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Relationship between vegetation, hydrology and fluvial landforms on an unregulated sand-bed stream in the Hunter Valley, Australia.

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Abstract.

A survey of fluvial landforms was conducted at Widden Brook, an unregulated sand-bed stream in the Hunter Valley, New South Wales (NSW), Australia, to investigate the physical factors associated with vegetation pattern in Riverine Oak Forest. Groundwater depth and chemistry (pH, dissolved oxygen and electrical conductivity) were measured using piezometers and submersible data loggers on three fluvial landforms (i.e. toe of bank, top of bank & floodplain) along five transects. Floristic composition, canopy cover, bare ground and leaf litter were assessed within 45 quadrats on the three landforms along the five transects. Elevation above the bed and flood return period were determined by cross-sectional survey and flood frequency analysis, while flow duration was determined from the gauge record. Canonical correspondence analysis demonstrated that vegetation composition was associated with average watertable depth and flood variables to a similar extent. The relative importance of these factors would be expected to vary with flood- and drought-dominated climatic periods on a scale of several decades. Floristic composition was moderately associated with the canopy cover of the dominant woody species, *Casuarina cunninghamiana* (Miq.), but weakly correlated with bare ground and groundwater chemistry. Suites of species were associated with particular fluvial landforms and their corresponding flood and watertable conditions. The reach examined has characteristics similar to both the semi-arid and mesic riparian ecosystems of the United States. The coarse sediments, high flood variability, short flood duration and dominance by a pioneer tree that relies on groundwater are similar to riparian ecosystems in the western United States, while the relatively broad floodplain and the development of a forest canopy that is associated with the distribution of understorey plants are similar to the mesic riparian systems in the eastern United States.

Keywords: flood frequency; floodplain vegetation; flow duration; riparian vegetation; groundwater

Introduction

Riparian vegetation pattern responds to three major gradients that are nested in both space and time: (i) continental/climatic gradients acting at the hydrological basin level; (ii) an intra-riparian longitudinal gradient reflecting changes along the length of a stream; and (iii) a transriparian gradient across a stream and floodplain (Mitsch & Gosselink 2000). The intra-riparian gradient reflects changes in elevation, stream gradient and fluvial processes (Mitsch & Gosselink 2000) such as erosion and deposition of sediment. The lateral transriparian gradient is a local topographical gradient that determines local moisture regime and soil development (Mitsch & Gosselink 2000). Flood disturbance (magnitude, frequency and duration) and hydrological conditions (including groundwater depth, amplitude and chemistry) are determined by processes at all three scales.

Despite large differences in climate, vegetation types and hydrogeomorphic processes, studies in the United States using multivariate gradient analysis to investigate the transriparian gradient have found that elevation is the main determinant of riparian vegetation pattern. This relationship has been demonstrated in bottomland hardwood forests in eastern United States (Menges & Waller 1983; Menges 1986; Lyon & Sagers 1998; Goebel et al. 2006), semi-arid riparian vegetation in western United States (Friedman et al. 1996) and in subalpine/montane riparian vegetation in the southern Rocky Mountains (Baker 1989). However the mechanisms responsible for this relationship with elevation are likely to differ in the eastern and western river systems.

Extensive bottomland hardwood forests occur on the broad alluvial floodplains of the eastern and central United States and are characterised by a mesic climate, strong seasonal hydrological pulses (i.e. inundated or saturated by surface or groundwater periodically through the growing season) and well-developed soils (Mitsch & Gosselink 2000). These eastern streams are usually perennial from the source to the mouth and moisture deficits (even during late summer) are usually not severe (Mitsch & Gosselink 2000). As flood duration is related to the size of the upstream drainage area and stream gradient, mid-western and eastern riparian ecosystems with small catchments (or low-order streams) are flooded for several days to several weeks during the spring thaw, whereas flooding on high-order rivers like the Mississippi may last up to several months (Mitsch & Gosselink 2000). Thus, the most important local environmental condition for vegetation in the high-order south-eastern riparian ecosystems in the United States is the moisture, or anaerobic gradient, which varies spatially and temporally across the floodplain (Mitsch & Gosselink 2000).

In contrast, the riparian systems in western United States often line low-order streams with steep gradients and narrow floodplains and are characterised by extreme and variable fluvial conditions and geomorphic responses (Mitsch & Gosselink 2000). Vegetation zonation is less likely to be associated with flood duration in these dry regions because the relatively steep stream gradients mean that the flood duration is short (Friedman et al. 1996). Rather, riparian vegetation pattern is expected to be most closely related to patterns of water availability (Hupp & Osterkamp 1996). In arid and semi-arid regions evapotranspiration usually exceeds precipitation (Mitsch & Gosselink 2000). As a result, riparian tree species in these environments are phreatophytes and obtain their water from groundwater or the capillary fringe of the groundwater table (Mitsch & Gosselink 2000). Stream geomorphic valley types are predictably associated with vegetation patterns in western United States, in a large part due to soil moisture regimes (Mitsch & Gosselink 2000). However, soil moisture and depth to groundwater are not the only factors governing plant establishment in these environments because high flood variability (large range of flood peak discharges) results in the periodic removal of plants from low elevations by floods and the vegetation consists of those species that can survive until the next flood (Mitsch & Gosselink 2000). Thus in river systems where flood variability is high, associations between vegetation and elevation may be due to the severe physical disturbance provided by catastrophic floods, in addition to soil moisture and groundwater depth gradients.

Fluvial geomorphic processes control the elevation and substrate of landforms within the channel (i.e. bars, benches and islands) and adjacent to the channel (banks, floodplains and terraces). Particular plant species are associated with specific fluvial landforms (Hupp & Osterkamp 1985) and vegetation pattern varies across fluvial landforms of different ages (Friedman et al. 1996). Where water is relatively abundant in the humid east of the United States, vegetation pattern is related to the distribution of landforms created by predictable flood disturbance or durations (Hupp & Osterkamp 1985). For example, in south-eastern bottomland forests newly formed point bars are colonised by a specific suite of species (Mitsch & Gosselink 2000). In semi-arid and arid regions with high flood variability, models of cottonwood (*Populus* sp.) recruitment and survival on the South and North Platte rivers (Johnson 1994) and their tributaries (Freidman et al 1996; Freidman & Lee 2002) emphasise the importance of the formation and removal of fluvial landforms. A similar model has been developed for the recruitment and survival of river oaks (*Casuarina cunninghamiana*) on Widden Brook in NSW, Australia (Erskine et al. 2009), the sand-bed stream that is the subject of this study.

Although flooding regimes and soil moisture gradients associated with specific fluvial landforms appear to be the most important determinants of riparian vegetation pattern, associations have been found with other environmental variables. Studies have shown that together with elevation, litter cover is associated with the riparian vegetation of a high-order stream in Canada (Day et al. 1988) and a semi-arid river system in eastern Colorado (Friedman et al. 1996). The latter study also found that litter cover was more strongly related to vegetation pattern than overstorey shade (Freidman et al. 1996). Menges (1986) demonstrated that light has a significant relationship with herbaceous composition in a mesic bottomland hardwood forest (independent of elevation). Some studies have found a strong correlation between soil pH and bottomland vegetation in the United States (Lyon & Sagers 1998), whilst a study of wetlands along a high-order stream in Quebec demonstrated a weak relationship (Jean & Bouchard 1993). These mixed results suggest that canopy cover and soil variables are likely to be of secondary importance in determining riparian vegetation pattern and/or their importance depends on the nature of the riparian system under study (i.e. the climate and associated vegetation type). The only studies using multivariate analysis to investigate relationships between groundwater depth and chemistry and riparian vegetation have all been conducted in Europe and involved cutoff channels (Bornette et al. 1998), an annually inundated alluvial depression (de Becker et al. 1999) and a montane floodplain with extensive peat formation (Bufková & Prach 2006). Thus, the findings of these studies are of limited relevance to the riparian ecosystem under investigation here.

In Australia, there are only a few studies using multivariate analysis to examine the transiparian gradient and all of them have been conducted on the River Murray; a regulated river in a semi-arid region dominated by eucalypt woodland. Blanch et al. (1999) investigated the relationship between littoral plants on the River Murray and water regime (i.e. flooding frequency and exposure to water depth classes), Walker et al. (1994) examined the association with physical channel characteristics and water depth, while Roberts and Ludwig (1991) examined the relationship of riparian vegetation with a current and wave-action gradient. The relationship between riparian vegetation and flow regimes have also been investigated in two contrasting river systems in Western Australia (Pettit et al. 2001; Pettit & Froend 2001), but there is a paucity of studies examining these kind of relationships in non-eucalypt dominated riparian vegetation in eastern Australia.

The aim of the current study was to investigate the degree to which the transiparian gradient (i.e. elevation, flood-related variables, watertable depth and groundwater chemistry) is correlated with vegetation composition on an unregulated, sand-bed stream in the Hunter

Valley, Australia. Widden Brook is characterised by high to very high flood variability, ceases to flow during dry periods and has been highly modified by past and current agricultural activities. For these reasons, the most relevant previous studies of sand-bed streams in terms of flow regime are those conducted on the Platte River and its tributaries in Nebraska and Colorado (see Johnson 1994; Friedman et al. 1996; Friedman and Lee 2002). These river ecosystems have also been highly impacted by livestock grazing (Mitsch & Gosselink 2000). On the basis of these studies we hypothesised that: (1) vegetation composition will be more strongly correlated with groundwater availability (i.e. watertable depth) than with flood-related variables; (2) flood frequency will be more strongly correlated with vegetation than flow duration, because flow durations on the floodplain of Widden Brook are relatively short; and (3) leaf litter will be moderately correlated, whilst canopy cover, percentage of bare ground and groundwater chemistry will be weakly correlated with vegetation composition.

Methods

Study area

The study area (Fig. 1) consisted of pastoral land in the riparian corridor of Widden Brook, which is a southern tributary of the Goulburn River in the upper Hunter Valley, NSW, Australia (150°22'E, 32°32'S). The site has a catchment area of about 650 km² and consists of a 12 km long reach of slightly sinuous, sand-bed channel, discontinuously flanked by bars, benches and floodplains that are intermittently grazed by livestock (cattle or horses). Benches are actively accreting flat-topped bodies of sediment occurring along the banks of a river between the bed and the main valley flat (Woodyer 1968; Woodyer et al. 1979; Erskine 1994; Erskine & Livingstone 1999) and are usually vegetated, elongate and discontinuous. Typical of Eastern Riverine Forest, the vegetation is dominated by a single tree species, *C. cunninghamiana* (Casuarinaceae), and the composition of the understorey varies considerably (Keith 2004). Other woody species within the study area (e.g. *Salix babylonica*, *Leptospermum polygalifolium*, *Acacia* spp.) are sparse and rarely extend further than the top of the bank. The density of mature *C. cunninghamiana* (river oak) individuals is variable, due to clearing of the bank and floodplain for grazing and pasture improvement since European settlement in the 1830s. Where remnant woodland survives on the floodplain, mean tree density varies from 70-883 stems ha⁻¹ (total basal area of 33 - 55 m² ha⁻¹). Dense stands of

younger *C. cunninghamiana* (about 13 m high) occur on benches within the channel and on the toe of the bank, particularly where grazing by livestock is low or has been excluded.

Fig. 1. Location of the study reach at Widden Brook, NSW. Inset – schematic of the layout of the five transects and 15 piezometer sites (not to scale).

The Widden catchment is located in the Permo-Triassic Sydney Basin which is a thick sequence of predominantly conglomerate, sandstone and siltstone (Beckett 1988). The area has a warm-temperate climate with annual average rainfall varying from 910 mm in the upper catchment to 649 mm immediately upstream of the study site. Long-term temperature records are only available for the upper catchment where average temperature at 0900 h varies

between 5.2°C (July) and 17.2°C (January), and at 1500 h, between 8.0°C (July) and 22.7°C (January).

Widden Brook is located in the Wollombi-Goulburn hydrologic area (Erskine & Livingstone 1999) which is characterised by low to moderate specific mean annual flood (mean annual flood per unit catchment area) and high to very high flood variability. The 1955 and 1971 floods were the two largest floods recorded between 1954 and 1977 at the former gauging station and had flood peak discharges which were 13.6 and 6.66 times greater than the mean annual flood, respectively. Both floods caused significant channel erosion. The monthly distribution of annual floods at the Widden gauging station shows that floods are most likely to occur between January and March (i.e. summer) or in June. Widden Brook ceases to flow during dry periods and the NSW Department of Water and Energy's Pinneena 9.2 surface water archive for the gauging station, Widden Brook at Widden, shows that zero flow occurred for at least 10% of the gauged period between September 1954 and April 1979 (Erskine et al. 2009).

Data collection

Five transects were established on the right bank of the stream, perpendicular to streamflow, to determine the floristic composition and environmental characteristics of three fluvial landforms: (i) the toe of the river bank, (ii) the top of the river bank and (iii) the floodplain. Three of the five transects were located on a reach with a relatively high floodplain containing a remnant population of large and senescing *C. cunninghamiana* as well as benches within the channel that support dense stands of younger *C. cunninghamiana*. The remaining two transects were located 11.1 km downstream on a reach with a lower floodplain, an absence of benches and occasional mature and juvenile *C. cunninghamiana*.

Fifteen piezometers were installed, with five located on each landform. The piezometers were constructed from 100 mm PVC slotted along the lower 0.5 to 1.5 m and installed to a depth of 3-4 m in the alluvial sediments according to the method adopted by the NSW Office of Water. Depth to the watertable was determined on 7-9 occasions between February 2006 and September 2008. Groundwater quality (pH, electrical conductivity and dissolved oxygen) was measured with a calibrated TPS 90-FLMV meter on 1-3 occasions between February 2006 and March 2007. Water quality could not be determined on a number of occasions, as some piezometers were dry. A flood occurred in June 2007 burying some piezometers, which were relocated and re-augered. Cross-sectional surveys of the channel and floodplain were

conducted along the five transects to determine the relative elevation of the piezometers (bank toe, top of bank and floodplain) above the channel bed, flood frequency and flow duration. Discharge corresponding to the ground surface at each piezometer was determined by Manning's equation and estimated roughness coefficients (Cowan 1956). Flood frequencies (i.e. return period) were calculated using the regional method of Boyd (1978). Flow durations were determined from the gauge record.

At each of the fifteen piezometers, three 2 m x 5 m quadrats were systematically placed (10 m apart), with the middle quadrat located so that the piezometer was in the centre (i.e. total of 45 quadrats). Quadrats were aligned next to each other and oriented with the longest axis parallel to the stream (i.e. all at the same elevation). In each quadrat, we recorded percent cover of all vascular plant species in the following cover classes: < 5%, 5-25%, 26-50%, 51-75%, 76-95% and 96-100%. Sampling (December 2008) coincided with the flowering of the warm-season herbaceous species, although cool-season annuals that had died but were still rooted in the ground were also recorded. Cover and type of bare ground (i.e. bed, bench or recent sand splays), leaf litter, large woody debris and projective foliage cover (i.e. canopy cover) were recorded. Species nomenclature follows Wheeler et al. (2002) for grasses and Harden (1990; 1991; 1992; 1994) for other species.

Data analysis

Average groundwater electrical conductivity (EC), pH, dissolved oxygen (DO) and watertable depth over the study period were calculated, as well as minimum, maximum and groundwater amplitude. The maximum recordable depth of the piezometer was used to calculate maximum watertable depth and groundwater amplitude when the piezometers were dry. Relative elevation was determined by subtracting the average elevation of the bed from the ground surface elevation at each piezometer. Large woody debris was in low abundance and was therefore not considered further. Environmental variables with skewed distributions were transformed. DO and flood return period were transformed by taking logarithms whilst percentage canopy cover, leaf litter and bare ground were arcsine transformed. Pearson correlations were conducted on environmental variables, while significant differences among landforms were determined by analysis of variance (ANOVA). Post hoc pair-wise comparisons were made using Bonferroni tests to protect against Type I errors. All analyses were conducted using SPSS version 12.

Canonical correspondence analysis (CCA) was conducted using CANOCO version 4.5 to determine the relationship between vegetation composition and the environmental variables. For the species abundance data, the midpoint of each cover class was used to average cover across the three quadrats. We removed infrequent species (< 5% frequency overall) from the dataset because rare species can unduly influence the analysis, particularly if they occur on sites with extreme environmental conditions. As the species abundance data showed skewed distributions they were transformed by taking the square root (ter Braak 1986). The square root transformation is also appropriate when the overall community pattern is of interest because it has the effect of down weighting the influence of highly abundant species (ter Braak 1986). Relative elevation, return period and flow duration were removed from the analysis because their high correlation with the watertable variables meant that they would add no unique contribution and result in unstable canonical coefficients (ter Braak 1995). The watertable variables were also highly correlated with each other, thus only average watertable depth was included in the analysis. Variance inflation factors of less than 5 indicated no multicollinearity (ter Braak & Smilauer 2002) between the variables that remained in the analysis (i.e. canopy cover, leaf litter, bare ground, average watertable depth, groundwater pH, EC and DO). CCA indicates the importance of environmental gradients by: (i) the magnitude of the eigenvalues, (ii) the statistical significance of the first eigenvalue as determined by Monte Carlo permutation tests and (iii) ecological interpretability (ter Braak & Verdonschot 1995; ter Braak 1995). The solution of the CCA is displayed as a triplot that shows the relationship between the weighted averages of each species, the environmental variables and the sites.

Results

On average, the elevation above the bed and depth to the watertable was lowest on the toe of the bank and similar on the top of bank and floodplain (Table 1). The cover of bare ground and flow duration was highest on the bank toe and similar on the top of the bank and floodplain (Table 1). Canopy cover and leaf litter showed a bimodal distribution, being highest on the floodplain, lowest on the top of the bank and moderate on the toe (Table 1). However, these differences were not significant. On average, watertable amplitude, flood return period, groundwater pH, EC and DO were similar across the three fluvial landforms (Table 1). With the exception of watertable amplitude, the watertable variables were highly correlated with each other and with the flood variables (Appendix 1). Relative elevation

above the bed was positively correlated with return period and the watertable variables, and was negatively correlated with flow duration and cover of bare ground. Although relative elevation, return period and flow duration were excluded from the CCA, the strong correlations with watertable depth suggest that any relationship demonstrated for average watertable depth (see below) would also be true for elevation above the bed, return period and flow duration. That is, the importance of flood-related variables in determining species composition cannot be separated from the importance of watertable depth. Therefore, although not stated explicitly hereafter, any interpretation regarding the importance of average watertable depth could equally be substituted with the variables “elevation above the bed”, “flood return period” or “flow duration”.

Table 1. Means ($\pm$ standard error) of environmental variables for each fluvial landform at Widden Brook ($n = 5$). EC, electrical conductivity; DO, dissolved oxygen. Means within rows followed by different superscripts differed significantly (Bonferroni test) at the $p < 0.05$ level.

	Mean $\pm$ SE		
	Toe of bank	Top of bank	Floodplain
Distance from the bed (m)	7 ± 3.3^a	20 ± 7.0^{ab}	56 ± 12.8^b
Relative elevation above bed (m)	0.59 ± 0.12^a	1.56 ± 0.24^b	1.60 ± 0.22^b
Flow duration (%)	2.39 ± 0.35^a	1.08 ± 0.26^b	0.93 ± 0.24^b
Return period (years)	1.18 ± 0.18^a	2.23 ± 0.54^a	2.54 ± 0.53^a
Average watertable depth (m)	0.86 ± 0.11^a	1.81 ± 0.24^b	1.90 ± 0.23^b
Watertable amplitude (m)	0.79 ± 0.08^a	0.77 ± 0.05^a	0.91 ± 0.08^a
Canopy cover (%)	27 ± 16.2^a	10 ± 4.5^a	42 ± 12.4^a
Leaf litter cover (%)	7 ± 4.5^a	0.5 ± 0.5^a	8 ± 3.5^a
Bare ground cover (%)	38 ± 9.8^a	14 ± 5.0^{ab}	0.3 ± 0.3^b
Groundwater pH	6.5 ± 0.09^a	6.5 ± 0.12^a	6.4 ± 0.24^a
Groundwater EC (dS m^{-1})	0.30 ± 0.07^a	0.35 ± 0.04^a	0.50 ± 0.04^a
Groundwater DO (ppm)	0.77 ± 0.24^a	0.85 ± 0.11^a	0.92 ± 0.25^a

A total of 124 plant species were recorded in the quadrats during the study, 72 of which had an overall frequency greater than 5%. Twenty-nine species were perennial, 40 species

were short-lived and the lifespan of three species was unknown. The first two axes of the CCA explained 34% of the variance of the weighted averages of species with respect to the environmental variables (Table 2). Similar studies of riparian vegetation have also found that a large percentage of the variance in community composition remains unexplained by the environmental factors (e.g. Menges 1986; Jean & Bouchard 1993; Bufková & Prach 2006; Goebel et al. 2006). Monte Carlo permutation tests indicated that the first canonical axis was statistically significant ($F = 1.85$, $p = 0.028$). The intra-set correlations (Table 2) showed that Axis 1 of the CCA conducted on the floristic community (species > 5 % frequency) was most strongly correlated with average watertable depth and moderately correlated with canopy cover, and therefore these two variables are most closely related to the dominant patterns in community composition.

The direction and length of the arrows in Fig. 2 indicate that the first axis of the CCA conducted on the entire floristic community was a watertable gradient, where the sites with a deep watertable also tended to have the highest canopy cover (right-hand side of Fig. 2) while sites with a shallow to intermediate watertable depth tended to have lower canopy cover (left-hand side of Fig. 2). Figure 2 shows that leaf litter and groundwater DO were moderately important environmental variables, whilst bare ground, groundwater pH and EC were of lesser importance. The weighted averages of species with respect to groundwater DO and average watertable depth resulted in similar rankings (arrows in the same direction in Fig. 2), but this similarity cannot be explained by the correlation between these two variables in the dataset (Appendix 1). However, there was a significant correlation between groundwater DO and canopy cover. Similar rankings of species with respect to canopy cover and leaf litter can be explained by a significant positive correlation between these two variables (Appendix 1). The second CCA axis was positively correlated with canopy cover and bare ground, but negatively correlated with average watertable depth (Table 2; Fig. 2). Thus, there appeared to be an (albeit weak) interactive effect of canopy cover and average watertable depth on vegetation pattern.

The ordination of species showed that the perennial vine, *Stephania japonica*, was most abundant on the site with the highest canopy cover and deepest watertable (Fig. 2). Other species associated with higher than average watertable depths and canopy cover included *Bromus driandrus*, *Carduus pycnocephalus*, *Conyza bonariensis*, *Einadia* sp., *Hordeum leporium*, *Silybum marianum*, *Sisymbrium officinale*, *Sisymbrium orientale*, *Solanum nigrum*, *Stellaria media* and *Urtica incisa*. Species that lie in the centre-right of the ordination (Fig. 2) were most abundant on sites with intermediate to deep watertables and either higher than

average canopy cover (*Austrostipa verticillata*, *Bidens subalternans*, *Bromus cartharticus*, *C. cunninghamiana*, *Chenopodium album*, *Ehrharta erecta*, *Lolium perenne/rigidum*, *Microlaena stipoides*, *Modiola caroliniana*, *Paspalidium distans*, *Petrorhagia velutina*, *Sonchus oleraceus* and *Taraxacum officinale*) or lower than average canopy cover (*Commelina cyanea*, *Gnapalium polycaulon*, *Hirschfeldia incana*, *Polygonum arenastrum*, *Rumex brownii* and *Sida rhombifolia*).

Table 2. Eigenvalues, species-environment correlation coefficients, cumulative variance and correlation coefficients of environmental variables with the first and second axes of the canonical correspondence analysis (CCA) conducted on the floristic and environmental data collected at Widden Brook.

	CCA	
	Axis 1	Axis 2
Eigenvalue	0.37	0.22
Species-environment correlation	0.96	0.93
Cumulative % variance		
Of species data	20.9	33.5
Of species-environment relation	35.2	56.4
Intra-set correlations		
Average watertable	0.86	-0.30
Canopy cover	0.62	0.35
Leaf litter	0.54	0.14
Bare ground	-0.23	0.28
Groundwater pH	0.41	0.04
Groundwater EC	0.02	-0.25
Groundwater DO	0.54	-0.17

Fig. 2. CCA ordination of species, samples (i.e. numbered sites) and environmental variables. Bare = percentage bare ground; DO = groundwater dissolved oxygen; EC = groundwater electrical conductivity; Litter = percentage cover of leaf litter; Ave WT = average watertable depth; Canopy Cover = projective foliage cover; pH = groundwater pH. See text for full specific names.

Species that lie in the centre-left of the ordination (Fig. 2) were most abundant on sites with shallow to intermediate watertable depths and either lower than average canopy cover (*Acetosella vulgaris*, *Bidens pilosa*, *Cineraria lyrata*, *Conyza canadensis*, *Cynodon dactylon*, *Hypochaeris radicata*, *Lactuca serriola*, *Oxalis* spp., *Paspalum dilatatum*, *Pennisetum clandestinum*, *Persicaria lapathifolia* and *Tagetes minuta*) or higher than average canopy cover (*Citrullus lanatus*, *Silene gallica*, *Trifolium repens* and *Verbena* spp.). Species with rhizomes or stolons (*A. vulgaris*, *C. dactylon*, *J. articulatus*, *P. distichum*, *P. clandestinum*, *P. australis* and *T. repens*) all lie in the left-hand side of the ordination suggesting that clonal species were most abundant on sites with lower than average watertable depths and canopy cover (Fig. 2).

Species that lie towards the top left-hand corner of the ordination (Fig. 2) were abundant on sites with a shallow watertable and lower than average canopy cover. *Aster subulatus*, *Cyperus fulvus*, *Juncus articulatus*, *Lythrum hyssopifolia*, *Persicaria decipens*, *Phragmites australis* and *Pseudognaphalium luteoalbum* were associated with the shallowest watertables, followed by *Anagallis arvensis*, *Cyclospermum leptophyllum*, *Digitaria ciliaris*, *Oenothera indecora*, *Oenothera stricta*, *Paspalum distichum*, *Plantago lanceolata*, *Polycarpon tetraphyllum*, *Rumex crispus*, *Salix babylonica*, *Setaria gracilis* and *Xanthium italicum* (Fig. 2). All of the *S. babylonica* individuals encountered were juvenile (< 2 m). The annual forb, *Persicaria hydropiper*, was most abundant on sites with a shallow watertable, moderate canopy cover and high bare ground (Fig. 2). This is consistent with *P. hydropiper* being associated with benches within the channel, as they have a sandy substrate, minimal groundcover and an overstorey of young *C. cunninghamiana* trees. Species that lie at the bottom left-hand side of the ordination (*Chondrilla juncea*, *Paronchychia brasiliensis*, *Portulaca oleracea*, *Urochloa panicoides* and *Urochloa piligera*) were most abundant on sites with little or no canopy cover, intermediate watertables and slightly higher groundwater EC.

All of these interpretations are based on the assumption that species have a unimodal distribution in relation to the environmental gradients (ter Braak 1986). However, a small number of species (*B. pilosa*, *C. pycnocephalus*, *C. cunninghamiana*, *C. lyrata*, *C. lanatus*, *P. dilatatum*, *P. distans*, *R. crispus* and *T. repens*) had bimodal distributions that result in their ordination close to the centre of Fig. 2. For example, the average cover of *C. cunninghamiana* was 24% ($\pm 12.9\%$) on the toe of the bank, 6% ($\pm 5.6\%$) on the top of the bank and 43% ($\pm 15.7\%$) on the floodplain.

Discussion

Average watertable depth and canopy cover are the most important environmental variables explaining vegetation pattern in the riparian corridor of Widden Brook. Whether the distribution of species is primarily determined by flood variables (i.e. elevation above the channel, flood return period and flow duration), or by watertable depth, cannot be established from a study conducted at one point in time because the flood variables and watertable depth are highly correlated. A number of authors (Hupp & Osterkamp 1985, 1996; Lite et al. 2005) have suggested that riverine vegetation is more strongly associated with elevation and fluvial landforms than with groundwater depth in humid regions, whereas water availability is more important than flood disturbance in semi-arid regions. Further, in drier climates vegetation persistence may depend on access to groundwater (Hupp & Osterkamp 1996). Although the climate of the study area is warm temperate, annual rainfall in the region has alternated between multi-decadal dry (1898-1947) and wet periods (1883-1897; 1948-2000) (Erskine et al. 2009) and Widden Brook ceases to flow during dry periods. Mean annual rainfall at the nearest long-term rainfall station to Widden Brook has varied significantly by over 100 mm (26 %) between dry and wet periods (Erskine et al. 2009). Erskine and Warner (1988, 1999) noted that there were statistically significant increases in flood frequency during wet periods in comparison to the dry period in this area. They called these alternating wet and dry periods, flood- and drought-dominated regimes respectively. Therefore, we would expect that the strength of associations between flood variables and groundwater depth and riparian vegetation pattern may depend on whether the study is conducted during a wet or a dry period. The timing of the current study was such that sampling occurred after a moderate-sized flood at the end of an extended dry period.

Groundwater

There was considerable variation in mean watertable depth among landforms due to local topography, suggesting that stratification of vegetation sampling by fluvial landform would be improved by also considering relative elevation above the bed. During the drier period of the study (2006), watertable depths on the floodplain could exceed 2.8 m, but on the toe of the bank they were never greater than 1.5 m. As the capillary fringe of the sandy soils would be in the order of 0.2 m, plants on the bank toe would need rooting depths > 0.6 m to access the capillary fringe 50% of the time and rooting depths > 1.3 m to access it during the drier

period. Plants on the floodplain would need rooting depths in excess of 1.8 m to access the capillary fringe 50% of the time and roots > 2.6 m during the drier period. Although the rooting depths of individual species in this study are unknown, Schenk & Jackson (2002) found that average rooting depths were 0.5 m for annuals, 1.0 m for perennial forbs/grasses and 3.3 m for trees in water-limited (< 1000 mm mean annual rainfall) ecosystems. Thus, many short-lived species in our study would only be able to access the capillary fringe on the bank toe sites with a particularly shallow watertable and only during wetter periods. This suggests that most short-lived species within the riparian corridor rely on surface moisture supplied by rainfall events or overbank flows, although those germinating on the bank toe would benefit from temporarily high watertables that occur after floods. Many perennial forbs and grasses in our study would be able to access the capillary fringe on the bank toe much of the time, but access to the watertable below the top of the bank and floodplain would depend on the rooting depth of the particular species, climatic conditions and local microrelief.

Mature individuals of *C. cunninghamiana*, the dominant woody species in this study, would probably be able to access the capillary fringe above the watertable on the bank toe, top of the bank and the floodplain most of the time. However, the depth of the watertable on the floodplain was spatially variable and exceeded the depth of some of the piezometers during the drier period. It is unknown whether the watertable is lowered below the rooting depth of *C. cunninghamiana* in some locations on the floodplain during extended dry periods. However, the large, senescing *C. cunninghamiana* individuals on the floodplain have clearly been able to access sufficient water during the droughts encountered over the last 50-60 years because vertical air photographs (see Erskine et al. 2009) indicate that they are more than 54 years old.

Australian studies (Morris & Collopy 1999; O'Grady et al. 2006) suggest that *C. cunninghamiana* uses groundwater opportunistically. Along the Daly River in the Northern Territory of Australia *C. cunninghamiana* uses groundwater, but as elevation within the riparian zone increases so does their use of soil water (O'Grady et al. 2006). The research of O'Grady and colleagues in tropical Australia indicates that the dominant tree species in riparian communities show some degree of dependency on groundwater supplies (Eamus & Froend 2006). Cottonwood (*Populus trichocarpa*), a dominant riparian species of the semi-arid south-western United States is an obligate phreatophyte because it uses groundwater exclusively in the fall (Mitsch & Gosselink 2000). Only the use of stable isotopes of water and water-potential techniques can confirm whether the river oaks of eastern Australia are obligate or facultative phreatophytes.

Consistent with our hypothesis, groundwater chemistry was only weakly correlated with vegetation pattern. In the Murray - Darling basin of south-east Australia, groundwater salinity affects the health of the dominant riparian trees (Overton et al. 2006). Some floodplains within the Murray-Darling basin act as a groundwater sink for the naturally saline regional aquifers of the western Murray Basin and although the groundwater is fresh in some parts of the floodplain (e.g. close to the river) in other areas electrical conductivity ranges from 35 – 85 dS m⁻¹ (Overton et al. 2006). Electrical conductivity levels recorded in the current study showed that the groundwater beneath the floodplain forest was fresh, explaining why no relationship with vegetation composition was found. The riparian vegetation of the semi-arid Murray – Darling basin often experiences groundwater salinities an order of magnitude greater than the vegetation at Widden Brook.

Flood disturbance

Extended periods of inundation are not characteristic of the flood regime on Widden Brook. Thus, with the exception of vegetation growing within the bed, floods exert much of their effect on the vegetation through physical disturbance (i.e. high energy flowing water and sediment deposition) and replenishment of the watertable. Typical of many rheophytes, *C. cunninghamiana* has fine stream-lined foliage and saplings with semi-rigid stems that are flexible under floodwaters. Flood return periods indicate that replenishment of the water-table via bank recharge would be quite common at the study site, whilst replenishment by vertical recharge on the floodplain would be relatively infrequent. Nevertheless, O’Grady et al. (2006) note that many riparian species along the Daly River in the Northern Territory, including *C. cunninghamiana*, depend on stored soil water at some time during the year and that flood events are important in recharging soil water stores. Seed fall in *C. cunninghamiana* occurs over a period of at least six months, with peaks in autumn or spring (Woolfrey & Ladd 2001). Recently germinated seedlings were observed on bars within the channel of Widden Brook during winter (July 2006), while Woolfrey & Ladd (2001) found that the density of *C. cunninghamiana* seedlings on the banks and in the channel of the Murrumbidgee River (ACT, Australia) reached a peak in September and then declined during the hotter, drier weather in October. Similar to other riparian trees, the seed rain of *C. cunninghamiana* is timed to take advantage of suitable seed bed conditions provided by floods (i.e. winter & summer).

In the current study, clonal perennial species (i.e. those with rhizomes or stolons) were most abundant on sites with lower than average watertable depths and canopy cover. The

clonal grasses (*P. australis*, *P. distichum*, *C. dactylon* and *P. clandestinum*) had their greatest abundance on the toe of the bank, consistent with rhizomes and stolons being able to resist the erosive forces of flowing water. Other morphological adaptations that allow perennial graminoids to tolerate frequent flooding include the location of their meristems close to the ground (Menges & Waller 1983). This morphology “confers mechanical tolerance and enables efficient regrowth” (Menges & Waller 1983, p. 465) after flood. Further, the flexible stems of grasses, sedges and rushes allow them to be completely flattened during flood providing little resistance to flow. The traits of clonal perennial grasses, allows them to not only survive moving water, but expand rapidly over the bare ground provided by flood scour or the deposition of sediment. Field experimentation in a floodplain meadow in northern Sweden has demonstrated that silt accumulation (up to 12 cm deep) favours clonal species with a strong ability for lateral spread (Xiong et al. 2001a).

Consistent with the ruderal annuals described by Menges & Waller (1983), fluvial processes provide short-lived species such as *A. subulatus*, *C. leptophyllum*, *D. ciliaris*, *L. hyssopifolia*, *P. luteoalbum*, *O. stricta* and *X. italicum* with disturbed, high light environments on the bank toe or top of the bank. We estimate that the toe of the bank at Widden Brook is, on average, flooded every year and inundated for 10.3 days per year, while the top of the bank is inundated for 4.5 days per year. Ruderal annuals of riparian zones grow at elevations that are inundated more frequently, but succeed by completing their life-cycle in the periods between floods (Menges & Waller 1983). Our study also identified a group of short-lived species (*C. bonariensis*, *H. leporium*, *S. nigrum*, *S. marianum*, *S. media*, *S. officinale* and *S. orientale*) that had their greatest abundance on the floodplain, and were analogous with Menges & Waller’s (1983) competitive ruderals. Annuals recolonise floodplains each year either from a persistent seedbank, annual reseeding of existing populations or re-introduction through dispersal (Menges & Waller 1983). The floodplain at Widden Brook is disturbed by flood relatively infrequently and therefore other mechanisms that provide sufficient bare ground and light (such as livestock grazing, death of cool-season annuals in summer or the patchy canopy of the *C. cunninghamiana* forest) may be responsible for the persistence of competitive ruderals on the floodplain.

Canopy cover & leaf litter

This study, and that of Menges (1986), found that the distribution of understorey species is associated with the cover of the forest overstorey (or light). Whilst the recruitment of

riparian and floodplain trees often depend on hydrogeomorphic processes (Johnson 1994; Friedman et al. 1996; Hupp & Osterkamp 1996; Scott et al. 1996; Erskine et al. 2009), the trees themselves affect habitat through above and belowground competition and the supply of leaf litter. In the mesic floodplain forest studies by Menges & Waller (1983) light was negatively correlated with elevation, but in our study canopy cover (and therefore light) showed a bimodal distribution with distance from the channel (i.e. moderate canopy cover on the toe of the bank, lowest cover on the top of the bank and highest cover on the floodplain). This was because canopy cover was provided by a single tree species, *C. cunninghamiana*, the abundance of which is a function of both fluvial geomorphic processes and historical clearing/grazing of the bank and floodplain.

At Widden Brook *C. cunninghamiana* germinates on the moist bare substrate provided by bars within the channel, but only establish where the bars build to higher elevations through the deposition of sediment to form benches (Erskine et al. 2009). As the benches build up, seedling mortality from the direct impacts of flow (i.e. flood scour and inundation) declines, but this may be partially offset by greater rates of mortality as watertables fall during dry periods (Erskine et al. 2009). Recruitment on benches is episodic and these benches (and the vegetation growing upon them) are periodically destroyed by catastrophic floods or a sequence of large floods in rapid succession (Erskine et al. 2009). Similarly, the successful establishment of *Populus* spp. and *Salix* spp. require bare, moist substrates (Scott et al. 1996). The provision of conditions that suit the establishment of these pioneer riparian trees will vary spatially and temporally depending on the dominant fluvial processes (Scott et al. 1996). Thus in Eastern Riverine Forest, canopy cover and its relationship with the riparian understorey is linked to the formation and removal of particular fluvial landforms within the channel (e.g. bars, benches and islands), which is both spatially and temporally patchy.

The cover of leaf litter in our study did not increase with elevation above the channel. As leaf litter was mainly supplied by *C. cunninghamiana*, its distribution was linked to the greater abundance of this species on the benches and the floodplain. Friedman et al. (1996) found that besides elevation, litter cover had a strong relationship with the composition of riparian vegetation in eastern Colorado, while vegetative cover, shade and sediment particle size had a weaker relationship. Similar to our study, Friedman et al. (1996) found that species had similar rankings with respect to litter cover and canopy cover as a result of a positive correlation between these two variables. The correlation between canopy cover and leaf litter means that the direct effect of leaf litter on riparian plant distribution is difficult to establish without experimentation. In a field experiment along the Vindel River in northern Sweden,

Xiong et al. (2001b) found that river-borne leaf litter may affect riparian vegetation by acting as a physical barrier, as well as by reducing light and soil temperature.

Conclusion

Contrary to our hypothesis, vegetation composition was associated with groundwater availability and flood-related variables to a similar degree. The relative strength of the correlation between riparian vegetation pattern and these two factors could not be separated because elevation above the bed, flood return period, flow duration and watertable depth are all highly correlated. For the same reason we could not determine whether flood frequency was more strongly correlated with vegetation composition than flow duration. However, we were able to identify suites of species associated with particular fluvial landforms and their corresponding flood and watertable conditions. We suggest that the strength of the relationship between flood and watertable variables and vegetation pattern would vary with the climatic cycle (i.e. flood- and drought-dominated periods) on a scale of several decades.

The correlation between vegetation pattern and canopy cover was stronger than predicted, whilst the weaker associations with percentage of bare ground and groundwater chemistry were consistent with our hypotheses. Canopy cover was provided by the dominant woody species, *C. cunninghamiana*, the cover of which is a function of geomorphic processes, clearing and grazing. The presence and absence of benches within our study reach, as well as differences in the relative height of the floodplain, illustrated how the spatial variability of fluvial landforms within sand-bed streams (on a scale of kilometres) can affect riparian vegetation pattern. As Mitsch & Gosselink (2000) note, plant zonation is not necessarily monotonic because floodplain level rarely rises uniformly from the river and microrelief can be complex, as in the case of natural levees next to streams.

The reach examined has characteristics similar to both the semi-arid and mesic riparian ecosystems of the United States. The coarse sediments, high flood variability, large geomorphic response and dominance of a pioneer tree that depends on groundwater is similar to riparian communities dominated by cottonwoods in the semi-arid regions of the western United States. However, the relatively humid environment has allowed vegetation on the broad floodplain to develop to the extent that the distribution of understorey plants is associated with canopy cover, which is similar to the mesic bottomland forests of the eastern United States.

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Appendix 1. Pearson correlation coefficients amongst the environmental variables examined at Widden Brook ($n = 15$). WT, watertable; GW, groundwater; * $P < 0.05$; ** $P < 0.01$.

	Relative elevation	Minimum WT depth	Maximum WT depth	WT amplitude	Average WT depth	Canopy cover	Leaf litter	Bare ground	GW pH	GW EC	GW DO	Flow Duration
Return Period	0.92**	0.92**	0.92**	-0.01	0.93**	0.36	0.45	-0.46	0.30	0.33	0.26	-0.90**
Flow Duration	-0.94**	-0.93**	-0.91**	0.06	-0.93**	-0.40	-0.43	0.54*	-0.25	-0.31	-0.41	
Groundwater DO	0.33	0.43	0.33	-0.40	0.32	0.69**	0.46	0.06	0.31	-0.08		
Groundwater EC	0.33	0.26	0.35	0.41	0.32	0.06	0.04	-0.68**	0.14			
Groundwater pH	0.37	0.45	0.34	-0.47	0.38	0.22	0.29	-0.06				
Bare ground	-0.58*	-0.51	-0.57*	-0.24	-0.56*	0.04	0.05					
Leaf litter	0.27	0.33	0.27	-0.26	0.28	0.76**						
Canopy cover	0.28	0.37	0.33	-0.17	0.29							
Average WT depth	0.99**	0.98**	0.99**	0.06								
WT amplitude	-0.24	-0.11	0.13									
Max. WT depth	0.98**	0.97**										
Min. WT depth	0.97**											