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Mangrove litter fall: Extrapolation from traps to a large tropical macrotidal harbour

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ABSTRACT

Mangrove litter is a major source of organic matter for detrital food chains in many tropical coastal ecosystems, but scant attention has been paid to the substantial challenges in sampling and extrapolation of rates of litter fall. The challenges arise due to within-stand heterogeneity including incomplete canopy cover, and canopy that is below the high tide mark. We sampled litter monthly for three years at 35 sites across eight mapped communities in the macrotidal Darwin Harbour, northern Australia. Totals were adjusted for mean community canopy cover and the occurrence of canopy below the high tide mark. The mangroves of Darwin Harbour generate an estimated average of 5.0 t ha^{-1} yr^{-1} of litter. This amount would have been overestimated by 32% had we not corrected for limited canopy cover and underestimated by 11% had we not corrected for foliage that is below the high tide mark. Had we made neither correction, we would have overestimated litter fall by 17%. Among communities, rates varied 2.6-fold per unit area of canopy, and 3.9-fold among unit area of community. Seaward fringe mangroves were the most productive per unit of canopy area but the canopy was relatively open; Tidal creek forest was the most productive per unit area of community. Litter fall varied 1.1-fold among years and 2.0-fold among months though communities exhibited a range of seasonalities. Our study may be the most extensively stratified and sampled evaluation of mangrove litter fall in a tropical estuary. We believe our study is also the first such assessment to explicitly deal with canopy discontinuities and demonstrates that failure to do so can result in considerable overestimation of mangrove productivity.

1. Introduction

Mangrove ecosystems produce large amounts of litter and decomposition of this may contribute significantly to the production of dissolved organic matter, and to nutrient recycling, in coastal ecosystems (Kathiresan and Bingham, 2001). Furthermore, mangrove forests have recently been recognised as amongst the most productive of tropical forests ecosystems, playing a significant part in the global carbon budget and therefore assuming a significance in relation to climate change that far exceeds what might be anticipated from their geographical extent (Donato et al., 2011). Numerous studies have measured rates of litter fall beneath stands of one or more species of mangrove (e.g. Woodroffe et al., 1988; Cunha et al., 2006; Chen et al., 2009), but estimation of total litter production for a complex mangrove system and its contribution to the overall productivity of a large tropical estuary is fraught with problems of both accuracy and precision, and has been rarely attempted (Jennerjahn and Ittekkot, 2002; Sanchez-Carrillo et al., 2009). Such attempts are warranted because of their contribution to a range of macro-ecological perspectives on coastal ecosystems (Saenger and Snedaker, 1993; Farnsworth, 1998; Jennerjahn and Ittekkot, 2002; Bouillon et al., 2008; Komiyama et al., 2008; Kristensen et al., 2008). They are also an important source of information for decisions about the exploitation and development of mangroves and adjacent water bodies (Ewel et al., 1998; Wolff, 2006; Meynecke et al., 2007; Burford et al., 2008), particularly given the threatened status of these communities in many regions (Kathiresan and Bingham, 2001). We estimated total litter fall in a large tropical embayment and its constituent mangrove communities. Our extrapolations deal explicitly with the sampling issues involved, generating a level of confidence that appears unparalleled in previous studies.

Mangrove forests often contain considerable floristic and structural variation. Species partition the intertidal region on inundation depth and frequency, soil type and soil and water salinity (Clough,

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1992), generating discrete communities or assemblages under differing combinations of conditions (Rodriguez, 1987; Bunt, 1996; Saenger, 2002). Even in the species-rich mangrove systems of Asia and the west Pacific where niches are finely partitioned, the structure and vigour of mangroves may also vary markedly within species and communities (Robertson et al., 1991; Devoe and Cole, 1998). It is to be expected that this will yield local spatial variation in rates of litter fall, and indeed, there is ample evidence that this is so (e.g. Twilley et al., 1986, 1997; Woodroffe et al., 1988; Wafar et al., 1997; Gwada and Kairo, 2001; Sherman et al., 2003). This variation can be substantial, with Shunula and Whittick (1999) reporting 2.5-fold variation, and Duke et al. (1981) five-fold variation among mangrove species within an estuary. Considerable local heterogeneity in rates of litter fall are also a feature of many terrestrial ecosystems including even tropical rainforests (Burghouts et al., 1998; Metcalfe et al., 2008).

Faced with this complexity, extrapolation may best be undertaken with carefully stratified sampling of litter fall. This also requires appropriate classification, mapping and estimation of area for each mangrove community. Additional challenges relate to the practicalities of sampling. Typically and especially in macrotidal systems, litter traps in mangroves are suspended from trees and elevated above the highest level to which the tide rises to avoid tidal flushing of litter (e.g. Duke et al., 1981; Woodroffe et al., 1988; Wafar et al., 1997; May 1999; Shunula and Whittick, 1999; Chen et al. 2009). In mangrove systems with a limited tide range, traps may be supported from below and placed randomly (e.g. Twilley et al., 1997). Sherman et al. (2003) placed litter traps randomly within plots but acknowledged being unable to sample portions of the mangrove stand subject to deeper tidal inundation. Unless canopy cover of the community is 100%, sampling under canopies is not random sampling of the community; failure to account for this sampling bias will result in overestimation of community- and estuary-wide rates of litter fall. Many authors have taken particular care not to extrapolate beyond the sampled canopies (e.g. Woodroffe et al., 1988), but others have extrapolated (Gong and Ong, 1990; Jennerjahn and Ittekkot, 2002; Burford et al., 2008; Sanchez-Carrillo et al., 2009) and these estimates may well thus be overestimates. Further, placement of traps above the high tide mark means that the part of the mangrove canopy that is inundated by the highest tides is not sampled. In an extensive literature search the only evidence we found of correction for this potential underestimation of litter fall is that Woodroffe (1982) fenced plots and collected litter off the ground. In terrestrial ecosystems, litter fall traps are typically placed either regularly or randomly and close to the ground (e.g. Stevenson and Coxson, 2003); in systems with marked canopy gaps, traps may be placed under woody plants and ecosystem-level estimates of litter fall corrected for canopy cover (Campanella and Bisigato, 2010).

Here, we provide community- and harbour-wide estimates of monthly and annual litter fall for Darwin Harbour, a large tropical embayment in northern Australia. We make use of an established mapping scheme for the Harbour's mangroves (Brocklehurst and Edmeades, 1996) to stratify sampling across eight mangrove communities. Litter fall was sampled monthly for three years in 70 traps at 35 sites. Our aims are firstly to provide litter fall estimates as a contribution to understanding spatial and temporal patterns of mangrove productivity and its contribution to Darwin Harbour (Burford et al., 2008), Woodroffe (1985), Woodroffe et al. (1988) by sampling more extensively in time and space, by sampling in a manner representative of the entire Harbour and stratified to reflect subsequent detailed mapping of its mangrove communities, and by incorporating corrections for incomplete canopy cover and unsampled canopy depth.

2. Study area and methods

2.1. Study area

Darwin Harbour (12°31′S, 130°49′E) is a macrotidal ria (tide range up to 8.1 m over a year) resulting from the post-glacial inundation and subsequent partial infill of a dissected lateritic-capped plateau (Semeniuk, 1985; McKinnon et al., 2006). We define the Harbour as the marine area enclosed by East Point and Charles Point (Fig. 1), consistent with Brocklehurst and Edmeades (1996). It has an area of c. 450 km^2, of which 190 km^2 is mangrove and 14 km^2 is

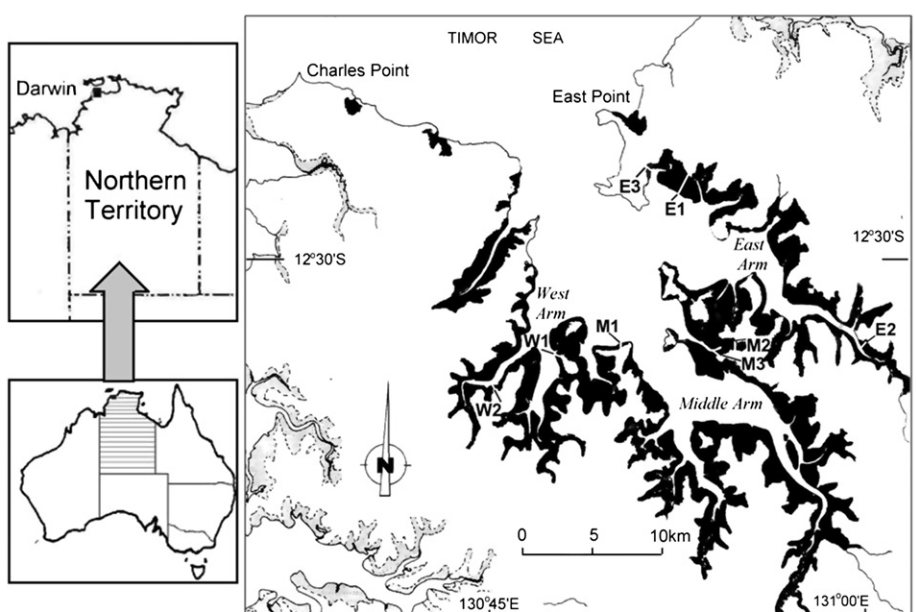

Fig. 1. Map showing Darwin Harbour with mangroves indicated in black and showing the location of the eight sampling transects (E1–E3, M1–M3, W1–W2) distributed across the three major arms of the Harbour. Grey shading indicates mangroves outside Darwin Harbour; inset shows the location of Darwin.