Aquatic Botany 136 (2017) 9–20

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Recovery of benthic primary producers from flood disturbance and its implications for an altered flow regime in a tropical savannah river (Australia)

Simon Townsend (Dr)[a,b,*], Julia Schult[b], Michael Douglas[a,c], Agnes Lautenschlager[d]

[a] Research Institute of Environment and Livelihoods, Charles Darwin University, Casuarina, NT, 0909, Australia
[b] Aquatic Health Unit, Department of Land Resource Management, P. O. Box 496, Palmerston, NT, 0831, Australia
[c] School of Earth and Environment, University of Western Australia, M087, Perth, Western Australia, 6009, Australia
[d] School of Life and Environmental Sciences, Deakin University, Warrnambool, Victoria, 3280, Australia

ARTICLE INFO

Article history:
Received 28 October 2015
Received in revised form 4 August 2016
Accepted 14 August 2016
Available online 17 August 2016

Keywords:
Spirogyra
Charophyte
Vallisneria
Flood disturbance
Resistance
Resilience
Climate change
Tropical river

ABSTRACT

Flood disturbances in the Australian tropical savannah occur annually during the wet season and play a central role in shaping river ecosystems. We examined the recovery of benthic primary producer biomass from wet season (January to March) flood disturbances in the Daly River. Recovery occurs during the subsequent period of predominately groundwater-fed flow. A 3.3 km long reach comprising a pool-run-pool-run sequence was surveyed on four dates for four plant groups: periphytic microalgae, visible filamentous *Spirogyra* spp., macroalgal *Chara* and *Nitella* spp., and the vascular macrophyte *Vallisneria nana*. Benthic primary producers had low resistance to flood disturbance, with the exception of *V. nana* which most likely survived through resistant rhizomes and leaves. Recovery following flood disturbance is possible when riverbed PAR exceeds the compensation irradiance of the primary producers, which occurs during the wet to dry season transition (April, May) as depth declines and water clarity improves. The total biomass of primary producers increased from 0.5 g dry weight m^{-2} in June to 15 g dry weight m^{-2} in November, indicating significant recovery. The temporal sequence of primary producer domination, from microalgae to macroalgae to *V. nana*, reflected plant size and growth rates. Inter-annual variability of wet season floods and dry season base-flows are hypothesized to affect the resistance and recovery of the four plant groups. Imposed on this natural variability, water resource developments will reduce flows, although this may be offset to a limited extent by more frequent flood disturbances of high magnitude caused by climate change.

1. Introduction

Disturbances play a central role in determining the structure of riverine communities (Resh et al., 1988; Lake, 2000), and are a primary evolutionary force for the selection of plant life-cycle traits (Grime, 2001). Disturbances are events during which conceivably damaging forces remove organisms of a population in a habitat, depleting available resources or degrading habitat structure (Lake, 2000). Disturbances however also create new space and resources for aquatic biota (Lake et al., 2006).

Flood disturbances create shear forces in the river channel that suspend sediments and detritus, move substrata and woody debris, and scour and abrade the streambed and banks (Poff et al., 1997). Floods in upland rivers are destructive pulse disturbances (Lake et al., 2006). Aquatic plants, from unicellular microalgae to large vascular plants, are typically damaged or removed by high flow disturbances (Lake, 2000). The recovery of primary producers contributes substantially to ecosystem recovery. For example, macrophytes provide physical habitat, which creates structural heterogeneity to support species diversity (Franklin et al., 2008), while benthic algae can underpin riverine food webs (Thorp and Delong, 2002).

Resistance and resilience are fundamental responses to disturbance (Lake, 2000). Resistance is a measure of the capacity of a species or a population to survive or withstand a disturbance, whilst resilience is the ability to recover from disturbance and constitutes a process of secondary succession (Lake et al., 2006). Aquatic plants with high resistance capacity can possess strong attachment

* Corresponding author at: Aquatic Health Unit, Department of Land Resource Management, P.O. Box 496, Palmerston, N.T., 0831, Australia.
E-mail addresses: simon.townsend@nt.gov.au (S. Townsend), julia.schult@nt.gov.au (J. Schult), michael.douglas@uwa.edu.au (M. Douglas), agnes.lautenschlager@deakin.edu.au (A. Lautenschlager).

http://dx.doi.org/10.1016/j.aquabot.2016.08.004
0304-3770/

structures, flexible bodies, and can regenerate vegetatively from deep root systems, rhizomes and tubers (Barrat-Segretain et al., 1999; Tremolieres 2004). Miler et al. (2012) found that the stem of the macrophyte *Ranunculus penicillatus* ((Dum.) Bab. 1874) has a basal breaking point, which acts as a mechanical fuse so the above-ground plant can be shed during a flood, allowing the root system to remain in the ground for fast post-flood regrowth. Highly resilient species, on the other hand, can colonize a streambed quickly after a flood. Biological traits such as high mobility, small size, rapid growth rates and vegetative reproduction are commonly associated with highly resilient species that underpin ecosystem recovery (Barrat-Segretain et al., 1999; Lake, 2000; Tremolieres 2004).

Tropical savannah rivers (e.g. Warfe et al., 2011) and some subtropical rivers (e.g. Paraná River, South America; Martins et al., 2013) are characterized by an annual flood pulse which has a major role in determining floodplain, backwater and channel macrophyte composition and biomass (e.g. Junk et al., 1989; Finlayson, 2005; Sousa et al., 2011; Warfe et al., 2011; Neiff et al., 2014; Schneider et al., 2015). Benthic plants can be removed from the river's main channel by flood disturbance, and recover during the following low flow period. Examples of this strategy include *Hydrilla verticillata* (L.f.) Royle and *Egeria najas* Planch. in the Paraná River (Sousa et al., 2010; Martins et al., 2013) and *Spirogyra* spp. in an Australian tropical river (Townsend and Padovan, 2005). Aquatic biota are adapted to the extreme seasonality of savannah river flows, with anthropogenic alterations to the flow regime likely to have far reaching consequences to aquatic biodiversity and ecological processes (Bunn and Arthington, 2002; Sousa et al., 2011; Warfe et al., 2011).

In the Australian tropical savannah, the currently low anthropogenic demand for water means that most rivers have near-natural flow regimes (Warfe et al., 2011; King et al., 2015) and provide an opportunity to understand the role of natural flood disturbances in river ecosystem structure and processes. Irrigated agricultural and silvicultural developments, amongst other consumptive uses of water, however, are expected to increase and modify the natural flow regime.

The Australian Government is promoting the development of water resources in the tropical savannah (Commonwealth of Australia, 2015). Two broad impacts on flow regime are most probable in the short term (up to 10 years). These are: (1) the diversion of wet season flows from the main channel or floodplain to storages for dry season irrigation (flood harvesting), which will affect the magnitude and timing of flood disturbances, and (2) groundwater extraction which will reduce groundwater-fed flows during the dry season (King et al., 2015) when ecological recovery from wet season flood disturbance occurs. Climate-change may also affect flow regime. Predictions for northern Australia suggest rainfall may either be marginally greater or lower, with a likelihood of more intense extreme rainfall events and increased frequency of severe cyclones (Morrongiello et al., 2011) which would produce more frequent, high magnitude wet season floods.

The primary aim of this study was to assess the recovery of benthic primary producers from wet season flood disturbance in the Daly River in the Australian tropical savannah. We use the term flood to refer to any wet season, high flow disturbance which is usually constrained by the river banks, rather than its strictly hydrological meaning of a high flow that spills over a river bank to flood surrounding land (Gordon et al., 2006). The Daly River is recognized for its Indigenous cultural (Jackson et al., 2012), biodiversity (Blanch et al., 2005), recreational and other values.

The study was conducted upstream of the lowland floodplain, and addresses the recovery of benthic primary producers within the main river channel. It complements other studies that focused on flood disturbance of macrophytes in tropical and subtropical floodplain lakes and secondary river channels (e.g. Padial et al., 2009; Sousa et al., 2011; Schneider et al., 2015), and contributes to addressing the paucity of Australian riverine vegetation studies compared to wetland and lake studies (Mackay et al., 2010).

We examine the recovery of microalgae, macroalgae and vascular plants from a wet season flood disturbance, and the role of the physical environment in shaping recovery. Another aim is to discuss the potential implications of anthropogenic and climate change driven alterations to flood disturbances on the resistance and recovery of benthic primary producers. The study will inform the ecologically sustainable development of the region's water resources.

2. Methods

2.1. Site description and location

The Daly River has a catchment area of ~52,000 km^2 (Fig. 1), and is largely undeveloped with only 6% of the natural vegetation cleared for intensive land-uses, principally agriculture and intensive pastoralism (Schult and Townsend, 2012). The dominant land-use however is cattle grazing in savannah woodland, whilst conservation is second-ranked. The river's flow regime is near-natural, with negligible impacts from reservoirs, and groundwater and river extractions (Schult and Townsend, 2012).

Rainfall is highly seasonal, which is characteristic of a tropical savannah climate. At Katherine township in the upper Daly catchment (Fig. 1), 63% of the 135 year average annual rainfall of 973 mm occurs during the wet season months of January to March, resulting in high wet season flows (Fig. 2A). Although the wet season rains are predictable, wet season flows nevertheless vary by two to three orders of magnitude among years (Fig. 2A) depending on the number and intensity of monsoonal weather events, rain depressions and cyclones. Daly River floods are deep and turbid (Townsend and Padovan, 2005), and have high velocities (~1 m s^{-1}) that produce drag and bed shear stress capable of moving sand and gravel.

Rainfall between June and October is negligible (4% of the annual average at Katherine township). Flow during this period is maintained by groundwater supplied predominately from karst aquifers, and is more predictable than wet season flows, varying by approximately a single order of magnitude between years (Fig. 2A).

The wet and dry seasons and the two transition periods between the two seasons are defined in this work with respect to the river's hydrography and flow source (King et al., 2015), rather than the region's weather. Flow is dominated by surface runoff in the wet season and by groundwater in the dry season. The transition from the wet-to-dry season (typically April and May) is marked by a gradual shift to groundwater dominance, and occurs during the recession limb of the seasonal flow regime (King et al., 2015). The dry-to-wet season transition (typically November and December) is marked by episodic storm runoff events which dilute the groundwater content of the river with turbid water (Townsend et al., 2012a). The wet, wet-to-dry, dry and dry-to-wet seasons however are not discrete but are used to communicate the different phases of the river's flow regime.

The study was conducted in the middle reach of the Daly River (Fig. 1), at an elevation of 22 m, where the river channel is bound by a 10–20 m upper bank that confines most wet season flow and a lower bank that confines dry season flow. The site is upstream of the river's lowland floodplain. Riparian vegetation along the lower bank is dominated by paperbark trees (*Melaleuca argentea* W. Fitzg) which do not shade the river significantly. The study reach comprised a pool-run-pool-run sequence of 3.3 km length (Fig. 1). The pools were approximately 420 m long and 2 m deep, whereas runs were almost three-times as long and half the depth. The riverbed area of the runs totalled 130,000 m^2 and 50,000 m^2 for the pools.