**Hydrology as a determinant of wood density in Australian riparian species**

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**Introduction**

Functional trait oriented approaches to understanding community assembly (McGill, Enquist, Weiher, & Westoby, 2006) have been *de mode* over the last decade, especially in plant ecology (Kattge et al., 2011). These approaches attempt to understand community assembly processes by linking morphological or physiological attributes of species to organismal success under given environmental conditions. Suites of traits can be conceptualized as axes of variation in terms of ‘ecological strategy’, and distribution of this variation across environmental gradients can provide insight into where these strategies are successful (Westoby, Falster, Moles, Vesk, & Wright, 2002).

Hydrology is widely considered to be the dominant abiotic force structuring riparian ecosystems. Hydrological variability in turn drives variation in moisture and substrate availability and flood disturbance, with cyclical resets to early successional conditions being characteristic of the riparian environment (Merritt, Scott, Poff, Auble, & Lytle, 2010). These are the conditions which are likely to dictate success of a particular ecological strategy. Several authors have recently suggested functional trait biology as a means of understanding the response of riparian plant communities to hydrological gradients (Catford et al., 2012; Merritt et al., 2010).

Woody plants determine the coarse physical structure of many riparian plant communities and are integral to the interplay of biological and physical elements that drive fluvial biogeomorphic processes (Corenblit, Steiger, Gurnell, Tabacchi, & Roques, 2009). Consequently, an understanding of the mechanisms of riparian woody plant community assembly will provide important insights into fluvial landscapes. Wood density (the ratio of kiln-dried mass to green volume of a wood sample (Cornelissen et al., 2003) is widely recognised as an important functional trait in plant ecology (Westoby & Wright, 2006), and has been proposed as one of just several key axes of variation within which all major plant ecological strategies can be described (Westoby et al., 2002). Wood density is in fact an emergent property of a combination of woody tissue traits, including vessel geometry and arrangement, and the density and proportion of surrounding lignified tissue (Chave et al., 2009). Combined variation in these traits corresponds to the wide range of ecological strategies among woody plants.

How might variation in wood density confer advantages to woody plant species in riparian environments? There is little direct evidence from riparian species, however general relationships between wood density and other ecological traits have been recognised from a variety of previous studies that can provide some insight into the importance of variation in wood density in riparian communities. Dense wood confers mechanical stiffness (D. S. Falster, 2006; Niklas & Spatz, 2010), as well as resistance to pathogens (Augspurger & Kelly, 1984) and herbivory (Coley, 1983), but requires more investment of biomass and is therefore more costly to construct per unit of stem height. According to this trade-off, it follows that several relationships between wood density and life-history strategy are apparent: studies of tropical rainforest species have shown an inverse relationship between growth rate and wood density (King, Davies, Tan, & Noor, 2006; Kraft, Metz, Condit, & Chave, 2010; L Poorter et al., 2008; Lourens Poorter et al., 2010; Wright et al., 2010), however no such relationship was found in a study of New Zealand tree species (Russo et al., 2010)Cohort survival was positively correlated with wood density in the same tropical rainforest studies (King et al., 2006; Kraft et al., 2010; L Poorter et al., 2008; Lourens Poorter et al., 2010; Wright et al., 2010). Following disturbance caused by a large cyclone in northern Queensland, Australia, wood density of rainforest trees was indicative of both damage sustained and subsequent recovery of biomass. Trees with dense wood were more likely to have experienced only minor damage, while of those trees that experienced major stem and branch damage, lower wood density trees were more likely to resprout and recover biomass faster post-disturbance (Curran, Gersbach, Edwards, & Krockenberger, 2008). In a study of 45 rainforest species in tropical Queensland, Falster and Westoby (2005) found that wood density increased with plant height along a successional gradient. Thus it seems likely that these observed relationships between wood density and recovery from disturbance at the individual level, as well as post-disturbance succession at the community level, may be true also for riparian systems.

In step with growing understanding of the role of woody plant tissue density in the biotic and physical structure of landscapes, the recent decade has seen an increase in understanding of the phylogenetic and environmental patterning of wood density variation. Phylogenetic analyses across two large wood density datasets (Swenson & Enquist, 2007; Zanne et al., 2010) have shown wood density to be highly conserved, with a large proportion of variation explained at the genus level. Strong phylogenetic signals in wood density variation have also been found in studies of coastal Californian angiosperms (Preston, Cornwell, & Denoyer, 2006) and Florida oaks (Cavender-Bares, Kitajima, & Bazzaz, 2004).

Wood density has been implicated in resilience to water stress. The proposed mechanism is stabilisation of xylem vessels by woody fibres against cavitation under conditions of negative vapour pressure. This hypothesis is controversial (Martinez-Cabrera et al).

Some studies (Weimann & Williamson, 2002; Swenson & Enquist, 2007), found little relationship between wood density and rainfall while others (Martínez-Cabrera, Jones, Espino, & Schenk, 2009; Preston et al., 2006), found that wood density was correlated with mean annual precipitation across a transcontinental gradient, and with soil moisture, respectively. High wood density, along with low SLA and low maximum height, has been associated with environmental stress tolerance and conservative use of resources **(Reich et al 2003, Westoby LHS 1998, Swenson & Enquist 2007).** For riparian plants, fluctuations in soil moisture driven primarily by hydrological patterns may therefore be an important driver of variation in wood density.

More basic investigations of the functional ecology of wood density are needed, particularly outside of the tropical rainforest systems that dominate the current literature.

ENVIRONMENTAL FILTERING AND SPECIALISATION PARAGRAPH

Do I need information about trait gradient analysis here?

In the sense that woody tissue determines plant responses to these to flooding disturbance and fluctuations in water availability, wood density is likely to be the primary indicator of riparian woody plant ecological strategy. Here we consider variation in wood density of dominant woody riparian plant species over a range of hydrological conditions, across 15 riparian sites within south-eastern Australia. We sought to address the following questions: (1) do riparian vegetation communities along hydrologically distinct classes of river exhibit differences in wood density? (2) is wood density related to the frequency and magnitude of flood disturbance? (3) is wood density related to water availability in the riparian zone? Further, we develop method based on Trait Gradient Analysis to ask: (4) do strong hydrological conditions induce specialisation in ecological strategy, as indicated by wood density?

**Methods**

**Study site selection**

Fifteen riparian sites were selected along gauged rivers within the South-East Coast and south-eastern Murray Darling drainage basins of Australia (see *Figure 1*). To differentiate rivers according to ecologically relevant components of hydrology, Olden and Poff (2003) described a statistical methodology for determining a minimally redundant set of hydrological descriptors. Kennard et al. (2010) followed this methodology to define a set of 120 hydrological metrics relevant to Australian rivers, which included metrics of central tendency and dispersion in all five dimensions of hydrological variation (magnitude, frequency, duration, timing, and rate of change). They then used these metrics to classify Australian river systems into twelve distinct flow regime classes, providing a foundation for analysing the properties of ecosystems across hydrological gradients. Sites in this study were drawn from rivers corresponding to ‘stable winter baseflow’, ‘unpredictable baseflow’ and ‘unpredictable intermittent’ hydrological classes, as described by Kennard et al. (2010). These are the best represented hydrological classes in eastern NSW and VIC, and represent a clear gradient over ecologically relevant hydrological parameters. Five sites per hydrological class were selected based on the criteria outlined below.

Gauged locations were selected that had >15 years of associated continuous hydrological data, and an absence of flow regulation, significant water extraction or catchment urbanisation (following Kennard et al., 2010). Of these, locations from the hydrological classes of interest were located within the study area. To minimise signals associated with human land-use, the following further criteria were used to shortlist possible study sites: intact native riparian vegetation cover (a band of native riparian vegetation extending >15 m from the channel edge), natural geomorphic condition (lack of significant human-induced erosional or depositional landforms), and minimal catchment clearing (catchment predominantly covered by native vegetation). These criteria were assessed using a combination of visual inspection of satellite photography (Google Earth, Microsoft Bing), information from the NSW Riparian Vegetation Extent dataset and the NSW Office of Water River Styles® geospatial dataset (NSW Office of Water, Department of Primary Industries). Large rivers with catchment area >1000 km2 were then removed. To select the 15 study sites from this shortlist, accessibility by road, permission from state or private landholders, and proximity of accessible areas to continuous hydrological monitoring stations were considered.

**MAP**

**Species abundance and trait data collection**

Data collection was undertaken between December 2012 and May 2013. At each site, a 10 m by 50 m plot was marked out, with the longest side abutting the channel edge. Criteria for selection of plot locations were: geomorphic homogeneity (the plot comprising only sloping bank where possible) and lack of anthropogenic disturbance such as built structures, roads or tracks, recent logging or clearing (in the last 20-30 years), herbicide spraying or animal grazing.

Proportional cover of woody vegetation was assessed at three strata levels: shrub (1-4 m), subcanopy (4-8 m) and canopy (>8 m). Species were identified using appropriate field guides, and were verified against herbarium specimens at the Macquarie University Herbarium. Hard to identify specimens were identified by staff at the Royal Botanic Gardens, Sydney.

# Wood samples were collected from dominant woody species present within the plot at >5% cover in shrub, sub canopy or canopy strata, and which had trunks robust enough to core. A 5.15 mm diameter, triple threaded increment borer (Haglöf Sweden) was used to extract a 100 mm wood sample from each of two individuals per species. Samples were extracted from the base of the main trunk, 10 cm above the leaf litter level, and air-dried at 20-45°C. On return to the laboratory, samples were rehydrated in deionised water and dissected into cylindrical sections of bark, sapwood and heartwood, using visual inspection of vessel occlusion as an indicator of tissue type. Sections were measured (x, y and z dimensions) with calipers (Mitzuni) to calculate wet volume, were then oven-dried at 80°C for 48 hours and weighed using a microbalance (Mettler Toledo). Wood density was then calculated as the ratio of oven dry mass to wet volume (g/cm3).

**Hydrological data analysis**

Hydrological data pertaining to each field site were collated from the PINNNENA CW 10.1 database (NSW Office of Water, Department of Primary Industries) and the NSW Office of Water Continuous Water Monitoring network website (<http://realtimedata.water.nsw.gov.au/water.stm>) (for NSW sites), and the Victoria State Government’s Water Measurement Information System website (<http://data.water.vic.gov.au/monitoring.htm>). Daily discharge rate data arrives as timestamped average daily flow datapoints in units of megalitres per day. Where possible 30 year time series were obtained, spanning years 1983 – 2012. Records were truncated for three sites, spanning 15, 19 and 28 years. Missing data were approximated using the Time Series Manager module in River Analysis Package (REF). Consistency of the resulting outputs were checked by visual inspection of hydrographs. For Mammy Johnson’s River, Mann River, Sportsman’s Creek and Wallagaraugh River, multiple linear regression was chosen as the most appropriate method. Linear interpolation was used for Jilliby Creek data.

To reduce Type 1 error, a minimal set of hydrological metrics was pared from the full set described by Kennard et al. (2010). These metrics describe variability in high flow magnitude and frequency as well as water availability in the riparian environment (see Table X). We used the Time Series Analysis module in River Analysis Package to generate these metrics. Low and high spell metrics were thresholded by the 5th and 95th percentiles, respectively. 20 year average return interval (ARI) flood magnitude was calculated with a flood independence value of 7 days between peak events. Colwell’s Indices were calculated using mean values over monthly time periods and a class distribution of 11 flow classes. Finally, metrics of flow magnitude were normalised by mean daily flow to allow for comparison between different sizes of river.

**References**

Augspurger, C. K., & Kelly, C. K. (1984). Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*, *61*(2), 211–217. doi:10.1007/BF00396763

Catford, J. a., Naiman, R. J., Chambers, L. E., Roberts, J., Douglas, M., & Davies, P. (2012). Predicting Novel Riparian Ecosystems in a Changing Climate. *Ecosystems*, *June*, 1–19. doi:10.1007/s10021-012-9566-7

Cavender-Bares, J., Kitajima, K., & Bazzaz, F. (2004). Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs*, *74*(4), 635–662. Retrieved from http://www.esajournals.org/doi/abs/10.1890/03-4007

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Amy, E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. doi:10.1111/j.1461-0248.2009.01285.x

Coley, P. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological monographs*, *53*(2). Retrieved from http://www.esajournals.org/doi/abs/10.2307/1942495

Corenblit, D., Steiger, J., Gurnell, A. M., Tabacchi, E., & Roques, L. (2009). Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. *Earth Surface Processes and Landforms*, *1810*, 1790–1810. doi:10.1002/esp

Cornelissen, J. H. C. A., Lavorel, S. B., Garnier, E. B., Díaz, S. C., Buchmann, N. D., Gurvich, D. E. C., … Poorter, H. I. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335–380.

Curran, T. J., Gersbach, L. N., Edwards, W., & Krockenberger, A. K. (2008). Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of North Queensland, Australia. *Austral Ecology*, *33*(4), 442–450. doi:10.1111/j.1442-9993.2008.01899.x

Falster, D. S. (2006). Sapling strength and safety: the importance of wood density in tropical forests. *The New phytologist*, *171*(2), 237–9. doi:10.1111/j.1469-8137.2006.01809.x

Falster, D., & Westoby, M. (2005). Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology*, *93*, 521–535. doi:10.1111/j.1365-2745.2005.00992.x

Gurnell, a. M., Pie, H., & Northwest, P. (2002). Large wood and fluvial processes. *Freshwater Biology*, *47*(4), 601–619.

Järvelä, J. (2002). Flow resistance of flexible and stiff vegetation: a flume study with natural plants. *Journal of Hydrology*, *269*, 44–54. Retrieved from http://www.sciencedirect.com/science/article/pii/S0022169402001932

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., … Wright, I. J. (2011). TRY - a global database of plant traits. *Global Change Biology*, *17*(9), 2905–2935. doi:10.1111/j.1365-2486.2011.02451.x

Kennard, M. J., Pusey, B. J., Olden, J. D., Mackay, S. J., Stein, J. L., & Marsh, N. (2010). Classification of natural flow regimes in Australia to support environmental flow management. *Freshwater Biology*, *55*(1), 171–193. doi:10.1111/j.1365-2427.2009.02307.x

King, D. a., Davies, S. J., Tan, S., & Noor, N. S. M. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, *94*(3), 670–680. doi:10.1111/j.1365-2745.2006.01112.x

Kraft, N. J. B., Metz, M. R., Condit, R. S., & Chave, J. (2010). The relationship between wood density and mortality in a global tropical forest data set. *The New phytologist*, *188*(4), 1124–36. doi:10.1111/j.1469-8137.2010.03444.x

Martínez-Cabrera, H. I., Jones, C. S., Espino, S., & Schenk, H. J. (2009). Wood anatomy and wood density in shrubs: Responses to varying aridity along transcontinental transects. *American journal of botany*, *96*(8), 1388–98. doi:10.3732/ajb.0800237

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–85. doi:10.1016/j.tree.2006.02.002

Merritt, D. M., Scott, M. L., Poff, N. L., Auble, G. T., & Lytle, D. a. (2010). Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. *Freshwater Biology*, *55*(1), 206–225. doi:10.1111/j.1365-2427.2009.02206.x

Mori, S., Itoh, a., Nanami, S., Tan, S., Chong, L., & Yamakura, T. (2013). Effect of wood density and water permeability on wood decomposition rates of 32 Bornean rainforest trees. *Journal of Plant Ecology*, 1–8. doi:10.1093/jpe/rtt041

Niklas, K. J., & Spatz, H.-C. (2010). Worldwide correlations of mechanical properties and green wood density. *American Journal of Botany*, *97*(10), 1587–94. doi:10.3732/ajb.1000150

Olden, J. D., & Poff, N. L. (2003). Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, *19*(2), 101–121. doi:10.1002/rra.700

Poorter, L, Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., … Wright, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, *89*(7), 1908–20. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/18705377

Poorter, Lourens, McDonald, I., Alarcón, A., Fichtler, E., Licona, J.-C., Peña-Claros, M., … Sass-Klaassen, U. (2010). The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *The New phytologist*, *185*(2), 481–92. doi:10.1111/j.1469-8137.2009.03092.x

Preston, K. a, Cornwell, W. K., & Denoyer, J. L. (2006). Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *The New phytologist*, *170*(4), 807–18. doi:10.1111/j.1469-8137.2006.01712.x

Russo, S. E., Jenkins, K. L., Wiser, S. K., Uriarte, M., Duncan, R. P., & Coomes, D. a. (2010). Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand. *Functional Ecology*, *24*(2), 253–262. doi:10.1111/j.1365-2435.2009.01670.x

Swenson, N., & Enquist, B. (2007). Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, *94*(3), 451–459. Retrieved from http://www.amjbot.org/content/94/3/451.short

Weimann, M., & Williamson, G. (2002). Geographic variation in wood specific gravity: effects of latitude, temperature and precipitation. *Wood and Fiber Science*, *34*(1), 96–107.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. a., & Wright, I. J. (2002). PLANT ECOLOGICAL STRATEGIES: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics*, *33*(1), 125–159. doi:10.1146/annurev.ecolsys.33.010802.150452

Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution*, *21*(5), 261–8. doi:10.1016/j.tree.2006.02.004

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., … Zanne, A. E. (2010). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, *91*(12), 3664–74. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/21302837

Zanne, A. E., Westoby, M., Falster, D. S., Ackerly, D. D., Loarie, S. R., Arnold, S. E. J., & Coomes, D. a. (2010). Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany*, *97*(2), 207–15. doi:10.3732/ajb.0900178