Contrasting water-uptake and growth responses to drought in co-occurring riparian tree species

Michael Bliss Singer,[1,2]* John C. Stella,[3] Simon Dufour,[4] Hervé Piégay,[5] Rob J.S. Wilson[1] and Laura Johnstone[3]

[1] *School of Geography and Geosciences, University of St Andrews, Irvine Building, North Street, St Andrews, KY16 9AL, UK*
[2] *Earth Research Institute, University of California Santa Barbara, Santa Barbara, CA 91306, USA*
[3] *Forest and Natural Resources Management Dept., College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA*
[4] *COSTEL/LETG, UMR 6554, Université Rennes 2, Rennes, France*
[5] *CNRS-UMR 5600, Université Lyon, ISIG Platforme Site ENS-Lyon, Lyon, France*

ABSTRACT

Growth responses of riparian trees to changes in water availability are poorly understood, thereby limiting understanding of regional drought implications in river corridors. We used dendrochronological methods to develop growth series and analysed oxygen isotopic ratios ($\delta^{18}O$) in α-cellulose from individual tree rings for two co-occurring riparian species, *Fraxinus excelsior* and *Populus nigra*. Trees were sampled along the Ain River (France) to assess growth and annual source water availability, inferred from tree-ring $\delta^{18}O$, compared with variations in streamflow and precipitation. Both species exhibited decreased growth during drought years, but *F. excelsior* demonstrated less variation in annual growth across sites compared with *P. nigra*. The latter species expressed a smaller range of $\delta^{18}O$ among individuals and years, but greater $\delta^{18}O$ sensitivity to river discharge, indicating a more consistent hyporheic water source. *P. nigra* also suffered more growth inhibition than *F. excelsior* in dry years when water tables were suppressed. These differences suggest contrasting patterns of water use, wherein *F. excelsior* uses primarily water from the vadose zone to maintain moderate growth rates, and *P. nigra* demonstrates more consistent phreatic water usage and suffers in drought years when water tables are suppressed. These observations are consistent with data on floodplain rooting depths, which show that *F. excelsior* maintains its roots above the gravel layer, whereas *P. nigra* generally roots deeply into phreatic zone gravels. These results indicate that surprisingly, poplars may be more sensitive to drought than ash trees and may be vulnerable to climate changes affecting water availability in riparian corridors. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS   tree rings; oxygen isotopes; drought; riparian forests; Mediterranean climate; water table; dendrochronology; water stress

Received 9 February 2012; Revised 29 April 2012; Accepted 2 May 2012

INTRODUCTION

The impacts of recent climate change on vegetation species ranges and community composition are increasingly recognized as a major concern with ecological and socioeconomic consequences (Walther *et al.*, 2002). Links between physical riverine processes and vegetation in riparian corridors are well appreciated (Baird and Wilby, 1999; Dawson and Ehleringer, 1991; Dufour and Piegay, 2008; Hupp and Osterkamp, 1996; Mahoney and Rood, 1998; Rood *et al.*, 2003; Scott *et al.*, 2000; Scott *et al.*, 1999; Sigafoos, 1964; Singer and Dunne, 2004a; Stella *et al.*, 2006; Stella *et al.*, 2011). Although riparian plant population response to hydro-geomorphic forcing is understood for certain species (Dufour and Piégay, 2010; Rodríguez-González *et al.*, 2010; Stromberg *et al.*, 2010), and physiological studies in controlled settings have discerned differences among co-occurring riparian species (Amlin and Rood, 2002; Stella *et al.*, 2010), research that compares species' responses *in situ* within a community is

relatively rare, but see Busch *et al.* (1992) and Horton *et al.* (2003). Even fewer studies evaluate relationships between growth and water availability for long-lived riparian trees over their lifespans (Leffler and Evans, 1999; Alstad *et al.*, 2008). For example, it is known that water table variability may stress or favour a given species, but determining thresholds for such changes is challenging. Studies of mature riparian *Fraxinus excelsior* have suggested that its growth can be affected by declines (Dufour and Piegay, 2008) or increases (Pont *et al.*, 2009) in the water table but found no obvious thresholds above or below which critical changes occur. Different tree species within the same forest stand may have contrasting growth responses to changes in their relative access to water based on their physiology (Lite and Stromberg, 2005; Marshall and Monserud, 2006) or their rooting depth. Thus, there is currently great uncertainty in predicting the response of riparian vegetation, in particular forest communities, to local and regional changes in water resources arising from meteorological drought and/or shifts in water table depth (Perry *et al.*, 2011). [Note: We use the term 'drought' *sensu lato* (Dracup *et al.*, 1980) to refer to dry conditions that have an impact on water partitioning in the riparian zone]. This shortcoming undermines the development of robust theories of forest succession in response to climate changes

---

*Correspondence to: Michael Bliss Singer, School of Geography and Geosciences, University of St Andrews, Irvine Building, North Street, St Andrews, KY16 9AL, UK.
E-mail: bliss@eri.ucsb.edu

(e.g. increased frequency of drought), reach-scale changes in hydrology by flow regulation, engineering or changes in channel bed or relative floodplain elevation (Singer and Dunne, 2006; Singer, 2007; Dufour and Piegay, 2008; Singer and Aalto, 2009; Singer, 2010) and pressure from invasive species (Busch and Smith, 1995). In addition, this uncertainty may threaten the success of river rehabilitation efforts in water-limited regions, especially in light of new research suggesting unanticipated lags in the response of lowland vegetation to changes in climate (Bertrand *et al.*, 2011).

Riparian tree growth response to water availability is generally well understood for controlled conditions (Daniels, 2008; Rood *et al.*, 2007; Stella and Battles, 2010), which has enabled analysis of annual variability due to climate using coupled approaches from traditional dendroclimatology and isotope dendrochronology (McCarroll and Loader, 2005). Such tree-ring isotope studies have primarily been conducted using trees that reside at their ecological limits, in order to maximize the climate signal and to minimize the 'noise' of local controls that are more variable in space and time. There has been far less work done in water-rich environments, including riparian zones, where subtle differences in physical boundary conditions, such as relative topographic position of tree roots with respect to fluctuating water sources, may affect water uptake, growth and survival (Daniels, 2008; Schifman *et al.*, 2012).

Riparian trees derive water from various sources depending on floodplain topography, rooting depth, seasonal precipitation regimes and temporal variation in river flows and groundwater depth. Differences in life history and physiology also play a role in water use amongst these sources. For example, some species are groundwater dependent (i.e. obligate phreatophytes) and cannot survive without access to perennial water sources, whereas other species are facultative phreatophytes and can use both soil and groundwater resources (Dawson and Ehleringer, 1991; Busch *et al.*, 1992).

Co-occurring tree species with contrasting morphology and physiology may express different growth responses to water availability, enabling detailed analysis of the relationships between water sources, water uptake and growth (Marshall and Monserud, 2006). These differences provide insight into ecohydrological processes that affect the development of stand composition and responses to perturbations such as the impact of climate change on water availability (e.g. water table decline) and physical modifications to the landscape (e.g. changes in relative elevation above a water source). Therefore, investigating relationships between water availability, water uptake and growth for co-occurring tree species with contrasting rooting depths holds promise for developing sound models of community-level changes in response to such perturbations in climatically sensitive regions (Dawson and Siegwolf, 2007).

Stable isotope ratios of oxygen in α-cellulose are particularly well suited for determining water sources of riparian trees (Dawson and Ehleringer, 1998; Marshall and Monserud, 2006). For example, if a tree is rooted in a phreatic zone that is undiluted by hyporheic river water

(Dawson and Ehleringer, 1991), its xylem water will be composed of a depleted $\delta^{18}O$ signature similar to groundwater, whereas a shallowly rooted tree at a site disconnected from a deep groundwater table will have an enriched xylem-derived cellulose $\delta^{18}O$ signature indicative of vadose zone moisture. Water in the vadose zone is generally derived from recent precipitation and is subject to high evaporative enrichment of $\delta^{18}O$ (Dawson and Ehleringer, 1998). In contrast, groundwater is typically depleted in $\delta^{18}O$ because it is sourced in percolated snowmelt (colder precipitation is more depleted than warmer precipitation (Dawson and Ehleringer, 1998). These water-source signatures will differ for individual rings within a given species depending on the annual position of the water table and the degree of mixing between precipitation, surface flow and groundwater during periods of xylem uptake (McCarroll and Loader, 2005).

On floodplain surfaces at fixed elevations within an alluvial river corridor, we would expect water sources for riparian trees would vary with annual streamflow levels during the growing season (Busch *et al.*, 1992). We outline three hydrologic scenarios. In years of average precipitation and streamflow, deep-rooting trees rely on water from the phreatic zone (primarily groundwater), whereas trees with shallow roots scavenge precipitation-derived soil moisture from the vadose zone (Smelko and Scheer, 2000; Schume *et al.*, 2004). In high-precipitation and high-flow years, groundwater in the phreatic zone is mixed with hyporheic river water, soils are wetted frequently by precipitation events and the water table rises into the vadose zone. Thus, a mixture of water sources is available to both deep-rooting and shallow-rooting species, although the particular mix that each can access may differ. Under drought conditions, precipitation is minimal and soil moisture is scarce; evaporative losses are great; the phreatic zone is depleted of river water; and the water table is suppressed. These three hydrological scenarios illustrate the complexity of the water sources available to riparian trees associated with climatic fluctuations.

In this paper, we compare radial growth and $\delta^{18}O$ in tree rings from two riparian species, *Fraxinus excelsior*, a deciduous ash, and *Populus nigra*, an obligate phreatophyte, which are both common along rivers throughout Europe (Marigo *et al.*, 2000; Guilloy-Froget *et al.*, 2002; Rood *et al.*, 2003; Lambs *et al.*, 2006). We analysed $\delta^{18}O$ within α-cellulose extracted from annual rings of trees growing at sites along the Ain River in the Rhône Basin (southeastern France) and compared their growth histories with variation in annual water sources, which we inferred from regional climate records and rooting depths, in relation to floodplain substrates with varying water retention capacity (fine vs coarse sediment layers). We discuss these patterns of growth, water use and root architecture to contrast survival strategies amongst mesophytic species, which can opportunistically use groundwater and obligate phreatophytes, which are more limited in their adaptability to variation in water sources.

METHODS

Study area

The Ain River (Figure 1) is a tributary of the Rhône River draining 3672 km^2 of the Jura Mountains, subject to winter flood peaks, which contains floodplain forests along a 40-km reach of sinuous, freely meandering gravel-bed river with a (slope) gradient of 0.0012–0.0018 (Dufour and Piegay, 2008). Seasonal variations in flow are influenced by total annual precipitation and groundwater discharge, which is prevalent in this zone of early Holocene glacial outwash (Marston *et al.*, 1995). Mean annual precipitation is 1150 mm year^{-1}, mean annual discharge is ~123 m^3 s^{-1}, and the 50-year flood of discharge is ~1700 m^3 s^{-1}. Bankfull discharge (~500 m^3 s^{-1}) occurs approximately 10 days per year. Floods occur primarily in winter and spring generated by frontal storms, but intense autumn precipitation events also contribute to flooding along the Ain (Marston *et al.*, 1995).

We sampled *F. excelsior* and *P. nigra* trees in two riparian forest stands along the Ain River (Figure 1). The two sites, which were typical of floodplain environments along the river (Dufour and Piegay, 2008), were situated at >2 m above the baseflow river stage, were underlain by coarse gravel substrates and contained a suitable number of individuals of both species. These sites were selected along an incised reach of river identified in Dufour and Piegay (2008), in order to maximize inter-annual variability in water sources in the relevant water storage reservoirs (vadose vs phreatic). We sampled co-located trees within these plots in order to assess these differences as expressed within trees with contrasting adaptation strategies and rooting depths.

Field data collection and tree-ring analysis

We collected two tree cores at breast height using 5-mm diameter increment borers from ten trees each of *P. nigra* and *F. excelsior* within the two riparian forest sites.

Visually healthy, mature (>30 years) trees were selected in order to characterize longer time series of growth and water source for each species. The 40 cores were cross-dated and ring-widths were measured under a microscope using Measure JTX Tree-Ring Measuring Program. Cross-dating was verified using cross-correlation analysis in the quality control program, COFECHA (Grissino-Mayer, 2002), and composite series were calculated.

From the raw ring width measurements, we calculated basal area increment (BAI), the annual increase in cross-sectional area of a tree, in order to obtain an unbiased estimate of annual growth for each tree and the composite series. BAI is considered a direct measure of wood production as it obviates the need for detrending that is a common processing step in tree-ring chronology construction; it also allows a direct comparison of productivity between the two species (Biondi *et al.*, 1994). BAI is calculated by differencing the computed basal area (BA) between successive years, where $BA = \pi (0.5*d)^2$, and d is the tree diameter measured at breast height (1.4 m above the ground). BAI is calculated for each year, t, as: $BAI_t = (BA_t - BA_{t-1})$, where subscript $t-1$ indicates the previous year (Biondi and Qeadan, 2008). In order to understand variability in growth among the species, we calculated the mean tree-level coefficient of variation in BAI among years.

Because precipitation is the primary source of vadose zone moisture during the peak of the growing season and river stage affects local groundwater table elevation, these water sources (precipitation P and river discharge Q) should strongly influence the water supply available to tree roots and therefore their growth rate, as well as the isotopic signatures of their ring cellulose. We ran correlation analyses of annual BAI against individual monthly values of P and Q using instrumental records of precipitation from the nearby Chatillon la Palud station and discharged from the Chazey-sur-Ain station along the Ain to define the annual periods that were most influential for total annual tree growth.
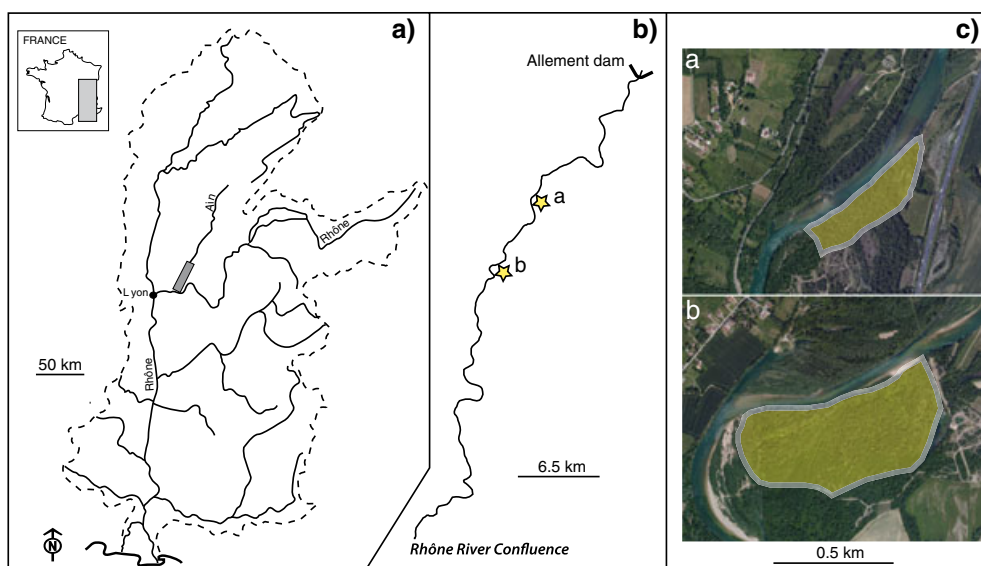

Figure 1. Maps of the following: (a) Rhône River basin in France; (b) study reach along the Ain River indicating selected study sites; and (c) detail of study sites along the Ain River between Barrage d'Allement and the Rhône River confluence. Yellow areas indicate study plots from which tree cores were extracted.

In conjunction with the tree ring measurements, we documented rooting depths and substrate stratigraphy at the two floodplain sites and at other locations along the Ain River, where recent lateral river migration exposed the root zone of individual *Fraxinus* ($n = 13$) and *Populus* ($n = 15$) trees. At the location of each tree, we measured the depth of fine sediment that resulted from overbank flood deposits. For each individual, we measured diameter at breast height, minimum and maximum root depth and the proportion of roots located in the overbank fine sediment layer. We compared maximum rooting depths between species using analysis of covariance (ANCOVA) with depth to fine sediment as a covariate.

Stable isotope analysis. Stable oxygen isotopes measured in tree ring cellulose provide a sensitive measure of water source as a product of biological–physical interactions in fluvial systems, more so than hydrogen isotopes (Waterhouse *et al.*, 2002), and there are established methods and protocols for their measurement (Edwards and Fritz, 1986; Roden and Ehleringer, 2000; Roden *et al.*, 2000; McCarroll and Loader, 2005). For each species, we selected for isotopic analysis cores from trees with the highest correlation to the composite ring-width series indicating robust crossdating ($n = 7$ trees for *F. excelsior* and $n = 6$ for *P. nigra*). The annual wood for 4 years (1976, 1985, 1992 and 2007) was extracted from the cores. These years were selected to represent a range of annual discharge and precipitation from dry to wet years. In addition, one tree of each species was selected for high-density sampling, which was accomplished by analysing separately the wood from most years from 1960 to 2008.

We extracted α-cellulose from the raw wood of dated tree rings by the Brendel method (Brendel *et al.*, 2000) and analysed these samples in a Finnegan Delta plus XP gas source mass spectrometer, coupled to a High Temperature Conversion/Elemental Analyzer peripheral to obtain oxygen isotopes. The standard deviation for $\delta^{18}O$ measurements in α-cellulose by this method is typically 0·2‰ (Waterhouse *et al.*, 2002) and it was 0·195‰ for all of our analyses.

Oxygen isotopic ratios were calculated as:

$$\partial^{18}O_{sample} = \left(\frac{\left(^{18}O/^{16}O \right)_{sample}}{\left(^{18}O/^{16}O \right)_{VSMOW}} - 1 \right) 1000$$

where Vienna Standard Mean Ocean Water (VSMOW) for $\delta^{18}O = 2·005 \times 10^{-3}$ ‰ and isotopic data were corrected against International Atomic Energy Agency standards for linearity and instrument drift.

Tree-ring cellulose is formed from sugars in the trunk, which exchange oxygen with xylem water and become fixed in the tree ring with no further exchange (McCarroll and Loader, 2005). Generally, isotopic ratios are corrected by the Craig–Gordon model for fractionations associated with evaporative enrichment (Flanagan *et al.*, 1991). This model requires information on isotopic composition of leaf water and fractionations associated with the equilibration between leaf water and relative humidity, which is a complex function of stomatal activity. However, all fractionations and the isotopic composition of atmospheric water vapour may be assumed to be similar within a specific site for a particular season, such that the primary species-specific differences in the isotopic composition of plant tissue arise from differences in the isotopic composition of xylem water (Marshall and Monserud, 2006). Thus, the isotopic signal of xylem water in cellulose varies primarily with different end-member water sources, wherein there is a 27‰ enrichment in $\delta^{18}O$ between water and cellulose, which is associated with carbonyl–water interaction during biosynthesis (Sternberg and DeNiro, 1983). Because water sources are generally stratified throughout the soil profile (e.g. perennial water table vs ephemeral vadose zone), $\delta^{18}O$ in xylem water often varies in woody plants with rooting depth (Snyder and Williams, 2000; Marshall and Monserud, 2006) relative to water sources. In this paper, we adopted the approach of Marshall and Monserud (2006) of directly comparing $\delta^{18}O$ preserved in tree ring cellulose for different species co-located in the same forest stand.

Isotopic signature of water changes through time, and we did not monitor these changes over the decades of interest. Therefore, in order to constrain (to first order) the differences in end-member water sources along the Ain, we collected groundwater from a spring near one of our sites in summer 2009 and analysed it for $\delta^{18}O$ using a gas bench peripheral to the mass spectrometer. We compared this value with average $\delta^{18}O$ in regional precipitation from the Global Network for Isotopes in Precipitation (GNIP) database (http://isohis.iaea.org, 2002–2008).

We also analysed tree-ring $\delta^{18}O$ data by first comparing the means and variances among species. Species means were tested using a linear mixed-effects model with year as a random factor. Differences in the $\delta^{18}O$ variance among species were tested using the variance ratio test (i.e. F-test), with data centred about the annual mean for each species to remove the annual environmental signal, primarily from large hydrologic variation among years. Each species' $\delta^{18}O$ response to the instrumental record of annual discharge was tested using a linear mixed-effects model with Q as a fixed factor and tree growth as a random factor to account for autocorrelation of annual samples within individuals.

RESULTS

Precipitation and discharge

The monthly correlations of P and Q with BAI indicate that the period of May–June–July (MJJ) is most highly and significantly correlated with tree growth for both ash and poplar in our study sites (Figure 2); these months are consistent with the main growing season. Furthermore, we find that averaged values of MJJ precipitation (P_{MJJ}) and MJJ discharge (Q_{MJJ}) are well correlated (Pearson's $R = 0·68$, $p < 0·0001$, $n = 47$; Figure 3a), suggesting a tight link between rainfall and runoff.
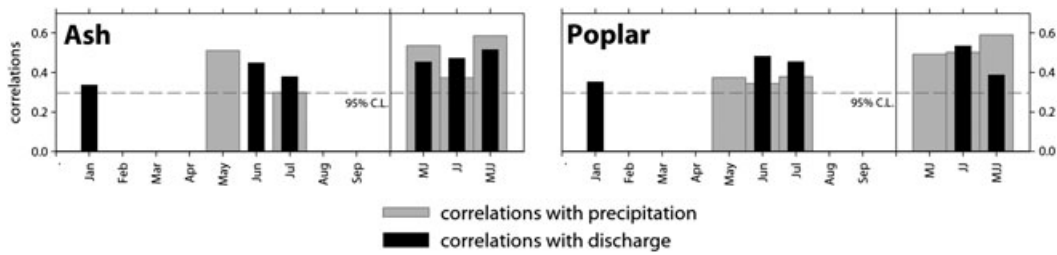
Figure 2. Correlations between tree growth (BAI by species – see Figure 3b) and monthly values of instrumental variables, *Q* and *P*. 'MJ', 'JJ' and 'MJJ' refer to averaged values for May–June, June–July, and May–June–July, respectively. Significance is indicated by the exceedance of the 95% confidence limits ('CL'). Months of October–December are not shown, as they yielded low correlations.

There are notable declines in both *P* and *Q* that occur many times over the last five decades, producing dry periods that could affect water sources and growth for the two riparian tree species. We specified several classes of dry period expressed during the growing season: (1) precipitation shocks (*Pshocks*) occur when $P_{MJJ} < 175$ mm (one standard deviation below mean P_{MJJ}); (2) discharge shocks (*Qshocks*) occur when $Q_{MJJ} < 42\,\text{m}^3\,\text{s}^{-1}$ (one standard deviation below mean Q_{MJJ}); and (3) drought years represent the co-occurrence of a *Pshock* and a *Qshock*. Each class of dry period occurred several times since 1960 (Figure 3a). *Pshocks* occurred in 1962, 1976, 1989, 1998 and 2003–2004. *Qshocks* occurred in 1964, 1976, 1989, 1991, 1998 and 2003–2004. Droughts

occurred in 1976, 1989, 1998 and 2003–2004. On the basis of empirical probabilities of the 47-year climatic record, *Qshocks* and *Pshocks* occur in ~10% of years.

Growth

Across the study area, *F. excelsior* growth was more consistent than *P. nigra* (i.e. annual ring widths varied less for individual trees and amongst trees within each year; Figures 3b and 4b). The mean of the coefficient of variation (CV) of annual BAI among individual trees is 0·49 for *F. excelsior* and 0·53 for *P. nigra*, indicating 8% proportionally greater variation in annual growth among *P. nigra* trees. Time series of tree growth for both species are presented for the full samples of trees (Figure 3b) and for the individuals for which we conducted high-density annual sampling of isotopes (Figure 4a).

Comparing the growth series with the defined dry periods shows that drought years (concurrent *Q* and *P* shocks) generally caused abrupt declines in growth of both species, although there were occasional 1-year lags between the dry year(s) and the growth response (e.g. 2003–2004 for *F. excelsior*, Figure 3b; 1998 for both
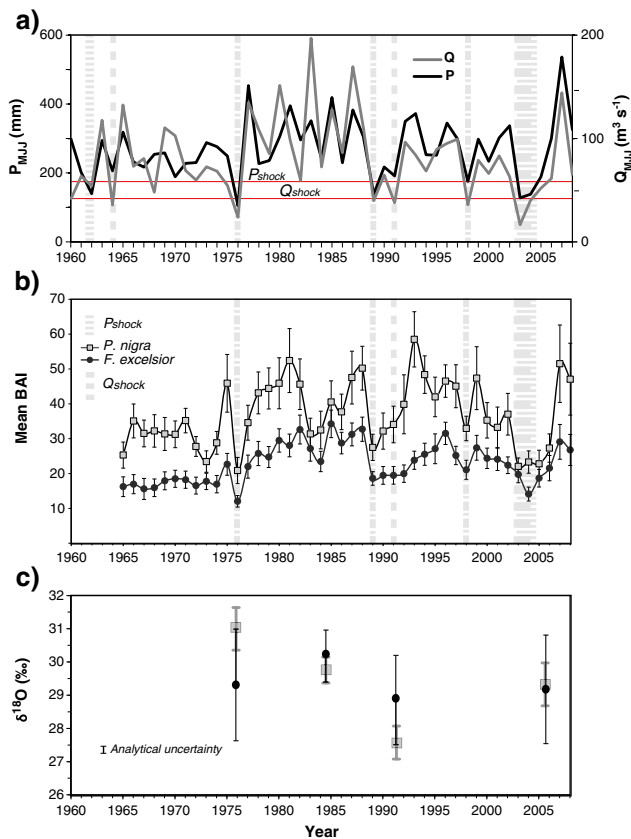

Figure 3. (a) Time series of May–July precipitation and discharge. Vertical dashed bars represent shocks and droughts, and horizontal lines represent thresholds for each (see text for description); (b) time series of mean annual BAI (pooled 20 trees for each species). Error bars are standard errors. Coefficient of variation in growth is 0·49 for *F. excelsior* and 0·53 for *P. nigra*; and (c) average values of $\delta^{18}O$ for a sample of trees for each species ±1 SD. Error bars are standard errors.
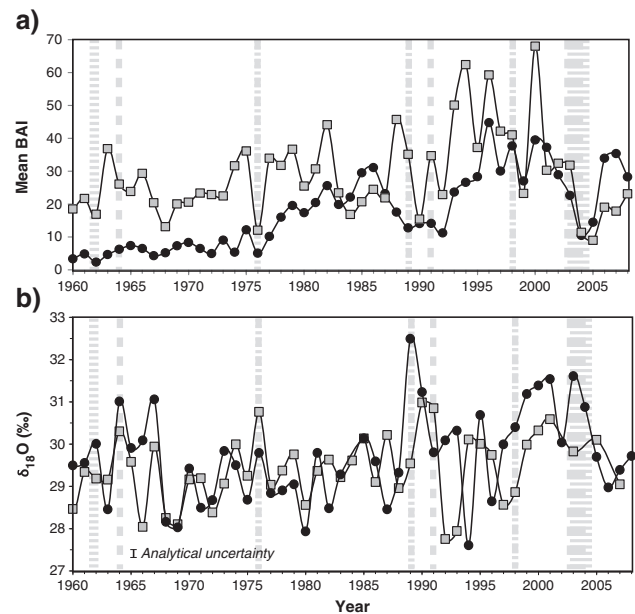

Figure 4. (a) Time series of mean BAI for two individual trees of each species for which we also have a full isotopic record. Error bars represent standard errors. (b) Time series of $\delta^{18}O$ for the same two individual trees as in Figure 4a. Standard deviation of $\delta^{18}O = 0\cdot82‰$ for *P. nigra* and 1·18‰ for *F. excelsior*. Vertical dashed bars as in Figure 3.

species, Figure 4a). However, shocks in Q alone apparently did not generally result in growth declines for either species (e.g. 1991, Figures 3b and 4b), and significant correlations between January Q and growth for both species (Figure 2) suggest that antecedent water table position is also important. Most droughts apparently cause a 1-year to 2-year suppression in tree growth for both species, followed by a rapid recovery (e.g. 1976, and 1998 droughts). However, other droughts induce a longer period of growth suppression well after the initial abrupt decline (e.g. 1991, and 2003–2004), indicating that the recovery period between dry periods plays a role in the growth response of both species. It should be noted that there are clearly additional years of growth decline in both species (e.g. 1983–2004) that exceed our conservative dry period thresholds, indicating that there are other regional factors that may affect growth rates in certain years (e.g. antecedent moisture in the vadose zone; discharge support for the water table in the months prior or following MJJ, Figure 2). Notably, growth of both species shows much less individual variability during droughts than for other years (Figure 3b), indicating a general regional signal of water stress.

Oxygen isotopes

The measured groundwater signature of $\delta^{18}O$ at Ricotti, France in June 2009 was -10.6‰ compared with the mean value for regional precipitation of -5.4‰ ± 2.9‰ SD at Avignon from GNIP. This indicates, consistent with our expectations, that precipitation in this region is generally enriched in $\delta^{18}O$ compared with groundwater. Given that precipitation becomes further enriched because of evaporative losses in the vadose zone, these marked differences provide good discrimination in $\delta^{18}O$, thus allowing for a relative comparison between phreatic zone versus vadose zone water sources used to construct cellulose in riparian trees.

Tree-ring $\delta^{18}O$ values for *F. excelsior* trees exhibited substantially more variability than for *P. nigra* within years, with higher variability in dry years (Figure 3c). The $\delta^{18}O$ variances were significantly different between the species ($F_{27,26} = 6.41$, $p < 0.0001$), and the average coefficient of variation (i.e. the mean of the CVs for each of the 4 years sampled) was 0.045 for *F. excelsior*, which was more than twice that of *P. nigra* (CV = 0.018). *P. nigra* had a more tightly coordinated response with $\delta^{18}O$ values changing by a proportional amount among years for most trees. Conversely, *F. excelsior* exhibited more individualistic responses both among trees and among years, leading to higher inter-annual variability and higher variability in $\delta^{18}O$ for any particular year (Figures 3c and 4c).

In contrast to the strong species difference in the variance of tree-ring $\delta^{18}O$ values, there was no difference in the grand mean $\delta^{18}O$ between the species across the 4 years sampled (mixed-effects model $t = -0.0754$, $p = 0.94$). This was due partly to offsetting, opposite trends by *F. excelsior* and *P. nigra* in wet and dry years. During droughts (e.g. 1976), $\delta^{18}O$ values for *P. nigra* trees were generally higher (i.e. more enriched) and rose presumably as the supply of depleted $\delta^{18}O$ water from the phreatic zone

became limited (i.e. as the water table was suppressed) and the relatively enriched water in the vadose zone dominated the water source $\delta^{18}O$ signature. In contrast, the mean values of $\delta^{18}O$ for *F. excelsior* did not vary among wet and dry years, and the overall range of values was greater in each year (Figures 3c and 5). These patterns indicate a contrasting sensitivity to climate. When each species was considered individually, the $\delta^{18}O$ values for *P. nigra* followed a negative relationship with mean annual river Q (Figure 5a), and this was a significant predictor in a mixed-effects model with individual trees as a random factor ($t = -6.55$, $n = 27$, $p < 0.00001$). The mixed-effects model for *F. excelsior* showed no relationship with Q ($t = -0.54$, $n = 28$, $p = 0.59$; Figure 5b).

Rooting depth

The maximum rooting depth was strongly related to the depth of overbank sediment (ANCOVA $F_{1,25} = 21.6$, $p < 0.0001$) and differed significantly between the species (ANCOVA $F_{1,25} = 18.1$, $p < 0.001$). *P. nigra* roots extended $> 40\%$ deeper into the substrate (124.5 ± 8.4 cm) than those of *F. excelsior* (87.4 ± 6.5 cm). In all cases, *F. excelsior* maximum rooting depth was less than or equal to the depth of fine sediment (Figure 6), indicating that these trees were rooted shallowly in fine-grained sediment of the vadose zone and did not penetrate gravel substrates
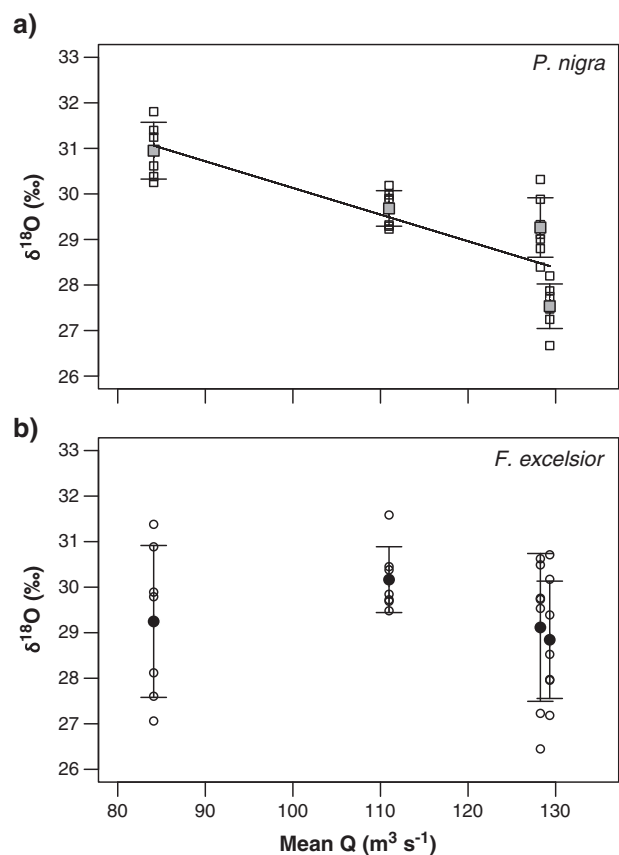

Figure 5. Plot of $\delta^{18}O$ versus mean annual Q for the following: (a) *P. nigra* and (b) *F. excelsior*. Large, filled symbols indicate mean values at a given Q level ± 1 SD. The solid line in (a) shows the population-level fixed-effect of Q in the linear mixed-effects model for *P. nigra*; the linear relationship was not significant for *F. excelsior*.
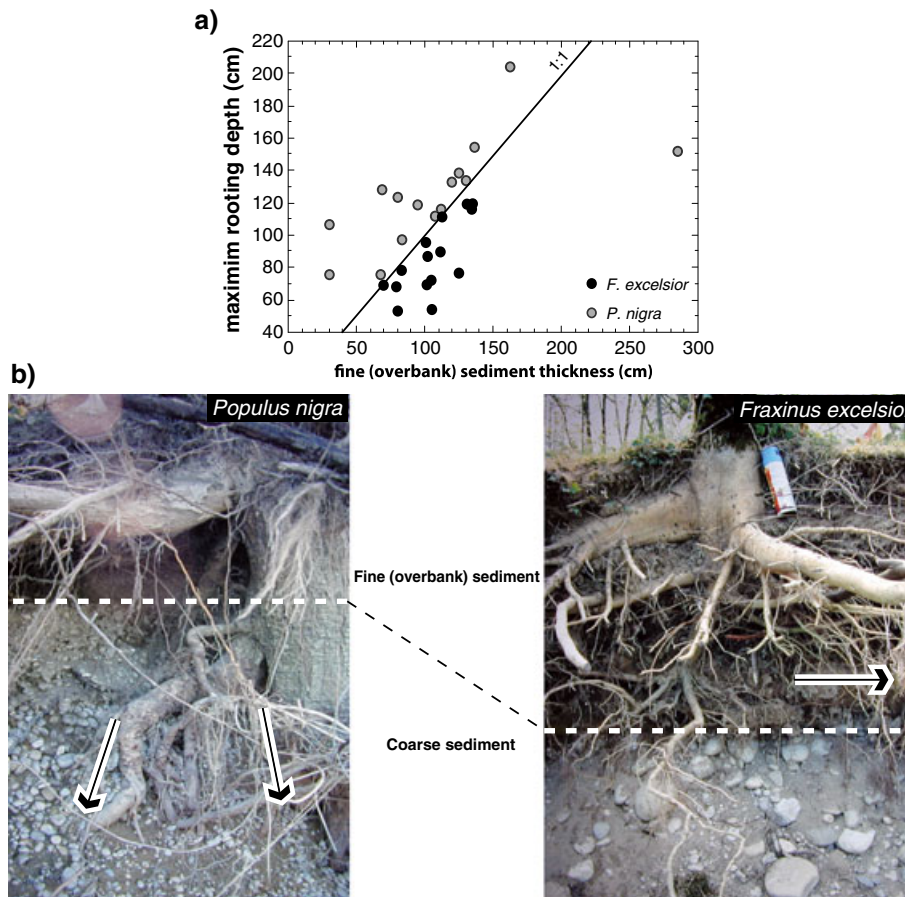
Figure 6. Rooting depth of co-occurring species: (a) measured rooting depths versus overbank fine sediment thickness for individuals of the two species located along the lower Ain River and (b) characteristic root morphology. Root systems were measured following Lucot *et al.* (1995).

(Figure 6b). *P. nigra*, in contrast, was deeply rooted in gravel substrates of the phreatic zone, below the level of fine sediment; this provided access to lower water tables (Figure 6a). The proportion of roots found within the fine sediment layer varied greatly as well; whereas all *F. excelsior* trees had 100% of roots within the fine sediment layer, *P. nigra* trees had a more variable, and on average substantially lower proportion in this zone ($62 \pm 33\%$, mean and 1 SD).

DISCUSSION

Previous research has identified a range of physiological responses in riparian trees to water stress, including leaf area reduction, decreased root biomass and root density and reduced stomatal conductance (Smith *et al.*, 1991; Busch and Smith, 1995; Rood *et al.*, 2003; Williams and Cooper, 2005; Stella and Battles, 2010), as well as reduced radial growth, branch abcission, canopy dieback and tree mortality (Scott *et al.*, 1999; Rood *et al.*, 2000; Dufour and Piegay, 2008; Stella *et al.*, 2010). The extent of these adjustments depends on local conditions of water availability and varies among tree species, as some are better able to cope with prolonged dry conditions through their root morphology, water use efficiency and other adaptive traits. Our results show that along the Ain River,

the shallowly rooted, mesophytic species *F. excelsior* (Figure 6) is well adapted to use water from a range of water sources, indicated by high variability in $\delta^{18}O$, and this is associated with a pattern of consistent inter-annual growth (Figure 3b). In contrast, *P. nigra* demonstrates a narrower range of annual isotopic variation among trees for any particular year (Figure 3c) and a stronger relationship between $\delta^{18}O$ and annual water supply (Figure 5a); together, these suggest a greater reliance on a perennial, phreatic water source among individuals for this species. This pattern of consistent *P. nigra* water source (indicated by low variation in $\delta^{18}O$) is associated with a more erratic pattern of inter-annual growth and is more closely tied to hydroclimatic fluctuations (Figures 3a and 3b), which drive changes in groundwater elevation and supply during the growing season. Such changes in water table can occur very rapidly in gravel substrates (e.g. typical of dynamic alluvial rivers such as the Ain), compared with fine sediments, because of high values of hydraulic conductivity. The high canopy water demand for *P. nigra* (Lambs and Muller, 2002), strongly suppressed growth during droughts (Figures 3b and 4b). This produced a shift to $\delta^{18}O$-enriched water during droughts, suggesting that this species is forced to use proportionally more vadose zone water during these periods, but it is not well adapted to maintaining robust growth and physiological functioning by switching water sources. These differences between

species are consistent with ecological roles for both species, that is, pioneer phreatophyte for *P. nigra* and post-pioneer with a wider range of appropriate conditions for *F. excelsior* (Marigo *et al.*, 2000).

Because of its incapacity to propagate roots in gravel (Figure 6), phreatic water is generally unavailable to *F. excelsior*, which establishes in floodplain areas located well above the level of mean stage for Q_{MJJ} (Dufour and Piegay, 2008). We analysed the stage-discharge relationship for each site and determined that the *Qshock* threshold corresponds to a water table elevation below the relative elevation of fine sediment (based on average fine sediments thickness in both plots, Figure 6). This suggests that in such dry years, ash trees at both sites are completely disconnected from the water table. Consistent with their rooting depth and root architecture (Figure 6), we surmise that in mean flow years, *F. excelsior* largely obtains xylem water from isotopically enriched vadose zone water, whereas *P. nigra* relies on isotopically depleted phreatic zone water (e.g. 1992, Figures 3a, 3c, 4b and 5a). Deviations from this pattern occur in very wet and very dry years, and they suggest a different mix of water source to each species. Because of the fixed nature of root architecture in mature trees, extreme years and particularly droughts have great potential to impact growth (Stromberg and Patten, 1996; Scott *et al.*, 2000).

During wet years that occur several years after a major drought (e.g. 1980, Figure 3a), high streamflow recharges the floodplain water table, introducing a high proportion of river water into the fine-grained vadose zone that overlies the coarse gravel substrate. This river water source provides (relatively) isotopically depleted water to the shallow root zone (Figure 6) of *F. excelsior* (e.g. 1980, Figure 4b), compared with the typically enriched water source in this soil stratum resulting from precipitation and subsequent evaporation. The opposite effect occurs during dry periods when *P. nigra* loses access to isotopically depleted phreatic sources (Busch *et al.*, 1992; Busch and Smith, 1995) and must subsist on vadose zone moisture using a more limited root system (Figure 6). The resulting prolonged water stress markedly reduces its annual growth (e.g. 1976, Figures 3a–c).

Dry periods, whether *P/Q* shocks or droughts, have a significant impact on both species, but their responses differ. Dry periods are often characterized by higher-than-normal temperatures and lower-than-normal precipitation, which reduce the quantity of runoff contributing to river discharge, the amount of water in the vadose zone and percolation into groundwater aquifers. These combined effects limit water availability to riparian trees through drying of the fine sediment layer overlying gravels and a suppression of the water table (Stromberg *et al.*, 1996). These factors also change the isotopic composition of the source water (e.g. vadose versus phreatic zone) and affect the quantity of water available for xylem uptake. Therefore, to maintain consistent growth, trees need to increase their water-use efficiency through stomatal control. However, the energy investment each species has made in terms of root growth has important implications for how well it responds to dry periods.

Because *P. nigra* devotes considerable resources into producing deep root networks (Figure 6), its more limited fine root distribution in the fine-grained vadose zone constrains water uptake during droughts. In other words, drought forces *P. nigra* into using vadose zone water as an emergency resource (Snyder and Williams, 2000) because its roots in this zone have a lower capacity to transmit water to the xylem. Thus, when the deeper roots cannot access phreatic water (e.g. during droughts), lower rates of uptake by the shallow roots from a relatively small pool of vadose zone water cannot satisfy canopy demand and thus induce stress on *P. nigra*, which markedly decreases growth (Figure 3). The most recent drought period of 2003–2004, had a particularly strong impact on *P. nigra* growth (Figures 3 and 4), which was substantially reduced for several years. It is clear that prolonged droughts of this kind and/or their increased frequency could have serious implications for this riparian species (Lambs *et al.*, 2006), although the stress impacts on trees and exact degree of increased mortality are unknown.

F. excelsior, on the other hand, is better adapted to water stress associated with the drying of the vadose zone, apparently allowing it to more successfully overcome droughts; however, the growth record indicates that it is still very susceptible to dry periods. It has lower baseline growth than *P. nigra* (Figure 3b) but has the ability to maintain moderate growth at low levels of water availability (Carlier *et al.*, 1992; Marigo and Peltier, 1996; Peltier and Marigo, 1999). Shocks certainly cause a rapid change in growth rates for *F. excelsior*, but the effect is generally short-lived (e.g. 1976, Figure 3b) and as droughts proceed, *F. excelsior* seems to grow consistently, albeit with sharp 1-year reductions, indicating a faster rate of recovery than for *P. nigra* (e.g. 2003–2004, Figure 3b).

Regional climate in this part of France is forecast to become drier and warmer. Figure 7 shows the modelled 20th century and projected future (under IPCC SRES A1B-A2 scenario) for the 5×5-km grid cell that includes the Ain River study sites (Meehl *et al.*, 2007). These models suggest that precipitation has declined by 1·83 mm per decade over the historical period ($R = 0·52$, $p < 0·0001$) and temperature has decreased by 0·05 °C per decade ($R = 0·63$, $p < 0·0001$). Future climate projections point to intensification of these trends in the coming decades (Figure 7) with precipitation and temperature declining by 5·09 mm ($R = 0·78$, $p < 0·0001$) and 0·36 °C ($R = 0·96$, $p < 0·0001$) per decade, respectively.

Regional climate models also predict increased frequency of dry periods, as well as longer droughts, concurrent with long-term trends in drying and warming. The impacts of such climatic changes could be pronounced for these two riparian tree species, but our findings suggest that *P. nigra* is particularly at risk. Its response to shocks and droughts in recent decades points to the fact that increased drought frequency and duration could have serious implications for poplars in the Ain floodplain and similar riparian environments in central and southern Europe. Regional water tables are likely to become more frequently depressed, and vadose zone water should become scarcer. This greater variation in water resources will lead to higher water stress for riparian
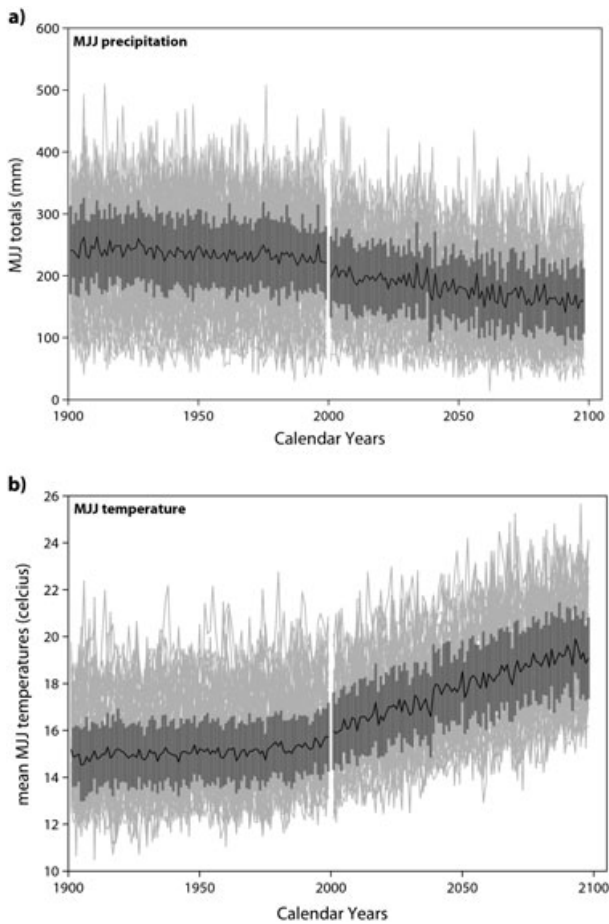
Figure 7. Simulated (1901–1999 and 2001–2098) mean annual temperatures and total annual precipitation for the 5 × 5-degree grid 43-38°N/3-8°E. The simulations, based upon the IPCC SRES A1B (A2) scenario, are taken from the World Climate Research Programme's (WCRP) Coupled Model Intercomparison Project (CMIP3) – (Meehl *et al.*, 2007). Light grey lines denote individual model time-series; the dark grey envelope highlights the inter-quartile range; and the black line delineates the median values.

et al., 2011), where water scarcity and climate change impacts are often amplified.

This paper focused on hydrologic–biologic interactions for co-occurring tree species with contrasting rooting depths along a particular reach of river. We have not addressed the longitudinal or lateral subsurface hydrological connectivity linking tree roots to available water in different transient reservoirs (vadose vs phreatic zone) on a range of floodplain surfaces with varying relative elevation above water levels (Piegay, 1997). Because it is understood that such hydrologic connectivity has direct relevance to ecology (Pringle, 2003; Michaelides and Chappell, 2009), this component of this problem should be addressed in future work, especially in the context of river rehabilitation efforts aimed at delivering more water to restored river reaches and of longitudinal sediment budget divergences and their consequences for floodplain accumulation [e.g. (Singer and Aalto, 2009; Singer and Dunne, 2001; Singer and Dunne, 2004b)]. Moreover, along the Ain, sediment starvation downstream of dams, channel incision and associated groundwater decline is projected to propagate downstream and to affect the most valuable riparian ecosystems, thus exacerbating the effects of the expected regional climate trend (Rollet, 2007). Nevertheless, this study has demonstrated that trees are good integrators of annual water partitioning between hydrologic reservoirs in the riparian corridor, and that the two-species approach, analysis of growth and isotopes in co-occurring trees with contrasting rooting depths, provides a window into the variability of such partitioning under drought conditions.

trees and possibly greater competition for soil water among individuals; together, these may shift the competitive advantage from *P. nigra* to *F. excelsior*, the better-adapted tree to variable water source conditions (Peltier and Marigo, 1999; Lemoine *et al.*, 2001). *P. nigra* will either need to grow increasingly deeper roots into the gravel substrate to maintain contact with the phreatic zone, or it will have to put more resources into developing increased density of roots in the vadose zone. Both adaptive strategies are possible for young trees but increasingly difficult for older, more established individuals. Furthermore, even if *P. nigra* can survive with few water resources (Lambs *et al.*, 2006), longer and more frequent droughts could trigger increased mortality of riparian poplars (Scott *et al.*, 1999; Lite and Stromberg, 2005; Rood *et al.*, 2007), decrease their establishment success (Stromberg *et al.*, 1996), and increase opportunities for recruitment and competitive release of more drought-adapted species (González *et al.*, 2010; Merritt and Poff, 2010). Thus, climate change has the potential to drive a change in the composition, in tree stand composition and biodiversity in riparian ecosystems. These potential impacts must be considered especially when evaluating impacts of flow management on regulated rivers in arid lands (Hughes and Rood, 2003; Perry

REFERENCES

Alstad KP, Hart SC, Horton JL, Kolb TE. 2008. Application of tree-ring isotopic analyses to recontruct historical water use of riparian trees. *Ecological Applications* **18**: 421–437.
Amlin N, Rood S. 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands* **22**: 338–346.
Baird AJ, Wilby RL (eds.).1999. *Eco-Hydrology: Plants and Water in Terrestrial and Aquatic Environments*. Routledge Ltd: London; 424.
Bertrand R, Lenoir J, Piedallu C, Riofrio-Dillon G, de Ruffray P, Vidal C, Pierrat J-C, Gégout J-C 2011. Changes in plant community composition lag behind climate warming in lowland forests. *Nature.* **479**: 517–520.
Biondi F, Myers DE, Avery CC. 1994. Geostatistically modeling stem size and increment in an old-growth forest. *Canadian Journal of Forest Research* **24**: 1354–1368.

Biondi F, Qeadan F. 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research* **64**: 81–96.

Brendel O, Iannetta PPM, Stewart D. 2000. A rapid and simple method to isolate pure alpha-cellulose. *Phytochemical Analysis* **11**: 7–10.

Busch DE, Ingraham NL, Smith SD. 1992. Water-uptake in woody riparian phreatophytes of the Southwestern United States—a stable isotope study. *Ecological Applications* **2**: 450–459.

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

Carlier G, Peltier J, Gielly L. 1992. Comportement hydrique du frêne (*Fraxinus excelsior* L) dans une formation montagnarde mésoxérophile. *Annals of Forest Science* **49**: 207–223.

Daniels JM. 2008. Distinguishing allogenic from autogenic causes of bed elevation change in late Quaternary alluvial stratigraphic records. *Geomorphology* **101**: 159–171.

Dawson TE, Ehleringer JR. 1991. Streamside trees that do not use stream water. *Nature* **350**: 335–337.

Dawson TE, Ehleringer JR. 1998. Plants, isotopes and water use: a catchment-scale perspective. In: Kendall C, McDonnell JJ (eds) *Isotope Tracers in Catchment Hydrology.* Elsevier Science B.V.: Amsterdam; 165–202.

Dawson TE, Siegwolf RTW. 2007. Using stable isotopes as indicators, tracers and recorders of ecological change: some context and background. In: Dawson TE, Siegwolf RTW (eds) *Stable Isotopes as Indicators of Ecological Change.* Academic Press-Elsevier: San Diego; 1–18.

Dracup JA, Lee KS, Paulson EG, Jr.. 1980. On the definition of droughts. *Water Resources Research* **16**: 297–302.

Dufour S, Piegay H. 2008. Geomorphological controls of *Fraxinus excelsior* growth and regeneration in floodplain forests. *Ecology* **89**: 205–215.

Dufour S, Piégay H. 2010. Channel mobility, hydro-geomorphic disturbances and understory vegetation in floodplain forests (Ain River, France). *Géomorphologie: relief, processus, environnement* **4**: 371–386.

Edwards TWD, Fritz P. 1986. Assessing meteoric water composition and relative humidity from $\delta^{18}O$ and ^2H in wood cellulose: paleoclimatic implications for southern Ontario, Canada. *Applied Geochemistry* **1**: 715–723.

Flanagan LB, Bain JF, Ehleringer JR. 1991. Stable oxygen and hydrogen isotope composition of leaf water in plant species under field conditions. *Oecologia* **88**: 394–400.

González E, González-Sanchis M, Cabezas Á, Comín F, Muller E. 2010. Recent changes in the riparian forest of a large regulated mediterranean river: implications for management. *Environmental Management* **45**: 669–681.

Grissino-Mayer HD. 2002. Research report evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* **57**: 205–221.

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

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.

Hughes FMR, Rood SB. 2003. Allocation of river flows for restoration of floodplain forest ecosystems: a review of approaches and their applicability in Europe. *Environmental Management* **32**: 12–33.

Hupp CR, Osterkamp WR. 1996. Riparian vegetation and fluvial geomorphic process. *Geomorphology* **14**: 277–295.

Lambs L, Loubiat M, Girel J, Tissier J, Peltier J-P, Marigo G. 2006. Survival and acclimatation of Populus nigra to drier conditions after damming of an alpine river, southeast France. *Annals of Forest Science* **63**: 377–385.

Lambs L, Muller É. 2002. Sap flow and water transfer in the Garonne River riparian woodland, France: first results on poplar and willow. *Annals of Forest Science* **59**: 301–315.

Leffler AJ, Evans AS. 1999. Variation in carbon isotope composition among years in the riparian tree. *Oecologia* **119**: 311–319.

Lemoine D, Peltier J-P, Marigo G. 2001. Comparative studies of the water relations and the hydraulic characteristics in *Fraxinus excelsior, Acer pseudoplatanus* and *A. opalus* trees under soil water contrasted conditions. *Annals of Forest Science* **58**: 723–731.

Lite SJ, Stromberg JC. 2005. Surface water and ground-water thresholds for maintaining Populus-Salix forests, San Pedro River, Arizona. *Biological Conservation* **125**: 153–167.

Lucot E, Badot PM, Bruckert S. 1995. Influence de l'humidité du sol et de la distribution des racines sur le potentiel hydrique du xylème dans des peuplements de chêne (Quercus sp) de basse altitude. *Annales des Sciences Forestières* **52**: 173–182.

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

Marigo G, Peltier JP. 1996. Analysis of the diurnal change in osmotic potential in leaves of *Fraxinus excelsior* L. *Journal of Experimental Botany* **47**: 763–769.

Marigo G, Peltier JP, Girel J, Pautou G. 2000. Success in the demographic expansion of *Fraxinus excelsior* L. *Trees-Structure and Function* **15**: 1–13.

Marshall JD, Monserud RA. 2006. Co-occurring species differ in tree-ring $\delta^{18}O$ trends. *Tree Physiology* **26**: 1055–1066.

Marston RA, Girel J, Pautou G, Piegay H, Bravard J-P, Arneson C. 1995. Channel metamorphosis, floodplain disturbance, and vegetation development: Ain River, France. *Geomorphology* **13**: 121–131.

McCarroll D, Loader NJ (2005) Stable isotopes in tree rings. In: Leng MJ (ed.) *Isotopes in Paleoenvironmental Research.* Springer: Dordecht, The Netherlands; 67–116.

Meehl GA, Covey C, Delworth T, Latif M, McAvaney B, Mitchell JFB, Stouffer RJ, Taylor KE. 2007. The WCRP CMIP3 multimodel dataset - a new era in climate change research. *Bulletin of the American Meteorological Society* **88**: 1383–1394.

Merritt DM, Poff NLR. 2010. Shifting dominance of riparian Populus and Tamarix along gradients of flow alteration in western North American rivers. *Ecological Applications* **20**: 135–152.

Michaelides K, Chappell A. 2009. Connectivity as a concept for characterising hydrological behaviour. *Hydrological Processes* **23**: 517–522.

Peltier JP, Marigo G. 1999. *Drought Adaptation in Fraxinus excelsior* L.: Physiological Basis of the Elastic Adjustment. Elsevier: Munich, ALLEMAGNE.

Perry LG, Andersen DC, Reynolds LV, Mark Nelson S, Shafroth PB. 2011. Vulnerability of riparian ecosystems to elevated CO2 and climate change in arid and semiarid western North America. *Global Change Biology*:n/a-n/a.

Piegay H. 1997. Interactions between floodplain forests and overbank flows: data from three Piedmont rivers of southeastern France. *Global Ecology and Biogeography Letters* **6**: 187–196.

Pont D, Piégay H, Farinetti A, Allain S, Landon N, Liébault F, Dumont B, Richard-Mazet A. 2009. Conceptual framework and interdisciplinary approach for the sustainable management of gravel-bed rivers: the case of the Drôme River basin (S.E. France). *Aquatic Sciences - Research Across Boundaries* **71**: 356–370.

Pringle C. 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes* **17**: 2685–2689.

Roden JS, Ehleringer JR. 2000. Hydrogen and oxygen isotope ratios of tree ring cellulose for field-grown riparian trees. *Oecologia* **123**: 481–489.

Roden JS, Lin GG, Ehleringer JR. 2000. A mechanistic model for interpretation of hydrogen and oxygen isotope ratios in tree-ring cellulose. *Geochimica Et Cosmochimica Acta* **64**: 21–35.

Rodríguez-González PM, Stella JC, Campelo F, Ferreira MT, Albuquerque A. 2010. Subsidy or stress? Tree structure and growth in wetland forests along a hydrological gradient in Southern Europe. *Forest Ecology and Management* **259**: 2015–2025.

Rollet AJ. 2007. Etude et gestion de la dynamique sédimentaire d'un tronçon fluvial à l'aval d'un barrage: le cas de la basse vallée de l'Ain. In, vol. PhD. Université Lyon 3, p 305.

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, Goater LA, Mahoney JM, Pearce CM, Smith DG. 2007. Floods, fire, and ice: disturbance ecology of riparian cottonwoods The review is one of a selection of papers published in the Special Issue on Poplar Research in Canada. *Canadian Journal of Botany* **85**: 1019–1032.

Rood SB, Patiño S, Coombs K, Tyree MT. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees-Structure and Function* **14**: 248–257.

Schifman LA, Stella JC, Volk TA, Teece MA. 2012. Carbon isotope variation in shrub willow (*Salix spp.*) ring-wood as an indicator of long-term water status, growth and survival. *Biomass and Bioenergy* **36**: 316–326.

Schume H, Grabner M, Eckmullner O. 2004. The influence of an altered groundwater regime on vessel properties of hybrid poplar. *Trees-Structure and Function* **18**: 184–194.

Scott ML, Lines GC, Auble GT. 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. *Journal of Arid Environments* **44**: 399–414.

Scott ML, Shafroth PB, Auble GT. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environmental Management* **23**: 347–358.

Sigafoos RS. 1964. *Botanical evidence of floods and flood-plain deposition*. US Geol. Survey: Reston, VA.

Singer MB. 2007. The influence of major dams on hydrology through the drainage network of the Sacramento Valley, California. *River Research and Applications* **23**: 55–72.

Singer MB. 2010. Transient response in longitudinal grain size to reduced gravel supply in a large river. *Geophysical Research Letters* **37**: L18403. DOI:10.1029/2010GL044381.

Singer MB, Aalto R. 2009. Floodplain development in an engineered setting. *Earth Surface Processes and Landforms* **34**: 291–304. DOI: 10.1002/esp.1725.

Singer MB, Dunne T. 2001. Identifying eroding and depositional reaches of valley by analysis of suspended-sediment transport in the Sacramento River, California. *Water Resources Research* **37**: 3371–3381.

Singer MB, Dunne T. 2004a. An empirical-stochastic, event-based program for simulating inflow from a tributary network: theoretical framework and application to the Sacramento River basin, California. *Water Resources Research* **40**: W07506. DOI: 10.1029/2003WR002725.

Singer MB, Dunne T. 2004b. Modeling decadal bed-material flux based on stochastic hydrology. *Water Resources Research* **40**: W03302. DOI: 10.1029/2003WR002723.

Singer MB, Dunne T. 2006. Modeling the influence of river rehabilitation scenarios on bed material sediment flux in a large river over decadal timescales. *Water Resources Research* **42**: W12415. DOI: 10.1029/2006WR004894.

Smelko S, Scheer L. 2000. Dendrochronological analysis of diameter growth and increment of Pedunculate oak (*Quercus robur* L.) in Danube floodplain forests. *Ekologia-Bratislava* **19**: 125–140.

Smith SD, Wellington AB, Nachlinger JL, Fox CA. 1991. Functional responses of riparian vegetation to streamflow diversion in the Eastern Sierra Nevada. *Ecological Applications* **1**: 89–97.

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.

Stella J, Battles J. 2010. How do riparian woody seedlings survive seasonal drought? *Oecologia* **164**: 579–590.

Stella J, Battles J, Orr B, McBride J. 2006. Synchrony of seed dispersal, hydrology and local climate in a semi-arid river reach in California. *Ecosystems* **9**: 1200–1214.

Stella J, Hayden M, Battles J, Piegay H, Dufour S, Fremier AK. 2011. The role of abandoned channels as refugia for sustaining pioneer riparian forest ecosystems. *Ecosystems* **14**: 776–790.

Stella JC, Battles JJ, McBride JR, Orr BK. 2010. Riparian seedling mortality from simulated water table recession, and the design of sustainable flow regimes on regulated rivers. *Restoration Ecology* **18**: 284–294.

Sternberg LdSLOR, DeNiro MJD. 1983. Biogeochemical implications of the isotopic equilibrium fractionation factor between the oxygen atoms of acetone and water. *Geochimica Et Cosmochimica Acta* **47**: 2271–2274.

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.

Stromberg JC, Patten DT. 1996. Instream flow and cottonwood growth in the eastern Sierra Nevada of California, USA. *Regulated Rivers: Research & Management* **12**: 1–12.

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.

Walther G-R *et al*. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.

Waterhouse JS, Switsur VR, Barker AC, Carter AHC, Robertson I. 2002. Oxygen and hydrogen isotope ratios in tree rings: how well do models predict observed values? *Earth and Planetary Science Letters* **201**: 421–430.

Williams CA, Cooper DJ. 2005. Mechanisms of riparian cottonwood decline along regulated rivers. *Ecosystems* **8**: 382–395.