



Influence of aquatic plant architecture on epiphyte biomass on a tropical river floodplain

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ABSTRACT

Tropical floodplains are highly productive because of seasonal replenishment of water and nutrients, which substantially boost primary productivity. This study examined how the architecture of aquatic macrophytes affect the light and water quality and consequently the attachment and biomass of epiphytes on a floodplain in northern Australia. Results show that macrophyte structural complexity is not only important for water column light penetration but also for the development of epiphytes on macrophytes. Emergent grasses with simple vertical structure and high plant densities, limit light penetration and consequently the development and biomass of epiphytic algae. In contrast, submerged macrophytes growing just below the water surface, allow greater light penetration. The complex architecture of submerged macrophytes also provides a large surface area for the development of a dense covering of epiphytic algae. Other plant structural forms (e.g., plants with floating leaves) have a simple structure, variable light penetration and low epiphytic algae biomass. The emergent grass *Pseudoraphis spinescens* (R.Br.) Vickery also had low light penetration but the horizontal alignment of stems across the water surface allow greater exposure to sunlight of the stems and the consequent development of epiphytic algae. We conclude that (1) the complex structure of submerged plants effectively creates a “false bottom” in deeper waters so that they function similarly to the floodplain’s littoral zone, and (2) that their extremely large surface area for attachment allows greater production of epiphytic algae than would occur on the sediment surface.

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Introduction

Tropical floodplains are highly productive because seasonal flooding results in the recurrent deposition of nutrient rich sediments (McClain and Richey, 1996; Junk and Wantzen, 2004). Flooding replenishes water on the floodplain, and substantially boosts primary (Junk and Piedade, 1997; Davies et al., 2008) as well as secondary production (Winemiller, 2004). Long inundation periods allow growth of aquatic macrophytes and algae (Junk and Piedade, 1997; Finlayson, 2005; Pettit et al., 2011), and also provide an opportunity for fish to move from the river channel or estuary onto the floodplain where they consume food sources needed for growth (Winemiller, 2004; Jardine et al., 2012). The most conspicuous contributors to tropical floodplain primary production are macrophytes (Piedade et al., 1991; Silva et al., 2009; Pettit et al., 2011). However in terms of secondary production, several investigations in tropical floodplain systems in South America

and Australia have found that algae and in particular periphyton (attached microalgae), despite forming an inconspicuous component of the total carbon biomass, provides the source material for the bulk of animal consumer biomass, with macrophytes and terrestrial carbon sources playing only a minor role (Hamilton et al., 1992; Lewis et al., 2001; Jardine et al., 2012). Therefore production of algae on the floodplain in the wet season is a very important component of the floodplain ecosystem (Jardine et al., 2012).

On the inundated floodplain, algal production can take place within the water column (phytoplankton) or as periphyton on substrates such as floodplain sediments (episammic) or hard surfaces (epilithic, epixylic) or attached to plants (epiphytic). Production of algae on the floodplain depends to a large extent on sufficient nutrients and light penetration (photic zone) to allow photosynthesis to take place. Macrophytes growing on the floodplain provide a convenient and useful substrate for attachment and growth of periphyton and these macrophytes have various structural forms including emergent, floating and submerged plants with varying morphologies. The structural complexity of these macrophytes types will influence periphyton attachment, with more complex shapes likely to allow greater light penetration through the water column for

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algae to utilise (Adams and McCracken, 1974) and provide greater surface area for attachment (Warfe and Burmuta, 2006; Hinojosa-Garro et al., 2010). As well as the structural complexity of forms, the alignment of these macrophytes in terms of the degree to which stems are in a vertical or horizontal plane, will also influence the level of exposure of stems to sunlight. Light attenuation has obvious implications for competition within aquatic plants as well as for the growth of epiphytic algae. The littoral zone at the edge of floodplain inundation is an area with high light penetration and available nutrients (Keizer et al., 2014) and therefore where the vast majority of benthic primary production is likely to take place (Strayer and Findlay, 2010). Aquatic plants growing near the water surface can, however, significantly increase the area available within the photic zone for the growth of attached epiphytic algae in deeper water. This access to light is likely to make macrophyte structure more important than biomass or surface area for the development of epiphytic algae (Jones et al., 2000). This study will investigate the relationship between the photic zone, macrophyte structure and alignment to the biomass of attached epiphytic algae within the flooded floodplain.

The relationship between aquatic macrophytes and epiphytic algae is generally considered in terms of importance as food and habitat. Plant stems and leaves provide a substrate for the attachment of epiphytes for grazing macroinvertebrates and small fish and protection from predation (Carpenter and Lodge, 1986). Epiphytes benefit macrophytes by diverting grazers and macrophytes benefit epiphytes by providing a substrate and nutrients (Hutchinson, 1975). High structural complexity of macrophytes are also likely to support the greatest abundance and diversity of macroinvertebrates, and by creating greater surface area and better access to light, the greatest epiphytic algae biomass (Warfe and Burmuta, 2006; Dibble and Thomaz, 2006). Our objective was to understand how the architecture and alignment of aquatic macrophytes affect the light and water environments and consequently the attachment and biomass of epiphytic algae on the Magela Creek floodplain in tropical northern Australia.

2. Methods

2.1. Study site

Magela Creek is a tributary of the East Alligator River, within Kakadu National Park, Northern Territory, Australia. Bounded by van Diemen Gulf and the Arafura Sea to the north and the sandstone plateau of western Arnhem Land to the south (Lat. 12.428050° S; Long. 132.869460° E). The creek flows down from the plateau, across the lowland coastal plains, and distributes water into an expansive clay-based floodplain of ~200 km² (Hart et al., 1987). The region is characterised by a monsoonal climate with distinct wet and dry seasons. The wet season hydro-period of flooded floodplain lasts around 3–5 months (usually November to March); however, this can vary greatly from year to year (Finlayson et al., 1990; Ward et al., 2014). Annual rainfall (~1300–1500 mm) is mostly from thunderstorms, tropical cyclones and monsoonal depressions (Gentilli, 1972; Finlayson, 2005). Following wet season rains, the Magela Creek floods and freshwater spreads over the floodplains, generating the rapid production of aquatic plants and animals. During the dry season the water gradually recedes into rivers, creeks and isolated waterholes, the grassland communities dieback and large patches are frequently burnt (Whitehead and McGuffog, 1997), as fire is used as a management tool to maintain health and diversity on the floodplains of Kakadu National Park (Bayliss et al., 2006).

Common aquatic habitat types on the floodplain include paperbark (*Melaleuca* spp.) forests, open perennial and annual

swamps, large perennial waterholes (ponds) and grass/sedge herbfields (Williams, 1979). Widespread grassland communities are dominated by: *Hymenachne acutigluma* (15% of the floodplain), *Pseudoraphis spinescens* (14%), and *Oryza meridionalis* (12%) (Finlayson et al., 1993). Invasive para-grass (*Urochloa mutica*) has replaced large areas of native vegetation occupying ~35% of the floodplain (Bayliss et al., 2006).

2.2. Vegetation types and sampling

Sampling took place in areas dominated by particular aquatic plant species that represent the main structural life form types on the Magela floodplain (Fig. 1). We categorized aquatic macrophytes into four different structural and stem alignment groups based on the classification by Den Hartog and van der Velde (1988):

- Helophytes—vertical emergent graminoids such as *H. acutigluma*, *O. meridionalis*, *U. mutica*, *Leersia hexandra* Sw., and *Eleocharis dulcis* (Burm.f.) Henschel.
- Horizontal helophytes—helophytes with horizontal stems growing just below the water surface, with only the terminal leaves and inflorescence emerging above the surface such as *P. spinescens*.
- Nymphaeids—with attached floating leaves including *Nymphaea violacea* Lehm. and *Nymphoides indica* (L.) Kuntze.
- Ceratophyllids—submerged plants with whorls of leaves at each nodes such as *Ceratophyllum demersum*, *Najas tenuifolia* R.Br. and *Utricularia aurea* Lour.

For each aquatic macrophyte structural type, three replicate patches of approximately 400–2500 m² in area were sampled. Within each site three randomly chosen 1 m² quadrats were placed and a visual estimate of plant cover was made for the quadrat and a sample of the aquatic macrophyte was taken. Samples of plant stems in the top 30 cm of the water column were collected so as not to disturb attached epiphytes and placed in buckets filled with water taken from the site. For each species, we cut sections of macrophyte leaves and stem (with the epiphytes attached to it) of approximately similar size and surface area. For each macrophyte sample we carefully removed attached epiphytes using a soft brush. Once removed, epiphytes were placed in zip-lock plastic bags and stored on ice for later measurement of biomass dry weight (mg). Although the sampled epiphyte community includes, not only algae, but bacteria, protozoa, meiofauna, algae is generally the largest proportion of this community (Hutchinson 1975; Messasz et al., 2009). Macrophyte samples for each quadrat were also placed in zip-lock bags and stored on ice for later measurement of surface area (m²) and dry weight (g). Measurement of surface area was made directly for simple stems and for more complex shapes the macrophytes sample was placed on a herbarium sheet, pressed and dried and then scanned using an area meter (LiCor L3100C). Plants were sampled on consecutive days in April 2013. We also measured the emergent vertical macrophytes *L. hexandra* and *E. dulcis* and associated epiphytes on consecutive days in May 2013.

At each sample site we used a Licor light meter (Light Logger, Licor 1400 Spherical Sensor—LI 193, measurements in $\mu\text{mol s}^{-1} \text{m}^{-2}$) to take readings of ambient light just above and below the water surface and at 20 cm intervals through the water column until no light penetrated (0% of ambient) or when the bottom was reached. Light measurements through the water column were also converted to a light attenuation coefficient (Kd) (Colley-Davies and Nagles, 2008) for each plant structural type. At each site, the physical and chemical characteristics of the water were determined through the water column using a multi-parameter meter ('Hydrolab', QUANTA, ECO Environmental, Perth, Western

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