Jul 1st, 12:00 AM

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Abstract: Many of Australia's tropical rivers are amongst the most ecologically intact in the world, but have been relatively little studied. Now, however, there is pressure for further development of these tropical land and water resources. To avoid repeating management mistakes that have been made elsewhere, it is essential to improve our understanding of how these rivers function. As part of the Tropical Rivers and Coastal Knowledge Research hub, we studied flow, nutrients, and primary production in the Daly River (N.T.), a perennial tropical river maintained in the dry season by ground-water and developed a dynamic simulation model to predict the coverage and biomass of each of five key plant and algae groups in the river. Flow is the key driver in this model, controlling both loss and growth terms for plants. When flow (and hence shear stress) is high, sloughing and bed-scouring contribute to loss of biomass, while shear stresses (and hence higher boundary layer thickness) limit the rate of transfer of nutrients to benthic plants. This paper will describe work to understand and model these dynamics, and will discuss what this might mean for the river's future.

Keywords: dynamic simulation model, environmental flow, shear stress, benthic plants, nutrient transfer, boundary layer transfers, primary production

1 INTRODUCTION

Many of Australia's tropical rivers are amongst the most ecologically intact in the world, but have been relatively little studied. By better understanding how these complex systems work, we can provide the information needed by land and water resource managers, to the benefit of farmers, pastoralists, commercial fishers and other industries that rely on healthy ecosystems. Plants, including algae, form the basis of the food web as well as being an important component of the habitat of aquatic animals and the aesthetic value of the Daly River. Changes in primary production (photosynthesis and subsequent growth and accumulation of plant biomass) and the relative abundance of different plants can affect the entire ecosystem and the biogeochemical functioning of the river.

Previous work in the Daly River (Rea et al. 2002; Townsend, S.A. and Padovan 2005; Townsend, S. A. and Padovan 2009) has demonstrated that it is an oligotrophic (low-nutrient) system in which the velocity of water and shear stresses play a key role in determining the coverage and biomass of plants, particularly *Spirogyra* and *Vallisneria*. Here, we aim to build on previous work to develop a dynamic simulation model of plant coverage and biomass in the Daly River, which can be used explore scenarios for the future of the River.

The input data used to drive the following model were derived from flow records from the Northern Territory government and observational data and process studies reported by Robson et al. (2010).

2   MODEL DESCRIPTION

Five benthic plant groups are represented in the model: *Spirogyra* (a benthic macroalgae), *Chara/Nitella* (benthic algae of more complex structure), *Vallisneria* (a flowering aquatic plant), *Schoenoplectus* (an emergent sedge), and periphyton (a mix of microalgae and bacteria that grows on submerged surfaces). The model simulates growth and biomass of these five groups throughout a 130 km stretch of the river.

The rate of change in biomass of each plant group is a result of the balance between growth and loss. Growth is controlled by light, nutrient availability and availability of suitable substrate. Losses are due to physical sloughing (enhanced at higher flows), grazing, and mortality due to other causes such as viruses (often higher when plant density is high). Our numerical model uses the following formulation:

$$\frac{dC_i}{dt} = C_i \mu_i - S_i - G_i$$

$$= C_i \mu_{max,i} f_{1,i}(I) \cdot f_{2,i}(N,P) \cdot f_3(C_1...C_5) - S_i(u_*,C_i) - G_i(C_i) \qquad (1)$$

where t is time in days, C_i is the areal biomass (mg chl a m^{-2}) of plant group i, μ_i is the current growth rate of plant group i (d^{-1}), S_i is the rate of sloughing under current flow conditions, G_i is the loss rate due to grazing and mortality other than through sloughing, $\mu_{max,i}$ is the maximum growth rate of group i under optimal conditions, $f_{1,i}(I)$ is a function of light reading the bottom of the water column (I), $f_{2,i}(N,P)$ is the nutrient limitation function, a function of the dissolved inorganic phosphorus concentration in the water, P, the dissolved inorganic nitrogen concentration in the water, N, and the shear velocity at the bottom of water column, u_*. $f_3(C_1...C_5)$ is a function of the current areal coverage of all plants, representing limitation by self-shading and limited substrate as biomass approaches the maximum. S_i represents the rate of loss due to physical sloughing (breaking away of algal biomass, especially at higher flows), which is a function of u_* and C_i. The rate of loss due to grazing and other mortality, G_i, is a function only of C_i, as grazers and viruses are not explicitly represented in the model.

The derivation of each of these terms and their basis in field measurements or previous literature is described in detail by Robson et al. (2010). Space limitations prohibit a full model description here. Distinctive or novel features of the model are:

- In this low-nutrient environment, growth of plants is primarily limited by the rate of nutrient transfer across the surface boundary layer in the water near leaf surfaces (not, as is more common in models of mesotrophic and eutrophic streams, by the rate of nutrient transfer through the cell wall). Hence, nutrient uptake is controlled by local shear stress (calculated from water velocity, depth and slope) as well as nutrient concentrations in the water. Similar models have previously been applied in a few cases to marine ecosystems, also subject to low nutrient concentrations (Stevens et al. 2003; Fram et al. 2008), but their use is uncommon in limnological models.

- The primary loss term is sloughing, a function of shear stress and biomass. A quadratic grazing and mortality loss term is also included, as is a term to represent competition for substrate and light.

- The model relies on input from a separate, two-dimensional hydrodynamic model that represents the bathymetry of the 130 km reach as 42,030 nodal points in 8,400

cross-sections across the width of the river. The productivity and biomass model is not spatially resolved, but reflects the spatial heterogeneity of the physical environment by grouping these nodes into 57 physical habitat categories. Each category is composed of a set of (often spatially disparate) nodes for which the relationships between flow and depth, and between flow and shear stress, match. At any given upstream flow, all points within a given category have approximately the same depth and shear stress.

Similar approaches have previously been taken in terrestrial habitat models, but the approach is unusual for a temporally dynamic model of an aquatic ecosystem. The approach has the advantage of greatly reducing the processing requirements of the model relative to those of a detailed, spatially resolved model, while retaining a representation of the key aspects of spatial heterogeneity in the physical environment. The main disadvantage of this approach is that it does not allow the impact of each cell on its neighbours to be simulated (e.g. the effect of upstream nutrient uptake reducing the nutrients available downstream).

- The model does not simulate stocks of other system components, such as nutrient concentrations in the water column or the fate of detrital plant material: where required, these are taken as time-varying inputs from observational data. The result is a simple model that makes full use of the available observational data, but that does not simulate feedback loops, which may become important in some management scenarios.

The model was initialised with minimal plant biomass at the start of the 2008 dry season (1 April). Minimum values were set to 0.1 mg chl a m^{-2} for periphyton, 0.01 mg chl a m^{-2} for *Schoenoplectus*, and 0.02 mg chl a m^{-2} for other plants. The model was then stepped forward with a daily time-step, forced with estimated nitrogen and phosphorus concentrations (derived from regular observations), flow (derived from stage height records) and light (from meteorological records and estimated depth and turbidity). The rate of change of plant biomass with time, dC_i/dt, and hence a time-series of C_i, was calculated at each time-step through the duration of the 2008 dry season (April to November 2008) for each plant group in each of 57 physical habitat types in the model.

3   RESULTS

The simulated areal biomass of each of the five plant groups included in the model is given in Figure 1, with observational results from (Robson et al. 2010) overlain. Observations taken at the same station at different times are connected by dashed black lines. The low resolution of the bathymetric data mean that it is not practical to attempt a point-by point comparison of observations with model results. Instead, we present the model results in terms of statistical probability. In each of the figures below, the lighter blue area indicates the full range of model output for areas with suitable substrate. The apricot-coloured line indicates the mean value. The darker blue area delineates the region between the 25th and 75th percentile, weighted by geographical area. If the model were perfect and the sampling sites chosen at random, we would expect around 50% of the observational data points to fall within the dark blue band, and all data points to fall within the lighter blue areas.

The model successfully reproduces the general ranges and relative abundance of the five plant groups, and shows a transition from a *Spirogyra*-dominated system in the early dry season to an increased abundance of *Nitella/Chara* and macrophytes later in the dry season.

The model underestimates the degree of spatial variability in *Spirogyra* (Figure 1a) in September and November and may over-estimate *Spirogyra* biomass in the mid dry-season. The high spatial variability simulated in the early part of the dry season is due mainly to spatial variations in shear velocity as flows recede following the wet season. Later in the dry season, lower shear velocities limit nutrient uptake by this fast-growing alga, and

biomass is reduced. The model's underestimation of spatial variability later in the dry season may indicate the simplified topography of our model system, or it may reflect the influence of grazing on *Spirogyra* in the real system and the feeding and habitat preferences of the animals that consume *Spirogyra*.

At the sampling sites in our study, both *Vallisneria* (Figure 1b) and *Nitella/Chara* (Figure 1c) increased gradually in the early part of the dry season, reaching a maximum in the mid-late dry season. The model reproduces this general pattern in both plants, but again underestimates the degree of spatial variability. It may also underestimate the early growth of both species and over-estimate the late dry-season growth of *Nitella*. In the case of *Vallisneria*, it is possible that early growth is enhanced by remnant plants that have survived through the wet-season: this possibility is not included in the model. In the case of *Nitella*, it is likely that we have not adequately specified the parameter values, given our reliance on literature values from other systems and complete lack of data regarding sloughing. Process studies of *Nitella* and/or *Chara* responses in the Daly River would improve our ability to model these species.

Schoenoplectus biomass (Figure 1d) was low, and grew slowly, both in the model output and in the field observations. This plant often does well in eutrophic (high nutrient) systems, and is used in sewage treatment wetlands (Zhang et al. 2009), so it might be expected to grow more strongly if nutrient concentrations were to increase. Given the low biomass and limited observational data (*Schoenoplectus* accounted for a negligible proportion of total chloropyhll *a* in 2008 observations), it is impossible to be confident that the model correctly simulates the dynamics of *Schoenoplectus*.

Periphyton biomass is relatively low and relatively consistent throughout the 2008 dry season in both the model and observational results (Figure 1e), but shows more spatial variability than most of the other plants simulated.
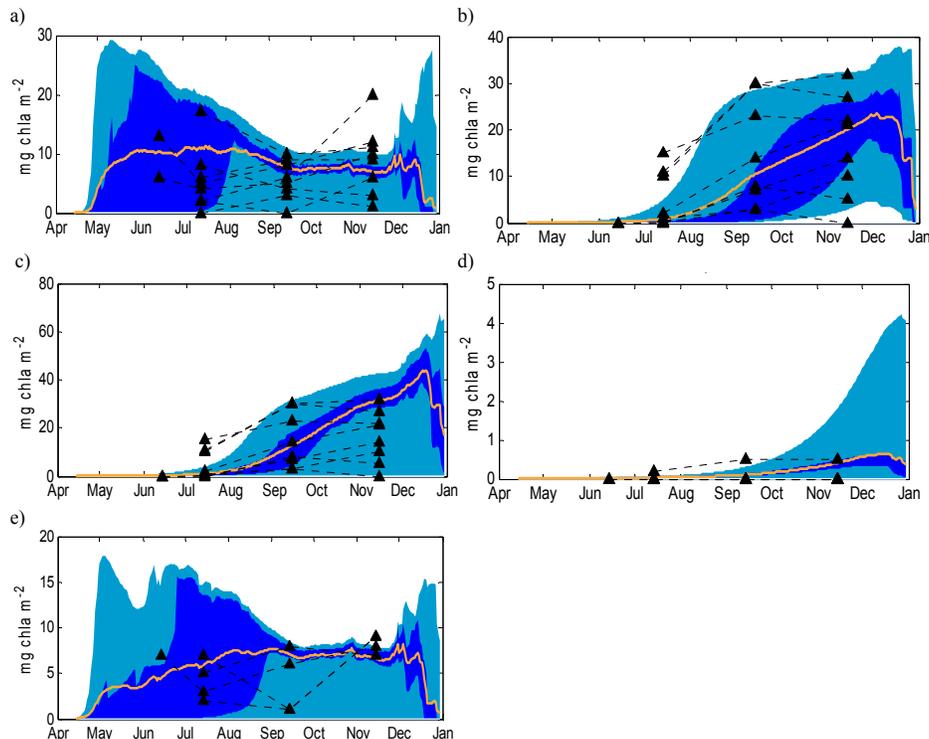

Figure 1 Simulated and observed plant biomass during 2008; a) *Spirogyra***; b)** *Vallisneria***; c)** *Nitella***; d)** *Schoenoplectus***; e) periphyton. Triangles indicate**

observational data points, the orange line indicates the area-weighted mean value from the model, the dark blue shaded area indicates the space between the 25th and 75th percentile of modelled values, and the lighter shaded area indicates the full range of model results.

3.1 Photosynthesis and primary production

The model can also be used to calculate the rate of photosynthesis necessary to support the simulated growth of benthic plants if we assume a fixed C:chl *a* ratio for each plant group, and a 1:1 ratio between carbon fixed and O_2 released. Figure 2 shows the results of this calculation. This calculation gives a result much lower than the actual photosynthesis calculated by Robson et al. (2010) from oxygen data (0.050 mmol O_2 L^{-1} in July, 0.074 mmol O_2 L^{-1} in September and 0.090 mmol O_2 L^{-1} in November). It has been noted previously (Webster et al. 2005) that it is likely that much of the photosynthesis occurring in the Daly River produces carbon that is released as extracellular carbohydrates rather than being incorporated into plant biomass, due to the strong nutrient limitation of the system. The difference between the photosynthesis required to support plant growth calculated here and the actual photosynthesis calculated by Robson et al. (2010) gives a measure of the amount of carbon that is fixed but does not contribute to the production of plant biomass.

3.2 Nitrogen and phosphorus stores

Model outputs can also be converted to nitrogen and phosphorus stores. Nitrogen and phosphorus stores in all five benthic plant groups gradually increase over the course of the dry season (

Figure 3) while water-column dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) gradually drop (approaching the detection limit in early September). Estimated water column total nitrogen (TN) and phosphorus (TP) stores decline faster than DIN and DIP stores in the first few months of the year and continue to decline until the last measurement in November 2008. The initial rapid decline in TN and TP stores in April to June may be associated with deposition of sediments on the river bed (Robson et al., 2010) as water velocities decline in the early part of the dry season. Nutrients associated with these sediments may subsequently become available to plants through gradual bacterial degradation. Simulated plant nutrient stores drop and water column stores rise at the start of the next wet season, when plant beds are disrupted by higher flows.

When dissolved inorganic nutrient concentrations in the water column drop to very low levels in the mid dry season, benthic plant biomass must be sustained by recycling of nutrients within the plant beds, degradation of organic detrital material in the water column or deposited sediment stores, or by new inputs (e.g. from atmospheric deposition or leaf litter). These model results suggest that the observed plant biomass growth does not require significant new nutrient inputs in the latter part of the dry season, i.e. nutrients present at the start of the dry season may be stored within the river and gradually converted to plant biomass. The maximum benthic plant nitrogen store of approximately 2.6 t of nitrogen in this stretch of the river represents only a tiny fraction of the total nitrogen load carried by the river during the wet season (approximately 3350 t, Robson et al. 2010).
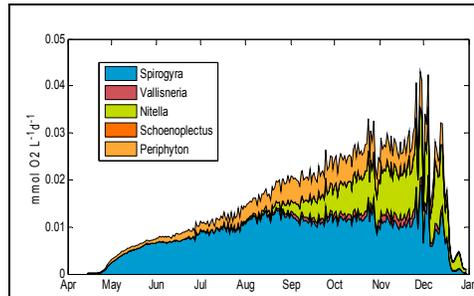
Figure 2 Photosynthesis required to support plant growth (averaged over the model domain).
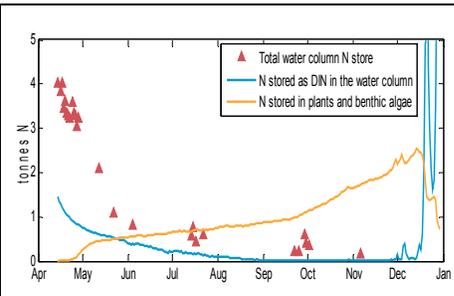

Figure 3 Changes in estimated water column and benthic plant nitrogen stores (integrated over the model domain) over the course of the 2008 simulation.

4   CONCLUSIONS

The model is able to reproduce many of the observed features of plant dynamics in the Daly River and may form a basis for a range of scenario simulations. From the results of our simulations, when combined with the results of the process studies reported by Robson et al. (2010) and previous work in the Daly River, we can conclude:

1. Primary production in the Daly River is strongly controlled by nutrient availability and the river is likely to be particularly sensitive to any change in nutrient loads.

2. Growth of plant biomass in the first half of the dry season is supported by uptake of nutrients from the water column. Towards the end of the dry season, plant biomass may be supported by recycling of nutrients stored within benthic communities and release of nutrients from sediment stores.

3. Plant biomass is strongly affected by seasonal changes in flows, with sloughing or scouring of benthic plant material at higher flows playing an important role in seasonal patterns and the distribution and relative abundance of different species.

ACKNOWLEDGEMENTS

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