Global Change Biology

Global Change Biology (2012) 18, 821–842, doi: 10.1111/j.1365-2486.2011.02588.x

REVIEW

Vulnerability of riparian ecosystems to elevated CO_2 and climate change in arid and semiarid western North America

LAURA G. PERRY*†, DOUGLAS C. ANDERSEN†, LINDSAY V. REYNOLDS*†, S. MARK NELSON‡ and PATRICK B. SHAFROTH†

*Department of Biology, Colorado State University, Fort Collins, CO, USA in cooperation with, †U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO, USA, ‡Bureau of Reclamation, Technical Service Center, Denver, CO, USA

Abstract

Riparian ecosystems, already greatly altered by water management, land development, and biological invasion, are being further altered by increasing atmospheric CO_2 concentrations ([CO_2]) and climate change, particularly in arid and semiarid (dryland) regions. In this literature review, we (1) summarize expected changes in [CO_2], 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_2] 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

Received 18 March 2011; revised version received 15 July 2011 and accepted 6 September 2011

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_2 concentration (hereafter [CO_2]) and associated climate change are likely to further alter dryland riparian ecosystems (Grimm *et al.*, 1997). Changes in [CO_2] and climate have direct, local effects on plant and animal survival, growth and phenology, biotic interactions, and soil processes (Fig. 1)

Correspondence: Laura G. Perry, tel. + 970 226 9196, fax +970 226 9230, e-mail: lperry@lamar.colostate.edu

Published 2011
This article is a US Government work and is in the public domain in the USA

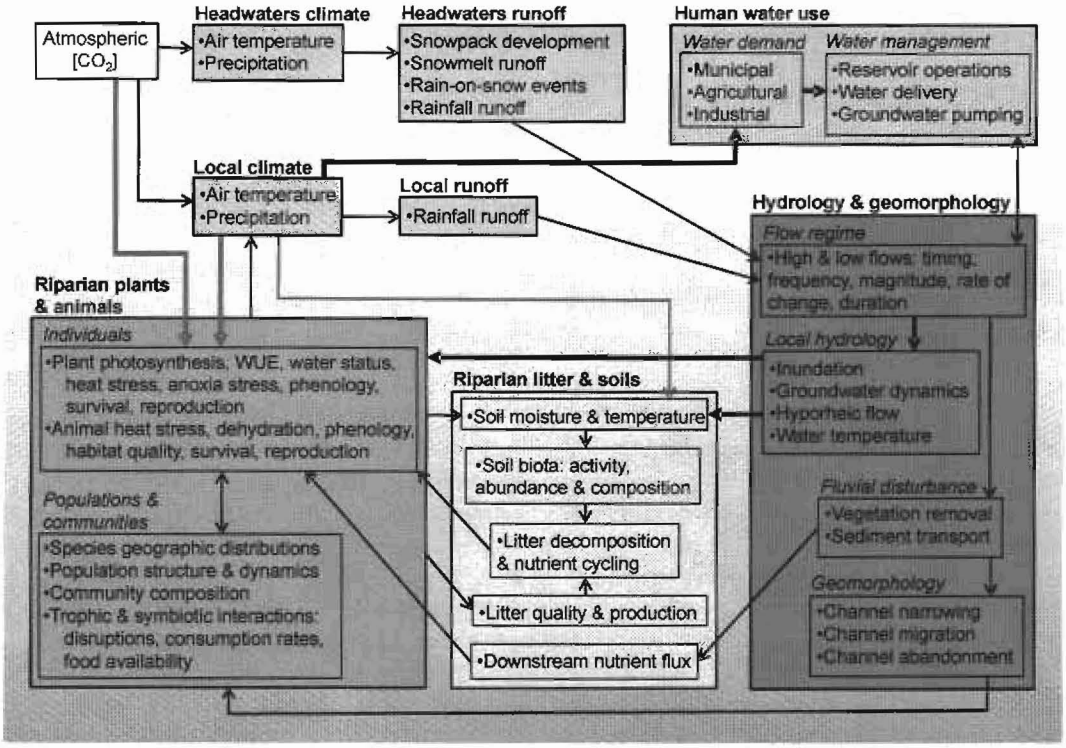

Fig. 1 Linkages between [CO_2] and climate change and components of riparian ecosystems in semiarid and arid western North America (SAWNA). Climate-change effects include both alteration of local weather conditions and alteration of climate in headwater regions leading to changes in flow regime. Direct 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

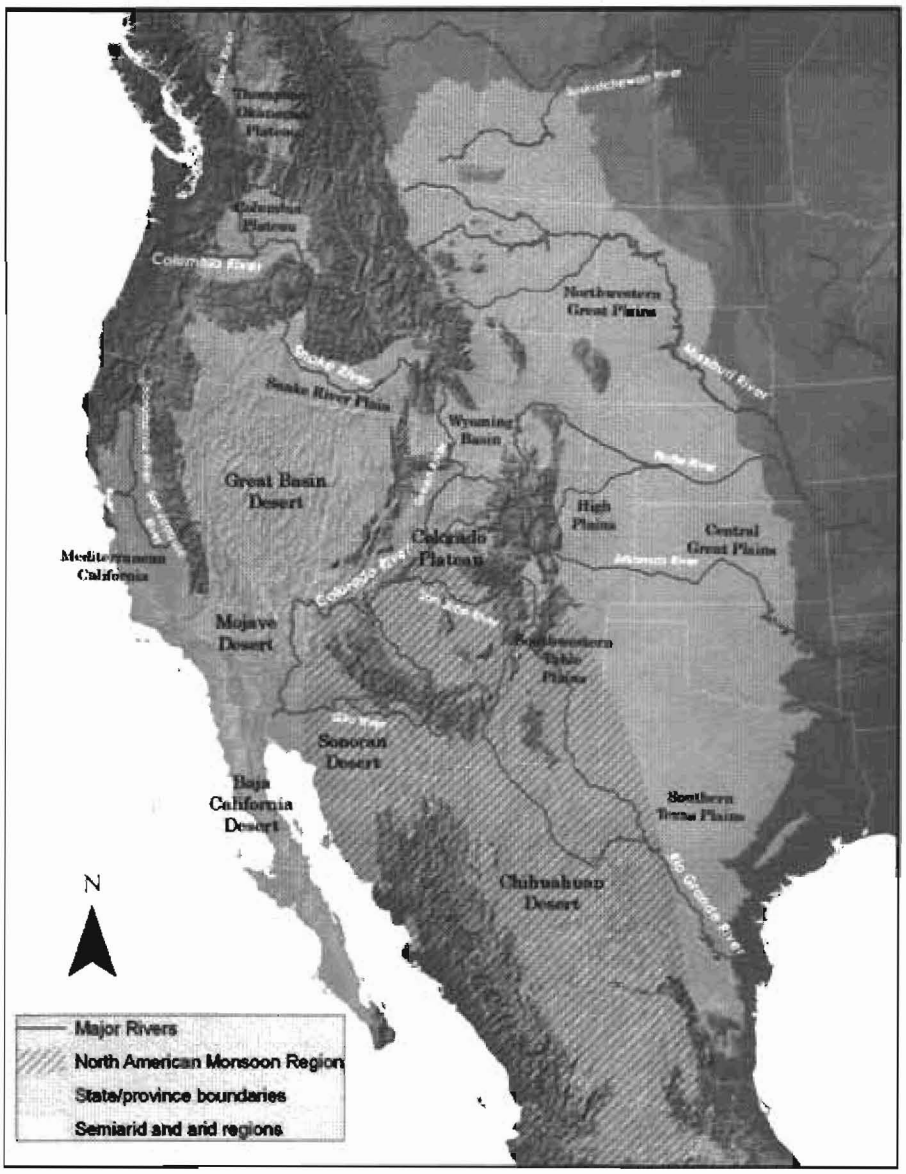

Fig. 2 Semiarid and arid regions of western North America (SAWNA), including subregions [adapted from CEC (1997)], major rivers, and the NA monsoon region [adapted from Adams & Comrie (1997)].

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_2] and temperature

Common name	Latin name	NA native/ introduced	Range in SAWNA	Ecophysiological responses	Citations
Plains cottonwood	*Populus deltoides* ssp. *monilifera* (Aiton) Eckenwalder	Native	East		
Rio Grande cottonwood	*P. deltoides* ssp. *wislizeni* (S. Watson) Eckenwalder	Native	Southeast		
Fremont cottonwood	*Populus fremontii* S. Watson	Native	Southwest	↑warming = earlier seed dispersal	Stella *et al.* (2006)
Black cottonwood	*Populus balsamifera* L. ssp. *trichocarpa* Brayshaw	Native	North	ca. 25 °C = optimal photosynthesis 35 °C = ca. 10% ↓photosynthesis	Bassman & Zwier (1991)
Narrowleaf cottonwood	*Populus angustifolia* James	Native	Higher elevations		
Peachleaf willow	*Salix amygdaloides* Andersson	Native	East		
Goodding's willow	*Salix gooddingii* C.R. Ball	Native	Southwest	↑warming = earlier seed dispersal	Stella *et al.* (2006)
Sandbar willow	*Salix exigua* Nutt.	Native	Throughout	↑warming = earlier seed dispersal	Stella *et al.* (2006)
Tamarisk (saltcedar)	*Tamarix ramosissima* Ledeb., *Tamarix chinensis* Lour., hybrids	Introduced	Throughout	ca. 25 °C = optimal photosynthesis 42 °C = ca. 50% ↓photosynthesis	Anderson (1982)
Russian olive	*Elaeagnus angustifolia* L.	Introduced	Throughout		
Eastern cottonwood	*P. deltoides* Bartram ex. Marsh ssp. *deltoides*	Native	n/a	↑[CO_2] = 40–50% ↑photosynthesis and 80% ↑growth ↑[CO_2] = 25–50% ↓stomatal conductance and 20–30% ↑WUE	Will & Teskey, (1997), McDonald *et al.* (2002), Murthy *et al.* (2005), Lewis *et al.* (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_2] and climate

[CO_2] 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_2] and climate change on riparian plants

Increased [CO_2] 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_2] 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 *et al.* (2001), Burn & Hag Elnur (2002), Regonda *et al.* (2005), Rood *et al.* (2005b)	Inconsistent predictions; varies with projected precipitation	Dettinger *et al.* (2004), Hayhoe *et al.* (2004), Vanrheenen *et al.* (2004), Milly *et al.* (2005), Christensen & Lettenmaier (2007)
Winter and early spring flow	10–60% increase	Regonda *et al.* (2005), Stewart *et al.* (2005), Miller & Piechota (2008), Rood *et al.* (2008)	Projected to increase further	Christensen *et al.* (2004), Dettinger *et al.* (2004), Knowles & Cayan (2004), Leung *et al.* (2004), Maurer (2007)
Late-spring and summer flow	10–20% decrease	Regonda *et al.* (2005), Stewart *et al.* (2005), Miller & Piechota (2008), Rood *et al.* (2008)	Projected to decrease further	Christensen *et al.* (2004), Dettinger *et al.* (2004), Hayhoe *et al.* (2004), Leung *et al.* (2004), Maurer (2007)
Spring snow melt flood timing	10–30 days earlier	McCabe & Clark (2005), Regonda *et al.* (2005), Stewart *et al.* (2005), Moore *et al.* (2007), Rood *et al.* (2008), Clow (2010)	Projected to shift still earlier	Christensen *et al.* (2004), Dettinger *et al.* (2004), Hayhoe *et al.* (2004), Leung *et al.* (2004), Stewart *et al.* (2004), Maurer (2007), Scibek *et al.* (2007)
Spring snow melt flood magnitude	Decrease in west Canada	Zhang *et al.* (2001)	Projected to decrease	Dettinger *et al.* (2004)
Spring snow melt flood rate of change	More gradual ascension in west Canada	Rood *et al.* (2008)		
Winter flood magnitude and frequency			Projected to increase in northwest United States and Canada	Leung *et al.* (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 $[CO_2]$ 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 $[CO_2]$ tends to increase photosynthesis and growth in C_3 plants (Ainsworth & Long, 2005; de Graaff *et al.*, 2006), including in cottonwoods (Table 1), which dominate SAWNA riparian ecosystems. In addition, increased $[CO_2]$ 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 $[CO_2]$ can increase plant productivity in dryland ecosystems (Morgan *et al.*, 2004).

Warming-induced drought, however, is likely to override the positive effects of $[CO_2]$-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

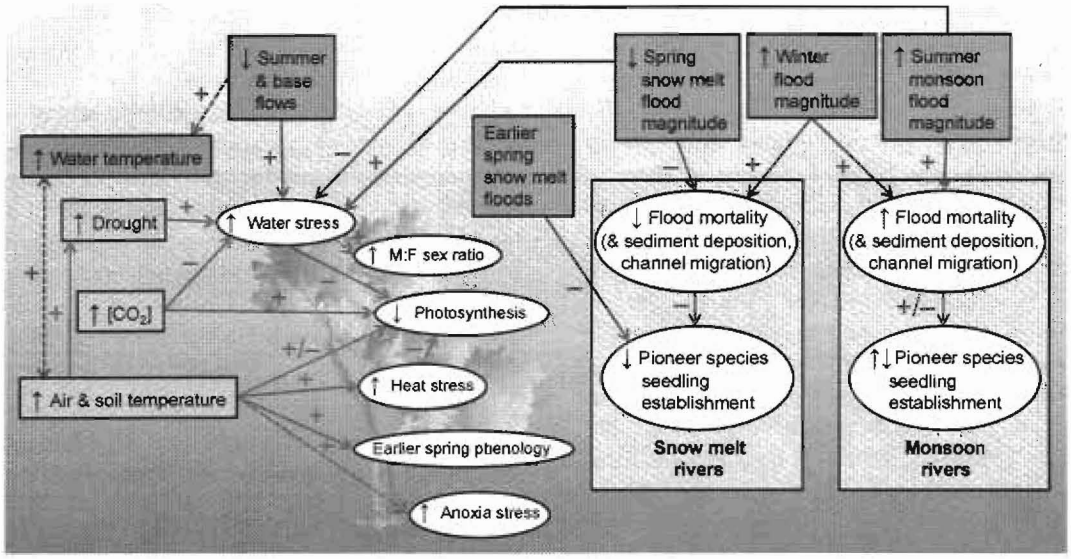

Fig. 3 Potential effects of elevated [CO_2], climate change, and climate-driven streamflow changes (rectangles) on riparian plants (ovals). Arrows within the rectangles and ovals indicate the net direction of expected change. Arrows between rectangles and ovals indicate linkages between environmental 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 °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 (50–55 °C) (Ferreira *et al.*, 2006). Slightly lower maximum temperatures (25–45 °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 °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; Kozlowski & 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_2] 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 individualistically 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_2] 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_2] 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_2] and climate change may also affect decomposition and nutrient cycling. Increased [CO_2] 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

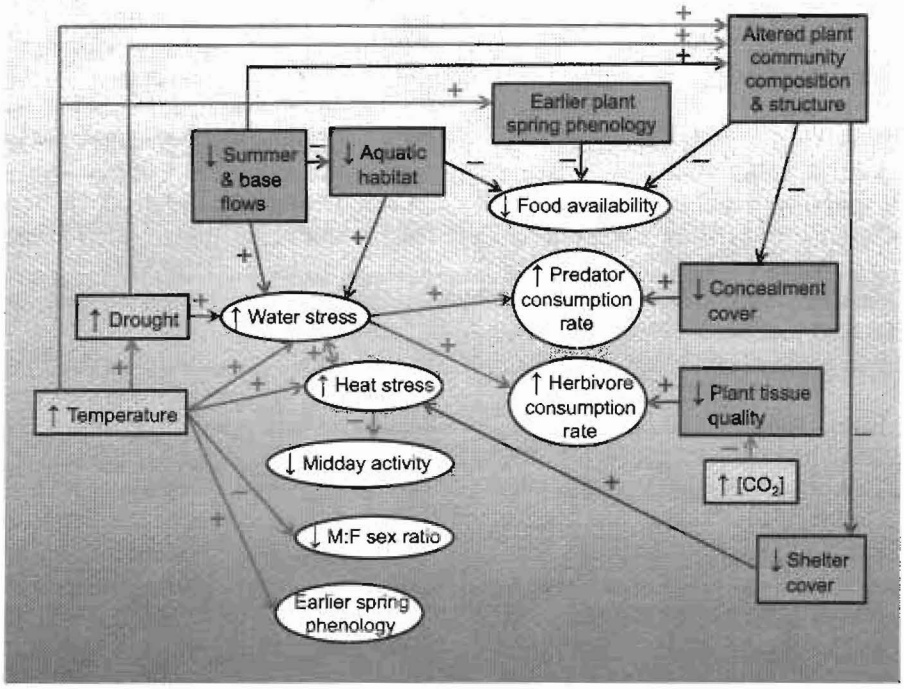

Fig. 4 Potential effects of elevated [CO_2], climate change, and climate-driven streamflow and plant community changes (rectangles) on riparian animals (ovals). Arrows within the rectangles and ovals indicate the net direction of expected change. Arrows between rectangles and ovals indicate linkages 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_2] 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_2] also may increase herbivore consumption rates. Increased [CO_2] 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_2] (Stiling & Cornelissen, 2007). Herbivore growth and abundance tend to decline under elevated [CO_2] 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_2] 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_2] may reduce consumption by insects that rely on [CO_2] gradients to locate fruit, flowers, prey, or ovipositioning sites (Guerenstein & Hildebrand, 2008), although increased [CO_2] does not reduce CO_2 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-armor 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_2] 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_2], 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_2] 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_2] 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_2] 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_2-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_2] 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_2] and climate change.

Acknowledgements

We thank Dana Blumenthal, Kevin McCluney, Julie Stromberg, and four anonymous reviewers for comments on earlier drafts of this manuscript. This work was funded by the Bureau of Reclamation, Research and Development Office, Science and Technology Program and the US Geological Survey, Invasive Species Program.

References

Abatzoglou JT, Redmond KT (2007) Asymmetry between trends in spring and autumn temperature and circulation regimes over western North America. *Geophysical Research Letters*, **34**, L18808, doi: 10.1029/2007GL030891.

Abrell L, Guerenstein PG, Mechaber WL, Stange G, Christensen TA, Nakanishi K, Hildebrand JG (2005) Effect of elevated atmospheric CO_2 on oviposition behavior in *Manduca sexta* moths. *Global Change Biology*, **11**, 1272–1282.

Adair EC, Binkley D (2002) Co-limitation of first year Fremont cottonwood seedlings by nitrogen and water. *Wetlands*, **22**, 425–429.

Adair EC, Binkley D, Andersen DC (2004) Patterns of nitrogen accumulation and cycling in riparian floodplain ecosystems along the Green and Yampa rivers. *Oecologia*, **139**, 108–116.

Adam JC, Hamlet AF, Lettenmaier DP (2009) Implications of global climate change for snowmelt hydrology in the twenty-first century. *Hydrological Processes*, **23**, 962–972.

Adams RA (2010) Bat reproduction declines when conditions mimic climate change projections for western North America. *Ecology*, **91**, 2437–2445.

Adams DK, Comrie AC (1997) The North American monsoon. *Bulletin of the American Meteorological Society*, **78**, 2197–2213.

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist*, **165**, 351–371.

Amlin NM, Rood SB (2002) Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands*, **22**, 338–346.

Andersen DC, Cooper DJ (2000) Plant-herbivore-hydroperiod interactions: effects of native mammals on floodplain tree recruitment. *Ecological Applications*, **10**, 1384–1399.

Andersen DC, Nelson SM (2002) Effects of cottonwood leaf beetle *Chrysomela scripta* (Coleoptera: Chrysomelidae) on survival and growth of Fremont cottonwood (*Populus fremontii*) in northwest Colorado. *American Midland Naturalist*, **147**, 189–203.

Andersen DC, Nelson SM (2006) Flood pattern and weather determine *Populus* leaf litter breakdown and nitrogen dynamics on a cold desert floodplain. *Journal of Arid Environments*, **64**, 626–650.

Andersen DC, Shafroth PB (2010) Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona. *Ecohydrology*, **3**, 325–338.

Andersen DC, Shafroth PB, Pritekel CM, O'Neill MW (2011) Managed flood effects on beaver pond habitat in a desert riverine ecosystem, Bill Williams River, Arizona USA. *Wetlands*, **31**, 195–206.

Anderson JE (1982) Factors controlling transpiration and photosynthesis in *Tamarix chinensis* Lour. *Ecology*, **63**, 48–56.

Andreadis KM, Lettenmaier DP (2006) Trends in 20th century drought over the continental United States. *Geophysical Research Letters*, **33**, L10403, doi: 10.1029/2006GL025711.

Arnell NW (1999) The effect of climate change on hydrological regimes in Europe: a continental perspective. *Global Environmental Change-Human and Policy Dimensions*, **9**, 5–23.

Auble GT, Scott ML, Friedman JM (2005) Use of individualistic streamflow-vegetation relations along the Fremont River, Utah, USA to assess impacts of flow alteration on wetland and riparian areas. *Wetlands*, **25**, 143–154.

Augspurger CK (2009) Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. *Functional Ecology*, **23**, 1031–1039.

Bale JS, Hayward SAL (2010) Insect overwintering in a changing climate. *Journal of Experimental Biology*, **213**, 980–994.

Barnett TP, Pierce DW (2009) Sustainable water deliveries from the Colorado River in a changing climate. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 7334–7338.

Barnett TP, Pierce DW, Hidalgo HG *et al.* (2008) Human-induced changes in the hydrology of the western United States. *Science*, **319**, 1080–1083.

Bassman JH, Zwier JC (1991) Gas exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa* x *Populus deltoides* clones. *Tree Physiology*, **8**, 145–159.

Beauchamp VB, Stromberg JC, Stutz JC (2006) Arbuscular mycorrhizal fungi associated with *Populus-Salix* stands in a semiarid riparian ecosystem. *New Phytologist*, **170**, 369–380.

Bengtsson L, Hodges KI, Esch M, Keenlyside N, Kornblueh L, Luo JJ, Yamagata T (2007) How may tropical cyclones change in a warmer climate? *Tellus Series A-Dynamic Meteorology and Oceanography*, **59**, 539–561.

Beerie AMM (1984) Germination and dormancy. In: *Advanced Plant Physiology* (ed. Wilkins MB), pp. 440–468. John Wiley & Sons, New York.

Bhattacharjee J, Taylor JP, Smith LM, Haukos DA (2009) Seedling competition between native cottonwood and exotic saltcedar: implications for restoration. *Biological Invasions*, **11**, 1777–1787.

Bidart-Bouzat MG, Imeh-Nathaniel A (2008) Global change effects on plant chemical defenses against insect herbivores. *Journal of Integrative Plant Biology*, **50**, 1339–1354.

Bolger DT, Patten MA, Bostock DC (2005) Avian reproductive failure in response to an extreme climatic event. *Oecologia*, **142**, 398–406.

Brand LA, Stromberg JC, Noon BR (2010) Avian density and nest survival on the San Pedro River: importance of vegetation type and hydrologic regime. *Journal of Wildlife Management*, **74**, 739–754.

Brekke LD, Miller NL, Bashford KE, Quinn NWT, Dracup JA (2004) Climate change impacts uncertainty for water resources in the San Joaquin River Basin, California. *Journal of the American Water Resources Association*, **40**, 149–164.

Bridgeland WT, Beier P, Kolb T, Whitham TG (2010) A conditional trophic cascade: birds benefit faster growing trees with strong links between predators and plants. *Ecology*, **91**, 73–84.

Briggs MK, Cornelius S (1998) Opportunities for ecological improvement along the lower Colorado River and delta. *Wetlands*, **18**, 513–529.

Brinson MM, Malvarez AI (2002) Temperate freshwater wetlands: types, status, and threats. *Environmental Conservation*, **29**, 115–133.

Briones MJI, Ostle NJ, Garnett MH (2007) Invertebrates increase the sensitivity of non-labile soil carbon to climate change. *Soil Biology & Biochemistry*, **39**, 816–818.

Brock JH (1994) Phenology and stand composition of woody riparian plants in the southwestern United States. *Desert Plants*, **11**, 23–32.

Brooker RW (2006) Plant-plant interactions and environmental change. *New Phytologist*, **171**, 271–284.

Burn DH, Hag Elnur MA (2002) Detection of hydrologic trends and variability. *Journal of Hydrology*, **255**, 107–122.

Busch DE, Smith SD (1995) Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern US. *Ecological Monographs*, **65**, 347–370.

Cain JW, Morrison ML, Bombay HL (2003) Predator activity and nest success of willow flycatchers and yellow warblers. *Journal of Wildlife Management*, **67**, 600–610.

Campbell CJ, Green W (1968) Perpetual succession of stream-channel vegetation in a semiarid region. *Journal of the Arizona Academy of Science*, **5**, 86–98.

Cane MA (2005) The evolution of El Niño, past and future. *Earth and Planetary Science Letters*, **230**, 227–240.

Cannon WA (1915) On the relation of root growth and development to the temperature and aeration of the soil. *American Journal of Botany*, **2**, 211–224.

Castelli RM, Chambers JC, Tausch RJ (2000) Soil-plant relations along a soil-water gradient in great basin riparian meadows. *Wetlands*, **20**, 251–266.

Cayan DR, Maurer EP, Dettinger MD, Tyree M, Hayhoe K (2008) Climate change scenarios for the California region. *Climatic Change*, **87**, S21–S42.

Cayan DR, Das T, Pierce DW, Barnett TP, Tyree M, Gershunov A (2010) Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21271–21276.

CEC (1997) *Ecological Regions of North America: Toward a Common Perspective*. Commission for Environmental Cooperation (CEC) Secretariat, Montreal.

Christensen NS, Lettenmaier DP (2007) A multimodel ensemble approach to assessment of climate change impacts on the hydrology and water resources of the Colorado River Basin. *Hydrology and Earth System Sciences*, **11**, 1417–1434.

Christensen NS, Wood AW, Voisin N, Lettenmaier DP, Palmer RN (2004) The effects of climate change on the hydrology and water resources of the Colorado River Basin. *Climatic Change*, **62**, 337–363.

Clow DW (2010) Changes in the timing of snowmelt and streamflow in Colorado: a response to recent warming. *Journal of Climate*, **23**, 2293–2306.

Coe SJ, Rotenberry JT (2003) Water availability affects clutch size in a desert sparrow. *Ecology*, **84**, 3240–3249.

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes in the western United States. *Science*, **306**, 1015–1018.

Cooper DJ, Merritt DM, Andersen DC, Chimner RA (1999) Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. *Regulated Rivers – Research & Management*, **15**, 419–440.

Cooper DJ, D'Amico DR, Scott ML (2003) Physiological and morphological response patterns of *Populus deltoides* to alluvial groundwater pumping. *Environmental Management*, **31**, 215–226.

Corbosiero KL, Dickinson MJ, Bosart LF (2009) The contribution of eastern North Pacific tropical cyclones to the rainfall climatology of the southwest United States. *Monthly Weather Review*, **137**, 2415–2435.

Daszak P, Scott DE, Kilpatrick AM, Faggioni C, Gibbons JW, Porter D (2005) Amphibian population declines at Savannah River site are linked to climate, not chytridiomycosis. *Ecology*, **86**, 3232–3237.

Denlinger DL, Yocum GD (1998) Physiology of heat sensitivity. In: *Temperature Sensitivity in Insects and Application in Integrated Pest Management* (eds Hallman GJ, Denlinger DL), pp. 7–53. Westview, Boulder, CO.

Dettinger MD, Cayan DR, Meyer M, Jeton AE (2004) Simulated hydrologic responses to climate variations and change in the Merced, Carson, and American River Basins, Sierra Nevada, California, 1900-2099. *Climatic Change*, **62**, 283–317.

Dewine JM, Cooper DJ (2008) Canopy shade and the successional replacement of tamarisk by native box elder. *Journal of Applied Ecology*, **45**, 505–514.

Diffenbaugh NS, Pal JS, Trapp RJ, Giorgi F (2005) Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15774–15778.

Dijkstra FA, Pendall E, Mosier AR, King JY, Milchunas DG, Morgan JA (2008) Long-term enhancement of N availability and plant growth under elevated CO_2 in a semi-arid grassland. *Functional Ecology*, **22**, 973–982.

Dijkstra FA, Blumenthal D, Morgan JA, Pendall E, Carrillo Y, Follett RF (2010) Contrasting effects of elevated CO_2 and warming on nitrogen cycling in a semiarid grassland. *New Phytologist*, **187**, 426–437.

Dixon AFG (1998) *Aphid Ecology: An Optimization Approach* (2nd edu). Chapman and Hall, London.

Drigo B, Kowalchuk GA, van Veen JA (2008) Climate change goes underground: effects of elevated atmospheric CO_2 on microbial community structure and activities in the rhizosphere. *Biology and Fertility of Soils*, **44**, 667–679.

Durst SL, Theimer TC, Paxton EH, Sogge MK (2008) Temporal variation in the arthropod community of desert riparian habitats with varying amounts of saltcedar (*Tamarix ramosissima*). *Journal of Arid Environments*, **72**, 1644–1653.

Ebersberger D, Niklaus PA, Kandeler E (2003) Long term CO_2 enrichment stimulates N-mineralisation and enzyme activities in calcareous grassland. *Soil Biology & Biochemistry*, **35**, 965–972.

Eheart JW, Tornil DW (1999) Low-flow frequency exacerbation by irrigation withdrawals in the agricultural midwest under various climate change scenarios. *Water Resources Research*, **35**, 2237–2246.

Ewert MA, Nelson CE (1991) Sex determination in turtles – diverse patterns and some possible adaptive values. *Copeia*, **1991**, 50–69.

Fagan WF (2002) Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, **83**, 3243–3249.

Ferreira S, Hjerno K, Larsen M *et al.* (2006) Proteome profiling of *Populus euphratica* Oliv. upon heat stress. *Annals of Botany*, **98**, 361–377.

Florsheim JL, Mount JF (2002) Restoration of floodplain topography by sand-splay complex formation in response to intentional levee breaches, Lower Cosumnes River, California. *Geomorphology*, **44**, 67–94.

Follstad Shah JJ, Dahm CN (2008) Flood regime and leaf fall determine soil inorganic nitrogen dynamics in semiarid riparian forests. *Ecological Applications*, **18**, 771–788.

Fontaine JJ, Decker KL, Skagen SK, van Riper C (2009) Spatial and temporal variation in climate change: a bird's eye view. *Climatic Change*, **97**, 305–311.

Frelich LE, Reich PB (2010) Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? *Frontiers in Ecology and the Environment*, **8**, 371–378.

Friedman JM, Osterkamp WR, Scott ML, Auble GT (1998) Downstream effects of dams on channel geometry and bottomland vegetation: regional patterns in the Great Plains. *Wetlands*, **18**, 619–633.

Friedman JM, Auble GT, Shafroth PB, Scott ML, Merigliano MF, Preehling MD, Griffin EK (2005) Dominance of non-native riparian trees in western USA. *Biological Invasions*, **7**, 747–751.

Friedman JM, Roelle JE, Gaskin JF, Pepper AE, Manhart JR (2008) Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. *Evolutionary Applications*, **1**, 598–607.

Friedman J, Roelle J, Cade B (2011) Genetic and environmental influences on leaf phenology and cold hardiness of native and introduced riparian trees. *International Journal of Biometeorology*, **55**, 775–787.

Geiger R (1965) *The Climate Near the Ground*. Harvard University Press, Cambridge, MA.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.

Gitlin AR (2007) *Applying Climate Predictions and Spatial Modelling to Prioritizing Riparian Habitat Restoration*. M.S. thesis, Northern Arizona University, Flagstaff.

Gladwin DN, Roelle JE (1998) Survival of plains cottonwood (*Populus deltoides* subsp. *monilifera*) and saltcedar (*Tamarix ramosissima*) seedlings in response to flooding. *Wetlands*, **18**, 669–674.

de Graaff MA, van Groenigen KJ, Six J, Hungate B, van Kessel C (2006) Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta-analysis. *Global Change Biology*, **12**, 2077–2091.

Graf WL (2006) Downstream hydrologic and geomorphic effects of large dams on American rivers. *Geomorphology*, **79**, 336–360.

Grantz K, Rajagopalan B, Clark M, Zagona E (2007) Seasonal shifts in the North American monsoon. *Journal of Climate*, **20**, 1923–1935.

Greenwood MJ, McIntosh AR (2010) Low river flow alters the biomass and population structure of a riparian predatory invertebrate. *Freshwater Biology*, **55**, 2062–2076.

Grimm NB, Chacon A, Dahm CN, Hostetler SW, Lind OT, Starkweather PL, Wurtsbaugh WW (1997) Sensitivity of aquatic ecosystems to climatic and anthropogenic changes: The Basin and Range, American Southwest and Mexico. *Hydrological Processes*, **11**, 1023–1041.

Groisman PY, Knight RW (2008) Prolonged dry episodes over the conterminous united states: new tendencies emerging during the last 40 years. *Journal of Climate*, **21**, 1850–1862.

Guerenstein PG, Hildebrand JG (2008) Roles and effects of environmental carbon dioxide in insect life. *Annual Review of Entomology*, **53**, 161–178.

Guilloy-Froget H, Muller E, Barsoum N, Hughes FMR (2002) Dispersal, germination, and survival of *Populus nigra* L. (Salicaceae) in changing hydrologic conditions. *Wetlands*, **22**, 478–488.

Hadley NF, Quinlan MC, Kennedy ML (1991) Evaporative cooling in the desert cicada – thermal efficiency and water metabolic costs. *Journal of Experimental Biology*, **159**, 269–283.

Hamlet AF, Lettenmaier DP (2007) Effects of 20th century warming and climate variability on flood risk in the western US. *Water Resources Research*, **43**, W06427, doi: 10.1029/2006WR005099.

Hamlet AF, Mote PW, Clark MP, Lettenmaier DP (2007) Twentieth-century trends in runoff, evapotranspiration, and soil moisture in the western United States. *Journal of Climate*, **20**, 1468–1486.

Haney JA, Turner DS, Springer AE, Stromberg JC, Stevens LE, Pearthree PA, Supplee V (2008) *Ecological Implications of Verde River Flows*. The Arizona Water Institute, The Nature Conservancy, and the Verde River Basin Partnership. Available at: http://azconservation.org/dl/TNCAZ_VerdeRiver_Ecological_Flows.pdf (accessed 11 November 2011).

Hanson AA, Sprague VG (1953) Heading of perennial grasses under greenhouse conditions. *Agronomy Journal*, **45**, 248–251.

Harms TK, Grimm NB (2008) Hot spots and hot moments of carbon and nitrogen dynamics in a semiarid riparian zone. *Journal of Geophysical Research-Biogeosciences*, **113**, G01020, doi: 10.1029/2007JG000588.

Harner MJ, Crenshaw CL, Abetho M, Stursova M, Follstad Shah JJ, Sinsabaugh RL (2009) Decomposition of leaf litter from a native tree and an actinorhizal invasive across riparian habitats. *Ecological Applications*, **19**, 1135–1146.

Harrisou FA, Berry PM, Henriques C, Holman IP (2008) Impacts of socio-economic and climate change scenarios on wetlands: linking water resource and biodiversity meta-models. *Climatic Change*, **90**, 113–139.

Hayhoe K, Cayan D, Field CB *et al.* (2004) Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 12422–12427.

Heath JE, Wilkin PJ (1970) Temperature responses of desert cicada, *Diceroprocta apache* (Homoptera, Cicadidae). *Physiological Zoology*, **43**, 145–154.

Hegland SJ, Nielsen A, Lazaro A, Bjerknes AL, Totland O (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters*, **12**, 184–195.

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.

Hodgkins GA, Dudley RW (2006) Changes in the timing of winter-spring streamflows in eastern North America, 1913-2002. *Geophysical Research Letters*, **33**, L06402, doi: 10.1029/2005GL025593.

Horton JL, Kolb TE, Hart SC (2001) Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant, Cell and Environment*, **24**, 293–304.

Horton JL, Hart SC, Kolb TE (2003) Physiological condition and water source use of Sonoran Desert riparian trees at the Bill Williams River, Arizona, USA. *Isotopes in Environmental and Health Studies*, **39**, 69–82.

Horton P, Schaefli B, Mezghani A, Hingray B, Musy A (2006) Assessment of climate-change impacts on alpine discharge regimes with climate model uncertainty. *Hydrological Processes*, **20**, 2091–2109.

Hultine KR, Bush SE, West AG, Ehleringer JR (2007) Population structure, physiology and ecohydrological impacts of dioecious riparian tree species of western North America. *Oecologia*, **154**, 85–93.

Hultine KR, Belnap J, van Riper C *et al.* (2010) Tamarisk biocontrol in the western United States: ecological and societal implications. *Frontiers in Ecology and the Environment*, **8**, 467–474.

Hungate BA, Chapin FS, Zhong H, Holland EA, Field CB (1997) Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia*, **109**, 149–153.

Hyvönen R, Agren GI, Linder S *et al.* (2007) The likely impact of elevated [CO_2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist*, **173**, 463–480.

IPCC (2007) *Climate Change 2007 Synthesis Report*. Intergovernmental Panel on Climate Change, Geneva.

IPCC (2008) *Climate Change and Water: IPCC Technical Paper VI*. Intergovernmental Panel on Climate Change, Geneva.

Jacobs SM, Bechtold JS, Biggs HC *et al.* (2007) Nutrient vectors and riparian processing: a review with special reference to African semiarid savanna ecosystems. *Ecosystems*, **10**, 1231–1249.

Johnson WC (1994) Woodland expansion in the Platte River, Nebraska – patterns and causes. *Ecological Monographs*, **64**, 45–84.

Johnson WC (1998) Adjustment of riparian vegetation to river regulation in the Great Plains, USA. *Wetlands*, **18**, 608–618.

Jones KB, Slonecker ET, Nash MS, Neale AC, Wade TG, Hamann S (2010) Riparian habitat changes across the continental United States (1972-2003) and potential implications for sustaining ecosystem services. *Landscape Ecology*, **25**, 1261–1275.

Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.

Kaszkurewicz A, Fogg PJ (1967) Growing seasons of cottonwood and sycamore as related to geographic and environmental factors. *Ecology*, **48**, 785–793.

Kaushal SS, Likens GE, Jaworski NA *et al.* (2010) Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment*, **8**, 461–466.

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823–11826.

Kerns BK, Naylor BJ, Buonopane M, Parks CG, Rogers B (2009) Modeling tamarisk (*Tamarix* spp.) habitat and climate change effects in the northwestern United States. *Invasive Plant Science and Management*, **2**, 200–215.

Kim J (2005) A projection of the effects of the climate change induced by increased CO_2 on extreme hydrologic events in the western US. *Climatic Change*, **68**, 153–168.

Knopf FL, Samson FB (1994) Scale perspectives on avian diversity in western riparian ecosystems. *Conservation Biology*, **8**, 669–676.

Knowles N, Cayan DR (2004) Elevational dependence of projected hydrologic changes in the San Francisco estuary and watershed. *Climatic Change*, **62**, 319–336.

Kozlowski TT, Pallardy SG (2002) Acclimation and adaptive responses of woody plants to environmental stresses. *Botanical Review*, **68**, 270–334.

Lamontagne S, Cook PG, O'Grady A, Eamus D (2005) Groundwater use by vegetation in a tropical savanna riparian zone (Daly River, Australia). *Journal of Hydrology*, **310**, 280–293.

Lawrence JE, Lunde KB, Mazor RD, Beche LA, McElravy EP, Resh VH (2010) Long-term macroinvertebrate responses to climate change: implications for biological assessment in mediterranean-climate streams. *Journal of the North American Benthological Society*, **29**, 1424–1440.

Lellouch M, Hyun K, Tognetti S (2007) *Ecosystem Changes and Water Policy Choices: Four Scenarios for the Lower Colorado River Basin to 2050*. Island Press, Washington, D.C.

Leung LR, Qian Y, Bian XD, Washington WM, Han JG, Roads JO (2004) Mid-century ensemble regional climate change scenarios for the western United States. *Climatic Change*, **62**, 75–113.

Lewis JD, Ward JK, Tissue DT (2010) Phosphorus supply drives nonlinear responses of cottonwood (*Populus deltoides*) to increases in CO_2 concentration from glacial to future concentrations. *New Phytologist*, **187**, 438–448.

Ligon JD (1969) Some aspects of temperature relations in small owls. *Auk*, **86**, 458–472.

Lin JL, Mapes BE, Weickmann KM *et al.* (2008) North American monsoon and convectively coupled equatorial waves simulated by IPCC AR4 coupled GCMs. *Journal of Climate*, **21**, 2919–2937.

Lins HF, Slack JR (1999) Streamflow trends in the United States. *Geophysical Research Letters*, **26**, 227–230.

Mac Nally R, Cunningham SC, Baker PJ, Horner GJ, Thomson JR (2011) Dynamics of Murray-Darling floodplain forests under multiple stressors: the past, present, and future of an Australian icon. *Water Resources Research*, **47**, W00G05, doi: 10.1029/2011WR010383.

Mahoney JM, Rood SB (1998) Streamflow requirements for cottonwood seedling recruitment – an integrative model. *Wetlands*, **18**, 634–645.

Martin TE (2007) Climate correlates of 20 years of trophic changes in a high-elevation riparian system. *Ecology*, **88**, 367–380.

Maurer EP (2007) Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. *Climatic Change*, **82**, 309–325.

McCabe GJ, Clark MP (2005) Trends and variability in snowmelt runoff in the western United States. *Journal of Hydrometeorology*, **6**, 476–482.

McCluney KE, Sabo JL (2009) Water availability directly determines per capita consumption at two trophic levels. *Ecology*, **90**, 1463–1469.

McDonald EP, Erickson JE, Kruger EL (2002) Can decreased transpiration limit plant nitrogen acquisition in elevated CO_2? *Functional Plant Biology*, **29**, 1115–1120.

McKechnie AE, Wolf BO (2010) Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, **6**, 253–256.

McLain JET, Martens DA (2006) Moisture controls on trace gas fluxes in semiarid riparian soils. *Soil Science Society of America Journal*, **70**, 367–377.

Memmott J, Craze PG, Waser NM, Price MV (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, **10**, 710–717.

Menzel A, Sparks TH, Estrella N *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976

Merritt DM, Cooper DJ (2000) Riparian vegetation and channel change in response to river regulation: a comparative study of regulated and unregulated streams in the Green River Basin, USA. *Regulated Rivers – Research & Management*, **16**, 543–564.

Merritt DM, Wohl EE (2002) Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. *Ecological Applications*, **12**, 1071–1087.

Merritt DM, Scott ML, Poff NL, Auble GT, Lytle DA (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshwater Biology*, **55**, 206–225.

Miller WP, Piechota TC (2008) Regional analysis of trend and step changes observed in hydroclimatic variables around the Colorado River Basin. *Journal of Hydrometeorology*, **9**, 1020–1034.

Milly PCD, Dunne KA, Vecchia AV (2005) Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, **438**, 347–350.

Mitchell NJ, Janzen FJ (2010) Temperature-dependent sex determination and contemporary climate change. *Sexual Development*, **4**, 129–140.

Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD (2009) New frontiers in competition for pollination. *Annals of Botany*, **103**, 1403–1413.

Moore JN, Harper JT, Greenwood MC (2007) Significance of trends toward earlier snowmelt runoff, Columbia and Missouri Basin headwaters, western United States. *Geophysical Research Letters*, **34**, L16402, doi: 10.1029/2007GL031022.

Morgan JA, Pataki DE, Korner C *et al.* (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia*, **140**, 11–25.

Morin X, Augspurger C, Chuine I (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology*, **88**, 2280–2291

Mortenson SG, Weisberg PJ, Ralston BE (2008) Do beavers promote the invasion of non-native *Tamarix* in the Grand Canyon riparian zone? *Wetlands*, **28**, 666–675.

Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005) Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society*, **86**, 39–49.

Murthy R, Barron-Gafford G, Dougherty PM *et al.* (2005) Increased leaf area dominates carbon flux response to elevated CO_2 in stands of *Populus deltoides* (Bartr.). *Global Change Biology*, **11**, 716–731.

Naiman RJ, Decamps H, McClain ME (2005) *Riparia: Ecology, Conservation, and Management of Streamside Communities*. Elsevier Academic Press, London, UK.

Naiman RJ, Bechtold JS, Beechie TJ, Latterell JJ, Van Pelt R (2010) A process-based view of floodplain forest patterns in coastal river valleys of the Pacific Northwest. *Ecosystems*, **13**, 1–31.

Nelson SM, Andersen DC (1999) Butterfly (Papilionoidea and Hesperioidea) assemblages associated with natural, exotic, and restored riparian habitats along the lower Colorado River, USA. *Regulated Rivers – Research & Management*, **15**, 485–504.

Nelson SM, Wydoski R (2008) Riparian butterfly (Papilionoidea and Hesperioidea) assemblages associated with *Tamarix*-dominated, native vegetation-dominated, and *Tamarix* removal sites along the Arkansas River, Colorado USA. *Restoration Ecology*, **16**, 168–179.

Nilsson C, Berggren K (2000) Alterations of riparian ecosystems caused by river regulation. *BioScience*, **50**, 783–792.

Nohara D, Kitoh A, Hosaka M, Oki T (2006) Impact of climate change on river discharge projected by multimodel ensemble. *Journal of Hydrometeorology*, **7**, 1076–1089.

Nord EA, Lynch JP (2009) Plant phenology: a critical controller of soil resource acquisition. *Journal of Experimental Botany*, **60**, 1927–1937.

Nunes JP, Seixas J, Pacheco NR (2008) Vulnerability of water resources, vegetation productivity and soil erosion to climate change in Mediterranean watersheds. *Hydrological Processes*, **22**, 3115–3134.

Ober HK, Hayes JP (2008) Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. *Forest Ecology and Management*, **256**, 1124–1132.

Palmer MA, Liermann CAR, Nilsson C, Florke M, Alcamo J, Lake PS, Bond N (2008) Climate change and the world's river basins: anticipating management options. *Frontiers in Ecology and the Environment*, **6**, 81–89.

Palmer MA, Lettenmaier DP, Poff NL, Postel SL, Richter B, Warner R (2009) Climate change and river ecosystems: protection and adaptation options. *Environmental Management*, **44**, 1053–1068.

Park S, Keathley DE, Han KH (2008) Transcriptional profiles of the annual growth cycle in *Populus deltoides*. *Tree Physiology*, **28**, 321–329.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, **13**, 1860–1872.

Patten DT (1998) Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands*, **18**, 498–512.

Pauley SS, Perry TO (1954) Ecotypic variation in the photoperiodic response in *Populus*. *Journal of the Arnold Arboretum*, **35**, 167–188.

Peterson TC, Zhang XB, Brunet-India M, Vazquez-Aguirre JL (2008) Changes in North American extremes derived from daily weather data. *Journal of Geophysical Research – Atmospheres*, **113**, D07113, doi: 10.1029/2007JD009453.

Pettit NE, Froend RH (2001) Availability of seed for recruitment of riparian vegetation: a comparison of a tropical and a temperate river ecosystem in Australia. *Australian Journal of Botany*, **49**, 515–528.

Piotrowski JS, Lekberg Y, Harner MJ, Ramsey PW, Rillig MC (2008) Dynamics of mycorrhizae during development of riparian forests along an unregulated river. *Ecography*, **31**, 245–253.

Pittock J, Connell D (2010) Australia demonstrates the planet's future: water and climate in the Murray-Darling basin. *International Journal of Water Resources Development*, **26**, 561–578.

Poff NL (1996) A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology*, **36**, 71–91.

Poff NL, Allan JD, Bain MB *et al.* (1997) The natural flow regime. *BioScience*, **47**, 769–784.

Poff NL, Olden JD, Merritt DM, Pepin DM (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5732–5737.

Pomeroy KE, Shannon JP, Blinn DW (2000) Leaf breakdown in a regulated desert river: Colorado River, Arizona, USA. *Hydrobiologia*, **434**, 193–199.

Poole GC, O'Daniel SJ, Jones KL *et al.* (2008) Hydrologic spiralling: the role of multiple interactive flow paths in stream ecosystems. *River Research and Applications*, **24**, 1018–1031.

Potter K, Davidowitz G, Woods HA (2009) Insect eggs protected from high temperatures by limited homeothermy of plant leaves. *Journal of Experimental Biology*, **212**, 3448–3454.

Purkey DR, Joyce B, Vicuna S, Hanemann MW, Dale LL, Yates D, Dracup JA (2008) Robust analysis of future climate change impacts on water for agriculture and other sectors: a case study in the Sacramento Valley. *Climatic Change*, **87**, S109–S122.

Rajagopalan B, Nowak K, Prairie J *et al.* (2009) Water supply risk on the Colorado River: can management mitigate? *Water Resources Research*, **45**, W08201, doi: 10.1029/2008WR007652.

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, **16**, 179–214.

Regonda SK, Rajagopalan B, Clark M, Pitlick J (2005) Seasonal cycle shifts in hydroclimatology over the western United States. *Journal of Climate*, **18**, 372–384.

Reich PB, Hungate BA, Luo YQ (2006) Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology Evolution and Systematics*, **37**, 611–636.

Reynolds LV, Cooper DJ (2010) Environmental tolerance of an invasive riparian tree and its potential for continued spread in the southwestern US. *Journal of Vegetation Science*, **21**, 733–743.

Richardson DM, Holmes PM, Esler KJ *et al.* (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions*, **13**, 126–139.

Richardson JS, Zhang YX, Marczak LB (2010) Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications*, **26**, 55–66.

Riechert SE, Hall RF (2000) Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider. *Journal of Evolutionary Biology*, **13**, 541–550.

Ringold PL, Magee TK, Peck DV (2008) Twelve invasive plant taxa in US western riparian ecosystems. *Journal of the North American Benthological Society*, **27**, 949–966.

van Riper C, Paxton KL, O'Brien C, Shafroth PB, McGrath LJ (2008) Rethinking avian response to *Tamarix* on the lower Colorado River: a threshold hypothesis. *Restoration Ecology*, **16**, 155–167.

Robinet C, Roques A (2010) Direct impacts of recent climate warming on insect populations. *Integrative Zoology*, **5**, 132–142.

Rood SB, Braatne JH, Hughes FMR (2003) Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiology*, **23**, 1113–1124.

Rood SB, Samuelson GM, Braatne JH, Gourley CR, Hughes FMR, Mahoney JM (2005a) Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment*, **3**, 193–201.

Rood SB, Samuelson GM, Weber JK, Wywrot KA (2005b) Twentieth-century decline in streamflows from the hydrographic apex of North America. *Journal of Hydrology*, **306**, 215–233.

Rood SB, Berg KJ, Pearce DW (2007) Localized temperature adaptation of cottonwoods from elevational ecoregions in the Rocky Mountains. *Trees – Structure and Function*, **21**, 171–180.

Rood SB, Pan J, Gill KM, Franks CG, Samuelson GM, Shepherd A (2008) Declining summer flows of Rocky Mountain rivers: changing seasonal hydrology and probable impacts on floodplain forests. *Journal of Hydrology*, **349**, 397–410.

Roy BA, Gusewell S, Harte J (2004) Response of plant pathogens and herbivores to a warming experiment. *Ecology*, **85**, 2570–2581.

Rustad LE, Campbell JL, Marion GM *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.

Sabo JL, Sponseller R, Dixon M *et al.* (2005) Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, **86**, 56–62.

Saxe H, Cannell MGR, Johnsen B, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369–399.

Schade JD, Marti E, Welter JR, Fisher SG, Grimm NB (2002) Sources of nitrogen to the riparian zone of a desert stream: Implications for riparian vegetation and nitrogen retention. *Ecosystems*, **5**, 68–79.

Scibek J, Allen DM, Cannon AJ, Whitfield PH (2007) Groundwater-surface water interaction under scenarios of climate change using a high-resolution transient groundwater model. *Journal of Hydrology*, **333**, 165–181.

Scott ML, Friedman JM, Auble GT (1996) Fluvial process and the establishment of bottomland trees. *Geomorphology*, **14**, 327–339.

Scott ML, Skagen SK, Merigliano MF (2003) Relating geomorphic change and grazing to avian communities in riparian forests. *Conservation Biology*, **17**, 284–296.

Scott ML, Nagler PL, Glenn EP *et al.* (2009) Assessing the extent and diversity of riparian ecosystems in Sonora, Mexico. *Biodiversity and Conservation*, **18**, 247–269.

Seager R, Vecchi GA (2010) Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21277–21282.

Seavy NE, Gardali T, Golet GH *et al.* (2009) Why climate change makes riparian restoration more important than ever: recommendations for practice and research. *Ecological Restoration*, **27**, 330–338.

Serrat-Capdevila A, Valdes JB, Perez JG, Baird K, Mata LJ, Maddock T (2007) Modeling climate change impacts and uncertainty on the hydrology of a riparian system: the San Pedro Basin (Arizona/Sonora). *Journal of Hydrology*, **347**, 48–66.

Shafroth PB, Auble GT, Stromberg JC, Patten DT (1998) Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands*, **18**, 577–590.

Shafroth PB, Stromberg JC, Patten DT (2000) Woody riparian vegetation response to different alluvial water table regimes. *Western North American Naturalist*, **60**, 66–76.

Shafroth PB, Stromberg JC, Patten DT (2002) Riparian vegetation response to altered disturbance and stress regimes. *Ecological Applications*, **12**, 107–123.

Shafroth PB, Cleverly JR, Dudley TL, Taylor JP, Van Riper C, Weeks EP, Stuart JN (2005) Control of *Tamarix* in the Western United States: implications for water salvage, wildlife use, and riparian restoration. *Environmental Management*, **35**, 231–246.

Shafroth PB, Wilcox AC, Lytle DA *et al.* (2010) Ecosystem effects of environmental flows: modelling and experimental floods in a dryland river. *Freshwater Biology*, **55**, 68–85.

Shaw JR, Cooper DJ (2008) Linkages among watersheds, stream reaches, and riparian vegetation in dryland ephemeral stream networks. *Journal of Hydrology*, **350**, 68–82.

Sipes SD, Tepedino VJ (1995) Reproductive biology of the rare orchid, *Spiranthes diluvialis* – breeding system, pollination, and implications for conservation. *Conservation Biology*, **9**, 929–938.

Skagen SK, Kelly JF, Van Riper C, Hutto RL, Finch DM, Krueper DJ, Melcher CP (2005) Geography of spring landbird migration through riparian habitats in southwestern North America. *Condor*, **107**, 212–227.

Smith JB, Wagner C (2006) Climate change and its implications for the Rocky Mountain region. *Journal of the American Water Works Association*, **98**, 80–92.

Snyder KA, Williams DG (2000) Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agricultural and Forest Meteorology*, **105**, 227–240.

Soykan CU, Sabo JL (2009) Spatiotemporal food web dynamics along a desert riparian-upland transition. *Ecography*, **32**, 354–368.

Sponseller RA, Grimm NB, Boulton AJ, Sabo JL (2010) Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. *Global Change Biology*, **16**, 2891–2900.

Steiger J, Tabacchi E, Dufour S, Corenblit D, Peiry JL (2005) Hydrogeomorphic processes affecting riparian habitat within alluvial channel-floodplain river systems: a review for the temperate zone. *River Research and Applications*, **21**, 719–737.

Stella JC, Battles JJ (2010) How do riparian woody seedlings survive seasonal drought? *Oecologia*, **164**, 579–590.

Stella JC, Battles JJ, Orr BK, McBride JR (2006) Synchrony of seed dispersal, hydrology and local climate in a semi-arid river reach in California. *Ecosystems*, **9**, 1200–1214.

Stella JC, Hayden MK, Battles JJ, Piégay H, Dufour S, Fremier AK (2011) The role of abandoned channels as refugia for sustaining pioneer riparian forest ecosystems. *Ecosystems*, **14**, 776–790.

Published 2011
This article is a US Government work and is in the public domain in the USA,

Stevens LE, Schmidt JC, Ayers TJ, Brown BT (1995) Flow regulation, geomorphology, and Colorado River marsh development in the Grand Canyon, Arizona. *Ecological Applications*, **5**, 1025–1039.

Stewart IT (2009) Changes in snowpack and snowmelt runoff for key mountain regions. *Hydrological Processes*, **23**, 78–94.

Stewart IT, Cayan DR, Dettinger MD (2004) Changes in snowmelt runoff timing in western North America under a 'business as usual' climate change scenario. *Climatic Change*, **62**, 217–232.

Stewart IT, Cayan DR, Dettinger MD (2005) Changes toward earlier streamflow timing across western North America. *Journal of Climate*, **18**, 1136–1155.

Stiling P, Cornelissen T (2007) How does elevated carbon dioxide (CO_2) affect plant-herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology*, **13**, 1823–1842.

Stromberg JC (2001) Influence of stream flow regime and temperature on growth rate of the riparian tree, *Platanus wrightii*, in Arizona. *Freshwater Biology*, **46**, 227–239.

Stromberg JC, Chew MK (1997) Herbaceous exotics in Arizona's riparian ecosystems. *Desert Plants*, **13**, 11–17.

Stromberg JC, Patten DT (1990) Flower production and floral ratios of a southwestern riparian tree, Arizona walnut (*Juglans major*). *American Midland Naturalist*, **124**, 278–288.

Stromberg JC, Tellman B (2009) *Ecology and Conservation of the Upper San Pedro Riparian Ecosystem*. University of Arizona Press, Tucson.

Stromberg JC, Tiller R, Richter B (1996) Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecological Applications*, **6**, 113–131.

Stromberg JC, Fry J, Patten DT (1997) Marsh development after large floods in an alluvial, arid-land river. *Wetlands*, **17**, 292–300.

Stromberg JC, Beauchamp VB, Dixon MD, Lite SJ, Paradzick C (2007a) Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in and south-western United States. *Freshwater Biology*, **52**, 651–679.

Stromberg JC, Lite SJ, Marler R *et al.* (2007b) Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecology and Biogeography*, **16**, 381–393.

Stromberg JC, Lite SJ, Dixon MD (2010) Effects of stream flow patterns on riparian vegetation of a semiarid river: implications for a changing climate. *River Research and Applications*, **26**, 712–729.

Syvitski JPM, Kettner A (2011) Sediment flux and the Anthropocene. *Philosophical Transactions of the Royal Society A – Mathematical Physical and Engineering Sciences*, **369**, 957–975.

Taub DR, Wang XZ (2008) Why are nitrogen concentrations in plant tissues lower under elevated CO_2? A critical examination of the hypotheses. *Journal of Integrative Plant Biology*, **50**, 1365–1374.

Taylor G, Tallis MJ, Giardina CP *et al.* (2008) Future atmospheric CO_2 leads to delayed autumnal senescence. *Global Change Biology*, **14**, 264–275.

Terry RC, Li C, Hadly EA (2011) Predicting small-mammal responses to climatic warming: autecology, geographic range, and the Holocene fossil record. *Global Change Biology*, **17**, 3019–3034.

Thackeray SJ, Sparks TH, Frederiksen M *et al.* (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313.

Thevs N, Zerbe S, Peper J, Succow M (2008) Vegetation and vegetation dynamics in the Tarim River floodplain of continental-arid Xinjiang, NW China. *Phytocoenologia*, **38**, 65–84.

Tockner K, Stanford JA (2002) Riverine flood plains: present state and future trends. *Environmental Conservation*, **29**, 308–330.

Vanrheenen NT, Wood AW, Palmer RN, Lettenmaier DP (2004) Potential implications of PCM climate change scenarios for Sacramento-San Joaquin River Basin hydrology and water resources. *Climatic Change*, **62**, 257–281.

Vartapetian BB, Jackson MB (1997) Plant adaptations to anaerobic stress. *Annals of Botany*, **79**, 3–20.

Vicuna S, Maurer EP, Joyce B, Dracup JA, Purkey D (2007) The sensitivity of California water resources to climate change scenarios. *Journal of the American Water Resources Association*, **43**, 482–498.

Vivoni ER, Aragon CA, Malczynski L, Tidwell VC (2009) Semiarid watershed response in central New Mexico and its sensitivity to climate variability and change. *Hydrology and Earth System Sciences*, **13**, 715–733

Wahid A, Gelani S, Ashraf M, Foolad MR (2007) Heat tolerance in plants: an overview. *Environmental and Experimental Botany*, **61**, 199–223.

Warner RE, Hendrix KM (1984) *California Riparian Systems: Ecology, Conservation, and Productive Management*. University of California Press, Berkeley. Available at: http://ark.cdlib.org/ark:/13030/ft1c6003wp/ (accessed 11 November 2011).

Webb RH, Leake SA (2006) Ground-water surface-water interactions and long-term change in riverine riparian vegetation in the southwestern United States. *Journal of Hydrology*, **320**, 302–323.

Webb RH, Leake SA, Turner RM (2007) *The Ribbon of Green – Change in Riparian Vegetation in the Southwestern United States*. University of Arizona Press, Tuscon.

Wiesenborn WD (2005) Biomass of arthropod trophic levels on *Tamarix ramosissima* (Tamaricaceae) branches. *Environmental Entomology*, **34**, 656–663.

Wiesenborn WD, Heydon SL (2007) Diets of breeding Southwestern willow flycatchers in different habitats. *Wilson Journal of Ornithology*, **119**, 547–557.

Wiesenborn WD, Heydon SL, Lorenzen K (2008) Pollen loads on adult insects from tamarisk flowers and inferences about larval habitats at Topock Marsh, Arizona. *Journal of the Kansas Entomological Society*, **81**, 50–60.

Will RE, Teskey RO (1997) Effect of irradiance and vapour pressure deficit on stomatal response to CO_2 enrichment of four tree species. *Journal of Experimental Botany*, **48**, 2095–2102.

Williams DG, Scott RL, Huxman TE, Goodrich DC, Lin G (2006) Sensitivity of riparian ecosystems in and semiarid environments to moisture pulses. *Hydrological Processes*, **20**, 3191–3205.

Wissmar RC (2004) Riparian corridors of eastern Oregon and Washington: functions and sustainability along lowland-arid to mountain gradients. *Aquatic Sciences*, **66**, 373–387.

Wolman MG, Miller JP (1960) Magnitude and frequency of forces in geomorphic processes. *Journal of Geology*, **68**, 54–74.

Wolock DM, McCabe GJ (1999) Estimates of runoff using water-balance and atmospheric general circulation models. *Journal of the American Water Resources Association*, **35**, 1341–1350.

Yang DQ, Kane DL, Hinzman LD, Zhang XB, Zhang TJ, Ye HC (2002) Siberian Lena River hydrologic regime and recent change. *Journal of Geophysical Research – Atmospheres*, **107**, 4694, doi: 10.1029/2002JD002542.

Zavaleta ES, Royval JL (2001) Climate change and the susceptibility of U.S. ecosystems to biological invasions: two cases of expected range expansion. In: *Wildlife Responses to Climate Change: North American Case Studies* (eds Schneider SH, Root TL), pp 277–341. Island Press, Washington, D.C.

Zhang XB, Harvey KD, Hogg WD, Yuzyk TR (2001) Trends in Canadian streamflow. *Water Resources Research*, **37**, 987–998.

Zoellick BW, Ulmschneider HM, Stanley AW (2005) Distribution and composition of mammalian predators along the snake river in southwestern Idaho. *Northwest Science*, **79**, 265–272.

Zvereva EL, Kozlov MV (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. *Global Change Biology*, **12**, 27–41.