

## REVIEW

# Vulnerability of riparian ecosystems to elevated CO<sub>2</sub> and climate change in arid and semiarid western North America

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## Abstract

Riparian ecosystems, already greatly altered by water management, land development, and biological invasion, are being further altered by increasing atmospheric CO<sub>2</sub> concentrations ([CO<sub>2</sub>]) and climate change, particularly in arid and semiarid (dryland) regions. In this literature review, we (1) summarize expected changes in [CO<sub>2</sub>], climate, hydrology, and water management in dryland western North America, (2) consider likely effects of those changes on riparian ecosystems, and (3) identify critical knowledge gaps. Temperatures in the region are rising and droughts are becoming more frequent and intense. Warmer temperatures in turn are altering river hydrology: advancing the timing of spring snow melt floods, altering flood magnitudes, and reducing summer and base flows. Direct effects of increased [CO<sub>2</sub>] and climate change on riparian ecosystems may be similar to effects in uplands, including increased heat and water stress, altered phenology and species geographic distributions, and disrupted trophic and symbiotic interactions. Indirect effects due to climate-driven changes in streamflow, however, may exacerbate the direct effects of warming and increase the relative importance of moisture and fluvial disturbance as drivers of riparian ecosystem response to global change. Together, climate change and climate-driven changes in streamflow are likely to reduce abundance of dominant, native, early-successional tree species, favor herbaceous species and both drought-tolerant and late-successional woody species (including many introduced species), reduce habitat quality for many riparian animals, and slow litter decomposition and nutrient cycling. Climate-driven changes in human water demand and associated water management may intensify these effects. On some regulated rivers, however, reservoir releases could be managed to protect riparian ecosystem. Immediate research priorities include determining riparian species' environmental requirements and monitoring riparian ecosystems to allow rapid detection and response to undesirable ecological change.

**Keywords:** biotic interactions, climate change, dehydration, heat stress, phenology, soil processes, streamflow, water management

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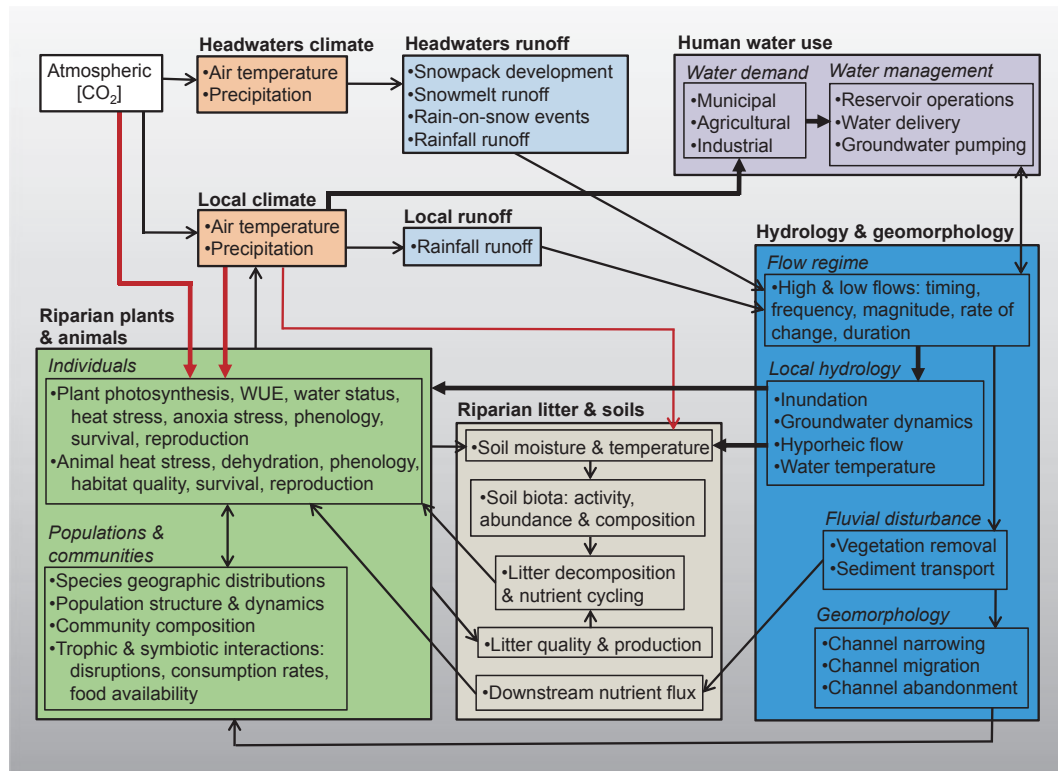
## Introduction

Riparian ecosystems provide critical biological habitat and increase regional biodiversity, particularly in arid and semiarid regions (hereafter, drylands) (Naiman *et al.*, 2005; Sabo *et al.*, 2005). Human activities have constricted many riparian communities (e.g., Jones *et al.*, 2010), expanded others (e.g., Johnson, 1994), and altered their composition and dynamics around the globe (Nilsson & Berggren, 2000; Tockner & Stanford, 2002). Flood control and water storage projects have promoted urban and agricultural development, leading

to deforestation, stream channelization, increased grazing, and nutrient pollution (Patten, 1998; Brinson & Malvarez, 2002). Flow regulation has reduced flood magnitude and frequency, altered flood timing, impeded sediment movement and seed dispersal, and reduced rates of fluvial geomorphic change (Poff *et al.*, 1997; Graf, 2006). Finally, introduced species have replaced native riparian species, particularly in anthropogenically disturbed areas (Richardson *et al.*, 2007).

Increases in atmospheric CO<sub>2</sub> concentration (hereafter [CO<sub>2</sub>]) and associated climate change are likely to further alter dryland riparian ecosystems (Grimm *et al.*, 1997). Changes in [CO<sub>2</sub>] and climate have direct, local effects on plant and animal survival, growth and phenology, biotic interactions, and soil processes (Fig. 1)

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**Fig. 1** Linkages between  $[CO_2]$  and climate change and components of riparian ecosystems in semiarid and arid western North America (SAWNA). Climate-change effects include both alteration of local weather conditions and alteration of climate in headwater regions leading to changes in flow regime. Direct effects of  $[CO_2]$  and climate change on riparian plants, animals, and soils are shown as red arrows. Linkages most in need of elucidation are shown as heavy arrows. Not all potential effects described in the text are shown.

(Rustad *et al.*, 2001; de Graaff *et al.*, 2006; Parmesan, 2006). In addition, climate change will influence riparian ecosystems via indirect, watershed-scale effects on hydrology, water management, and fluvial geomorphology (Fig. 1). Riparian community dynamics are strongly influenced by hydrology and associated fluvial processes sensitive to climate change, including base streamflow, flood magnitude and timing, and water management and use (Poff *et al.*, 1997; Merritt *et al.*, 2010). Climate change is expected to alter riparian hydrology substantially in drylands around the world (Barnett *et al.*, 2008; Nunes *et al.*, 2008; Pittock & Connell, 2010).

Climate-change effects on rivers in semiarid and arid western North America (hereafter, SAWNA) have recently been the subject of considerable research, and may provide insights into likely effects of climate change on dryland rivers globally. Most of this research has focused on hydrology, but also has important and largely unexplored ecological implications. SAWNA riparian ecosystems are temporally and spatially dynamic, changing in size, location, geomorphology, and species composition in response to natural variation in climate and hydrology (Webb *et al.*, 2007), novel

flow regimes from human water management (Poff *et al.*, 2007), and biological invasion (Friedman *et al.*, 2005). These ecosystem dynamics make it challenging to attribute temporal trends in SAWNA riparian ecosystems to increased  $[CO_2]$  or climate change. Therefore, predicting effects of climate change will require examining effects of analogous environmental changes caused by natural climatic variation or water management, as well as testing effects with controlled field and laboratory experiments. Here, we review the literature concerning likely effects of rising  $[CO_2]$  and climate change on SAWNA riparian ecosystems. Specifically, we (1) summarize expected changes in climate, hydrology, and water management, (2) consider likely effects of those changes on riparian plants, animals, biotic interactions, and soil processes, and (3) identify knowledge gaps that hinder predictions of riparian ecosystem responses, environmentally sound water management planning, and adaptation measures.

### Study area

The SAWNA region (Fig. 2) includes deserts, plains, and high plateaus, and is characterized by low annual



Fig. 2 Semiarid and arid regions of western North America (SAWNA), including subregions [adapted from CEC (1997)], major rivers, and the NA monsoon region [adapted from Adams & Comrie (1997)].

precipitation and high warm-season temperatures, leading to high evapotranspiration (CEC, 1997). Precipitation tends to be lower and temperatures tend to be warmer at southern latitudes than at northern latitudes. Outside of the North American (hereafter, NA) monsoon region (Fig. 2), most precipitation falls during winter or spring. Within the monsoon region, some areas receive most precipitation during late summer, whereas others receive a mixture of summer and winter precipitation (Adams & Comrie, 1997). SAWNA river reaches vary widely in drainage area, valley width, channel gradient, streamflow hydrology, groundwater hydrology, parent bedrock material, and sediment

dynamics (Poff, 1996; Naiman *et al.*, 2005). Most large SAWNA rivers are regulated by dams, whereas many smaller SAWNA rivers remain relatively free-flowing (Poff *et al.*, 2007). Riparian forests vary in species composition across the region, but are dominated by native cottonwood trees (*Populus* spp. L.) and willows (*Salix* spp. L.), and the introduced trees tamarisk (saltcedar; *Tamarix* spp. L.) and Russian olive (*Elaeagnus angustifolia* L.) (Table 1) (Friedman *et al.*, 2005; Scott *et al.*, 2009). Riparian ecosystems support a large proportion of SAWNA invertebrate, amphibian, reptile, mammal, and breeding bird species (Warner & Hendrix, 1984; Knopf & Samson, 1994; Naiman *et al.*, 2005), are critical

**Table 1** Dominant woody plant species in SAWNA riparian ecosystems, and available information on their responses to [CO<sub>2</sub>] and temperature

Common name	Latin name	NA native/ introduced	Range in SAWNA	Ecophysiological responses	Citations
Plains cottonwood	<i>Populus deltoides</i> ssp. <i>monilifera</i> (Aiton) Eckenwalder	Native	East		
Rio Grande cottonwood	<i>P. deltoides</i> ssp. <i>wislizeni</i> (S. Watson) Eckenwalder	Native	Southeast		
Fremont cottonwood	<i>Populus fremontii</i> S. Watson	Native	Southwest	↑warming = earlier seed dispersal	Stella <i>et al.</i> (2006)
Black cottonwood	<i>Populus balsamifera</i> L. ssp. <i>trichocarpa</i> Brayshaw	Native	North	ca. 25 °C = optimal photosynthesis 35 °C = ca. 10% ↓photosynthesis	Bassman & Zwier (1991)
Narrowleaf cottonwood	<i>Populus angustifolia</i> James	Native	Higher elevations		
Peachleaf willow	<i>Salix amygdaloides</i> Andersson	Native	East		
Goodding's willow	<i>Salix gooddingii</i> C.R. Ball	Native	Southwest	↑warming = earlier seed dispersal	Stella <i>et al.</i> (2006)
Sandbar willow	<i>Salix exigua</i> Nutt.	Native	Throughout	↑warming = earlier seed dispersal	Stella <i>et al.</i> (2006)
Tamarisk (saltcedar)	<i>Tamarix ramosissima</i> Ledeb., <i>Tamarix chinensis</i> Lour., hybrids	Introduced	Throughout	ca. 25 °C = optimal photosynthesis 42 °C = ca. 50% ↓photosynthesis	Anderson (1982)
Russian olive	<i>Elaeagnus angustifolia</i> L.	Introduced	Throughout		
Eastern cottonwood	<i>P. deltoides</i> Bartram ex. Marsh ssp. <i>deltoides</i>	Native	n/a	↑[CO <sub>2</sub> ] = 40–50% ↑photosynthesis and 80% ↑growth ↑[CO <sub>2</sub> ] = 25–50% ↓stomatal conductance and 20–30% ↑WUE	Will & Teskey, (1997), McDonald <i>et al.</i> (2002), Murthy <i>et al.</i> (2005), Lewis <i>et al.</i> (2010)

Nomenclature follows the USDA plants database (<http://www.plants.usda.gov>). Eastern cottonwood does not occur in SAWNA, but ecophysiological responses are included here because it is closely related to plains and Rio Grande cottonwood.

habitat for Neotropical migrant birds (Skagen *et al.*, 2005), and supply the allochthonous stream inputs that support aquatic communities (Naiman *et al.*, 2005).

### Observed and projected changes in [CO<sub>2</sub>] and climate

[CO<sub>2</sub>] has increased from ca. 280 to ca. 390 ppm (by volume) since 1750, and could exceed 850 ppm by 2100 (IPCC, 2007). SAWNA mean annual temperatures increased by 0.5–2 °C between 1948 and 2002 (Mote *et al.*, 2005; Stewart *et al.*, 2005; Miller & Piechota, 2008), largely as a result of human-induced increases in atmospheric aerosols and greenhouse gases (IPCC, 2007; Barnett *et al.*, 2008). Winter and spring temperatures

increased significantly (Mote *et al.*, 2005; Abatzoglou & Redmond, 2007), spring warm spells shifted earlier (Regonda *et al.*, 2005), and autumn temperatures remained relatively stable (Abatzoglou & Redmond, 2007). Most climate models predict that SAWNA mean annual temperatures will rise by another 2–4 °C in the 21st century (Christensen & Lettenmaier, 2007; Cayan *et al.*, 2008; Seager & Vecchi, 2010).

Trends and predictions for SAWNA precipitation are less clear. Some studies detected increases in precipitation (Mote *et al.*, 2005; Hamlet *et al.*, 2007) and seasonal delays in monsoon rainfall (Grantz *et al.*, 2007) over the last 50–100 years, whereas others found little change (Stewart *et al.*, 2005; Miller & Piechota, 2008). Most precipitation variation can be accounted for by the El Niño

Southern Oscillation and the Pacific Decadal Oscillation (Wolock & McCabe, 1999; Regonda *et al.*, 2005; Grantz *et al.*, 2007; Hamlet *et al.*, 2007). Predictions of future precipitation vary considerably, but most models predict increases in northern NA and decreases in mid- and southern NA (Christensen & Lettenmaier, 2007; IPCC, 2008; Seager & Vecchi, 2010). In particular, winter and spring precipitations are projected to decline in southwestern NA (Seager & Vecchi, 2010). Monsoon rainfall is especially difficult to predict (Lin *et al.*, 2008) and is ignored in most global climate models (Serrat-Capdevila *et al.*, 2007). The frequency and magnitude of extreme rainfall events increased across the United States in the last century (Peterson *et al.*, 2008), and further increases are predicted (Diffenbaugh *et al.*, 2005). In southwestern NA, more intense dissipating tropical cyclones (Bengtsson *et al.*, 2007) may increase late summer rainstorm intensity (Corbosiero *et al.*, 2009), and more frequent El Niño conditions (Cane, 2005) could increase winter precipitation from Pacific frontal storms.

Warming has reduced total snow cover and April 1 snow water equivalents over much of SAWNA in the last century (Barnett *et al.*, 2008; Stewart, 2009). Climate models predict continued declines in mountain snowpack (Cayan *et al.*, 2008; IPCC, 2008; Adam *et al.*, 2009).

Together, warming and changes in precipitation increased SAWNA drought frequency, severity, and duration over the last 50–100 years (Andreadis & Lettenmaier, 2006; Groisman & Knight, 2008). Droughts occur frequently in western NA (CEC, 1997), but recent droughts have been small compared to intense droughts that occurred during a warm period between 900 and 1300 AD (Cook *et al.*, 2004). Several models predict that droughts will intensify in the next century in southwestern NA because of both increased evaporation and decreased precipitation (Cayan *et al.*, 2010; Seager & Vecchi, 2010). Even at northern latitudes, increased evaporation due to warming is likely to outweigh projected increases in precipitation, leading to greater aridity (Smith & Wagner, 2006).

### Observed and projected changes in river hydrology

Warmer temperatures, smaller snowpacks, and precipitation changes are altering SAWNA river flow regimes (i.e., timing, frequency, magnitude, rate of change, and duration of high and low flows) (Regonda *et al.*, 2005; Stewart *et al.*, 2005; Barnett *et al.*, 2008; Clow, 2010). First, spring snow melt peak flows now occur substantially earlier than they did a century ago, and models predict even earlier peaks in the future (Table 2). This change is most apparent for rivers with headwaters at lower elevations, where warmer winter temperatures

lead to rainfall instead of snowfall, rain-on-snow events, and earlier snow melt (McCabe & Clark, 2005; Regonda *et al.*, 2005), but it is also evident at higher elevations (Clow, 2010).

Second, flood frequency and magnitude may be increasing in some regions and decreasing in others. Although few studies have reported trends in peak flow magnitudes in SAWNA rivers (Table 2), simulations suggest that spring flood magnitudes have declined over the last century in cold-winter basins (winter mean temperature  $<-6$  °C) (Hamlet & Lettenmaier, 2007) and models predict smaller spring snow melt peak flows in the future due to smaller snowpacks in the headwaters (Table 2). In contrast, simulations suggest that winter flood magnitudes in California and the northwestern United States [where rivers flow through both humid and dryland areas (Fig. 2)] have increased in moderate-winter basins (winter mean temperature  $-6$  to  $1$  °C) (Hamlet & Lettenmaier, 2007) and models predict larger and more frequent winter floods in the northwestern United States as rain-on-snow events and winter snow melt become more common in the headwaters (Table 2). Predictions of more intense summer monsoon rainstorms and more frequent winter frontal rainstorms in the monsoon region suggest that flooding also will increase on monsoon-dominated rivers (Vivoni *et al.*, 2009).

Third, low flows are projected to become lower on SAWNA rivers under climate change. Late-spring and summer flows have declined on snow melt-dominated rivers over the last century because of smaller snowpacks and earlier snow melt in the headwaters, and are projected to decline further under future climate scenarios (Table 2). Total annual flows and/or base flows in the Colorado River (snow melt-dominated), the San Pedro River (monsoon-dominated), and the Rio Grande (snow melt- and monsoon-dominated) are projected to decline across a range of future climate scenarios because of greater evapotranspiration and perhaps lower precipitation (Nohara *et al.*, 2006; Christensen & Lettenmaier, 2007; Serrat-Capdevila *et al.*, 2007).

### Direct effects of [CO<sub>2</sub>] and climate change on riparian plants

Increased [CO<sub>2</sub>] and climate change will affect riparian plant physiology, phenology, and geographic distributions in many of the same ways that they affect upland plants. However, in riparian ecosystems many of these direct effects will interact with concurrent effects of climate change on streamflow (Figs 1 and 3). We discuss direct effects first, and then discuss interactions with indirect, streamflow-mediated effects. Although increased [CO<sub>2</sub>] and climate change are expected to

**Table 2** Trends in streamflow and model projections of future streamflow in semiarid and arid western North America (SAWNA) snow melt-dominated rivers

Flow component	Historical trends		Model projections	
Total annual flow	Few trends, but 10–50% decrease in northwest United States and Canada	Lins & Slack (1999), Zhang <i>et al.</i> (2001), Burn & Hag Elnur (2002), Regonda <i>et al.</i> (2005), Rood <i>et al.</i> (2005b)	Inconsistent predictions; varies with projected precipitation	Dettinger <i>et al.</i> (2004), Hayhoe <i>et al.</i> (2004), Vanrheenen <i>et al.</i> (2004), Milly <i>et al.</i> (2005), Christensen & Lettenmaier (2007)
Winter and early spring flow	10–60% increase	Regonda <i>et al.</i> (2005), Stewart <i>et al.</i> (2005), Miller & Piechota (2008), Rood <i>et al.</i> (2008)	Projected to increase further	Christensen <i>et al.</i> (2004), Dettinger <i>et al.</i> (2004), Knowles & Cayan (2004), Leung <i>et al.</i> (2004), Maurer (2007)
Late-spring and summer flow	10–20% decrease	Regonda <i>et al.</i> (2005), Stewart <i>et al.</i> (2005), Miller & Piechota (2008), Rood <i>et al.</i> (2008)	Projected to decrease further	Christensen <i>et al.</i> (2004), Dettinger <i>et al.</i> (2004), Hayhoe <i>et al.</i> (2004), Leung <i>et al.</i> (2004), Maurer (2007)
Spring snow melt flood timing	10–30 days earlier	McCabe & Clark (2005), Regonda <i>et al.</i> (2005), Stewart <i>et al.</i> (2005), Moore <i>et al.</i> (2007), Rood <i>et al.</i> (2008), Clow (2010)	Projected to shift still earlier	Christensen <i>et al.</i> (2004), Dettinger <i>et al.</i> (2004), Hayhoe <i>et al.</i> (2004), Leung <i>et al.</i> (2004), Stewart <i>et al.</i> (2004), Maurer (2007), Scibek <i>et al.</i> (2007)
Spring snow melt flood magnitude	Decrease in west Canada	Zhang <i>et al.</i> (2001)	Projected to decrease	Dettinger <i>et al.</i> (2004)
Spring snow melt flood rate of change	More gradual ascension in west Canada	Rood <i>et al.</i> (2008)		
Winter flood magnitude and frequency			Projected to increase in northwest United States and Canada	Leung <i>et al.</i> (2004), Kim (2005)

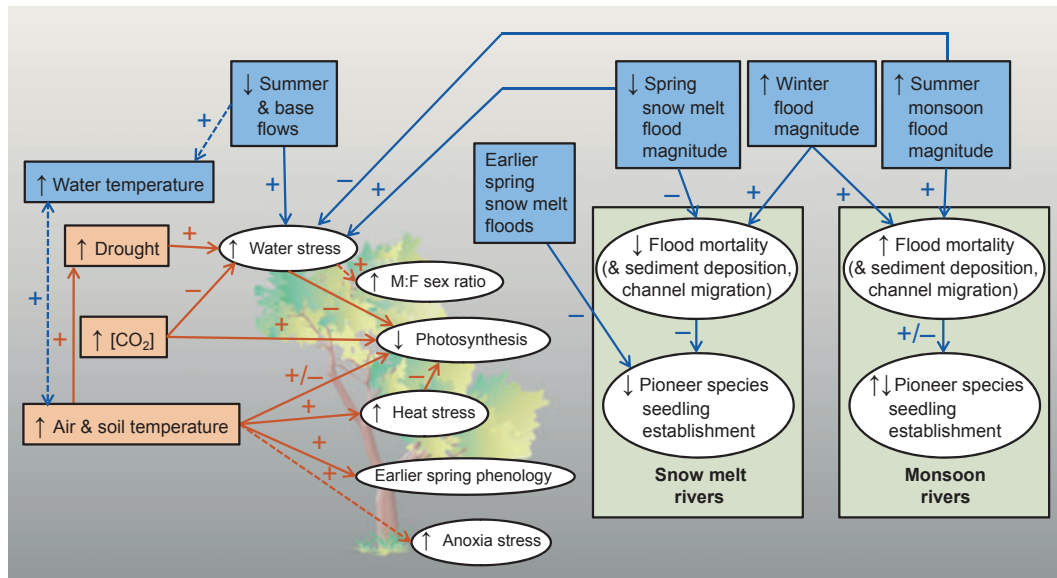
affect interspecific competition and facilitation (Brooker, 2006), little is known about plant interactions in SAWNA riparian communities except for competitive suppression of tamarisk (*Tamarix* spp. L.) seedlings by native tree seedlings (Dewine & Cooper, 2008; Bhattacharjee *et al.*, 2009) and suppression of cottonwood (*Populus* spp. L.) and tamarisk seedlings by closed-canopy shade (Reynolds & Cooper, 2010). Therefore, we limit discussion to likely effects on individual plants, populations, community structure, and spatial distributions.

#### Physiology and growth

Increased [CO<sub>2</sub>] and warming are likely to have conflicting effects on SAWNA riparian plant photosynthesis, water status, and growth (Fig. 3). Greater carbon availability due to increased [CO<sub>2</sub>] tends to increase photosynthesis and growth in C<sub>3</sub> plants (Ainsworth &

Long, 2005; de Graaff *et al.*, 2006), including in cottonwoods (Table 1), which dominate SAWNA riparian ecosystems. In addition, increased [CO<sub>2</sub>] reduces stomatal conductance and thus increases water use efficiency (WUE) in cottonwoods (Table 1) and many other plants (Ainsworth & Long, 2005). Increased plant WUE due to increased [CO<sub>2</sub>] can increase plant productivity in dryland ecosystems (Morgan *et al.*, 2004).

Warming-induced drought, however, is likely to override the positive effects of [CO<sub>2</sub>]-induced increases in WUE on plant water status (Frelich & Reich, 2010), especially where changes in streamflow further reduce water availability. Relatively drought-intolerant riparian species such as cottonwoods and willows (*Salix* spp. L.) may be particularly vulnerable to lower groundwater tables during more frequent or intense droughts. Cottonwoods respond to moderate water deficits with reduced stomatal conductance, photosynthesis, shoot elongation and trunk expansion, and to



**Fig. 3** Potential effects of elevated  $[CO_2]$ , climate change, and climate-driven streamflow changes (rectangles) on riparian plants (ovals). Arrows within the rectangles and ovals indicate the net direction of expected change. Arrows between rectangles and ovals indicate linkages between environmental drivers and plant responses, with + and – symbols indicating positive and negative effects, respectively, of the expected change in the environmental driver on the plant process or characteristic. For example, the – symbol for the linkage between water stress and photosynthesis indicates a negative effect of increased water stress on photosynthesis, contributing to a net reduction in photosynthesis. +/- symbols indicate that the effect could be in either direction. Direct effects of elevated  $[CO_2]$  and climate change on riparian plants are shown with orange arrows. Indirect, streamflow-driven effects are shown with blue arrows. Dashed arrows indicate linkages that are particularly uncertain. Effects of changes in flood timing and magnitude are shown separately for plants on snow melt-dominated and monsoon-dominated rivers. Note that winter floods in snow melt rivers are only projected to increase in the northwestern United States. Also, earlier snow melt peaks will affect seedling establishment only for species that rely on particular timing of seed release relative to snow melt peak flows, such as cottonwoods and willows. Together, these effects will have complex, species-specific and community-specific impacts on riparian plant growth, survival, recruitment, population dynamics, geographic distributions, and community composition and structure. Not all potential linkages discussed in the text are shown.

severe water deficits with xylem cavitation, branch sacrifice, and crown die-back (Rood *et al.*, 2003). Some studies suggest that Goodding's willow (*Salix gooddingii* C.R. Ball) is more drought-tolerant than Fremont cottonwood (*Populus fremontii* S. Watson) (Busch & Smith, 1995; Stella & Battles, 2010), whereas others suggest that Goodding's willow is less drought-tolerant (Horton *et al.*, 2001), making it difficult to predict how increased drought will affect relative abundances of dominant native tree species. Increased drought is less likely to affect species that are substantially more drought-tolerant, such as introduced tamarisk and Russian olive (*E. angustifolia* L.) (Stromberg *et al.*, 2007b; Reynolds & Cooper, 2010).

Warming, particularly higher maximum temperatures, will also increase riparian plant heat stress and thus reduce growth. Temperatures  $>45\text{ }^{\circ}\text{C}$ , which is at the upper end of recent SAWNA maximum air temperatures (<http://www.wrcc.dri.edu>), damage or kill leaf tissue of most plant species, although at least one desert riparian plant (an Asian poplar, *Populus euphratica*

Oliv.) tolerates higher temperatures ( $50\text{--}55\text{ }^{\circ}\text{C}$ ) (Ferreira *et al.*, 2006). Slightly lower maximum temperatures ( $25\text{--}45\text{ }^{\circ}\text{C}$ ) can reduce germination, growth, flowering, fruit ripening, and seed set (Wahid *et al.*, 2007). Among SAWNA riparian species, high temperatures reduce photosynthesis in tamarisk and black cottonwood (Table 1), reduce growth in velvet mesquite (*Prosopis velutina* Woot.) (Cannon, 1915) and Arizona sycamore (*Platanus wrightii* S. Watson) (Stromberg, 2001), and increase fungal infection in thinleaf alder [*Alnus incana* (L.) Moench spp. *tenuifolia* (Nutt.) Breitung]. Warming is generally expected to shift temperatures closer to optimal for tree photosynthesis (Saxe *et al.*, 2001; Hyvönen *et al.*, 2007), and may, for example, increase black cottonwood photosynthesis in Montana where current average growing season temperatures are  $<25\text{ }^{\circ}\text{C}$  (<http://www.wrcc.dri.edu>), the optimum for that species (Table 1). In contrast, photosynthesis may decrease in SAWNA riparian plants where growing season temperatures already approach or exceed the optimum, such as for tamarisk (Table 1) in areas with current

average growing season temperatures >25 °C, including parts of Arizona, New Mexico, Utah, and Colorado (<http://www.wrcc.dri.edu>).

Warming also may increase or decrease anoxia, and thus affect riparian plants. Soil anoxia can develop whenever water tables are high, including in riparian wetlands on lower geomorphic surfaces and briefly on higher surfaces inundated during floods. The duration of anoxia strongly affects riparian wetland community composition (Castelli *et al.*, 2000). Under climate change, lower water tables due to more frequent or intense drought may reduce anoxia. When water tables are high, however, warmer soil temperatures may increase anoxia, and production of toxic anaerobic metabolites, by increasing root and microbial respiration (Vartapetian & Jackson, 1997).

### Phenology

Warming will likely advance spring phenology of riparian plants (Menzel *et al.*, 2006; Parmesan, 2007). Emergence from winter dormancy, loss of cold-hardiness, and spring budburst are largely controlled by temperature in most temperate perennials (Rathcke & Lacey, 1985; Kozłowski & Pallardy, 2002), including cottonwoods (Pauley & Perry, 1954; Kaszkurewicz & Fogg, 1967). To break dormancy, plants must be exposed to thresholds of chilling and then warming temperatures, which vary among species, genotypes, bud types, developmental stages, depths of dormancy, and photoperiods. The few phenological studies of SAWNA riparian plants suggest that fewer chilling days under climate change may inhibit floral initiation in reed canarygrass (*Phalaris arundinacea* L.) (Hanson & Sprague, 1953) and more warming days will hasten seed dispersal in Fremont cottonwood, Goodding's willow and sandbar willow (Table 1).

Warming is less likely to affect riparian plant autumn leaf senescence and initiation of winter dormancy, which are thought to be controlled by photoperiod and light quality in most temperate plants (Berrie, 1984), including cottonwoods (Pauley & Perry, 1954; Friedman *et al.*, 2011). Ecotypic variation in NA tamarisk, however, suggests that the cues triggering autumn phenology can evolve rapidly (Friedman *et al.*, 2011). Also, warmer autumn temperatures, if they occur, may slow development of cold-hardiness, which is induced by cold temperatures in most temperate plants, including cottonwood (Park *et al.*, 2008), and could affect the phenology of seed dispersal of autumn-fruiting riparian trees such as Arizona sycamore (*P. wrightii* S. Watson), box elder (*Acer negundo* L.), netleaf hackberry [*Celtis laevigata* Willd. var. *reticulata* (Torr.) L.D. Benson], and velvet ash (*Fraxinus velutina* Torr.) (Brock, 1994).

Increased [CO<sub>2</sub>] may delay autumn leaf senescence in some riparian species, as it can in upland poplars (*Populus* spp. L.) (Taylor *et al.*, 2008).

Earlier spring emergence, with or without delayed autumn senescence, can extend the plant growing season and increase productivity (Hyvönen *et al.*, 2007), soil resource uptake (Nord & Lynch, 2009), and frost injury when late spring frosts occur despite warmer spring temperatures (Morin *et al.*, 2007; Augspurger, 2009). Changes in phenology also may result in mismatches between the timing of plant resource requirements and resource availability (Hegland *et al.*, 2009; Nord & Lynch, 2009).

### Geographic distributions

Climate-change effects on riparian plant physiology, growth, and phenology may alter species' geographic distributions (Parmesan, 2006; Kelly & Goulden, 2008). Plant species that are limited by cold temperatures and favored by low precipitation, such as tamarisk (Friedman *et al.*, 2008), may spread northward and to higher elevations as temperatures increase and/or precipitation declines (Zavaleta & Royval, 2001; Kerns *et al.*, 2009). Conversely, species that are limited by warm temperatures, perhaps including Russian olive (Friedman *et al.*, 2005), may decline in the south and at low elevations. Ecotypic variation in cold or heat tolerance {e.g., in plains cottonwood [*Populus deltoides* Bartram ex. Marsh spp. *monilifera* (Aiton) Eckenwalder] and tamarisk (Friedman *et al.*, 2008)} may lead to incremental northward or upward migration by populations adapted to warmer temperatures (Jump & Penuelas, 2005).

In riparian ecosystems, warming will also result in movement of plant species and ecotypes upstream, because rivers and riparian corridors connect high and low elevations with distinct climates. SAWNA riparian ecosystems exhibit strong gradients in plant community composition and structure between downstream and upstream areas, changing from plains and Fremont cottonwood (*P. fremontii* S. Watson) to narrowleaf cottonwood (*Populus angustifolia* James) forests and from deciduous to coniferous forests (Patten, 1998). Under climate change, plant species and ecotypes that are currently restricted to relatively low elevations, such as some black cottonwood ecotypes (Rood *et al.*, 2007), desert willow [*Chilopsis linearis* (Cav.) Sweet], catclaw acacia (*Acacia greggii* A. Gray), netleaf hackberry [*C. laevigata* Willd. var. *reticulata* (Torr.) L.D. Benson], Fremont cottonwood, green ash (*Fraxinus pennsylvanica* Marsh) and mule-fat [seepwillow; *Baccharis salicifolia* (Ruiz & Pav.) Pers.] (Campbell & Green, 1968), may expand upstream. Species that are currently limited to



middle elevations, such as narrowleaf cottonwood, Arizona sycamore (*P. wrightii* S. Watson), and Arizona walnut [*Juglans major* (Torr.) A. Heller] (Campbell & Green, 1968; Gitlin, 2007), may shift still further upstream. Species currently at the upper limits of river basins, or at the upper limits of perennial flow in small streams, may disappear from those basins. Because riparian species are likely to respond individually to warming, community composition and structure along longitudinal riverine gradients will change as species shift differentially upstream.

### Indirect effects on riparian plants mediated by streamflow

#### *Importance of flow regime to riparian vegetation*

Changes in flow regime, regardless of the cause, can substantially alter riparian plant communities because species' presence and vigor depend on fluvial geomorphic processes and surface water and groundwater hydrology (Poff *et al.*, 1997; Nilsson & Berggren, 2000; Naiman *et al.*, 2005; Merritt *et al.*, 2010). Floods drive disturbance regimes through erosion, transport, and deposition of sediments, vegetation, and debris (Wolman & Miller, 1960). In particular, the magnitude and frequency of floods over multi-decadal time scales structure the dynamics, complexity, and quality (e.g., size, shape, sediment texture) of the fluvial landforms on which riparian plants grow (Naiman *et al.*, 2005). Many dominant riparian species (e.g., cottonwoods, willows) are pioneer species that require bare, moist substrates created by floods via scour, sediment deposition, channel migration, or channel abandonment for seed germination (Scott *et al.*, 1996; Cooper *et al.*, 2003; Stella *et al.*, 2011) and strict hydrologic conditions for seedling establishment (Mahoney & Rood, 1998; Cooper *et al.*, 1999). Furthermore, many riparian plants obtain most of their water from alluvial groundwater sustained by infiltrating streamwater (Snyder & Williams, 2000; Horton *et al.*, 2003), and additional water from inundation during floods. Finally, many riparian plants rely in part on hydrochory for seed and vegetative propagule dispersal (Merritt & Wohl, 2002). Species vary greatly in their responses to streamflow-associated stresses (i.e., drought, high water tables, inundation, burial, and mechanical stress).

Climate-change effects on hydrology and riparian ecosystems will occur within the context of already large temporal variation in flow regime on western rivers. Unregulated rivers exhibit decades-long cycles of channel widening and narrowing due to natural variation in climate and flood magnitude, which in turn create cycles in riparian forest community composition

(Johnson, 1998; Webb & Leake, 2006). Moreover, riparian ecosystems along regulated rivers are still adjusting to novel flow regimes from human water management. Changes in snow melt timing, flood magnitude, and low flows under climate change may strengthen or diminish current trends in geomorphology and ecology on different river reaches.

#### *Spring snow melt flood timing*

Earlier spring floods on snow melt rivers may reduce riparian tree recruitment by de-synchronizing the spring flow peak and seed release (Rood *et al.*, 2008). Seed release in cottonwoods and some willow species occurs over just a few weeks and must coincide with or immediately follow the spring flow peak for the short-lived seeds to settle in environments favorable for germination and long-term survival (Mahoney & Rood, 1998; Merritt & Wohl, 2002; Stella *et al.*, 2006). Warming is likely to advance seed release timing as well as spring flood timing, but advances in spring flood timing are likely to exceed advances in seed release timing, because spring plant phenology is also constrained by photoperiod (Rood *et al.*, 2008).

#### *Flood magnitude*

Reduced spring flood magnitude on snow melt rivers may dramatically alter riparian plant communities by stabilizing channels and exposing lower geomorphic surfaces, reducing the fluvial disturbance that drives patch dynamics, and reducing hydrologic connectivity between the channel and floodplain (Poff *et al.*, 1997). Reduced disturbance can lead to channel and floodplain narrowing, and thus to transient increases in suitable establishment sites for pioneer species and forest expansion (Johnson, 1994). Long-term reduction in sediment transport and deposition and rates of channel migration and abandonment, however, eventually shrinks the areas where pioneer species establish (Scott *et al.*, 1996; Friedman *et al.*, 1998; Shafroth *et al.*, 2002). Over time, as pioneer forests age, reduced disturbance favors shade-tolerant, mid- and late-successional species (Johnson, 1998), drought-tolerant species on higher geomorphic surfaces, and herbaceous species on lower surfaces (Stevens *et al.*, 1995; Merritt & Cooper, 2000). Some introduced species are likely to be favored, including shade-tolerant Russian olive (Reynolds & Cooper, 2010), drought-tolerant tamarisk (Stromberg *et al.*, 2007b), and numerous herbaceous exotics {e.g., cheatgrass (*Bromus tectorum* L.), Canada thistle [*Cirsium arvense* (L.) Scop.], and leafy spurge (*Euphorbia esula* L.) (Stromberg & Chew, 1997; Ringold *et al.*, 2008)}.

In contrast, increased summer and winter flood magnitude in the monsoon region and increased winter flood magnitude in the northwestern United States may increase fluvial disturbance, resulting in greater geomorphic complexity and patch diversity, younger and more heterogeneous tree age structure, lower herbaceous perennial abundance, and greater abundance of annuals (Wissmar, 2004; Stromberg *et al.*, 2007a, 2010). Increased winter floods might also increase cottonwood and willow recruitment and abundance. For example, many cottonwoods and willows established in the Southwest during a period of frequent winter floods in the late 20th century, on surfaces created by channel widening and floodplain deposition following large floods in the early 20th century (Webb & Leake, 2006). More intense summer floods, however, would provide moisture too late for cottonwood and willow seed germination, and could scour away seedlings established following winter floods (Stromberg *et al.*, 2007a). Increased summer floods would favor germination of tamarisk seeds, which are released throughout the summer (Shafroth *et al.*, 1998), but could also increase tamarisk seedling mortality (Gladwin & Roelle, 1998; Shafroth *et al.*, 2010). Floods large enough to deposit high, thick layers of coarse sediment may create surfaces that support xeric pioneer shrubs (Stromberg *et al.*, 1997, 2010).

#### *Summer and base flows*

Lower late-spring and summer flows on snow melt rivers may reduce survival and growth of shallow-rooted plants, such as seedlings and juvenile trees, that become water-limited during that period (Rood *et al.*, 2008). Rapid groundwater declines can kill riparian tree seedlings when root growth is insufficient to maintain contact with moist soil (Mahoney & Rood, 1998; Shafroth *et al.*, 1998; Amlin & Rood, 2002). Even mature phreatophytic trees are adversely affected when water tables drop too far or too quickly (Rood *et al.*, 2003). Declining low flows may increase root depths of surviving phreatophytes (Shafroth *et al.*, 2000) and shift plant community composition toward more drought-tolerant native and introduced species. Lower flows also may skew tree sex ratios; Arizona walnuts [*J. major* (Torr.) A. Heller; monoecious] produce more male than female flowers under drier conditions (Stromberg & Patten, 1990), and male cottonwoods (dioecious) and box elders (*A. negundo* L.; dioecious) tolerate drought stress better than females (Hultine *et al.*, 2007). Corridors of mesic riparian vegetation will contract where reduced flows lower the water table and reduce soil moisture under higher geomorphic surfaces (Rood *et al.*, 2003; Auble *et al.*, 2005).

Lower base flows in monsoon rivers may have effects similar to, but more pronounced than, those in snow melt rivers, including declines in drought-intolerant cottonwoods, willows, and perennial herbs, increases in drought-tolerant species and annuals, declines in canopy height and cover due to changes in species composition, and narrowing of the mesic riparian zone (Serrat-Capdevila *et al.*, 2007; Stromberg *et al.*, 2010). Some reaches may shift from perennial to intermittent flow, dramatically changing community composition and reducing patch diversity. Introduced species tolerant of intermittent flow (e.g., tamarisk), may become dominant (Stromberg *et al.*, 2007a, 2010; Shaw & Cooper, 2008), and obligate wetland species requiring a consistently shallow water table may disappear (Stromberg *et al.*, 1996; Castelli *et al.*, 2000). The combination of lower base flows and larger floods in monsoon rivers may particularly benefit tamarisk over other woody species and annuals over other herbaceous species, because they are both adapted to drought and require disturbance for establishment (Stromberg *et al.*, 2010).

#### *Interactions between direct and streamflow-mediated effects*

Lower summer and base flows will exacerbate effects of increased drought frequency and intensity on water availability under climate change (Fig. 3). Thus, water stress is even more likely to drive plant responses to increased [CO<sub>2</sub>] and climate change in SAWNA riparian ecosystems than in upland dryland ecosystems (Morgan *et al.*, 2004). Together, lower growing-season streamflows and increased drought will likely increase plant mortality, decrease growth and recruitment, and shift species' relative abundances in favor of more drought-tolerant species.

Lower summer and base flows also may exacerbate effects of warming on riparian plant heat stress, photosynthesis, anoxia stress and phenology by further increasing soil temperatures. Lower water tables reduce vadose zone soil moisture, which affects soil heating and cooling (Geiger, 1965). Furthermore, warmer surface water temperatures, due to warmer air temperatures (Kaushal *et al.*, 2010) and perhaps lower river stage, can increase soil temperature through heat transfer during hyporheic flow (Poole *et al.*, 2008).

#### **Effects on riparian litter and soil processes**

Climate-driven changes in streamflow will interact with direct effects of climate change on litter decomposition and nutrient cycling in riparian ecosystems (Fig. 1). Warming has conflicting effects on decomposition and nutrient cycling, because it increases biochemical

reaction rates and detritivore activity (e.g., Briones *et al.*, 2007) but also increases evaporation, reducing the soil moisture required for microbial activity (Rustad *et al.*, 2001). In mesic upland ecosystems, warming tends to accelerate nitrogen (N) mineralization, suggesting that the positive effects of warming on microbial activity outweigh the negative effects of lower soil moisture (Rustad *et al.*, 2001). At the same time, increased [CO<sub>2</sub>] can increase soil microbial abundance by increasing root exudation of carbon-rich metabolites (Drigo *et al.*, 2008), and can increase soil moisture by increasing plant WUE, and thus increase either microbial N immobilization (Hungate *et al.*, 1997; Dijkstra *et al.*, 2010) or N mineralization (Ebersberger *et al.*, 2003; Dijkstra *et al.*, 2008). Few warming studies have been conducted in drylands, however, where soil moisture might be more important (Dijkstra *et al.*, 2010). In SAWNA riparian ecosystems, observational studies suggest that decomposition and nutrient cycling are slowest in warm, dry microclimates, and seasons (Naiman *et al.*, 2005; Andersen & Nelson, 2006; Harms & Grimm, 2008; Harner *et al.*, 2009). Projected lower summer and base flows and smaller spring floods under climate change increase the likelihood that the negative effects of lower soil moisture will outweigh the positive effects of warming on microbial and detritivore activity in these ecosystems, leading to slower decomposition and nutrient cycling.

Changes in litter quality and production under increased [CO<sub>2</sub>] and climate change may also affect decomposition and nutrient cycling. Increased [CO<sub>2</sub>] tends to reduce plant litter N slightly, but not enough to slow decomposition (Reich *et al.*, 2006). Changes in plant community composition, however, can affect decomposition by altering the relative abundance of species with different litter chemistry (Reich *et al.*, 2006). For example, a shift from predominantly Fremont cottonwood litter to predominantly tamarisk litter can slow decomposition (Pomeroy *et al.*, 2000), and greater contributions of velvet mesquite (*P. velutina* Woot.) and Russian olive litter can accelerate decomposition (Williams *et al.*, 2006; Harner *et al.*, 2009). In addition, greater drought stress can reduce total litter production in SAWNA riparian ecosystems, leading to slower N mineralization and lower soil inorganic N concentrations (Follstad Shah & Dahm, 2008).

Changes in flow regime will also affect nutrient retention and transport. Downstream N flux in SAWNA riparian ecosystems is largely mediated by inundation and surface and hyporheic flows during floods (Andersen & Nelson, 2006; Harms & Grimm, 2008). Lower flood magnitudes on snow melt rivers may reduce downstream N flux, whereas greater flood magnitudes on monsoon rivers and in the northwestern

United States may increase downstream N flux. Lower soil moisture due to warming, lower summer and base flows, and smaller spring floods may increase N retention by reducing denitrification (McLain & Martens, 2006). Downstream flux of less soluble nutrients (e.g., phosphorus) will depend on how climate and flow regime changes affect watershed sediment budgets.

Changes in decomposition and N cycling may affect plant productivity. Low N availability limits riparian plant growth in at least some SAWNA riparian ecosystems (Adair & Binkley, 2002). Most plant-available N in these ecosystems comes from litter decomposition and associated N mineralization or from sediment deposition and streamwater during floods (Schade *et al.*, 2002; Adair *et al.*, 2004). Slower decomposition and N cycling due to lower soil moisture, lower total litter production, and greater tamarisk relative abundance may further reduce plant growth under climate change. Lower soil moisture and decreased flooding also may alter riparian plant nutrient uptake by reducing abundance of mycorrhizal fungi associated with cottonwoods, willows, moist conditions, and disturbance (Beauchamp *et al.*, 2006; Piotrowski *et al.*, 2008).

## Effects on riparian animals

### *Heat stress and dehydration*

Warmer maximum temperatures will increase heat stress in riparian animals. Terrestrial animals have an upper lethal limit (ULL) to body temperature ( $T_b$ ), above which they exhibit heat torpor or coma, and unless cooling ensues, death. ULLs vary among species and with acclimatization, but typically range from ca. 42 to 46 °C (Denlinger & Yocum, 1998).

For riparian ectotherms (i.e., most arthropods, reptiles, amphibians), which control  $T_b$  behaviorally through orientation, movement and choice of microhabitat, warming is likely to alter behavior and physiology, and may reduce survival. For example, the Apache cicada (*Diceroprocta apache* Davis), a facultatively riparian, diurnally active insect and an important food item for the federally at-risk yellow-billed cuckoo (*Coccyzus americanus* L.), seeks shade when  $T_b > 39.2$  °C, reduces  $T_b$ -raising behaviors such as flight and courtship 'singing' at ambient temperatures ( $T_a$ ) > ca. 40 °C, and exhibits heat-induced torpor when  $T_b > 45.6$  °C (Heath & Wilkin, 1970). Unlike most insects, Apache cicadas also respond to  $T_b > 37$ –38 °C by extruding water for evaporative cooling (Hadley *et al.*, 1991).

Non-mobile ectotherms (e.g., eggs, pupae) may be particularly vulnerable to warming, because they cannot move to cooler areas and instead must rely on parents or earlier life stages to select sites with favor-

able microclimates. For example, hawkmoths (*Manduca sexta* L.) lay their eggs on the undersides of leaves of the facultatively riparian plant sacred thorn-apple (*Datura wrightii* Regel), where evaporative cooling from plant transpiration buffers the eggs from fatally high  $T_a$  (Potter *et al.*, 2009). Chemical cues for egg laying or pupation on particular plant species may become maladaptive if leaf temperatures increase, for example because of reduced stomatal conductance under elevated  $[CO_2]$  or an increase in plant heat tolerance and hence a reduction in transpiration.

Reptiles with temperature-dependent sex determination (TSD), including western box turtles (*Terrapene ornata* Agassiz) and mud turtles (*Kinosternon* spp.) (Ewert & Nelson, 1991), also may be particularly vulnerable to warming. Small increases in temperature (2 °C) during incubation can dramatically skew sex ratios in TSD species (Ewert & Nelson, 1991). For most TSD species, warmer temperatures increase female relative abundance, which may not reduce population viability as long as some males are produced (Mitchell & Janzen, 2010). Consistent very high temperatures during incubation, however, may produce single-sex cohorts and trigger demographic collapse.

For riparian endotherms (i.e., birds, mammals), which maintain  $T_b$  within a few degrees of ULL and prevent overheating by evaporative cooling, more frequent and severe heat waves are likely to increase mortality from heat stress and dehydration. Evaporative cooling is generally limited by size and physiology. For example, the elf owl (*Micrathene whitneyi* Cooper), a small raptor associated with southwestern desert riparian vegetation, has difficulty using evaporative cooling to maintain a normal  $T_b$  (36–38 °C) when  $T_a \approx 40$  °C, and dies when  $T_b = 42.2$  °C (Ligon, 1969). Furthermore, evaporative cooling can lead to acute dehydration. Evaporative water loss in the elf owl rises from ca. 3 to ca. 15 mg  $H_2O\ g^{-1}\ h^{-1}$  when  $T_a$  rises from 38 to 45 °C (Ligon, 1969). Small or young birds may be particularly vulnerable to dehydration during extreme heat waves because of their limited water storage capacity and, for nestlings, their lack of access to water (McKechnie & Wolf, 2010). For small mammals, warming may alter community structure, increasing abundance of more heat-tolerant species, decreasing abundance of less heat-tolerant species, and potentially altering the relative abundance of granivores, omnivores, and herbivores (Terry *et al.*, 2011).

Changes in streamflow under climate change may compound effects of warming on animal dehydration by reducing surface water availability (Figs 1 and 4). Reduced summer and base flows could increase the frequency or duration of zero-flow periods (Stromberg *et al.*, 2010) or lower water tables and reduce riparian

wetland inundation (Stromberg *et al.*, 1996), thus restricting access to water. For example, bat reproduction in the Colorado Front Range decreases during warm and dry years with low streamflow, perhaps because female bats require surface water near roost sites for adequate lactation (Adams, 2010). Low surface water availability may also decrease riparian bird reproduction (Coe & Rotenberry, 2003).

### Phenology

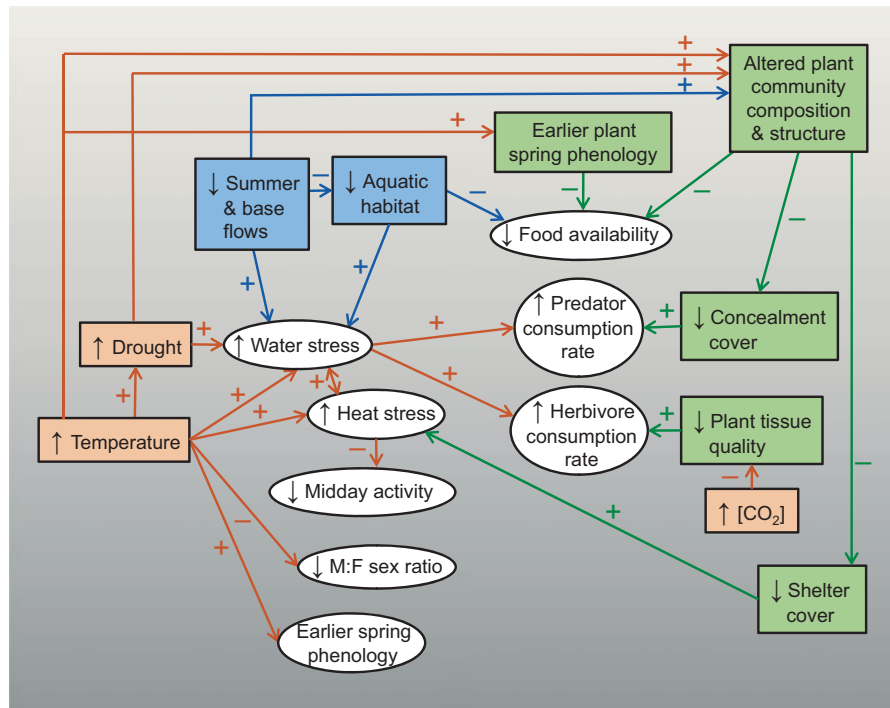
Effects of warming on animal phenology in riparian ecosystems are likely to be similar to effects in other ecosystems. Across Europe and NA, warming is advancing the timing of butterfly first flights, frog breeding, and bird migration and nesting (Parmesan, 2006). Warming is also accelerating insect development, leading to earlier hatching, pupation, and adult emergence and more generations per growing season (Robinet & Roques, 2010). Furthermore, warming can accelerate initiation and termination of cold-season and dry-season insect diapause, and may sometimes desynchronize diapausing life stages from the critical photoperiods that induce diapause (Bale & Hayward, 2010; Robinet & Roques, 2010).

### Geographic distributions

Warming effects on riparian animal physiology, survival, behavior, and phenology may alter animal geographic distributions similarly to plants, with species expanding northward, to higher elevations and upstream (Parmesan, 2006; Robinet & Roques, 2010). Warmer winter temperatures are likely to increase animal survival in the colder parts of SAWNA (Bale & Hayward, 2010), while warmer summer temperatures may decrease fitness in hotter areas. As in other ecosystems, however, changes in some animal distributions may be limited by species' dispersal abilities (Robinet & Roques, 2010). Northward or upward dispersal to cooler climates sometimes may require long-distance mobility (e.g., flight or large size), because many SAWNA rivers flow east-west (Fig. 2) or contain long segments of inhospitable habitat (e.g., canyons with little or no floodplain).

### Habitat quality

Changes in riparian plant community composition, structure, and phenology, whether due to changes in  $[CO_2]$ , temperature, precipitation, streamflow, geomorphology, or soil processes, are likely to reduce habitat quality for many riparian animals, including shelter cover (e.g., shade), concealment cover and nest sites



**Fig. 4** Potential effects of elevated  $[CO_2]$ , climate change, and climate-driven streamflow and plant community changes (rectangles) on riparian animals (ovals). Arrows within the rectangles and ovals indicate the net direction of expected change. Arrows between rectangles and ovals indicate linkages between environmental drivers and animal responses, with + and – symbols indicating positive and negative effects, respectively, of the expected change in the environmental driver on the animal process or characteristic. For example, the – symbol for the linkage between aquatic habitat and food availability indicates a negative effect of reduced aquatic habitat on food availability, contributing to a net reduction in food availability. Direct effects of elevated  $[CO_2]$  and climate change on riparian animals are shown with orange arrows. Indirect, streamflow-driven effects are shown with blue arrows and indirect, plant community-driven effects are shown with green arrows. Note that sex ratios will be affected only in reptiles with temperature-dependent sex determination (TSD). Together, these effects will have complex, species-specific and community-specific impacts on riparian animal survival, recruitment, population dynamics, geographic distributions, community composition and structure, and trophic and symbiotic interactions. Not all potential linkages discussed in the text are shown.

(Fig. 4). For example, at least four of the changes in SAWNA riparian vegetation expected under climate change are likely to negatively affect riparian birds. First, lower plant structural diversity due to reduced flooding and associated geomorphic change may reduce bird diversity, particularly of canopy-foraging and tall-shrub-foraging guilds (Scott *et al.*, 2003). Second, decreases in mature cottonwood stands and increases in tamarisk may reduce bird population size, particularly of canopy- and shrub-nesting species (van Riper *et al.*, 2008; Brand *et al.*, 2010). Third, decreases in preferred nest trees may increase nest predation (Martin, 2007). Finally, advances in plant springtime phenology may reduce food and refuge quality for Neotropical migratory birds that stop in SAWNA riparian habitats en route to northern breeding areas. Spring temperatures are increasing more rapidly in these birds' migratory habitats than summer temperatures in their breeding habitats, potentially leading to trade-offs between early migration with better migration habitat

vs. later migration with better breeding habitat (Fontaine *et al.*, 2009).

Other animals also may be negatively affected by changes in SAWNA riparian vegetation. For example, butterfly species richness and abundance of phreatophyte-dependent butterflies decline with lower cottonwood and willow abundance, herbaceous species richness and patch diversity, and with greater tamarisk abundance (Nelson & Andersen, 1999; Nelson & Wydoski, 2008). Likewise, reptile and amphibian diversity and density are lower in tamarisk stands than in other riparian vegetation, perhaps because of lower plant structural diversity (Shafroth *et al.*, 2005). In addition, lower total canopy cover and reduced shade due to greater plant water stress and altered plant community composition may increase animal heat stress.

Changes in riparian hydrology also may reduce habitat quality for animals that rely on surface water for shelter or reproduction. Amphibians and arthropods that spend some life stages in water may be particularly

sensitive to reduced surface water, aquatic habitat, and habitat connectivity (Fagan, 2002; Daszak *et al.*, 2005). Beaver (*Castor canadensis* Kuhl) and other semi-aquatic mammals may decline on reaches that shift from perennial to intermittent flow. Floods can damage or destroy beaver dams (Andersen & Shafroth, 2010), so larger flood magnitudes on monsoon rivers and in the northwestern United States also may reduce beaver abundance. Changes in beaver populations in turn could affect local and downstream communities, as beavers are formidable herbivores and beaver dams increase lentic habitat and reduce sediment flux (Andersen *et al.*, 2011).

Climate change is likely to improve habitat quality for some animals in riparian areas, however. In particular, diversity and abundance of upland animal species may increase in riparian areas as riparian animal populations decline with lower water availability. Also, lower flood magnitudes on snow melt rivers may increase beaver dam persistence (Andersen & Shafroth, 2010) and small mammal abundance (Andersen & Cooper, 2000). Greater tamarisk abundance and lower cottonwood and willow abundance also may benefit some species, such as bird species that appear to prefer dense tamarisk stands [e.g., Abert's towhee (*Pipilo aberti* Baird), blue grosbeak (*Passerina caerulea* L.), Say's phoebe (*Sayornis saya* Bonaparte), and yellow-breasted chat (*Icteria virens* L.) (van Riper *et al.*, 2008; Brand *et al.*, 2010)].

### Effects on riparian trophic and symbiotic interactions

#### *Disrupted interactions*

As in uplands, changes in riparian species distributions or phenology may disrupt plant–herbivore, plant–pollinator, parasitoid–host, and predator–prey interactions (Parmesan, 2006; Thackeray *et al.*, 2010). Such disruptions may pose particularly large problems for plants that lose access to specialist pollinators and for specialist pollinators and herbivores that lose access to hosts (Memmott *et al.*, 2007). For example, Ute lady's tresses (*Spiranthes diluvialis* Sheviak), a federally threatened SAWNA riparian orchid, may fail to reproduce if disassociated from its pollinators, native bumblebees (*Bombus* spp.) (Sipes & Tepedino, 1995). Similarly, cottonwood leaf beetles (*Chrysomela scripta* F.), which emerge from diapause with warming spring temperatures and forage on the earliest cottonwood foliage or flowers (Andersen & Nelson, 2002), may lose access to food if their phenology shifts so that they emerge before cottonwood budburst. Changes in species distributions or phenology could also intensify competition or shift competitive dominance given fewer or different pollinators,

flowers, plant tissue, or prey items (Mitchell *et al.*, 2009). Many disrupted interactions, however, may be replaced by novel generalist interactions (Hegland *et al.*, 2009). Wide arrays of native and introduced riparian plants, prey, and pollinators are available to form novel associations in SAWNA riparian ecosystems (Wiesenborn & Heydon, 2007; Durst *et al.*, 2008; Wiesenborn *et al.*, 2008; Bridgeland *et al.*, 2010).

#### *Consumption rates*

There are many reasons to expect that increased [CO<sub>2</sub>] and climate change will increase riparian herbivore, pollinator, and predator consumption rates (Fig. 4). Warming may increase temperature-dependent metabolic rates in ectotherms, and thus increase their energy demands and consumption (Gillooly *et al.*, 2001). Warming also may promote wintertime and springtime activity (Roy *et al.*, 2004), and increase the time that desert herbivores or predators spend browsing or hunting in the shade of riparian vegetation. More frequent or intense droughts and lower summer and base streamflows may intensify predation in riparian areas, because mammalian predators remain closer to rivers during dry periods (Soykan & Sabo, 2009) and prey organisms requiring surface water may be forced to aggregate in smaller areas. Reduced inundation due to lower flows and smaller spring floods also may increase small mammal populations in riparian areas, and thus increase herbivory and bird nest predation (Andersen & Cooper, 2000; Cain *et al.*, 2003). Furthermore, lower flows may increase predator access to riverine islands (Zoellick *et al.*, 2005).

Lower plant tissue nutritional quality due to elevated [CO<sub>2</sub>] also may increase herbivore consumption rates. Increased [CO<sub>2</sub>] can reduce plant tissue N concentrations, including in cottonwood (McDonald *et al.*, 2002), by increasing tissue carbon, lowering N demand, and lowering N supply from transpiration-driven mass flow (Taub & Wang, 2008). It also can increase plant tissue concentrations of carbon-rich secondary metabolites that reduce palatability (Bidart-Bouzat & Imeh-Nathaniel, 2008). Insect herbivores tend to increase consumption to compensate for lower plant tissue N under elevated [CO<sub>2</sub>] (Stiling & Cornelissen, 2007). Herbivore growth and abundance tend to decline under elevated [CO<sub>2</sub>] despite increased consumption, but not when temperatures are also increased (Zvereva & Kozlov, 2006; Stiling & Cornelissen, 2007).

Greater water stress also may increase consumption rates of insect herbivores and predators that obtain water from plant tissue and prey. For example, when SAWNA riparian wolf spiders (*Hogna antelucana* Montgomery) do not have access to moist microcli-

mates or surface water, they increase consumption of field crickets (*Gryllus alogus* Rehn) to maintain their water balance (McCluney & Sabo, 2009). Furthermore, the crickets increase consumption of green (i.e., moist) leaf litter to maintain *their* water balance. Because the spider–cricket interaction relies on plant-available groundwater, reductions in groundwater could affect plant, detritivore, and predator populations in a trophic cascade.

Increased [CO<sub>2</sub>] and climate change may reduce consumption by some riparian species, however. For example, greater plant water stress may increase phloem viscosity and thus reduce feeding efficiency of sap-feeders (Dixon, 1998), which are common on tamarisk (Wiesenborn, 2005) and narrowleaf-Fremont hybrid cottonwoods (*P. angustifolia* × *fremontii*) (Bridgeland *et al.*, 2010). Furthermore, increased [CO<sub>2</sub>] may reduce consumption by insects that rely on [CO<sub>2</sub>] gradients to locate fruit, flowers, prey, or ovipositioning sites (Guerenstein & Hildebrand, 2008), although increased [CO<sub>2</sub>] does not reduce CO<sub>2</sub> receptor sensitivity or host detection in hawkmoths (*M. sexta* L.) (Abrell *et al.*, 2005).

#### Food availability

Changes in SAWNA riparian plant and animal community composition may reduce food availability for many herbivores and predators (Fig. 4). Decreases in native woody phreatophytes and increases in tamarisk may reduce food availability for beaver (*C. canadensis* Kuhl), which prefer cottonwood and willow over tamarisk (Mortenson *et al.*, 2008), and for the myriad insect herbivores and secondary consumers that occupy cottonwoods and willows (Wiesenborn & Heydon, 2007; Durst *et al.*, 2008; Bridgeland *et al.*, 2010), but increase food availability for the tamarisk leafhopper (*Opsius stactogalus* Fieber) and armored scales (*Chionaspis* spp.), which make up most arthropod biomass on tamarisk (Wiesenborn, 2005). Lower arthropod diversity or abundance in turn may reduce bird reproduction by reducing bird prey availability (Bolger *et al.*, 2005) or increasing nest predation by predators (e.g., snakes, skunks) that might otherwise consume arthropods (Martin, 2007). Changes in plant community composition and structure also may reduce abundance and biomass of nocturnal flying insects (Ober & Hayes, 2008), thereby reducing food availability for bats and other nocturnal aerial insectivores. Warmer streamwater and intermittent flows may reduce abundance of some aquatic insects (Lawrence *et al.*, 2010; Sponseller *et al.*, 2010), which as adults are important riparian prey (Richardson *et al.*, 2010). Lower prey abundance could be particularly detrimental to predators such as the grass spider (*Agelenopsis aperta* Gertsch) that have

adapted to high prey abundance in riparian ecosystems by developing behaviors that maximize predator avoidance rather than prey capture (Riechert & Hall, 2000).

#### Indirect effects mediated by human activities

Climate-change effects on human activities (e.g., water management, land conversion) and associated socioeconomic drivers will strongly affect riparian ecosystems (Harrison *et al.*, 2008; Purkey *et al.*, 2008). Changes in water demand and environmental regulation, with or without climate-induced changes in streamflow, could trigger changes in reservoir storage, dam management, and groundwater pumping (Fig. 1; Vicuna *et al.*, 2007; Purkey *et al.*, 2008; Barnett & Pierce, 2009). Many studies predict increased water demand in drylands because of human population increases and climate change (IPCC, 2008), although water conservation or agricultural land-use change could mitigate those trends (Lellouch *et al.*, 2007; IPCC, 2008). A model of water yield, demand, and delivery on the Colorado River predicted water delivery shortages (i.e., scheduled deliveries exceed supply) in 60–100% of years by 2060 (Barnett & Pierce, 2009).

Along regulated rivers, changes in water management to maintain reservoir storage and deliver water to municipal, agricultural, and industrial users are likely to reduce flow variability, particularly by decreasing flood magnitude and/or frequency. These reductions in flooding, together with reduced sediment supply below dams (Syvitski & Kettner, 2011), may supersede the effects of other projected changes in flood magnitude (Table 2) on riparian geomorphology and ecology (Fig. 1). On some river reaches, earlier and larger irrigation water withdrawals could also substantially reduce late-spring and summer flows (Eheart & Tornil, 1999), compounding projected reductions in streamflow and further increasing plant and animal water stress.

Human adaptation measures – actions that increase resilience and reduce vulnerability of natural and human systems (IPCC, 2007) – will also shape riparian ecosystem responses to climate change (Naiman *et al.*, 2005). Adaptation options for riparian ecosystems will vary across watersheds and may include both proactive and reactive approaches (Palmer *et al.*, 2008, 2009). Proactive management is aimed at maintaining or increasing system resilience to climate change in advance of changes occurring. Examples include increasing the scale of protected area networks and connected private lands (Heller & Zavaleta, 2009), securing water rights for environmental flows (Palmer *et al.*, 2008), implementing water conservation measures or cropping pattern adjustments (Lellouch *et al.*, 2007; Purkey *et al.*,

2008), and restoring riparian vegetation to increase habitat connectivity, promote linkages between aquatic and terrestrial ecosystems, expand thermal refugia for wildlife, and protect genetic diversity (Heller & Zavaleta, 2009; Seavy *et al.*, 2009). On some regulated rivers, it also may be possible to modify water management operations proactively to mitigate climate-change effects on streamflow (Rood *et al.*, 2005a; Palmer *et al.*, 2009; Merritt *et al.*, 2010). Reactive management is aimed at responding to ongoing or past impacts through active measures such as revegetation, introduced species removal, and rare species protection (Palmer *et al.*, 2008, 2009). Outcomes of adaptation measures can be predicted by linking models of future climate scenarios, land cover, water demand and water management (e.g., Brekke *et al.*, 2004; Vicuna *et al.*, 2007; Harrison *et al.*, 2008; Purkey *et al.*, 2008; Rajagopalan *et al.*, 2009) to biological response models (Harrison *et al.*, 2008).

A global assessment of major river basins identified three in SAWNA (Columbia, Sacramento, and Colorado) that are almost certain to need management intervention to mitigate climate-change impacts (Palmer *et al.*, 2008). Along highly regulated mainstem reaches of these rivers, intensively managed and site-specific approaches will be necessary, such as active revegetation along the lower Colorado River (Briggs & Cornelius, 1998). Along reaches that might still receive high flows from unregulated tributaries, measures such as levee breaching could enhance floodplain connectivity (Florsheim & Mount, 2002). Furthermore, efforts to de-arm bends and reconnect abandoned channels isolated by land conversion could increase opportunities for rivers to meander and create new surfaces for pioneer forest establishment. Along individual tributaries, more adaptation options are possible. In the lower Colorado River basin, where water management has already severely altered the main stem and virtually all tributaries, proactive management efforts are ongoing, including securing water rights, establishing protected area corridors, and institutionalizing environmental flows along the San Pedro (Stromberg & Tellman, 2009), Bill Williams (Shafroth *et al.*, 2010), and Verde rivers (Haney *et al.*, 2008).

## Conclusions

Semiarid and arid western North American riparian ecosystems are likely to change dramatically under increased [CO<sub>2</sub>] and climate change. Lower late-spring and summer streamflows will compound effects of increased drought due to warming, leading to strong reductions in water availability. Greater water stress

will alter plant community composition and structure, favoring drought-tolerant species and reducing abundance of currently dominant, drought-intolerant cottonwoods and willows. Tamarisk seems especially likely to increase, but other drought-tolerant species may increase instead if the recently released biocontrol tamarisk beetle (*Diorhabda carinulata* Desbrochers) reduces tamarisk abundance (Hultine *et al.*, 2010). These changes in plant community composition, together with scarcer surface water, are likely to reduce habitat quality for many riparian animals, leading to lower riparian animal diversity and abundance and greater abundance of animals associated with drier conditions. Lower soil moisture may also slow litter decomposition and nutrient cycling.

At the same time, like in uplands, warming will increase heat stress and alter phenology, inducing northward, upward and upstream shifts in geographic distributions and disrupting specialized biotic interactions. Furthermore, increased [CO<sub>2</sub>], together with warming, may alter plant photosynthetic rates and tissue chemistry. Together, warming, reduced surface water, increased water stress, and altered plant community composition and tissue chemistry may increase herbivore and predator consumption rates.

Semiarid and arid western North America is environmentally diverse, however, and many climate-change effects will vary in size or direction across the region. At northern latitudes, projected increases in precipitation may partly offset increases in water stress due to warming and lower summer streamflows, whereas at southern latitudes, projected decreases in precipitation are likely to intensify water stress. Similarly, warming is less likely to induce heat stress at cooler, northern latitudes than at warmer, southern latitudes. Ecosystems in the monsoon region and the northwestern United States may have greater flood magnitudes and hence increased geomorphic complexity and early-successional species abundance under climate change, whereas ecosystems in the rest of SAWNA may have lower flood magnitudes and hence reduced geomorphic complexity and increased late-successional species abundance. Finally, local variation in geology and soils may influence climate-change effects. For example, changes in flood magnitude may affect geomorphic dynamics more on wide, alluvial floodplains with space for channel migration than in narrow, constrained valleys. Furthermore, ecosystems on coarse-textured soils with low water-holding capacity, such as on steep stream gradients or younger geomorphic surfaces, may be more vulnerable to reduced water availability than ecosystems on fine-textured soils (Naiman *et al.*, 2005).



Climate-change effects will occur within the context of ongoing changes in SAWNA riparian ecosystems caused by flow regulation, groundwater pumping, deforestation, stream channelization, livestock grazing, nutrient pollution, and biological invasion (Patten, 1998; Brinson & Malvarez, 2002; Graf, 2006). Climate change may contribute to some of these changes, and be moderated by others. For example, climate change appears likely to facilitate invasion by exotic, drought-tolerant or late-successional woody and herbaceous plant species. Furthermore, on relatively pristine rivers, climate change may mimic some of the effects of flow regulation and groundwater pumping on flood magnitude and water availability, resulting in even more widespread hydrologic change. Conversely, on regulated rivers, flow regulation may often override effects of climate change on streamflow. Also, nutrient pollution may partly offset the negative effects of lower soil moisture on nutrient cycling and plant productivity.

Because we lack understanding of fundamental niche parameters for most dryland riparian species, site-specific, quantitative predictions of ecosystem responses to increased [CO<sub>2</sub>] and climate change remain highly speculative. In particular, our ability to make more specific predictions is hampered by lack of knowledge of (1) direct effects of [CO<sub>2</sub>] and temperature on physiology, phenology, growth and survival for most dryland riparian species, (2) biotic interactions and their effects on population dynamics, community structure, and ecosystem processes, and (3) effects of surface and hyporheic flows on soil and air temperatures, riparian vegetation, and soil processes. Predictions of climate-change effects are also limited by uncertainty in projected (4) streamflow on rainfall-dominated rivers and (5) human water demand and water management.

Long-term biological monitoring along representative regulated and unregulated rivers might detect effects of ongoing abiotic change, especially on short-lived taxa, but will not clearly distinguish effects of increased [CO<sub>2</sub>] and climate change from effects of ongoing natural dynamics, human water management, and biological invasion. Therefore, controlled experiments are needed to test cause-and-effect hypotheses suggested by field observations. In particular, CO<sub>2</sub>-enrichment and warming experiments, which have not been conducted in riparian ecosystems, could elucidate effects on plant physiology, water status and growth, trophic interactions, and soil processes. On a larger scale, streamflow on some regulated rivers might be managed to test effects of projected streamflow changes or environmental flows designed to mitigate climate-change impacts.

Globally, increased [CO<sub>2</sub>] and climate change may affect riparian ecosystems in other dryland regions via some of the same mechanisms we expect to operate in SAWNA. Warming is hastening snow melt peak flows, increasing winter flows, and decreasing summer flows in some snow melt rivers in Europe (Arnell, 1999; Horton *et al.*, 2006), Asia (Yang *et al.*, 2002), and eastern NA (Hodgkins & Dudley, 2006). Where these rivers flow through dryland regions, effects may be analogous to those in SAWNA, because low flows limit plant and animal survival and growth (Lamontagne *et al.*, 2005; Thevs *et al.*, 2008; Greenwood & McIntosh, 2010), floods drive patch dynamics (Steiger *et al.*, 2005), and seed dispersal is timed to coincide with high flows (Pettit & Froend, 2001; Guilloy-Froget *et al.*, 2002) in riparian ecosystems around the world. However, differences in climate, hydrology, geomorphology, and ecology (e.g., Jacobs *et al.*, 2007; Naiman *et al.*, 2010; Mac Nally *et al.*, 2011) will lead to unique responses to increased [CO<sub>2</sub>] and climate change.

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