

# Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds

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## SUMMARY

1. Riparian vegetation composition, structure and abundance are governed to a large degree by river flow regime and flow-mediated fluvial processes. Streamflow regime exerts selective pressures on riparian vegetation, resulting in adaptations (trait syndromes) to specific flow attributes. Widespread modification of flow regimes by humans has resulted in extensive alteration of riparian vegetation communities. Some of the negative effects of altered flow regimes on vegetation may be reversed by restoring components of the natural flow regime.

2. Models have been developed that quantitatively relate components of the flow regime to attributes of riparian vegetation at the individual, population and community levels. Predictive models range from simple statistical relationships, to more complex stochastic matrix population models and dynamic simulation models. Of the dozens of predictive models reviewed here, most treat one or a few species, have many simplifying assumptions such as stable channel form, and do not specify the time-scale of response. In many cases, these models are very effective in developing alternative streamflow management plans for specific river reaches or segments but are not directly transferable to other rivers or other regions.

3. A primary goal in riparian ecology is to develop general frameworks for prediction of vegetation response to changing environmental conditions. The development of *riparian vegetation-flow response guilds* offers a framework for transferring information from rivers where flow standards have been developed to maintain desirable vegetation attributes, to rivers with little or no existing information.

4. We propose to organise riparian plants into non-phylogenetic groupings of species with shared traits that are related to components of hydrologic regime: life history, reproductive strategy, morphology, adaptations to fluvial disturbance and adaptations to water availability. Plants from any river or region may be grouped into these guilds and related to hydrologic attributes of a specific class of river using probabilistic response curves.

5. Probabilistic models based on riparian response guilds enable prediction of the likelihood of change in each of the response guilds given projected changes in flow, and

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facilitate examination of trade-offs and risks associated with various flow management strategies. Riparian response guilds can be decomposed to the species level for individual projects or used to develop flow management guidelines for regional water management plans.

*Keywords:* environmental flows, hydrologic alteration, plant water relations, riparian vegetation, vegetation models

## Introduction

Riparian vegetation is a key element of riverine ecosystems, providing many ecological, aesthetic and economic benefits, including terrestrial wildlife habitat structure, food resources, stabilising geomorphic properties along banks and floodplains, and energy subsidies to aquatic and terrestrial ecosystems (Pusey & Arthington, 2003). Riparian and riverine aquatic plant species have evolved within the context of flowing water habitats. The selective pressures of particular flow regimes on riverine biota, including vegetation, have resulted in a range of morphological, life history and phenological adaptations (Lytle & Poff, 2004). Assemblages of species exhibit traits that enable them to disperse, survive and reproduce in response to specific flow components: flow timing, frequency, magnitude, duration and predictability (Mahoney & Rood, 1998a; Karrenberg, Edwards & Kollmann, 2002; Middleton, 2002). Thus, there is often a strong interconnection between a river's natural flow regime and the trait composition of its riparian species.

Natural flows of water and sediment in rivers have been altered by humans in ecologically significant ways by storage and redistribution of water from dams, diversion structures and canals and constructed waterways (Poff *et al.*, 1997; Naiman, Décamps & McClain, 2005). Globally, this human water infrastructure is extensive; the current capacity of reservoirs is enough to store seven times the volume of water in all the world's rivers (Naiman *et al.*, 2005). Human water development fragments river systems (Nilsson *et al.*, 2005) causing once-connected river segments to function largely independently of one another (Graf, 1999) and modifies natural flows of water and sediment (Petts, 1984) all of which have direct effects on riverine ecosystems. Ninety per cent of bottomland forests in the south-

eastern United States and in Europe are 'functionally extinct' due to human water development and agriculture (Tockner & Stanford, 2002), and many formerly distinct river systems have become homogenised by water management (Poff *et al.*, 2007).

Infrastructural developments that alter flow regimes have significantly changed river processes and aquatic and riparian ecosystems worldwide, but at the same time offer opportunities for restoration of riverine ecosystems through environmental flow management. In this study, we explore approaches and tools for determining stream flow requirements specifically to sustain native riparian vegetation growing along channel margins and across river bottomlands. Understanding specific adaptations of organisms to components of the flow regime is leading to the development of a range of tools for determining the flow necessary to sustain the physical and biological diversity of riverine ecosystems. Over 200 methods have been developed for determining in-stream flows for ecological benefits (Tharme, 2003), of which about 70% are based largely upon the minimum flow requirements (e.g. flow depth and current velocity) for aquatic biota, primarily fish (Annear, 2004). Whereas species- and cover-specific models have been developed for riparian vegetation at specific sites, a more general framework is necessary.

We review the models that have been developed for linking attributes of riparian vegetation to flow regime by providing an overview of the key physical factors that shape the flow-dependent characteristics of riparian vegetation. We provide an overview of theory, methods and models for quantitatively linking individual plants, plant populations and riparian plant communities to specific streamflow attributes. We begin by highlighting the key physical factors that shape the flow-dependent characteristics of riparian vegetation. Finally, we describe how these tools can be used to quantify flow regimes necessary to support

desired vegetation attributes. We also introduce the concept of 'riparian vegetation-flow response guilds' – groups of species that respond in similar ways to similar flow components.

#### *Physical processes that influence riparian plant communities*

Although riparian plant communities are influenced by all of the factors that structure communities in uplands, gradients of water availability and fluvial disturbance govern plant community organisation along streams. The stratigraphic characteristics of river-deposited sediment (layers and lenses of sorted material) differ in water-holding capacity, height of capillary rise, hydraulic conductivity, aeration, nutrient levels and water balance throughout the soil column (Merigliano, 2005). The position of landforms relative to the channel creates a number of important physical gradients including frequency and duration of flooding, exposure to shear forces, deposition and scour, the characteristics of the sediment deposited and its water-holding capacity and depth to water table (Hupp & Osterkamp, 1985; Auble, Friedman & Scott, 1994; Richards, Brasington & Hughes, 2002; Bornette *et al.*, 2008). This linkage between fluvial geomorphic processes and riparian vegetation dynamics creates the topographic diversity, soil moisture gradients, fluvial disturbance patches and distinctive microhabitats that characterise riparian ecosystems.

Substrate stratigraphy and texture influence the rate of movement of shallow ground water from uplands and sideslopes as well as within the hyporheic zone (Harner & Stanford, 2003; Merigliano, 2005; Renofalt, Merritt & Nilsson, 2007). Stratigraphic complexity resulting from a spatially complex disturbance history, influences turnover and aeration of ground water in the rooting zone of plants, the rate of onset and the level of anoxia and the biogeochemical environment in the rhizosphere (Renofalt *et al.*, 2007). The frequency of high flows and associated biochemical conditions in the rooting zone may enable an ebb and flow of terrestrial species into and out of the riparian zone over time, contributing to 'temporal diversity' of river margins. Less frequent flood events (>10 year recurrence interval floods) are important as they may enhance native riparian species diversity through maintaining habitat heterogeneity and

hindering non-native species less well adapted to scour and burial associated with flooding (Stromberg, 1993; Stromberg, Wilkins & Tress, 1993).

Fluvial disturbance varies in its duration, intensity, frequency and extent (Keddy, 2002) and is one of the key processes influencing vegetation composition and structure on river floodplains. The mechanical disturbance resulting from high flows regulates the rate of formation and destruction of landforms across the bottomland, the turnover of substrates near the channel, rates of channel migration, overbank deposition and floodplain development. Intense mechanical disturbance and flow characteristics also influence plant species composition by eliminating 'non-riparian' species that are intolerant of the physical disturbance regime, while providing riparian obligates with conditions they require for establishment, survival and reproduction (Stromberg *et al.*, 1993; Merritt & Wohl, 2006).

Fluvial geomorphic processes introduce significant complexity into efforts to model riparian vegetation change in response to changing flow regimes (Bradley & Smith, 1984; Nilsson & Svedmark, 2002; Nilsson *et al.*, 2003). Our ability to model and predict channel change in response to stochastic flood events or even to very precise prescribed floods is limited, confounding the uncertainty in predicting vegetation response. Empirical studies examining past rates of meandering, relationships between discharge and sediment transport, and detailed two- and three-dimensional hydraulic and sediment transport models offer opportunities for examining geomorphic change in response to altered flow regimes that cannot be ignored in predicting vegetation response to flow components (Richter & Richter, 2000; Richards *et al.*, 2002; Perucca, Camporeale and Ridolfi, 2006).

Lateral and taproot development of plants may vary as a function of the conditions under which they grow (Cronk & Fennessy, 2001). Trees and herbs that develop their root systems in relation to a highly variable flow and groundwater regime may form more vertically extensive root systems than those developed under relatively stable surface and groundwater environments (Scott, Lines & Auble, 2000; Shafroth, Stromberg & Patten, 2000). This may predispose plants established under stable groundwater regimes to greater moisture stress during channel dewatering, groundwater pumping or prolonged drought than plants established under more variable

groundwater regimes (Scott, Shafroth & Auble, 1999; Scott *et al.*, 2000).

All of these factors influence and sometimes obscure the direct relationship between surface water and the characteristics and vulnerability of riparian vegetation to changes in the flow regime. These stream-level complexities make developing general rules for managing and setting standards for river flows challenging.

#### *Characterising flow regime*

Ecologically relevant elements of streamflow include the magnitude, frequency, duration, timing, rate of change in flow and interannual variability and sequencing of flows. Classifications of flow regimes have identified distinct patterns of streamflow at continental and global scales (Poff & Ward, 1989; Poff, 1996; Puckridge *et al.*, 1998; Poff *et al.*, 2006a, Kennard *et al.*, 2010). Assessing similarities among flow regimes and characterising broad categories of hydrologic patterns can be useful for developing ecological generalisations among rivers in different regions and transferring information from well-studied rivers to rivers with little data (Snelder, Biggs & Woods, 2005; Arthington *et al.*, 2006).

Although a number of hydrologic indicators has been developed and used for aquatic taxa (Poff & Ward, 1989; Poff & Allan, 1995; Monk *et al.*, 2007), this has not yet been achieved for riparian vegetation. Beyond the flow-related metrics affecting aquatic taxa, riparian taxa are influenced by channel incision, channelisation, increases in floodplain soil salinity and other physical factors (Busch & Smith, 1995; Overton *et al.*, 2006). Flow-related changes in nutrient biogeochemistry can influence floodplain soil processes, such as altered levels of mycorrhizal activity and decomposition rates (Ellis, Crawford & Molles, 2002; Beauchamp, Stromberg & Stutz, 2006). Thus, in addition to the direct effects of flow, riparian vegetation communities may be responding to flow indirectly through a wide range physical and biotic factors.

#### *Linking riparian vegetation to streamflow*

Development of a quantified relationship between flow and riparian vegetation for use in a flow prescription or impact assessment requires making difficult choices about the hydrologic variables and the

vegetation metrics to represent. Altered flow regimes may cause changes in plant species richness (Nilsson *et al.*, 1991a; Jansson *et al.*, 2000), plant growth and productivity (Stromberg & Patten, 1990), community composition (Merritt & Cooper, 2000; Merritt & Wohl, 2006) and loss of riparian forests (Rood & Mahoney, 1990; Braatne *et al.*, 2007). Understanding these linkages and quantifying the relationships statistically contributes to the defensibility of flow prescriptions. Water is an important limiting resource for plants; thus fitness, vulnerability to pathogens and herbivory, richness, productivity, biomass, competitive ability, population structure and community composition are supported by and respond directly to water availability. Each vegetation attribute varies in what it reveals about the characteristics of the vegetation, its sensitivity to flow regime (Table 1) and in how confounded it is with other environmental and biological factors not associated with flow regime.

Considerations regarding the temporal and spatial scale over which a chosen variable should be measured are also very important. Measures of the physiological characteristics of individual plants may be the most sensitive to short-term changes in flow regime but reveal little about the important ecological consequences of changes in streamflow (Table 1). Measures of the attributes of a population of a particular species or multiple species at the reach scale may better integrate changes in flow regime over longer periods of time but may be less sensitive to subtle changes in flow regime. In turn, attributes measured at the community level may better integrate long-term patterns of flow regime. The choice of measurement at the level of the individual, population or community or some combination will largely depend upon the vegetation attributes that are deemed important, along with established goals for maintenance and restoration of riparian vegetation. There are a number of formal approaches that have been used to link metrics of riparian vegetation at different scales to hydrologic regime (summarised in Table 2).

#### *Individuals and populations*

Understanding the autecology of a species is necessary for developing cause-and-effect relationships between attributes of flow and life-stages of that species (Van Der Sman, Joosten & Blom, 1993).

Organisational level	Metrics	Acute sensitivity to hydrologic alteration	Reflective of chronic hydrologic alteration
Individual	Xylem water potential	****	*
	Transpiration	****	*
	Photosynthesis	****	*
	CO <sub>2</sub> flux	****	*
	Canopy volume	***	*
	Shoot/root growth	**	****
	Incremental growth	**	**
	Leaf size	**	**
	Leaf thickness	**	**
Population	Age/stage/size class distribution	*	****
	Population growth rate	*	****
	Variability	*	****
Community	Richness	*	**** (varies)
	Diversity	*	**** (varies)
	Composition	**	****
	Cover	***	****
Stand Structure/productivity	Biomass	***	****
	Vegetation volume	**	****
	Vertical structure	**	****

**Table 1** Metrics of riparian vegetation and their sensitivity to hydrologic alteration and ability to reflect responses to chronic changes in flow regime

Number of asterisks indicate the authors' conceptions of relative strength.

Determining hydrologic requirements for survival from germination, to reproductive age, to senescence as well as interactions with physical and biotic factors such as channel change processes and competition are necessary for specifying flow requirements.

The germinant-seedling stage may be the most vulnerable in the life history for most species so an understanding of the 'regeneration niche' (*sensu* Grubb, 1977) of species or groups of species of concern is particularly important in managing flow regime. Although there are few formal rules for linking the regeneration niche to flow regime along rivers, the wealth of information about riparian poplar (*Populus* L.) autecology, specifically recruitment, led to the development of some very useful models such as the 'recruitment box' (Mahoney & Rood, 1998). The model formalises *Populus* autecology at an early life-stage and integrates phenology of seed release, the range of river stages that define the optimal position on the floodplain for seedling survival (high enough on the floodplain to avoid scour by subsequent floods; low enough to avoid moisture stress), and the rate of stream stage/groundwater decline suited to maximum rates of *Populus* seedling root extension (*c.* 2.5 cm day<sup>-1</sup>). Although this elegant

model was developed for *Populus* in western North America, the concept has been applied to *Salix* L. (Rood *et al.*, 2005) and could be readily transferable to other sexually reproducing riparian species with specialised recruitment traits. The model could also be used to prevent establishment of undesirable species by decoupling the timing of seed release from the availability of suitable habitat (Shafroth *et al.*, 1998, 2008; Sprenger, Smith & Taylor, 2001; Stokes & Cunningham, 2006). The recruitment box model has been widely used to aid in the design of flow regimes to enhance recruitment for riparian forest restoration (Rood *et al.*, 2003, 2005). The model assumes that river stage and alluvial groundwater decline are closely coupled, which may not hold along gaining river reaches, in fine-textured substrates and at sites with complex substrate stratigraphy (Cooper *et al.*, 1999; Merigliano, 2005).

Once individuals have successfully passed from germinant-seedling to juvenile stage, hydrologic processes (e.g. water availability) may be a key determinant of growth, long-term survival and mortality (Stromberg & Patten, 1990, 1991). Physiological responses to changing hydrologic conditions can occur over short periods of time yet can have long-

**Table 2** Models linking riparian vegetation and attributes of flow regime at individual, population and community scales

Model level	Citations	Hydrologic variable/s tested	Best hydrologic variables	Vegetation attribute	Analysis tool	Assumptions	Locations
Individual/ establishment	Mahoney & Rood, 1998a,b	Timing of peak, rate of stage decline	All	Seedling survival	Recruitment box model	Static channel geometry, coarse textured substrate	Oldman River, Alberta, Canada
Individual/ maintenance	Busch & Smith, 1995; Cooper <i>et al.</i> , 1999; Scott <i>et al.</i> , 1999	Depth to ground water	Depth to ground water	Xylem pressure potential, leaf thickness, leaf area, canopy volume, annual branch growth	Logistic regression, linear regression	Static channel geometry	Bill Williams and Colorado R.; AZ, U.S.A.; eastern CO, U.S.A.; Green R., UT, U.S.A.
Individual/ cover types	King, Allen & McCoy, 1998	Water level	Water level	Stress, mortality and regeneration, tree relative importance values	Probit analysis		Ouachita and Saline R., AR, U.S.A.
Population	Lytle & Merritt, 2004; Griffith & Forseth, 2005; Smith, Caswell & Mettler-Cherry, 2005	Distributions of floods, droughts, timing of peak, rates of change in flow; timing of flood, timing of drawdown	Distributions of floods, droughts, timing of peak, rates of change in flow; timing of flood, timing of drawdown	Population growth rate, stage-based population growth rate, sensitivities, elasticities, variability in population growth rate, aerial cover of life-stages	Stochastic structured/ matrix modelling	Quasi-equilibrium channel	Yampa R., CO, U.S.A.; Illinois R., IL, U.S.A.
Population	Clipperton <i>et al.</i> , 2003	Flow exceedance probability	n/a	<i>Populus</i> recruitment, growth, health (qualitative)	Qualitative coupling of requirements for recruitment, growth and maintenance		Saskatchewan R. basin, Alberta, Canada
Population	Pearlstone, McKellar & Kitchens, 1985; Phipps, 1979	Depth to ground water, flood frequency, inundation duration	Depth to ground water, flood frequency, inundation duration	Growth, dispersal, death, of five tree species	Numerical modelling	Static channel geometry	Santee R., SC, U.S.A.; White R., AR, U.S.A.
Community/ individual	Franz & Bazzaz, 1977; Auble <i>et al.</i> , 1994; Auble, Scott & Friedman, 2005; Auble & Scott, 1998; Friedman <i>et al.</i> , 2006	Flow duration	Flow duration	Response curves of plant associations, response curves of individual species	Numerical modelling, response curves (Gaussian, logistic regression)	Static channel geometry	East-central IL; Gunnison R, CO, U.S.A.; San Miguel R, CO, U.S.A.

Table 2 (Continued)

Model level	Citations	Hydrologic variable/s tested	Best hydrologic variables	Vegetation attribute	Analysis tool	Assumptions	Locations
Individual/stand	Stromberg & Patten, 1990, 1991	Annual flow volume, flow volume -1 and -2 years, cumulative flow previous 4 years, season flow volume (Oct.-Mar., Apr.-June, July-Sep.)	Annual flow volume the year of growth	Tree incremental growth, canopy vigour, mortality	Linear regression		Rush Creek and Bishop Ck., CA, U.S.A.
Individual/community	Stromberg, 1993	Mean growing season flow volume, mean and median annual flow volume, flood magnitude	Growing season flow volume, flood magnitude	Abundance (foliage area, stem basal area, stand width), species richness	Second-order linear regression	Static channel form	Verde R., Arizona, U.S.A.
Cover types/functional groupings	Rains, Mount & Larsen, 2004	Depth to ground water, flooding	Depth to ground water	Response curves of plant associations	Numerical groundwater model (MODFLOW), Bayesian classification	Static channel form	Little Stony Ck., CA
Cover types	Johnson, 1992	Water development		Change in riparian cover types	Compartmental simulation model/numerical modelling		Missour R., MI, U.S.A.
Cover types	Springer <i>et al.</i> , 1999; Baird, Stromberg & Maddock, 2005	Depth to ground water		Woody vegetation cover, cover seedling establishment, cover juvenile survival habitat	Numerical groundwater model (MODFLOW) and conceptual vegetation model	Static channel geometry	Verde R., AZ, U.S.A.
Cover types	Primack, 2000	Inundation duration (classes)	Inundation duration (classes)	Cover types	Cover types	Static channel geometry	Pere Marquette catchment, Michigan, U.S.A.
Community/biomass	Camporeale & Ridolfi, 2006	Stream discharge	Stream discharge	Probability of vegetation biomass	Stochastic modelling		Hypothetical

Table 2 (Continued)

Model level	Citations	Hydrologic variable/s tested	Best hydrologic variables	Vegetation attribute	Analysis tool	Assumptions	Locations
Stand characteristics	Perucca <i>et al.</i> , 2006	Distance from river (parabolic function to represent a position between anoxic and dry)	Distance from river (parabolic function to represent a position between anoxic and dry) Depth to ground water	Biomass	Fluid dynamic model, river meandering model, numerical simulation, logistic model	River dynamics 'induce vegetation patterns'	Hypothetical (using data from SC, U.S.A., Pearlstine <i>et al.</i> , 1985)
Stand characteristics	Stromberg <i>et al.</i> , 1993	Depth to ground water	Stand biomass (leaf area index and vegetation volume), stand structure (maximum canopy height and basal area), leaflet variables (primary leaflet area, primary leaflet length and secondary leaflet number), xylem water potential	Stand biomass (leaf area index and vegetation volume), stand structure (maximum canopy height and basal area), leaflet variables (primary leaflet area, primary leaflet length and secondary leaflet number), xylem water potential	Second-order linear regression		Hassayampa R., San Pedro R., Tanque Verde Ck., AZ, U.S.A.
Cover types/functional groupings	Toner & Keddy, 1997	Depth, duration and timing of flooding, fraction of the growing season flooded, last day of first flood, length of the second flood, mean depth of flooding, number of floods per growing season, number of days of drawdown preceding midseason floods, time of second flood	Depth, duration and timing of flooding	Presence-absence of woody cover	Logistic regression	Static channel geometry	Ottawa R. Ontario, Canada
Cover types/functional groupings	Richter & Richter, 2000	Duration of flooding above threshold (effective discharge)	Duration of flooding above threshold (effective discharge)	Abundance of patch types	Numerical model simulations	Flood driven meandering drives forest succession; channel maintenance approach	Yampa R., CO, U.S.A.

term repercussions for the morphology and fitness of the individual (Smith *et al.*, 1998). Plants may experience water stress in response to rising solar radiation and temperature and/or reduced soil moisture or groundwater levels over the course of hours. Stomatal conductance, transpiration, net carbon assimilation, leaf internal CO<sub>2</sub> concentration, carbon isotope discrimination (an index of time-integrated carbon concentration and water-use efficiency) and xylem water potential can change as plants increase their water-use efficiency or become stressed in response to anoxia, water availability or changes in atmospheric conditions. Such measurements have led to the development of thresholds of groundwater depletion for riparian species through measuring the onset and consequences of chronic water stress (Stromberg *et al.*, 1993; Scott *et al.*, 1999; Cooper, D'Amico & Scott, 2003).

Plant attributes that can collectively express negative, short- to long-term (hours–weeks) response to reduced water availability include wilting, chlorosis and discoloration of leaves, abscission, leaf death and reduction in canopy volume. Extreme water stress may result in xylem cavitation and branch dieback in trees and shrubs ('drought pruning'), which can relieve overall water stress in the individual by reducing leaf area (Tyree *et al.*, 1994). There are also compensatory interactions among vegetation response variables, such as branch die-off or stand mortality in response to severe moisture stress that reduce stress in surviving branches and individuals within a riparian forest stand (Tyree *et al.*, 1994; Scott *et al.*, 1999).

In modelling individual species, it is important not only to know its distribution across the landscape, but also to understand how it performs at the population level (e.g. recruitment, overall fitness). Knowledge about structure (age- or size-class distributions) of a population is helpful in determining what life-stage is most influenced by flow regime changes. Age- or size-class distributions, evidence of successful recruitment or some functional assessment of life-stage can yield significant insight into the structure of the population and indicate 'bottlenecks' that may negatively affect one or more life-stages (e.g. recruitment failure). Age-class distributions may also provide insight into event-driven recruitment that may be statistically related to hydrologic characteristics (Auble & Scott, 1998; Birken & Cooper, 2006; Rathburn *et al.*, 2009).

Tolerance of plants to inundation, fluvial processes (scour and burial), anoxia and drought vary as a

function of developmental stage for many species adapted to riverine environments (Smith *et al.*, 1998; Friedman & Auble, 1999). In riparian areas, many colonising species germinate and establish on freshly deposited alluvium near the channel, whereas adults persist as channel migration and floodplain accretion and/or abandonment cause local soils to become more xeric over time. Thus, a species may be a specialist requiring specific conditions to establish and exhibit more generalist traits during later stages of development (Shipley *et al.*, 1989). The better we understand the specific relationships between flow-related processes and the survival and mortality of plants at different stages, the greater an opportunity we have for modelling populations and examining differences in population growth rates in response to different combinations of environmental factors (Lytle & Merritt, 2004).

The integration of dynamic numerical modelling and spatial mapping of site and stand dynamics is useful for predicting the extent and characteristics of change under various simulated flow regimes, providing a continuum of change that enables an evaluation of trade-offs associated with various flow regimes (Phipps, 1979; Pearlstine *et al.*, 1985). Matrix-structured population modelling also provides a powerful framework for determining whether populations are growing, stable or declining and identifying how growth rates are influenced by various processes (e.g. floods, droughts, seasonal rates of change in flow). Matrix models can be used to examine growth rates of populations and life-stages within populations in contrasting environments, in populations subjected to experimental treatments and in simulations over long periods of time to project the outcome of changing conditions (Caswell, 2001). Matrix population modelling has rarely been used in developing flow standards to manage plant populations along rivers (however see Lytle & Merritt, 2004; Griffith & Forseth, 2005; Smith *et al.*, 2005).

Incorporating stochastic processes into matrix models has been applied to species for which vital rates are tightly coupled to river flow regime (Lytle & Merritt, 2004; Smith *et al.*, 2005). Smith *et al.* (2005) used the information from structured population models to recommend winter and spring floods and the date that drawdown should occur to reduce the probability of extinction of a threatened floodplain species. Lytle & Merritt (2004) developed a structured

population model for riparian *Populus* trees by incorporating stochastic processes (flooding, drought and rates of river stage decline) that are tightly linked to *Populus* vital rates. The simulations revealed subtle patterns such as the importance of chance occurrences of sequences of annual flows most favourable to stand recruitment. Through simulating human or climate-driven changes in flow regime, changes in population structure could be observed and ecological limits of acceptable hydrologic alteration evaluated (Poff *et al.*, 2010). Though not dealing with geomorphic processes explicitly, hydrologically based models such as these account for fluvial processes to some extent because such processes are driven by river hydrology.

Matrix population modelling has great potential for projecting the outcomes of altered flow regime on riparian plant populations. There are opportunities for extending the applications of matrix models through incorporating more realism such as continuous environmental responses, channel change, spatial structure, multiple interacting species, autocorrelative and cross-correlative effects and additive or antagonistic effects of multiple environmental conditions. Including spatial structure and examining metapopulations (extinction, dispersal, colonisation) subjected to different stochastic environmental variations would permit an evaluation of the threat of extinction for a species and the role of alterations to the floodplain ecosystem in its decline.

#### Individual distributions

Fitting a distribution or function to presence–absence or abundance data of a species along an environmental gradient (e.g. flow-related) or gradients is a way to simultaneously test a hypothesis about its niche (*sensu* Hutchinson, 1957) and to develop a framework for prediction of its distribution under changing conditions (Guisan & Thuiller, 2005). Species distributions provide insight into the breadth of the species' realised niche and indicate ecological amplitude and its environmental optima along environmental gradients (Fig. 1).

Flow-related variables have universally been found to be strong predictors of species distributions in wetland and riparian ecosystems (Franz & Bazzaz, 1977; Shipley, Keddy & Lefkovitch, 1991; Merritt & Cooper, 2000). Abundance or probability of presence of a species can be estimated as a function of one or more variables quantifying hydrologic conditions. If

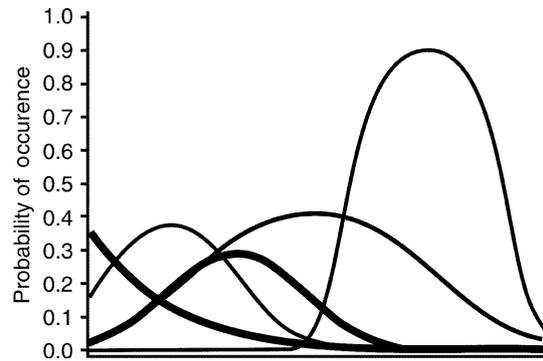


Fig. 1 Probabilistic species response curves. The independent variable may be any of a number of flow-related gradients such as exceedance probability, flow duration, flood frequency and intensity, frequency and duration of fluvial disturbance. Different lines represent different species (in the conventional view) or different guilds.

the distribution of flow conditions change in the riverscape, the statistical models may be used to estimate likelihood of response by riparian vegetation (Franz & Bazzaz, 1977; Auble *et al.*, 1994; Auble *et al.*, 2005; Friedman *et al.*, 2006).

Spatially explicit predictive models may be used to examine probabilities of spatial distributions of species and likely change in response to simulated changes in flow variables such as inundation duration. Such methods may be used to set bounds on flow alteration through providing a means of predicting the magnitude of change in the distribution of individual species under alternative flow scenarios.

An alternative to probabilistic modelling of each species individually is indirect and direct gradient analysis using a variety of ordination techniques (Jongman, ter Braak & Van Tongeren, 1995). Regressing flow-related variables against ordination axis scores can reveal which variables the species are collectively organised along, and provide an indication of the flow-related variables that best account for variation in community structure (Vanderijdt, Hazelhoff & Blom, 1996). These techniques bridge the gap between analysing individualistic responses of species and examining patterns in community structure.

Collectively, the flora in a riparian area may contain a diverse assemblage of species with numerous combinations of tolerances and requirements, some of which may be in direct conflict. Niche-based modelling quantifies this and estimates how different flow regimes in different years could provide for the

requirements of a range of species. Another important consideration of niche-based modelling is that the temporal response of different species to changes in flow regime varies widely. Short-lived species such as annuals could respond on the scale of a single season, but longer-lived species could require decades or even centuries to respond. Furthermore, the predictions from niche-based models only provide an estimate of the probability of change given a change in the gradient modelled. A variety of stochastic biotic and physical factors (fire, herbivory, competition, disease, fluvial disturbance) influence the distributions of species and if not explicitly incorporated into the model, these factors increase the uncertainty of predictions (Auble *et al.*, 2005).

### Communities

Although altered hydrologic attributes result in individualistic responses by species in accordance with their life-history attributes, collective responses may be revealed as changes in community attributes, plant communities, plant cover types and plant functional groupings (Nilsson, Gardfjell & Grelsson, 1991b; Jansson *et al.*, 2000; Merritt & Cooper, 2000). Dealing with vegetation response to flow alteration as a whole obviates many of the limitations of generalising the response of individual species (Franz & Bazzaz, 1977).

Collective attributes of the community (e.g. richness, diversity, cover, biomass) are linked to hydrologic attributes of rivers and may respond in predictable ways to specific hydrologic alterations (Stromberg & Patten, 1991; Nilsson & Jansson, 1995; Jansson *et al.*, 2000; Nilsson & Berggren, 2000; Lite, Bagstad & Stromberg, 2005). Plant associations or dominant cover types show strong affinities for specific hydrologic attributes such as inundation duration (Franz & Bazzaz, 1977; Auble *et al.*, 1994; Friedman *et al.*, 2006) and depth to ground water (Rains *et al.*, 2004; Camporeale & Ridolfi, 2006).

Classifying communities into cover types can be achieved by examining dominant woody species (Friedman *et al.*, 2006), growth forms (woody versus herbaceous cover; Toner & Keddy, 1997) or using ordination and clustering techniques to classify cover types (Auble *et al.*, 1994). These community or cover types may then be modelled to relate spatial distribution or probability of occurrence of cover types to attributes of the flow regime or ground water (Rains

*et al.*, 2004). Johnson (1992) developed a compartmental simulation model of changes in riparian cover types (successional stages) in response to projected changes in meander rates caused by water development along the Missouri River, North Dakota, U.S.A. Richter & Richter (2000) simulated successional stages of *Populus*-dominated riparian forest by relating stand formation to meandering rate along the Yampa River, CO, U.S.A. They further related meandering to flow regime and suggested an acceptable amount of extractable water that would ensure high flows adequate to maintain a reasonable level of meandering. Flow permanency (fraction of the season flooded) is an important predictor of woody versus herbaceous cover types (Toner & Keddy, 1997), shifts in zonation of cover types in response to altered flow (Auble *et al.*, 1994) and richness of vegetation (Lite *et al.*, 2005). The presence-absence of herbaceous and woody vegetation was correctly predicted 80% of the time in a model incorporating only long-term (7–18 years) averages of flood timing along the Ottawa River, Canada (Toner & Keddy, 1997).

Other attributes used to characterise vegetation include biomass, vegetation volume, growth rates and stand physical structure (Stromberg & Patten, 1990, 1991; Stromberg *et al.*, 1993). These attributes can be regressed against flow variables, and the relationships used to estimate stand characteristics in response to flow alteration scenarios. One advantage of these empirical regression approaches is that a full range of vegetation metrics can be quantified, enabling an evaluation of trade-offs between flow alteration and measurable riparian conditions. A disadvantage of these techniques is that the relations are often very river and site-specific, limiting transferability of relationships to other rivers even in the same hydroclimatic region.

### Functional groups

To facilitate generalisation across systems, grouping species by some shared functional attribute can be a practical way to generalise and transfer patterns from one system to the next. Stream ecologists have developed functional classifications of species into groups 'with similar biological and ecological traits that are expected to respond consistently along specific environmental gradients' (Poff *et al.*, 2006b). Although different species respond to different components of

river flow regime (e.g. some require elevated baseflows versus high flows for the creation of open-patches), groups of riparian plant species that respond in similar ways to specific attributes of stream flow regime or processes associated with them can be identified.

Because traits are a product of natural selection, trait convergence may occur in communities experiencing similar selective pressures (Southwood, 1977). When selective pressures, such as flow and fluvial disturbance regimes are similar, convergence of traits can occur even across biogeographic boundaries and phylogenies. The reproductive phenology of pioneer riparian tree species in relation to seasonal floods around the world, root morphologies for water acquisition and sexual versus vegetative reproductive strategies, provide some examples of such trait convergence. Riparian *Populus deltoides* Bartram ex Marsh. in western North America (Braatne, Rood & Heilman, 1996) and *Eucalyptus camaldulensis* Dehnh. and *Melaleuca raphiophylla* Schauer in Australia release short-lived seeds for a short period of time in synchrony with the recession of floods (Pettit & Froend, 2001). The capacity to produce deep taproots exemplifies the convergence of root morphologic traits in phreatophytes in the northern (e.g. many species of Salicaceae, *Prosopis velutina* Woot.) and southern hemispheres (e.g. *Eucalyptus sideroxylon* A. Cunn ex Woolls). Selection for sexual reproduction and annual growth form in plants associated with rivers that experience frequent, channel-forming fluvial disturbances versus vegetative and perennial reproductive strategies along relatively stable channels with less seasonal flow variability provides another example of trait convergence (Cronk & Fennessy, 2001; Samuelson & Rood, 2004).

The ecological guild or functional group concept provides a framework for identifying riverine species with shared responses to environmental variation (Leonard & Orth, 1988; Poff & Allan, 1995; Lamouroux, Poff & Angermeier, 2002; Poff *et al.*, 2006b). Austen, Bayel & Menzel (1994) distinguished between structural guilds (groups of species that use similar resources) versus guilds that function as a 'super species' or groups of species that collectively respond to environmental variation in a similar manner. We adopt the latter concept of guilds in developing our framework for riparian vegetation.

The selection of meaningful traits for categorising species into guilds or functional groups requires a

solid mechanistic understanding of the relationships between traits and environmental gradients. Such specific trait linkages, statistical correlations among traits, and evolutionary lability of traits provide a basis for predicting responses of communities to changes in physical processes (Poff *et al.*, 2006b).

#### *Towards the development of riparian vegetation-flow response guilds*

To overcome the shortcomings and limitations of the site-specific nature of the individual, population and community models developed in the studies reviewed, we propose a general framework for modelling riparian vegetation-stream flow relations. The foundation of this framework is the rich plant ecology literature in which functional approaches to grouping plants are well-developed (Grime, 1979; Shipley *et al.*, 1989; Keddy, 1992, 2002; Lavorel *et al.*, 1997; Tilman *et al.*, 1997).

We define groups of riparian plant species that respond in similar ways to quantifiable flow attributes as *riparian vegetation-flow response guilds* (hereafter *riparian response guilds*). We categorise the riparian response guilds broadly into five categories: life history, reproductive strategy, morphology, fluvial disturbance and water balance (Table 3). Non-phylogenetic associations of plant communities have been used to predict ecosystem response to disturbance (Grime, 1979), water depth and exposure (Shipley *et al.*, 1989), resource gradients (Rajaniemi *et al.*, 2006) and groundwater decline (Baird *et al.*, 2005). Because juvenile and adult traits may be independent of one another in wetland and riparian plants (Shipley *et al.*, 1989), it is necessary to examine these life-stages independently during the development of trait matrices. Such functional classifications provide a broader framework for prediction of response to changes in environmental variables than do analyses of individual species response curves, communities and cover types along gradients (as outlined above and in Table 2). We propose a riparian response guild framework that considers key attributes of riparian vegetation (Table 3).

#### *Life-history guild*

The life-history guild is composed of traits that reflect trade offs between individual fecundity and survivor-

**Table 3** Flow response guilds for riparian vegetation

Flow response guild	Traits	Relevant flow component
Life history	Longevity (life span) Annual–perennial–biennial	Frequency of extreme floods
Reproductive strategy	Vegetative–sexual–combined Timing in synchrony with flow component	Magnitude of extreme flow (flood transported ice, wood, material, shear) Timing of high, low flow
Morphology	Growth form (e.g. herbaceous–woody, graminoid–shrub–tree) Rooting depth (phreatophytic) Root morphology (lateral–taproot, shallow–deep) Size at maturity (canopy height, vegetation volume)	Flow duration Magnitude and duration of low and high flow Water table depth and inter- and intra-annual variability Flow permanence, groundwater depth, flow variability
Fluvial disturbance	Furrowed bark Flexible stems Re-sprouting ability Adventitious roots and stems (scour-burial)	Magnitude and frequency of high flow High sediment flux
Water balance	Stomatal control Critical water stress level – xylem water pressure potential Aerenchyma (tolerance of anoxia) Oxygen diffusion to roots Drought-induced dormancy Tolerance of submergence Rate of root extension	Magnitude/duration low flow Magnitude/duration low flow Duration of high flow Water table depth and inter- and intra-annual variability Rate of stage decline

Because such traits may vary over the developmental stages of plants, the same species may be divided into different guilds at different life-stages.

ship within species. Traits in this guild include life span of the individual, a key determinant of response time to a change in hydrologic conditions. The life span of species groups has relevance to the response of such groups to changes in timing and duration of disturbance as well as the length of time between such disturbances (Southwood, 1988). For example, annual or other short-lived plants may be present or absent as a function of seasonal flow regime whereas long-lived riparian forest species may persist for a century or more after the flow-related processes necessary for forest stand formation have ceased (Howe & Knopf, 1991; Friedman & Lee, 2002). Life span (as opposed to classification as annual or perennial) is a quantitative measure of typical length of life. Different life-history guilds may be used to develop an understanding of the sequence and duration of responses that should be anticipated following a change in flow regime.

#### *Reproductive strategy guilds*

Reproductive strategies include: (i) phenology (timing of seed release); (ii) type of regeneration (sexual versus vegetative); (iii) reproductive cycle of the plant

(annual, biennial, short and long-lived perennial); (iv) seed longevity or propensity for dormancy and (v) length of time to first reproduction. Because of the typical temporal variability of the flow regime and high resource heterogeneity in riparian areas, numerous reproductive strategies may co-exist in these systems (Naiman *et al.*, 2005). Phenological adaptations include delayed flowering during submergence and dispersal timed to increase the likelihood of suitable habitat availability during dispersal (Fenner, Brady & Patton, 1985; Pettit & Froend, 2001). Reproductive specialists (responsive to attributes of flow regime) are expected to be sensitive to changes in the timing of various flow components and rates of change in flow. Plants growing in wetlands and stable or uniform riparian habitats exhibit a high propensity for asexual or vegetative reproduction, but sexual reproduction is favoured in highly variable or heterogeneous habitats (Cronk & Fennessy, 2001; Keddy, 2002). Indeed rivers or river reaches that have more stable flows and less extreme flooding (higher elevation streams, spring-fed streams, swamps, regulated rivers) tend to be dominated by perennial species with vegetative reproduction strategies (Merritt & Cooper,

2000; Friedman *et al.*, 2006; Merritt & Wohl, 2006). Whereas many pioneer species have short-lived seeds, seed longevity can also function as an important reproductive adaptation to disturbance, as species that can form a seed bank may be the first to establish following disturbance (Keddy, 2002).

#### *Morphology guilds*

Canopy height, canopy volume, root depth and root architecture are among the structural traits of plants responsive to and reflective of hydrologic variability (Stromberg & Patten, 1990; Scott *et al.*, 2000). When changes in flow permanence, total annual discharge and depth to groundwater occur, communities may shift in predictable ways according to traits associated with water acquisition (e.g. root morphology). Shifts from tall forest species to shorter shrublands or meadow may reflect a directional or threshold response to water depletion (Lite & Stromberg, 2005). The presence of woody and herbaceous vegetation may also be tightly linked to timing and sequencing of floods and duration of inundation (Toner & Keddy, 1997). Linkages between physiognomy of the vegetation and flow regime could guide managers in structuring flows to provide specific native habitat types such as multi-layered forest canopies for neotropical songbirds or moist meadows for obligate riparian mammals.

#### *Fluvial disturbance guilds*

Several trait 'syndromes' exist in river ecosystems around the world as co-evolved adaptations to fluvial disturbances. These syndromes are likely to vary as a function of natural patterns of disturbance in these systems (magnitude and frequency of flooding). Furrowed bark, flexible stems and the ability to re-sprout after stems are damaged are all traits that are common to groups of disturbance-adapted woody species living along rivers throughout the world. Several genera share these traits within families (e.g. Salicaceae). These adaptations are readily identified for individual species, and the relative importance of such guilds in the riparian community should exhibit a strong relationship to characteristics of the flow regime.

The ability to root adventitiously from stems is an adaptation both to burial of stems by sediment and to acquisition of oxygenated water in inundated areas (Cronk & Fennessy, 2001). Whereas terrestrial plants

rarely experience burial by sediment, burial is a frequent occurrence along free-flowing rivers. Plants may possess tubers, rhizomes and/or pointed shoots to facilitate upward penetration through sediment following burial. Adventitious rooting from stems enables a plant to acquire nutrients, water and oxygen from the accumulated sediment around its stem following burial. Such traits should be more prevalent in riparian areas with frequent fluvial disturbances and become less prevalent in systems that have naturally low or altered levels of disturbance. Altered disturbance patterns are likely to have a more severe effect on seedlings and earlier growth stages for most species; however, if seeds are available following disturbance or fresh deposits of alluvium provide centres or nodes of colonisation.

The proportion of the riparian community with adaptations to disturbance should be higher in systems with high frequency and magnitude of disturbance. Shifts in this guild will occur in accordance with magnitude and direction of the change at a rate determined to some degree by the life-history traits of those species included in the guild.

#### *Water balance guilds*

In hydrologically variable riparian environments plant species often have adaptations to conditions associated with periods of flooding as well as periods of drought (Blom *et al.*, 1994; Naumburg *et al.*, 2005). Species vary greatly in their ability to regulate their water pressure potential (through stomatal closure or other leaf morphologic traits; Pockman & Sperry, 2000). Many species of riparian plants, particularly in arid regions, require access to a permanent or seasonal water supply and are intolerant of low internal water pressure potentials (Cronk & Fennessy, 2001). Other species may have an affinity for fine-textured substrates with high water-holding capacity, or may be able to use water at low soil water pressure potentials (Naumburg *et al.*, 2005). Some riparian species can use different water sources over the course of the season, with various proportions of transpired water coming from ground and soil water depending on relative availability (Busch & Smith, 1995; Smith *et al.*, 1998). Such species may be better adapted to extended periods of low flow caused by drought, groundwater pumping and water extraction (Stromberg *et al.*, 2007). Plants along streams where

surface water has been diverted may exhibit morphologic responses to enhance water-use efficiency, such as reduced leaf size, increased leaf thickness and reduced leaf area (Smith *et al.*, 1991).

Generally, the 'water balance' riparian response guild spans a trait gradient from tolerance of anoxic conditions associated with prolonged flooding to tolerance of periodic soil desiccation. At intermediate positions along soil hydrologic gradients lie groups of riparian species with traits appropriate to hydrologically variable conditions. These species include those individual species with adaptations to conditions of both moisture excess and scarcity as well as transient, species that occur only when favourable conditions exist.

### Summary

As with individual species, plant distributions can be fitted to entire guilds along various gradients to place predictions of trait occurrences in the context of hydrologic characteristics (Fig. 1). Once such response curves have been constructed and calibrated for specific stream types within hydroclimatic regions, the response of guilds to a range of hydrologic alterations may be predicted and used to inform management decisions. By using standard hydrologic components and community attributes applicable to all streams, the riparian response guild framework facilitates prediction of riparian plant community attributes and likely responses to flow regime alteration and is generalisable across catchments and regions.

### Discussion and conclusions

We may enhance our ability to make predictions across a broader range of systems by using the riparian response guilds framework. The next steps toward implementing such a framework will involve quantifying attributes of regional lists of species and determining the guilds to which they belong. Probabilistically modelling the distributions of species guilds along quantified gradients of water availability (flow duration or inundation duration) and fluvial disturbance (frequency, magnitude, duration) will enable us to evaluate and refine the riparian response guild framework, and begin to apply it to flow management. At the species level, it is desirable to fit species response surfaces to environmental predic-

tors that represent (i) *limiting* or *regulating factors* (those that control ecophysiology); (ii) *disturbances* (perturbations that remove or redistribute biomass) and (iii) *resources* (compounds that can be assimilated by organisms; Guisan & Thuiller, 2005). At the guild level, predictors for fitting response surfaces to functional groups could be similarly selected according to functional attributes of the guild. In riverine environments, these might include factors such as flow duration, recurrence interval, stream power, shear stress, critical shear stress or other flow and fluvially mediated variables.

This approach has the potential to overcome many of the shortcomings of conventional modelling approaches. Because distributions are most often developed empirically at sites, they include only species currently at the sites and thereby exclude other species which may have been extirpated or those suited to current or future site conditions. Accordingly, they may be difficult to apply beyond the range of site-specific calibration, as relationships between stream-flow and the response variables may vary by site (Auble *et al.*, 1994; Friedman *et al.*, 2006). Modelling multiple species at a site along with some model component that connects them may provide a probabilistic view of community dynamics but may be difficult to summarise as clear and explicit management prescriptions. By contrast, application of riparian response guilds enables the scientist and manager to talk in general but practical terms about the probable changes in vegetation attributes (guild shifts).

Because of the increasing demand for water worldwide, changing climate, the continued modification of rivers and the desire to maintain viable features of ecologically functioning rivers, the development of intuitive and transferable frameworks for flow management is timely. One central aim of community ecology is to predict the composition of communities in response to changing environmental conditions (Keddy, 1992). Such prediction often requires some balance between considering the details of specific sites and species (reductionist) and theory so general (holistic) that it cannot be easily conveyed to managers and translated into management strategies (Lavelle *et al.*, 1997). Statistically linking riparian vegetation-flow response guilds to hydrologic gradients, regionally calibrating these relationships and using them to guide river flow management provides an important development toward such a framework.

This flow management framework provides a level of generalisation that can be used to establish flow standards on individual streams and catchments and to facilitate transferability of flow standards to related streams in the hierarchical river classification. This approach also helps obviate the need to prescribe river and site-specific recommendations of flow by allowing development of some general guidelines for multiple streams within particular streamflow classes (Poff *et al.*, 2010). The use of the riparian vegetation-flow response guilds framework provides a sound riparian vegetation component to an holistic approach to river and environmental flow management (*sensu* Tharme, 2003; Arthington *et al.*, 2006).

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