stage changed pre- and post-dam construction to understand how water levels may be related to observed changes.

RESULTS

Cottonwood flow–ecology relationships

Of the several StateMod-compatible flow metrics analysed, percent alteration of the wet-year 90-day maximum flow produced the best quantile regression model of broadleaf cottonwood abundance ($p = 0.015$, $n = 41$; Table 1). This model describes the constraint imposed by flow alteration. For example, a 50% reduction in the wet-year 90-day maximum flow is expected to reduce the potential abundance of cottonwood by 53% (Fig. 2). The relationship was insensitive to the function used (linear or quadratic), averaging across replicates, or bootstrap section selection (linear coefficients between 1.03 and 1.20). There was a moderately strong correlation ($r = -0.76$) between the wet-year 90-day maximum flow and the multivariate Index of Flow Modification metric that it is intended to replace. The wet year 90-day maximum flow was also the best predictor variable for cottonwood

Table 1 Comparison of models of cottonwood abundance as a function of flow alteration as represented by a variety of metrics (data from Merritt and Poff 2010). The coefficients and constants describe a 90th percentile boundary calculated using quantile regression (abundance = constant + coefficient × flow alteration). The wet year 90-day maximum flow produced the best model. The multi-metric Index of Flow Modification (IFM, Merritt and Poff 2010) is included for comparison.

Flow alteration metric	Constant	Coefficient	N	p-value
5-year return	0.8550	−0.3013	45	0.564
10-year return	1.0008	0.0320	46	0.459
90-day max.	1.0485	1.2062	44	0.027
30-day max.	1.0347	1.0405	44	0.095
7-day max.	0.9997	0.4779	49	0.032
1-day max.	1.0895	1.0541	45	0.041
Wet year 90-day max	1.0051	1.0379	41	0.015
Wet year 30-day max	1.1323	1.0725	43	0.184
Wet year 7-day max	1.0000	0.0000	46	0.782
Wet year 1-day max	1.2153	0.9687	41	0.950
IFM LN($Y + 1$)	0.7756	−1.2723	64	0.001
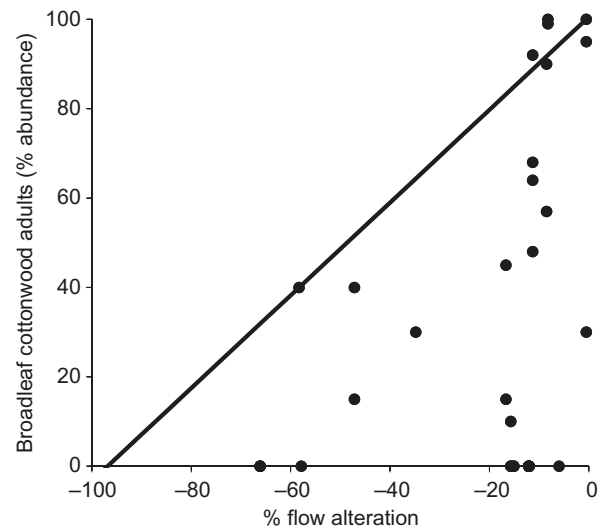
Fig. 2 Per cent abundance of adult cottonwood as a function of flow alteration. The solid line is the 90th percentile quantile regression model that best describes the abundance of adult broadleaf cottonwood as constrained by peak flow reduction. The model is % abundance = 1.038 × % flow alteration + 1.005 (rank score p-value = 0.015), where % flow alteration is the difference under current and natural conditions of the 90-day peak flow magnitude in the wettest three out of 10 years.

recruitment and was closest to the Index of Flow Modification in explanatory power (Table 2).

In comparing the narrowleaf data (abundance *vs* flow alteration) to the broadleaf flow–ecology relationship, we found that all reaches where reservoir storage in the watershed is <75% of mean annual

Table 2 Measures of performance for models of recruitment of broadleaf cottonwood that use a simpler alternative independent variable as compared to the multi-metric Index of Flow Modification (IFM) from (Merritt and Poff 2010). Of the models considered, the best fit between the model and the data (i.e. lowest AIC) used the wet year 90 day maximum as the independent variable.

	AIC	p-value Pr(>Chi), d.f. 114
5-year return flow (daily)	105.7	0.0009
90-day max.	113.0	0.0562
Wet year 7-day max.	109.6	0.0077
Wet year 1-day max.	106.1	0.0012
Wet year 90-day max.	103.6	0.0003
IFM	93.6	<0.0001

flow, narrowleaf abundance was below the broadleaf 90th percentile line (Fig. 3). We also found that there are four reaches with narrowleaf abundance values above the 90th percentile line despite pronounced flow alteration. All of these reaches had reservoir storage >90% of mean annual flow.

In addition to flow alteration, water balance emerged as a physical factor that may also be governing narrowleaf abundance. Narrowleaf cottonwood generally is found only below approximately 2650 m, but we found that among our sites the precise limit was influenced by the geomorphic settings. At the highest elevations (above 2500 m),
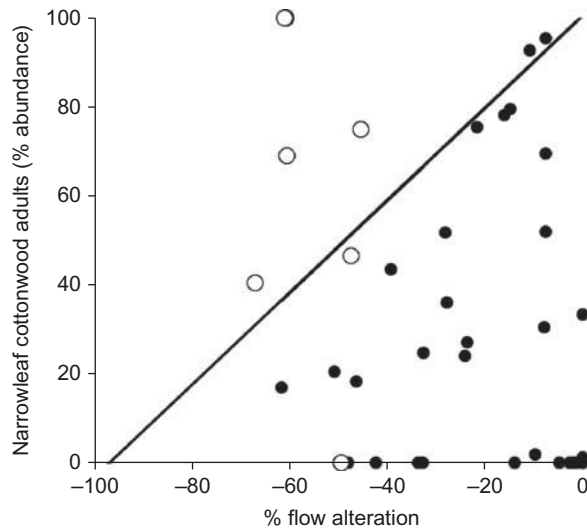
Fig. 3 Narrowleaf cottonwood abundance *vs* flow alteration together with the broadleaf cottonwood flow–ecology relationship (solid line). Open circles represent sections where upstream reservoir storage capacity is 90% or more of annual runoff, and black dots—less than 75%.

narrowleaf were found only in steep, confined settings where streamside soils appeared less moist. At these higher elevations we observed wetter soils by unconfined streams, and at these locations willow tended to be dominant. The interaction between valley confinement and water balance may explain this moisture gradient, with willow being more abundant than narrowleaf cottonwood in unconfined valleys with positive water balance (Fig. 4), although we did not collect detailed soil moisture or groundwater data that would allow us to analyse this result more closely.

Temporal changes downstream from large reservoirs

Reduced flows have lowered water levels of the Colorado River downstream from Granby Dam (data obtained for USGS 09019500 because the datum has remained unchanged), where the 75th percentile water level was 0.35 m lower than predam (using stage recorded for streamflow measurements, comparing 1934–1949 to 1983–2011 for April–October; Granby Dam was completed in 1950). Note that even the pre-dam data post-date most of the Grand Ditch (constructed from 1890 to 1936), which intercepts the flow of 13 headwater tributaries of the Colorado River. Woods (2001) reported large flow reductions by Grand Ditch (more than 50% of August flow below the ditch), which translates to an approximately 10% reduction in mean flow downstream from Granby Dam.

Reduced high flows downstream from Granby Dam also resulted in reduced frequency of channel scouring and subsequent reduction in the active channel area. The active channel as measured in aerial photos exceeded 15 m in many locations before Granby Dam was built. The change in unvegetated channel width at this site was pronounced, narrowing by 63% (comparing aerial photograph 10/25/1938 to 8/20/2007; Fig. 5), while the channel location remained relatively constant.

During this same period, narrowleaf forest increased in extent by colonizing 36 of the 61 gravel bars that were unvegetated in 1938. The other 25 bars were colonized by willow, such that all 61 bars are now vegetated. This narrowleaf colonization was more pronounced upstream from a tributary that serves as major sediment source (cottonwoods colonized 32 of the 36 bars upstream from the source). Conversely, most colonization by
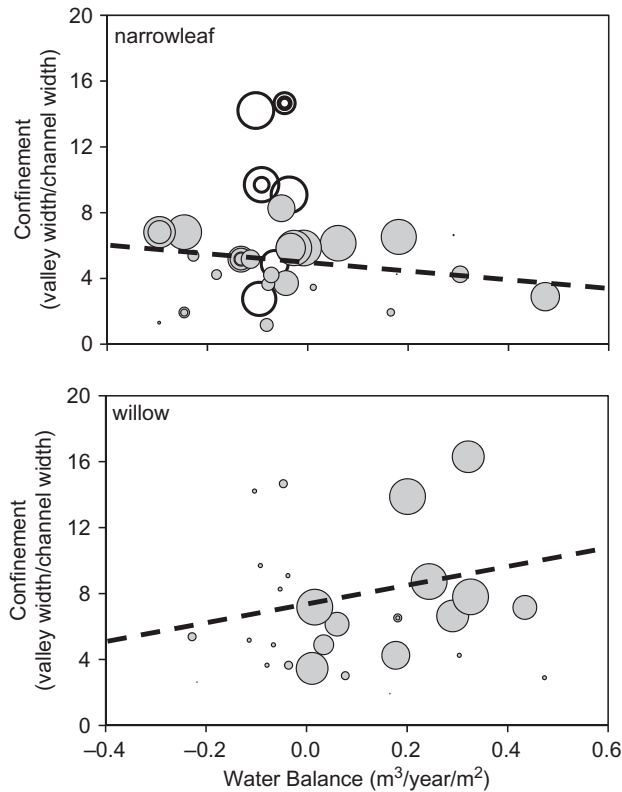
Fig. 4 Confinement *vs* water balance for sites with narrowleaf cottonwood (top) and willow (bottom). Size of each data point represents abundance. Trendlines that indicate apparent moisture gradients from low moisture for confined streams with negative water balance to high moisture for unconfined streams with a positive water balance are weighted least-squares regression with the confinement–water balance relationship weighted by abundance of narrowleaf (*F* statistic: 0.80 on 1 and 40 DF, *p*-value: 0.38) and willow (*F* statistic: 1.447 on 1 and 35 DF, *p*-value: 0.2371). Data points from river segments with 90% or more reservoir storage upstream are distinguished by open circles.

willow occurred downstream from the sediment source (13 of the 17 bars dominated by willow). The Fraser River, a tributary to the Colorado River, provides a temporal reference over the same period (1938–2011), with no major dams used for its transbasin diversions. Willow remains dominant for the Fraser reach upstream from the Colorado confluence, with scattered narrowleaf trees only colonizing two bars. Unlike the Colorado River, unvegetated bars are still present today along the Fraser River (10 bars in 1938, and 10 bars in 2011, over the same 2.4-km reach). The location of bars has changed for all but one bar, reflecting active meandering of the Fraser River channel, in contrast to the more stable Colorado.

DISCUSSION

We were able to define a flow–ecology model for broadleaf cottonwood (*Populus deltoides* and *P. fremontii*) where the flow metric was compatible with StateMod, an existing hydrologic model that provides daily flow estimates for natural and current flow management conditions. The relationship was expressed as a constraint (quantile regression 90th percentile; Cade and Noon 2003) because both natural flow variability and other factors outside the flow managers' control, such as logging or cattle grazing, can also limit cottonwood abundance. In their application of this model to riparian forests across watersheds totalling more than 53 000 km², Sanderson *et al*. (2012a, 2012b) found that the characterization of this flow–ecology relationship worked well with this hydrologic model.

Our application of the broadleaf cottonwood model to narrowleaf cottonwood revealed that narrowleaf cottonwood has a more complicated relationship to streamflow alteration than do broadleaf cottonwoods. For all 32 reaches where reservoir storage was <75% of mean annual flow, the broadleaf model was supported for narrowleaf. For four of the seven reaches where reservoir storage was ≥90% of mean annual flow, narrowleaf cottonwood was abundant despite peak flow reduction of 45–61%.

Analysis of other physical conditions at our narrowleaf sites, combined with our aerial photograph analysis, offered some insight into possible factors that may explain high cottonwood abundance downstream from large reservoirs. Our analysis of aerial photographs showed clearly that narrowleaf woodlands have expanded since dam construction, colonizing 32 of 36 gravel bars that were unvegetated prior to dam construction. During this period of narrowleaf expansion, active channel width decreased 63%. Similar reductions in channel width, followed by a period of cottonwood recruitment, have been documented in other western rivers (Johnson 1994, Shafroth *et al.* 2002).

Changes in multiple flow-mediated processes likely combine to result in these changes. In addition to reduced supply of fine sediment (Ward and Eckhardt 1981, Verstraeten and Poesen 2000), flow regulation has lowered stream water levels (75th percentile water level was 0.35 m lower at flow recorder site after Granby Dam) and reduced riparian flooding. This likely translated to lower groundwater levels, as it has upstream from Granby Dam, as described by Woods (2001). These changes have

Fig. 5 Aerial photographs of the Colorado River above Troublesome Creek (Lat. 40.055°N, Long. 106.29°W), comparing pre-dam 1938 (23 October) to post-dam 2005 (17 June). The active channel decreased on average 63% during this period, and point bars and islands have been colonized by narrowleaf cottonwood and willows.

likely resulted in less scouring of higher flood-plain surfaces and reductions in the extent of saturated soils, both of which would allow cottonwood and/or willow to successfully recruit on bare surfaces, as we observed in the aerial photographs.

Cottonwood establishment following flood flow attenuation is well-documented. It is less clear if observed changes occur over a few years or several decades. In one detailed study (Johnson 1994), cottonwood expansion did not stabilize until more than five decades after major reservoirs that altered flow were constructed. Establishment of new trees at our narrowleaf sites is still occurring, based on our observation of many seedling and juvenile trees, suggesting that either we are in a century-long process of

equilibration, or other dynamics are operating that support narrowleaf recruitment despite flood flow alteration (or some combination of the two). Given that the reduction in seedling recruitment following flood attenuation is well established elsewhere, it may be that the post-dam recruitment we observed has resulted from clonal processes. To understand how clonal recruitment may be maintained under conditions of highly altered flood flows, it is worthwhile to contrast the biology and habitat of narrowleaf and broadleaf cottonwoods (Table 3).

Disturbance promotes both seedling and clonal recruitment in cottonwoods. However, the mechanisms by which that recruitment is promoted by disturbance differ between the two modes of

Table 3 Contrast between broadleaf and narrowleaf cottonwoods, in terms of typical distributions and life history traits. These characteristics reflect our field observations during the present study, along with information provided in the papers cited.

	Broadleaf cottonwood	Narrowleaf cottonwood	Source
Systematics			
Species	*Populus deltoides* and *P. fremontii*	*P. angustifolia*	Weber and Wittmann (2001)
Section (sub-genus)	*Aigeiros* "cottonwoods"	*Tacamahaca* "balsam poplars"	Eckenwalder (1984)
Related species	*P. nigra* (Eurasia)	*P. balsamifera*; *P. trichocarpa*	
Elevation and climate			
Altitude	Lower	Higher	Boles and Dick-Peddie (1983), Keim *et al.* (1989), Carsey *et al.* (2003), Floate (2004)
Temperature	Warmer	Cooler	Kalischuk *et al.* (2001)
Precipitation	Lower (arid to moist)	Higher (semi-arid to moist)	Boles and Dick-Peddie (1983)
Growth season	Longer	Shorter	Kalischuk *et al.* (2001)
Typical river environment			
Stream order	Often higher (larger rivers)	Lower	
Slope	Gradual	Steeper	
Alluvial sediments	Finer (sands and silt)	Coarser (sand and gravel to boulder)	Cooper *et al.* (1999)
Flow dynamics	More gradual	Flashier	
Channel dynamics for recruitment	Point bar migration (depositional)	Channel avulsion, braiding, (erosional)	Roberts (1999)
Valley form	Unconfined, meandering channel	Unconfined at lower elevation, to confined at higher elevation	Boles and Dick-Peddie (1983)
Ecophysiology			
Flood (inundation) tolerance	Moderate	Higher	Rood *et al.* (2010)
Drought tolerance	Moderate	Lower	Rood *et al.* (2010)
*Life history**			
Reproduction	Almost exclusively sexual	Extensively clonal	Rood *et al.* (1994), Gom and Rood (1999), Roberts (1999)
Root suckering	Rare	Extensive	Rood *et al.* (1994), Gom and Rood (1999), Roberts (1999)
Flood training	Sparse	Common	Gom and Rood (1999)
Branch propagation	Rare	Sparse	Rood *et al.* (2003)
Coppice regrowth	Common	Extensive	Rood *et al.* (2003)

*Occurrence sequenced as: rare, sparse, common, extensive.

recruitment. Roberts (1999) proposed that erosional processes are critical for stimulating root-suckering by narrowleaf cottonwood, in contrast to depositional processes for broadleaf cottonwood seedlings. Root-suckering can also be triggered by disturbances unrelated to flooding. High-energy streams (slope >4%), canyons and gorges were excluded from this study based on the assumption that landslides in this setting can trigger recruitment independent of flow (Friedman *et al.* 2006). Beaver also trigger root suckering by chewing bark and downing trees (Gom and Rood 1999, Friedman *et al.* 2006), and we observed beaver damage at 23 out of 68 sections. Other research has demonstrated that fire can act as a recruitment-generating disturbance (Rood *et al.*

2007). Ranchers in Colorado report that tractors and other equipment used in haying operations can also induce narrowleaf suckering, presumably through the scarification of shallow roots. We also observed root-suckering at Windy Gap (Colorado River), where one in six trees had been toppled by winds that reached 134 km/h (personal observation, T. Wilding 2011).

Reproductive traits are not the only point of differences between narrowleaf and broadleaf cottonwoods (Table 3). Rood *et al.* (2010) demonstrated that narrowleaf cottonwoods have higher flood-tolerance and lower drought-tolerance than broadleaf cottonwood hybrids (*P. × jackii*), concluding that narrowleaf cottonwood is a "willow-like" cottonwood. We observed a transition from narrowleaf

forest to willow shrublands (*Salix* spp. excluding *S. exigua*) with increasing precipitation (for wide valleys), and it is possible that excess moisture constrains narrowleaf cottonwoods at their upper elevation limit. Other authors have observed a transition from cottonwood on coarse soils to willow on finer textured soils that better retain moisture (McBride and Strahan 1994, Roberts 1999). If narrowleaf cottonwoods are intermediate between willows and broadleaf cottonwoods in terms of flood and drought tolerance (see Amlin and Rood 2002, Francis *et al.* 2005, Guilloy *et al.* 2011), then beavers could hasten the transition from narrowleaf to willow by constructing dams that both increase flooding and increase the accumulation of fine sediment that retains soil moisture (Westbrook *et al.* 2006, 2011). In contrast, reduced streamflow caused by water development could reduce soil saturation, thereby making soils more suitable for narrowleaf cottonwood and increasing abundance.

The ability of the scientific community to discern causality among the various factors associated with the observed differences between broadleaf and narrowleaf cottonwoods is additionally confounded by the differences in elevation and geomorphic settings in which the species occur. Our findings suggest that, unlike broadleaf cottonwood, narrowleaf cottonwood may persist or even expand in particular instances where flood flows are strongly attenuated, although it is unknown if or how this persistence can be maintained into the future. As such, there are some conditions under which a model of flood flow attenuation that performs well for broadleaf cottonwood does not perform well for narrowleaf cottonwood. However, broadleaf and narrowleaf cottonwoods also clearly have important similarities, and results from this study suggest that a flow–ecology model of streamflow alteration as a constraint on cottonwood recruitment is useful when applied to both broadleaf and narrowleaf cottonwoods in basinwide assessments of the risk for cottonwood reduction resulting from flood flow attenuation.

SUPPLEMENTARY MATERIAL

Supplementary materials for this paper can be accessed at: http://dx.doi.org/10.1080/02626667.2014.880786.

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