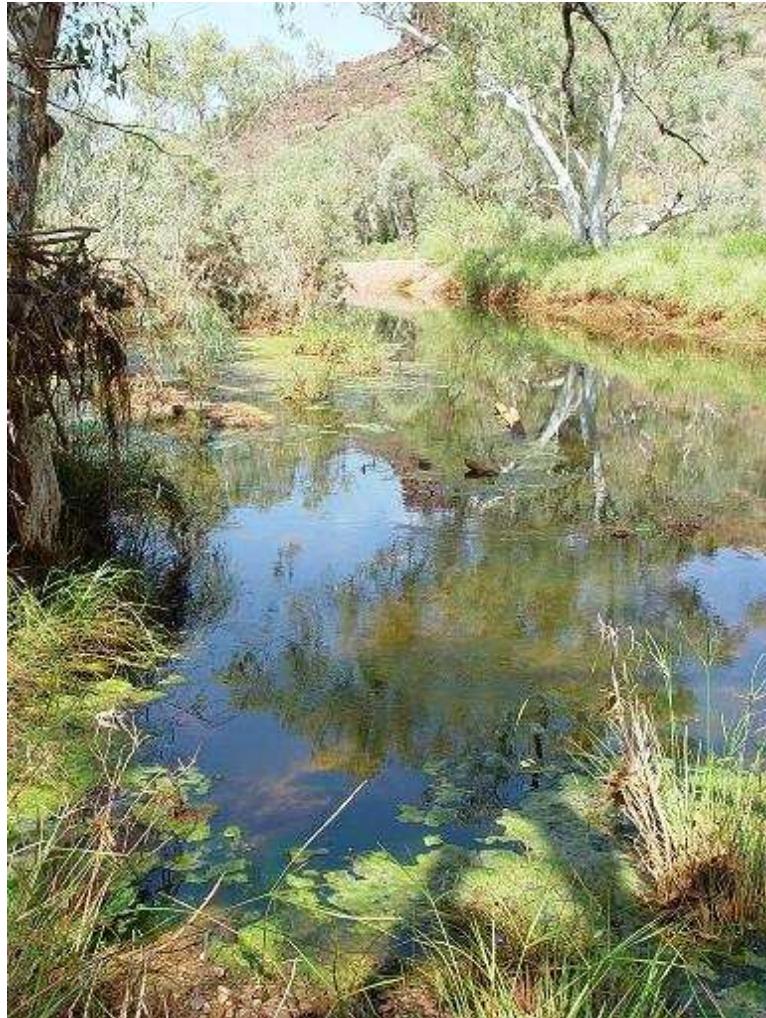


Soil biogeochemistry and flooding in intermittent streams of the semi-arid Pilbara region



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This thesis is presented for the degree of Doctor of Philosophy

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Statement of Candidate Contribution

I hereby declare that this thesis is my own composition, except where otherwise stated. All sources have been acknowledged and my contribution is clearly identified. This thesis was completed during the course of my enrolment in the degree of Doctor of Philosophy at the University of Western Australia, and has not previously been accepted for a degree at this or any other institution.

Credit for certain material is due to:

Chapter 3, 4, 6, and 7: Stable isotope samples were processed by Lidia Bednarek and Doug Ford at the Western Australian Biogeochemistry Centre (UWA).

Chapter 5: Experiments undertaken to determine soil moisture release curves were conducted in collaboration with Mr Gary Cass (UWA).

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Signed.....

Date.....

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Tiddalick - The Frog Who Caused a Flood[†]

*In the time of dreaming
Before the earth was old
Myths were in the making
Legends yet untold*

*Here began a story
Of one huge enormous frog
Solemn in his glory
He drank from every bog*

*Tiddalick the great one
Had to quench his mighty thirst
He drank from all the waterholes
So much he nearly burst*

*He drained the lake and river
The stream and billabong
Soon there was no water left
It was very wrong*

*Others now grew thirsty
There was no sign of rain
Hot sun scorched the arid earth
No water did remain*

*Tiddalick's swollen stomach
Was squelchy round and wide
He was so big he couldn't move
The water was inside*

*Animals assembled
Men gathered with them too
They had to end this great distress
And work out what to do...*

*The kookaburra had a plan
We need to make him laugh
To hold his side and open wide
We need to show some gaffe*

*If only we can do that
The water will pour out
We all must work together
To end this mighty drought...*

*The kangaroo and platypus
Wombat and emu
All tried their best to make him laugh
But Tiddalick stayed blue*

*Some danced and some told stories
Others somersaulted
Tiddalick grew tired and bored
And slept when antics halted*

*The last to try was Norang the Eel
He was their final hope
He turned himself into a hoop
And wriggled like a rope*

*The rope stood upright on the sand
Then it began to spin
It went round like a whirlwind
Tiddalick began to grin*

*Then out slopped some water
Before it reached the sand
Man and beast began to drink
It worked like they had planned...*

*As his belly rumbled
The frog rocked to and fro
With his hands upon his sides
A stream began to flow*

*Tiddalick's mouth was open wide
With water gushing out
A surging tidal river
Spewed like a water spout*

*It swept away the animals
And covered all the sand
A shining lake of water
Had spread over the land...*

Roenfeldt, R. (1980) *Tiddalick: The Frog Who Caused a Flood*. Penguin Books Australia (reproduced with permission)

[†]The story of Tiddalick (or 'Tiddilik') the desert water-holding frog is based on a Central Aboriginal legend aimed at teaching water conservation and environmental stewardship.

Note

This thesis was prepared as independent scientific manuscripts. While every effort has been made to remove repetition, there unavoidably remains some possibility of overlap between chapters.

Species Authorities

Acacia aneura Benth.
Acacia citrinoviridis Tindale & Maslin
Acacia coriacea DC.
Acacia pruinocarpa Tindale
Acacia pyrifolia DC.
Acacia sclerosperma F.Muell.
Acacia tumida Benth.
Acacia victoriae Benth.
Acacia wanyu Tindale
Acacia xiphophylla E.Pritz.
Acetosa vesicaria (L.) A.Love
Callitris columellaris F.Muell.
Cenchrus ciliaris L.
Corymbia calophylla (Lindl.) K.D.Hill & L.A.S.Johnson
Cymbopogon ambiguus A. Camus
Cynodon dactylon (L.) Pers.,
Eremophila longifolia (R.Br.)F.Muell.
Eriachne mucronata R. Br.
Eucalyptus brevifolia F.Muell
Eucalyptus camaldulensis Dehnh.
Eucalyptus gamophylla F.Muell.
Eucalyptus kingsmillii Maiden & Blakely
Eucalyptus marginata Sm.
Eucalyptus microtheca F.Muell.
Eucalyptus victrix L.A.S.Johnson & K.D.Hill
Hakea lorea R.Br.) R.Br. subsp. *lorea*
Melaleuca glomerata F.Muell.
Melaleuca leucadendra (L.)L.
Pinus pinaster Aiton
Senna artemisioides (DC.) Randell ssp. x *artemisioides*
Spirogyra fluviatilis Hilse
Triodia basedowii E.Pritz
Triodia pungens R.Br.
Triodia wiseana C.A.Gardner
Vachellia farnesiana (L.) Wight & Arn.

Abstract

Most of Australia, and large areas of many other continents, is drained by intermittent rivers and streams, however comparatively few biogeochemical studies have been completed for these systems. Intermittent, dryland streams are highly dynamic environments subject to unpredictable and sporadic flow. Natural disturbance from lengthy drought periods and sudden floods are typical for these systems. Without adequate baselines for natural disturbances, it is difficult to quantify other effects from anthropogenic disturbance such as dewatering, land clearing, and urbanisation, or climate change.

This thesis presents work from a four-year study examining the biogeochemistry of nitrogen (N), phosphorus (P) and carbon (C) in soils and sediments of two intermittent streams (Barnett Creek and Pirraburadoo Creek) in the Pilbara region of north-west Australia. The Pilbara is an area of ancient geology and highly weathered environments that is undergoing rapid development yet is poorly understood from an ecological perspective. The principal objectives of this thesis were to determine: i) how flooding affects the spatio-temporal patterns of nutrients in intermittent stream landscapes; ii) the role of flooding in N and C mineralisation and microbial dynamics; and iii) the connections between benthic algae, microbes and nutrient availability in channel sediments. To address these objectives, three field studies and two incubation experiments were conducted.

Field studies at Barnett Creek indicated that flooding reduced the spatial heterogeneity of available soil nutrients and microbes in the stream landscape, and that topography (relative elevation) in the stream landscape was of less importance in influencing nutrient and microbial patterns than flooding or landscape position. Indeed, stream bed topography changed little throughout study period and did not appear to significantly affect nutrient distributions. The riparian zone was shown to be a hot spot (potential source), and floodplains a cold spot (potential sink), for nitrate ($\text{NO}_3\text{-N}$) and organic carbon (OC). Microbial community profiles were unaffected by floods, while overall soil microbial biomass (by phospholipid fatty acid analysis) was reduced by flooding. Different riparian vegetation communities were biogeochemically similar across the study period, despite dissimilarities in species composition and canopy cover. Using kriging, a visual

presentation of biogeochemical patchiness across the stream landscape and within channel beds highlighted the spatio-temporal divergence and convergence throughout the hydrologic period.

Laboratory incubation studies indicated that N mineralisation is affected both by landscape position and water availability. A distinct mineralisation ‘flush’ occurs in Pilbara soils and sediments, with up to 70 % of N mineralised being released in the first 48 h after rewetting. Addition of *Eucalyptus* litter stimulated soil microbial activity and produced rapid N immobilisation. The results indicated that landscape position was less important in controlling microbial activity than soil saturation when water-filled pore space was > 40 %. Large pulses of water availability resulting in full soil saturation appeared to cause a slower release of mineralisation products, compared to small pulse events that stimulated a rapid cycle of C and N mineralisation-immobilisation.

Field studies at Pirraburadoo Creek indicated that microbial biomass and activity increased in benthic algal mats during mat senescent stages, and decreased after flooding when mat biomass peaked. Benthic algae grew rapidly in gravel run environments after flooding, while declining in pools, and demonstrated moderate N limitation and strong P limitation. Pools had two to eight times greater NO₃-N, three to five times more total N, and two to three times more labile P, OC and total C than either pools after flooding, or runs before or after flooding. Hence, the pools at Pirraburadoo Creek represented a local, interflood store of nutrients in otherwise nutrient-poor landscape, when connectivity to upstream reaches or upland environments was weak or non-existent.

This thesis provides the first detailed analysis of soil and sediment biogeochemical responses to flooding for intermittent streams in the Pilbara region and for semi-arid Australia. Further pressing questions raised by this work include: What is the key pulse size and frequency for maintaining Pilbara riparian communities as well as soil microbial function? How do the spatio-temporal nutrient and microbial patterns observed persist over (i) multi-decadal scales, (ii) mega-spatial (larger landscape to regional) scales, (iii) different flood frequency-magnitude regimes, and (iv) different stream sizes? Stream biogeochemistry is a burgeoning field, and it is therefore reasonable to expect such existing gaps in knowledge may be addressed in the near future.

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CHAPTER 1

General Introduction

This thesis presents work from a four-year study examining the soil biogeochemistry of nitrogen (N), phosphorus (P) and carbon (C) in soils and sediments of two intermittent streams (Barnett Creek and Pirraburadoo Creek) in the semi-arid Pilbara region of north-west Australia. To provide a contextual foundation for the experiments detailed in Chapters 3 to 7, in this chapter I provide an overview of intermittent streams in dryland (arid and semi-arid) regions, cycling of N, P and C in soils and aquatic systems, and microbial and benthic algal communities. As the introductory sections of each of the five experimental chapters, as well as the discussion in the synthesis chapter (Chapter 8), provide further targeted and detailed reviews of relevant literature, this chapter is intended as a general introduction rather than as an exhaustive review of the biogeochemistry of intermittent streams in dryland landscapes.

1.1 DRYLAND STREAMS

1.1.1 Intermittent streams

Intermittent or temporary rivers, streams (i.e. smaller rivers) and ponds are found in many parts of the world, and are essentially natural bodies of water which experience a recurrent dry phase, irrespective of whether this phase is seasonal, annual or extra-annual (Boulton & Suter, 1986; Rains *et al.*, 2006; Williams, 1987). Ephemeral, temporary, episodic and intermittent rivers and streams have been variously discriminated on the basis of a number of characteristics including connectivity, channel structure and flow rates, volumes and frequencies (Bayly & Williams, 1973; Nanson *et al.*, 2002; Uys & O'Keeffe, 1997). The ability to maintain certain biological assemblages, particularly aquatic macroinvertebrates, has also been used as an indicative factor in some studies (Feminella, 1996; Kirkby *et al.*, 1983; Schneider & Frost, 1996). Here, the term 'intermittent' is preferred for its use in the description of

more or less structurally stable channels in semi-arid regions that are periodically, if not predictably, inundated (Bayly & Williams, 1973; Nanson *et al.*, 2002). While often used interchangeably with ‘river’ as a term for flowing water, ‘stream’ emphasises smaller waterways, including those that may form the upper reaches (sections) of a river catchment.

More than half of the land area of Australia, and significant proportions of many other continents, is drained by intermittent rivers and streams. However comparatively few ecological or biogeochemical studies have been completed for these systems in comparison to permanent, and usually temperate waterways in the Northern Hemisphere (Boulton & Suter, 1986; Williams, 1983). Possible reasons for this neglect include the remote and unpredictable nature of these systems; indeed, Australian streams are highly dynamic, disturbance-intensive systems, with an interannual variability more than twice that of average river flows worldwide (Chiew & McMahon, 1993). Intermittent drainage is prevalent throughout the subtropical dry climatic zone of the continental interior (Fig. 1.1).

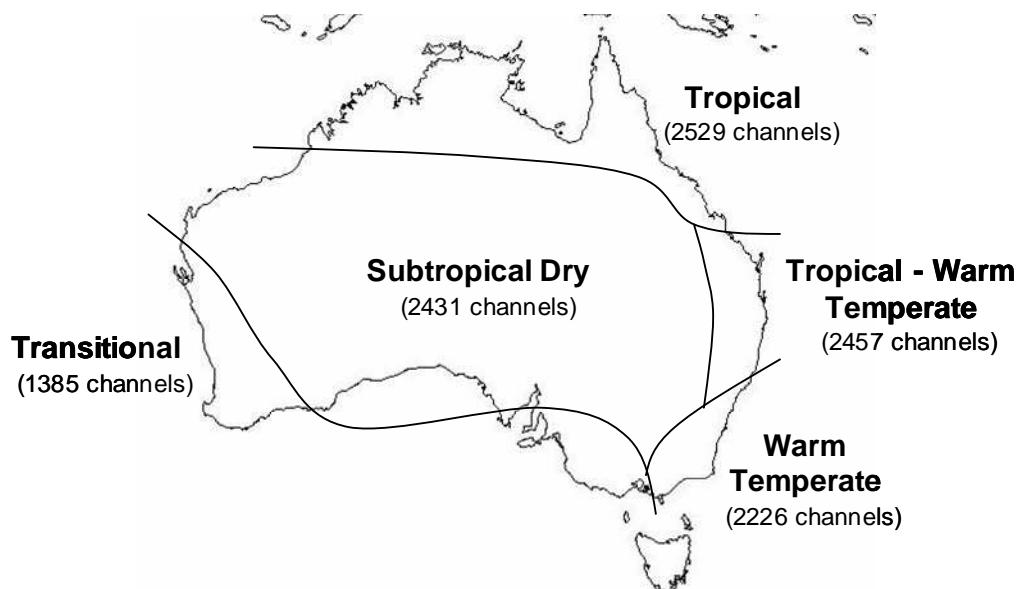


Fig. 1.1 Climatic zones in Australia relevant to drainage, with total number of river channels per zone (Lake, 1995).

1.1.2 Flood pulses

Intermittent streams are characterised by unpredictable, sporadic flow and are highly dynamic environments capable of moving large quantities of water and sediment during flash floods, while remaining dry and poorly connected to their floodplains for often many months or years during interflood periods (Bunn *et al.*, 2006). In dryland regions, such intermittent rivers and streams provide the principal form of drainage (Boulton & Suter, 1986). Water availability in such systems is generally determined by pulsed events, which may include spectacular flash floods, followed by months or even years of drought (Austin *et al.*, 2004; Comin & Williams, 1994; Fisher & Minckley, 1978; Huxman *et al.*, 2004). A pulsed hydrograph for one Australian intermittent river system, the Cooper Creek system, can be contrasted with the more predictable drainage of permanent systems such as the Colombia River in North America or the Mekong River of south-east Asia (Fig. 1.2). Drying-rewetting cycles are often most pronounced in dryland ecosystems with a strongly seasonal precipitation, but wet-dry cycles are common in a variety of ecosystems (Kieft *et al.*, 1987; Pulleman & Tietema, 1999).

Flood pulses have long been recognised for their importance in maintaining ecosystem functions in drylands (Noy-Meir, 1973). In contrast, quantification of their controlling role in biogeochemical cycles has seldom been attempted (Austin *et al.*, 2004; Baldwin & Mitchell, 2000; Marti *et al.*, 1997; Valett *et al.*, 2005). The large changes in water availability associated with drought-flood systems are clearly the major ‘drivers’ of element cycling in drylands (Gebauer & Ehleringer, 2000; Schimel & Parton, 1986), yet quantitative information remains relatively scarce. The rapid and often aseasonal nature of floods, as well as the difficulties involved in conducting research in such largely remote and inhospitable environments, has mostly precluded detailed studies.

In general, nutrient transformation and flows within a landscape are increased by disturbance (Forman & Godron, 1986). Flooding stimulates decomposition and redistribution of organic matter (Baker *et al.*, 2001; Day, 1983) causing biogeochemical ‘hot spots’ (patches with disproportionately high reaction rates relative to the surrounding matrix) and ‘hot moments’ (short periods of time that exhibit disproportionately high reaction rates relative to longer intervening time periods) (McClain *et al.*, 2003).

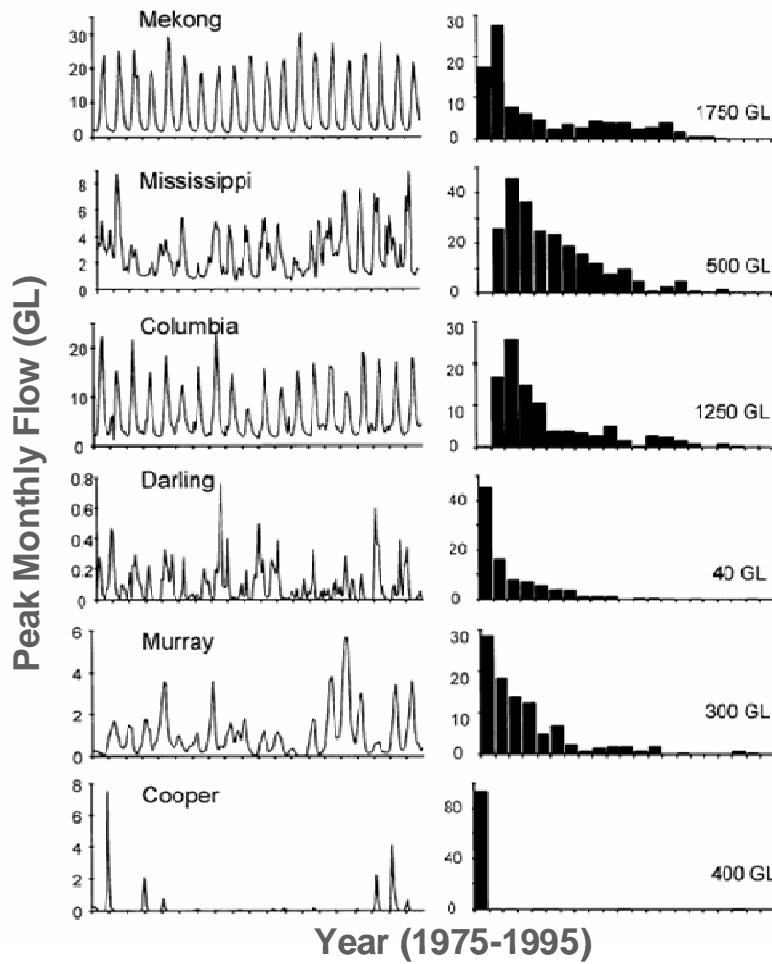


Fig. 1.2 Hydrographs and relative flow-frequencies (peak monthly flows, GL) for rivers in various climatic regions over 20-year intervals. Note the extremely unpredictable flow of intermittent Cooper Creek in inland Australia (Walker *et al.*, 1995).

In the context of nutrient dynamics, hot spots and hot moments may therefore also refer respectively to patches and periods with disproportionately higher resource availability (indicative of nutrient transformation rates).

Water can also leach nutrients and cause erosion of rock and other materials (Bormann & Likens, 1967). The Flood Pulse Concept (Junk *et al.*, 1989) also supports inundation as the primary driving force for productivity and biotic interactions in large river-floodplain systems. The magnitude of the effect of water pulses on C and nutrient pools will, however, depend on the distribution of resource availability and soil organisms, both of which will in turn be strongly affected by spatio-temporal patterns in vegetation, topographic position and soil texture (Austin *et al.*, 2004), as discussed below.

1.1.3 Landscape linkages

Traditionally, rivers and streams have been considered single, internally homogeneous elements of the terrestrial landscape which are linked by flows across static boundaries. More recently, heterogeneity within these environments has been appreciated as an integral part of individual stream landscapes or ‘riverscapes’ (Wiens, 2002). Interrelationships among stream topography, flooding and connectivity have been emphasised in recent studies (Bechtold & Naiman, 2006; Ward *et al.*, 2002).

Stream landscapes have generally been treated as linear conduits, in which water flows play a key role in connecting landscape patches (Hansen & di Castri, 1992; Junk *et al.*, 1989; Ward, 1998; Ward *et al.*, 2002). Hydrological connectivity has been conceptualised in four dimensions for lotic ecosystems (Fig. 1.3): longitudinal, lateral, vertical and temporal (Amoros *et al.*, 1987; Ward, 1989). Productivity fluctuations resulting from connections on the longitudinal dimension (upstream-downstream gradient) are described by the River Continuum Concept (Vannote *et al.*, 1980). Exchanges between riparian-influenced upstream (first or second-order) streams with their larger downstream members (third-order streams and greater) are a significant element of this concept. Meanwhile, lateral connectivity encompasses the permanent and episodic links between the main course of a river and its floodplain (Junk *et al.*, 1989; Ward & Stanford, 1995). Transported energy and materials are moved into riparian and upland environments, while the products of primary production in these environments are laterally transferred to the stream channel. Lateral and longitudinal elements are combined in some models, such as the concept of nutrient spiraling, where downstream transport of nutrients is integrated with lateral processing by bank sediments and riparia (Elwood *et al.*, 1983; Fisher *et al.*, 1998; Newbold, 1992). Vertical connectivity includes exchanges between the surface and groundwater, particularly in the hyporheic zone beneath and lateral to the channel bed, which may add to or remove nutrients from surface sediments (Boulton, 1993; Dahm *et al.*, 1998; Dent *et al.*, 2007). Lastly, the temporal dimension is required to account for changes in momentary, seasonal, annual and historic scales (Amoros & Bornette, 2002).

Where streams flow intermittently, landscape connectivity is often reduced and processes may be limited during dry periods to small-scale exchanges between nearby patches (Pringle *et al.*, 1988). Patches may, for example, represent different vegetation communities within the riparian zone, floodplain waterbodies, or microhabitats within the stream channel. Regardless of their nature, all landscape patches will vary on spatio-temporal scales in their ability to perform certain ecosystem functions, and to interact with surrounding patches across boundaries (Wiens, 2002). Environments subject to extreme disturbance, such as dryland streams, may present particularly useful testing grounds for the concepts of patch dynamics and disturbance ecology.

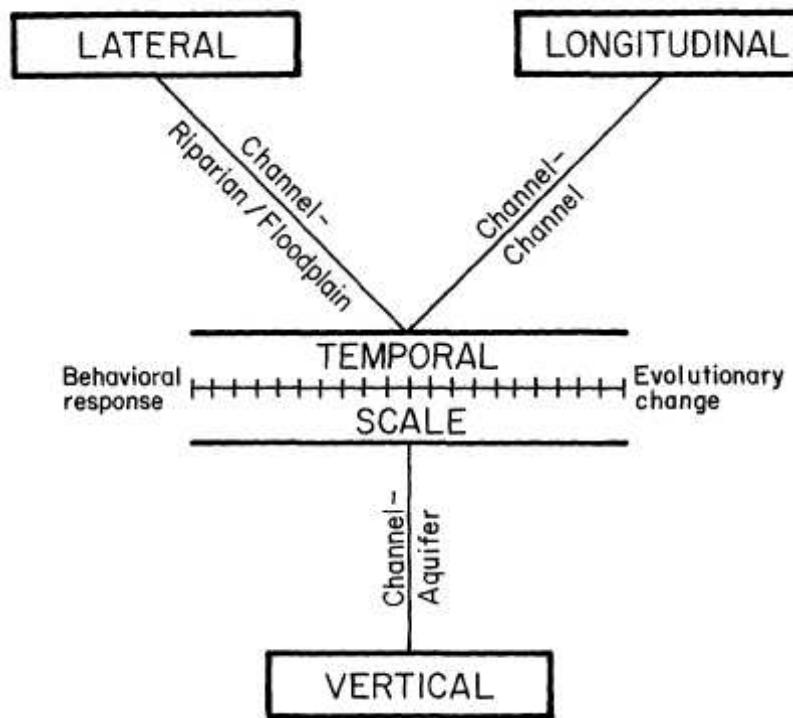


Fig. 1.3 A conceptualisation of the four dimensions of lotic ecosystems (Ward, 1989).

1.1.4 Riparian zones

Riparian zones include all land adjoining, directly influencing or influenced by a river, extending from the edges of water bodies to the edges of upland or floodplain communities (Naiman *et al.*, 2005b). Riparian zones are terrestrial areas which act as aquatic-terrestrial ‘interfaces’ (*sensu* Naiman & Decamps, 1997), integrating interactions between aquatic (channels and banks) and terrestrial (floodplains or uplands) components of a landscape (Harms & Grimm, 2008; Schade *et al.*, 2002).

While typically associated with lotic waters, lentic (standing) waters such as lakes and wetlands all possess some form of riparia (Naiman & Decamps, 1997; Naiman *et al.*, 2005b). Highly dynamic environments, riparian zones are characterised by strong energy regimes, substantial habitat heterogeneity and a diversity of ecological processes and multidimensional gradients (Naiman *et al.*, 2005a). Often representing the interface between aerobic and anaerobic environments, they are sites of substantial biogeochemical activity (Addy *et al.*, 2002; Bunn, 1993). Massive floods in dryland streams may have a long-lasting impact on riparian zones and can demolish whole reaches of riparian forest (Jacobson *et al.*, 1995). Plant community persistence in dryland riparian zones depends upon the ability of species to withstand extreme cycles of flooding and drying (Brock *et al.*, 2006).

Riparian vegetation forms an important component of the stream landscape, helping retain and process nutrients, and providing habitat (Lynch & Catterall, 1999; Naiman *et al.*, 2005b). This is particularly vital in dryland conditions, where vegetative cover may be sparse in the surrounding environment (Aguiar & Sala, 1999). Vegetation can also trap sediments and nutrients moving through the landscape and modify channel structure through processes such as bank stabilisation (Lee *et al.*, 2000; Simon & Collison, 2002). Importantly, like other ecological interfaces, riparia play an important role in connection of landscape elements (Naiman & Decamps, 1997). This is particularly important in dryland settings, where riparian vegetation provides a link between the relatively mesic environment of the river channel, and the xeric floodplains or uplands. Jacobs *et al.* (2007) summarised key differences between riparian communities in mesic and semi-arid riparian systems, with a focus on riparian zones in savanna ecosystems (Table 1.1). This summary underscores the relative high heterogeneity of dryland riparia, and the consequences for productivity and nutrient transformation.

Table 1.1 Summary of the major difference between mesic and semi-arid riparia ('ecotones'; Jacobs *et al.*, 2007).

| Ecological properties | Mesic catchment | Semi-arid catchment |
|--|---|--|
| Moisture availability | Less variable, leading to more efficient nutrient cycling. | More variable, giving rise to pulse-like patterns in nutrient availability. |
| Nutrient distribution | Less variable. | Highly heterogeneous at various scales, influencing nutrient delivery to riparian corridors. |
| Upland vegetation configuration | High plant density, thick litter layer in uplands, vertical movement of water resulting in subsurface-dominated runoff. This maximises opportunities for soil retention and transformation of carbon and nutrients. | Open, non-vegetated spaces result in soil surface crusting and surface-dominated runoff; larger dendritic drainage networks. This results in limited opportunities for soil modification of runoff; faster, more intense hydrologic response to rain events. |
| Distribution of riparian vegetation in catchment | Lower-order streams flanked by riparian communities that are able to intercept and trap sediments and nutrients from the uplands. | Lower order streams sometimes devoid of flanking riparian vegetation so that sediment and nutrients often pass directly from uplands to aquatic environments during rainstorms. |
| Riparian vegetation configuration | Patchy cover; more or less productive than uplands. | More continuous cover where present; often more productive than uplands. |
| Hill slope lateral transfers | Deep infiltration, slow lateral movement. High contributions to groundwater. | Shallow rapid lateral movement. Retention in soil / bedrock interface layers. Slow recharge to groundwater. Rapid overland flow and sediment movement during extreme events. |
| Longitudinal delivery | Hydrologically 'losing' streams less common. | Hydrologically 'losing' streams common, especially during the dry season leading to reversal of water and nutrient movement from surface water to riparian sediments. |
| Nutrient processing | Discontinuity between phenology of upland and riparian vegetation less common, resulting in less pulse-like nutrient delivery and retention in riparian vegetation. | Enhanced phenology and evergreen vegetation in riparian areas contrasts with the uplands. This enhances early season nutrient delivery and retention in riparian vegetation. |

1.2 SOIL BIOGEOCHEMISTRY OF DRYLAND STREAMS

1.2.1 Soils and sediments in the stream landscape

Soils and sediments in stream landscapes are highly variable, and often form a complex vertical and horizontal mosaic of different physiochemical types as a result of frequent erosional and depositional disturbances (Naiman *et al.*, 2005b). Soil texture and mineralogy affect most aspects of soil biogeochemistry and strong correlations are generally observed among soil organic matter (OM) content, rates of nutrient mineralisation and water availability (Hassink *et al.*, 1993; Naiman *et al.*, 2005b). The physical structure of the soil will also influence the size and distribution of pore spaces between particles, and the amount of surface area available for adsorption of organic and inorganic substances (Naiman *et al.*, 2005b). The ability of soils to hold water is particularly important in intermittent stream environments, where retained moisture can continue to drive biogeochemical processes after recession of flood waters (Naiman & Decamps, 1997).

In dryland environments, bulk soil is composed mainly of inorganic phases such as silicates, oxides and often carbonates, with extremely low (usually $\leq 1\text{-}2\%$) organic matter (Amundson, 1989). The products of weathering tend to remain *in situ*, leading to significant accumulations of duricrusts (thin and hardened surface layers) and evaporates in suitable locations (Bull & Kirkby, 2002). In the Australian drylands, weathering over many millions of years ensures that stocks of many nutrient elements are depleted, and that nutrient availability may instead depend upon the slow turnover and cycling of organically bound nutrients (Adams & Attiwill, 1986; Bull & Kirkby, 2002). This is particularly true for the central Pilbara, where an Archaean (2.5 to 3.8 bya) geological setting supports very low N and P contents, which are further depleted through successive weathering and leaching (Twidale, 1994). As a result, maintenance of soil fertility is a key issue affecting both natural and managed systems both in the Pilbara and elsewhere in dryland Australia (Islam *et al.*, 1999, 2000; Morton *et al.*, 1995).

1.2.2 Biogeochemical cycling

The biogeochemistry of dryland streams is shaped by the high internal heterogeneity of the matrix of soils and sediments - a ‘boom-bust’ ecology with extreme fluxes in nutrient availability. All organisms require nutrients for growth, particularly C, P and N (Prosser *et al.*, 1999). Concentrations and cycling activities of these and other elements are generally referred to as their biogeochemistry, and are intricately linked to overall ecosystem functioning (Gorham, 1991). In any given ecosystem, nutrient inputs may be derived from many different sources, including geological, atmospheric and biological (Bormann & Likens, 1967). In intermittent streams, these inputs may shift from those derived from in-stream production after rains, to floodplain production after severe floods, or to residual riparian production during dry periods.

An element is generally considered bioavailable if it is present as, or can be readily transformed to a free ion species, suitable for uptake by plants and other organisms (Barber, 1995). Amongst other factors, nutrient bioavailability depends on soil chemistry, the type and abundance of OM, and the presence of sufficient soil solution for transfer (Jjemba, 2004). Soil nutrients may be present in organic (immobilised or non-labile) or inorganic (labile) pools (White, 1979b). Particulate or dissolved forms may be particularly significant in aquatic systems (Findlay & Sinsabaugh, 2003; Wetzel, 2001). Inorganic nutrients are immediately available for uptake by plants and soil organisms while organic forms must be subject to decomposition or other processes before they are bioavailable (White, 1979b). In dryland soils however, nutrients and OM may accumulate during dry periods, as low soil water potentials preclude decomposition processes and uptake by organisms (Austin *et al.*, 2004; Barber, 1995). Competition between microbial sequestration of nutrients (immobilisation) and the release of nutrients in inorganic forms (mineralisation) also plays a significant role in net nutrient availability within ecosystems (Harte & Kinzig, 1993; Mulholland, 1996).

Spatial dimensions of nutrient cycling are particularly important in stream landscapes due to the strong advective forces (Mulholland, 1996). However, there is surprisingly little information on nutrient dynamics in dryland intermittent systems, and particularly for floodplain river systems (Baldwin & Mitchell, 2000). Previous studies have tended to deal with components of the stream landscape in isolation, rather than addressing

simultaneous processes in, or connections between, upland / floodplain, riparian and channel environments. As these ecosystem components do not operate in isolation, profiling pool sizes, nutrient fractions and transformations across the whole stream landscape is necessary to understand the exchanges which occur with re-establishment of hydrological connectivity after flood pulses.

A generalised nutrient cycle for a stream landscape is presented in Fig. 1.4, demonstrating the interdependence of nutrient processes across a stratified landscape. In addition, each landscape unit is expected to possess an internal patchiness of soil characteristics (see Section 1.2.1) and vegetation, that will subsequently favour or inhibit different nutrient processes (Bechtold & Naiman, 2006; Pringle *et al.*, 1988; van Coller *et al.*, 2000; Wu & Loucks, 1995). In dryland streams, this internal patchiness is expected to change considerably with changes in hydrological connectivity, as patches re-connect and disconnect. Understanding these changes can provide for integrated management of dryland streams, by determining their reliance on, and significance for, biogeochemical function in adjacent landscape units such as upland and floodplain environments.

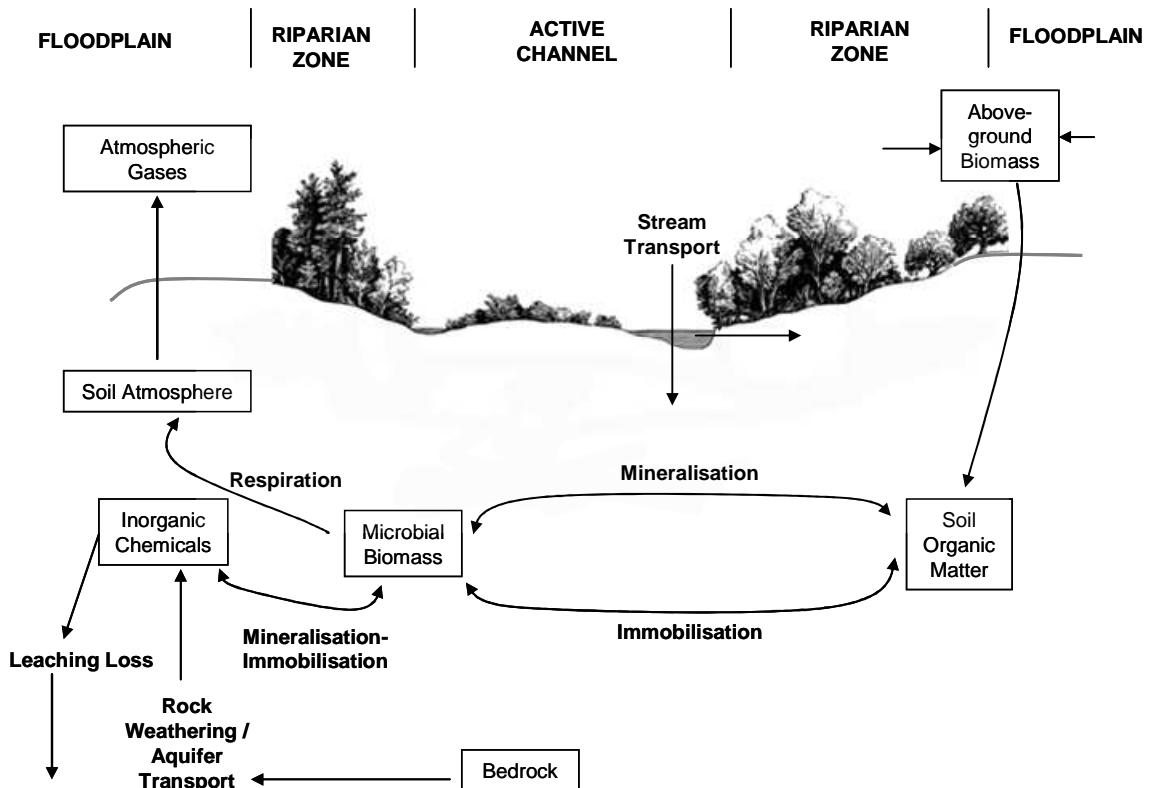


Fig. 1.4 Generalised nutrient cycle for a stream landscape, including active channel, riparian zone and floodplain. Arrows indicate direction of nutrient flow.

Tracking transformations of nutrients in the natural environment is a challenging task, which has promoted the development of a number of techniques and tools, such as methods of measuring stable isotopes at natural abundance, isotopic dilution, and element stoichiometry (Di *et al.*, 2000; Elser *et al.*, 2000; Grimm, 1992; Viaroli *et al.*, 2004; West *et al.*, 2006). One promising tool, which has been applied to ecosystem science and biogeochemistry in recent decades, is stable isotope analysis (Adams & Grierson, 2001). Processes that are otherwise unobservable or difficult to measure, such as water sources, nutrient transformation rates, or food web structure, can be detected through the use of the stable isotopes of N, C, oxygen or hydrogen (Amundson, 1989). For example, Bunn *et al.* (2003) used stable isotope analysis of C and N to determine C sources for aquatic consumers in the arid Cooper Creek system of central Australia, while Connin *et al.* (2001) examined changes in C and N isotopic discrimination to classify litter decomposition stages in Chihuahuan Desert soils in the United States. Insights can be improved considerably when this technique is used in concert with other data sources such as combining stable isotope results with the chemical, physiological or genetic profiling of soil microorganisms, such as stable isotope probing (SIP; Manefield *et al.*, 2002; West *et al.*, 2006). For example, Ewing *et al.* (2007) used a combination of multiple techniques including phospholipid fatty acid analysis (PLFA), stable isotope and DNA analyses to elucidate the spatial variability of microbial communities and the impact of this variability on C and N cycling in Mojave Desert soils.

1.2.3 Carbon transformations

In dryland streams, available C may vary considerably based on source and OM decomposition stage. Terrestrially derived carbon may be less frequently utilised by aquatic consumers in such hydrologically disconnected systems than for those consumers in permanent, mesic streams, though episodic floods may introduce vast quantities of terrestrial materials. C is used by most organisms as a source of energy and as the raw material for cellular construction. C transformations and cycling are closely linked to the N, P and sulphur (S) cycles and to the movement of energy through ecosystems, and form the bulk (usually > 50 %) of the plant and animal residues forming OM (Andreux *et al.*, 1990; Jjemba, 2004).

Within terrestrial and aquatic environments, C is present in a number of classes including coarse litter or OM, dissolved OM (DOM), particulate OM (POM), and dissolved inorganic and OC (White, 1979a). DOM, defined as OM passing through a 0.45 µm filter (Zsolnay, 2003), is the largest fraction of C in many permanent aquatic systems (Findlay & Sinsabaugh, 1999; Mulholland, 1981). In contrast, coarse particulate forms of OM (POM, particle size >0.45 µm) may dominate in intermittent systems, and form large accumulations in the stream channel and riparian zone which are subsequently redistributed by floods (Jacobson *et al.*, 1999). Regardless, the precise composition of different C pools in dryland streams may be highly variable, as are the processes that link them to form the general C cycle (Fig. 1.5).

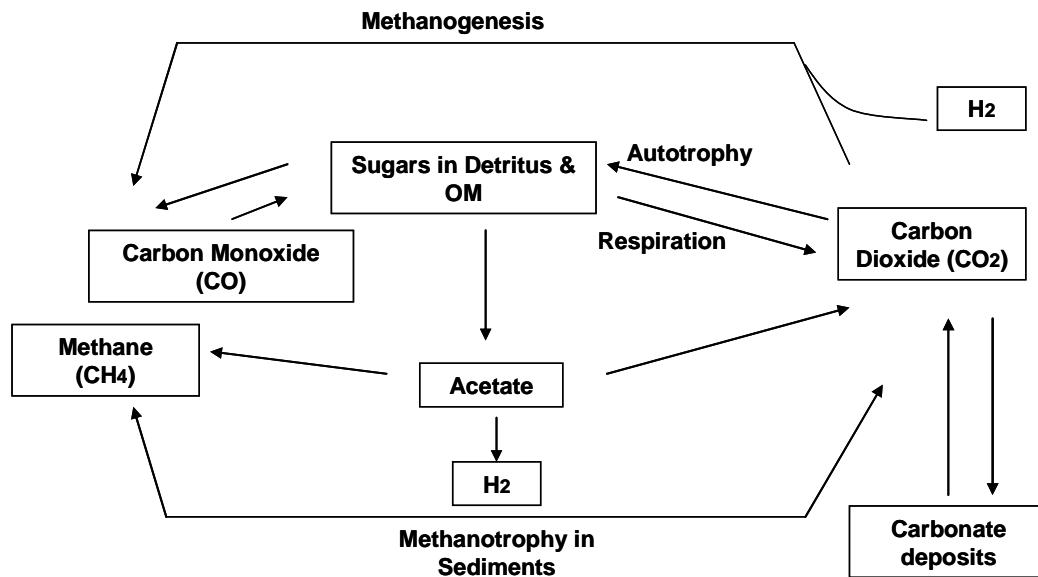


Fig. 1.5 Generalised carbon cycle, incorporating aerobic and anaerobic transitions (Jjemba, 2004). Arrows indicate direction of carbon flow.

Algae and cyanobacteria play major roles in fixing atmospheric CO₂ in aquatic systems (Atlas & Bartha, 1993a). Incorporated into OM, this C is eventually returned to the soil as detritus, and incorporated into heterotrophic biomass or liberated through respiration (Fig. 1.5). In anoxic environments, such as flooded river sediments, significant amounts of C may be cycled through digestion of OM by methanotrophic bacteria (Boon *et al.*, 2004; Hlavacova *et al.*, 2005). Invertebrates also mediate C transformations through OM breakdown, feeding on algae and microbial biofilms and acting as a food source for larger organisms (Boulton, 1999). Shredders, a functional group of stream invertebrates, may play a particularly important role in reducing bacterially conditioned litter from

coarse POM (CPOM) to finer particles < 1 mm in diameter, i.e. fine POM (FPOM; Cummins *et al.*, 1989). While the diversity of invertebrates in dryland streams is typically lower than in mesic streams, densities can be extremely high, concomitant with the boom-bust ecology of dryland systems (Boulton *et al.*, 2006; Grimm & Fisher, 1989).

The bioavailability of C to heterotrophs is highly dependent upon C chemistry, including the relative proportion of N and the presence of large and complex polymers such as lignins, waxes and phenols (Jjemba, 2004; Nannipieri *et al.*, 2003). In many ecosystems in Australia, high concentrations of structural proteins in plant material and unpredictable fire and rainfall patterns mean that organic materials with low bioavailability may accumulate on the soil surface, without decomposition, for long periods (Boulton, 1991; Towns, 1985). This is particularly true during the dry seasons of northern Australia, when litterfall is greatest (Chen *et al.*, 2003), and moisture limits the activity of decomposers. In dryland stream landscapes, fallen and stream-transported coarse (or large) woody debris are often the most significant (though low bioavailability) C stores, however little is known of their dynamics or biogeochemical influence (Jacobson *et al.*, 1999). Further information could help in tracking mass movements of C, and elucidate how wood redistribution affects retention and transformation of other nutrients in the dryland landscape.

1.2.4 Nitrogen transformations

In contrast to other biogeochemical aspects, N dynamics have been considered in depth for a few well-studied dryland systems (Dodds *et al.*, 2002; Grimm, 1992; Grimm & Petrone, 1997; Tank & Dodds, 2003), though rarely in combination with other cycles, such as C and P cycles. Nitrogen (N) is a major constituent of amino acids (and hence proteins), nucleic acids, amino sugars and their polymers, and chlorophyll (Atlas & Bartha, 1993b), and is available to plants and microorganisms primarily in the form of ammonium ($\text{NH}_4\text{-N}$) and nitrate ($\text{NO}_3\text{-N}$) (Hopkins, 1995; Naiman & Decamps, 1997). However, typically $\leq 5\%$ or less of soil N occurs in these two forms, as the vast majority is held within OM which must be mineralised before its N content is bioavailable (Ashman & Puri, 2002a).

In intermittent streams, shifts between extremes of water and oxygen availability ensures that spatio-temporal variability in N processes can be extreme at any of several scales (McClain *et al.*, 2003). Local N limitation is to be expected under these conditions (Grimm & Fisher, 1986; Holmes *et al.*, 1996). Indeed, in most soils and sediments, competing N process may dominate in proximate locations (Ashman & Puri, 2002b). Inorganic N ions are highly soluble, and hence form small, actively cycled reservoirs in freshwater systems (Atlas & Bartha, 1993b). However, under successive flood-drought regimes, losses through volatilisation of ammonia, denitrification, and leaching may progressively reduce the availability of these forms and, indeed, the total pool of soil N (Noy-Meir, 1974; Patrick & Tusneem, 1972; Reddy & Patrick, 1984).

1.2.5 Phosphorus transformations

When water is not limiting, P availability is as likely as N to limit biological productivity in dryland stream systems, except where local or regional geology supports certain P-rich minerals, e.g. apatite. Phosphorus occurs in both inorganic and organic forms in soils and sediments (Barber, 1995), and in aquatic habitats, P is most commonly present in particulate or soluble forms (Fig. 1.6; Atlas & Bartha, 1993b). Due to a combination of adsorption, co-precipitation and biotic assimilation (Fig. 1.6), particulate forms of P are dominant in riparian corridors (Naiman *et al.*, 2005b). While certain aspects of the P cycle in aquatic settings have been fairly well-researched, such as connections to algal blooms (Carpenter *et al.*, 1998; Correll, 1998), most transformations are poorly understood.

In most soils and sediments, the concentration of bioavailable soil P is generally low (Cosgrove, 1977; Ehrlich, 1981) – usually only ~ 0.01 % of the total stored P (Ashman & Puri, 2002a). P availability is further restricted by soil pH, due to the tendency of P to precipitate in neutral and alkaline conditions in the presence of bivalent metal ions such as calcium, magnesium and iron (Ashman & Puri, 2002a; Atlas & Bartha, 1993b). Iron and aluminum oxides and clays are capable of adsorbing large amounts of P from soil solutions (Fristedt, 2004). Very little P is delivered through atmospheric deposition, with most instead being released by the weathering of bedrock. However, this P remains relatively immobile and becomes progressively tightly bound to soils and sediments (White, 1979b).

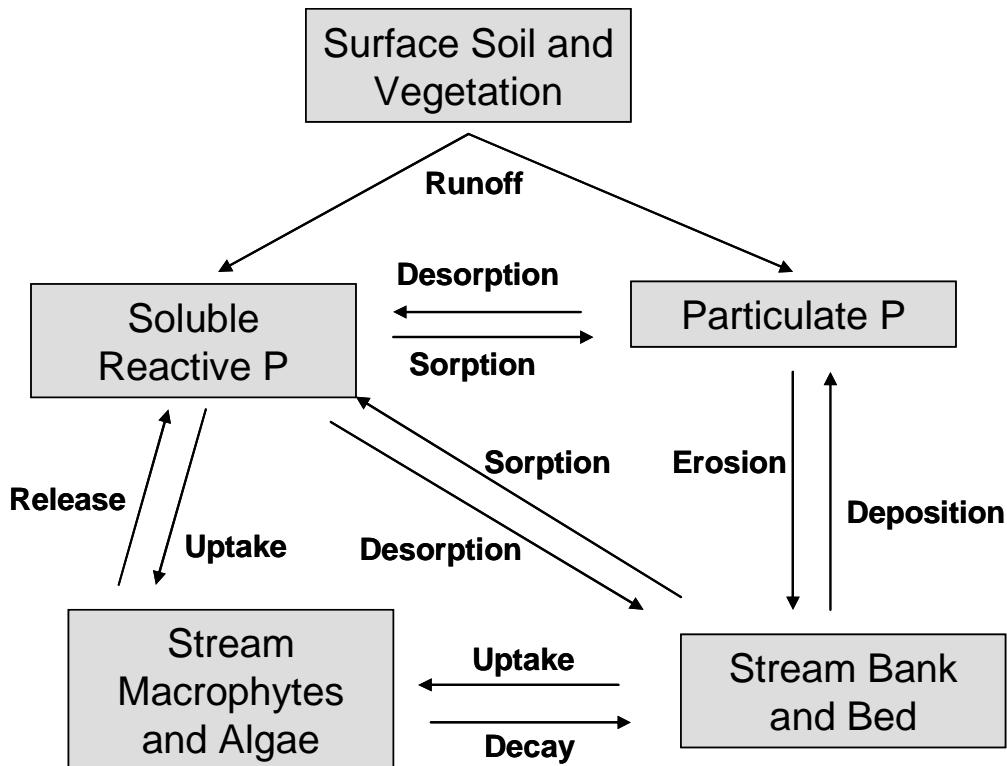


Fig. 1.6 Phosphorus transformations between terrestrial and aquatic environments. Arrows indicate direction of phosphorus flow.

Orthophosphate (PO_4^{3-}) is the only inorganic form of P present in soils and sediments, and the only form used by autotrophs (Ashman & Puri, 2002b; Correll, 1998). Consequently, the small amounts of P available to organisms are those in active circulation and productivity is P limited in many natural systems, and particularly freshwater ecosystems (Atlas & Bartha, 1993b; Naiman & Decamps, 1997). In general, these small pools of P are highly prone to disturbance by either natural or anthropogenic causes (Atlas & Bartha, 1993a). This is likely to be particularly true for dryland systems, where thin topsoils are susceptible to removal or degradation by natural or anthropogenic disturbance. Understanding P distribution and dynamics can therefore assist in long-term maintenance of soil fertility in dryland regions.

1.3 MICROBIAL AND BENTHIC ALGAE IN DRYLAND STREAMS

1.3.1 Soil microbial communities

Microbes are ubiquitous (Hart *et al.*, 1996) and ‘drive’ the biogeochemical cycles of most ecosystems (Burke *et al.*, 2003; Radajewski *et al.*, 2003; Zelles, 1999). Microbial populations are highly active and turn over quickly, and are generally diverse in both species composition and metabolic capabilities (function) – a characteristic that facilitates complex processes such as decomposition or N fixation (Ashman & Puri, 2002b; Jorgensen, 1980; Pomeroy, 1974). Nutrients mobilised by microbially mediated transformations may be available for plant growth or be sequestered by other microbes (Atlas & Bartha, 1993b).

In general, soil microbes are highly heterogeneous in their spatial distribution (Gallardo & Schlesinger, 1992), and their distribution is linked to the availability of suitable substrates (i.e. OM) and moisture, particularly in dryland systems (Kuske *et al.*, 2002; Skopp *et al.*, 1990; Stark & Firestone, 1995). During drought, microbes can form protective structures such as mucilaginous films, thickened cell walls or cysts in order to persist in a dormant stage until favourable conditions return (Ashman & Puri, 2002b). Flooding presents different challenges to microbes, as soils become submerged and anaerobic. Previous research into links between microbial activity, community dynamics and environmental conditions have mostly focused often on temperature limitations (Katterer *et al.*, 1998) rather than the effects of fluxes in water availability. In general, little is known about microbial functioning in natural systems in response to extreme environmental events such as severe flooding or prolonged drought. Part of the difficulty resides in the rapidity of microbial responses to ecosystem disturbance, and in linking community composition to function.

Within soils, microbes often live closely bound to mineral and organic material, increasing the difficulty of studying their community composition and activity (Ashman & Puri 2002a). Past studies have relied on culturing specific microbes within the laboratory – time-intensive methods which cannot be extrapolated easily to natural conditions (Aumen *et al.*, 1983). More recent studies have utilised techniques such as genetic profiling, enzyme activity analysis and PLFA to profile the composition and

functioning of natural microbial communities (Burke *et al.*, 2003; Zelles *et al.*, 1997). PLFA has proved particularly useful in measuring changes in biomass and relative shifts community composition, as fatty acids are rapidly turned over in the natural environment and hence effectively provide a qualitative and quantitative snapshot of the living microbial community (Petersen *et al.*, 1991; Sinsabaugh *et al.*, 1999; Vestal & White, 1989). Understanding the composition and dynamics of soil microbial communities is vital in modeling ecosystem biogeochemistry, as microbial profiles are closely linked to biogeochemical function.

1.3.2 Benthic algal communities

Freshwater algae are a morphologically and evolutionarily diverse group, and are prevalent in most aquatic environments (Stevenson, 1996). Benthic algae are attached to or associated with organic and inorganic substrata, such as submerged rocks and woody debris (Burkholder, 1996), and often live in close association with meiofauna (animals approximately 0.05-1 mm in length), fungi, bacteria and detritus (Fig. 1.7) within a biofilm community (Lock *et al.*, 1984; Peters, 2006). Highly variable in space and time, benthic algal communities are often the dominant primary producers in shallow aquatic environments (Havens *et al.*, 2001). Besides this role, they are significant in providing habitat and in stabilising substrata (Spork *et al.*, 2000) and their abundance and community composition been used to assess stream health (Biggs & Kilroy, 2000) and water quality (Vis *et al.*, 1998; Whitton & Kelly, 1995).

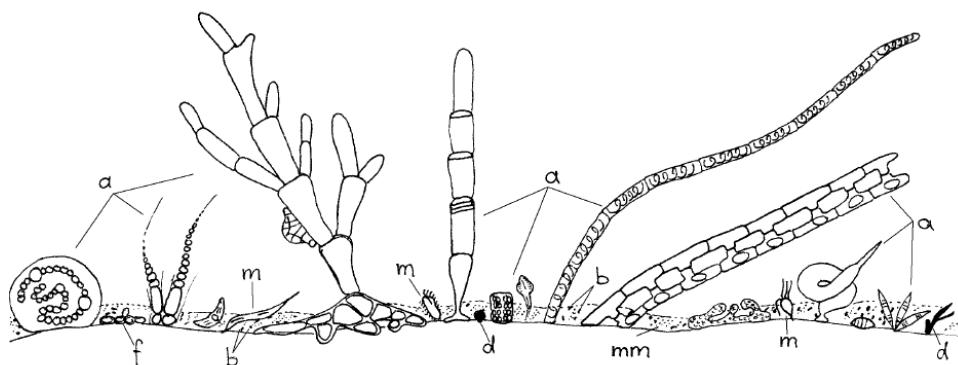


Fig. 1.7 Diagram of a typical benthic algal community, dominated by benthic algae (a), associated with meiofauna (m), fungi (f), bacteria (b) and detritus (d), embedded in a mucopolysaccharide matrix (mm). From Kahlert (2001).

Benthic algal communities occupy the interface between oxygen-depleted sediments and the overlying aerobic water column, and hence can be expected to support a diverse array of competing nutrient processes. In general, it may be expected that benthic algae assist in total nutrient supply through fixation of atmospheric gases, utilisation of substratum nutrients, uptake from stream water, incorporation of detritus (e.g. litter) and through provision of habitat for bacteria and fungi involved in nutrient transformation processes (Mulholland, 1996). Algal filaments also reduce current velocity, and hence create an adjacent boundary layer of water where retention and local cycling of nutrients (e.g. N) may be facilitated (Grimm & Petrone, 1997; Wetzel, 1993). The relationships between benthic algal communities and nutrient turnover in aquatic systems are not fully resolved, particularly for intermittent streams experiencing large spatio-temporal changes in water and nutrient availability. In these streams, understanding the dynamics of benthic algae can help quantify in-stream production, and nutrient exchanges occurring between sediments and the water column during wet periods.

1.4 PREVIOUS BIOGEOCHEMICAL STUDIES OF INTERMITTENT DRYLAND STREAMS IN AUSTRALIA AND ELSEWHERE

A small number of biogeochemical studies has been conducted in Australian dryland streams systems (e.g. Bunn *et al.*, 2003; Esslemont *et al.*, 2007; Francis & Sheldon, 2002; Lamontagne *et al.*, 2006). However, these studies have focused almost exclusively on large systems (i.e. rivers), rather than small streams. Internationally, while large river systems have also been the focus of most biogeochemical studies (e.g. Jacobson *et al.*, 2000; Lewis *et al.*, 2007; Tibbets & Molles, 2005), a greater pool of active researchers means that there exist some well-studied small stream systems, primarily in North America, such as the Sycamore Creek system in Arizona (e.g. Dent *et al.*, 2007; Fisher *et al.*, 1982; Grimm, 1987; Heffernan & Sponseller, 2004). While large rivers have an obviously significant regional influence, small intermittent streams cover the vast majority of the Australian continent, and processes occurring in these feeder tributaries as a whole significantly affect the biogeochemistry of downstream reaches. As such, we require comprehensive profiles of biogeochemical function in small streams (as to be provided in this thesis) in order to scale-up to region-wide processes.

Dryland streams are disproportionately sensitive to environmental pressures such as climate change, pastoralism and cultivation, water harvesting, and salinisation (Kingsford, 2006). While water quality, macroinvertebrates, and algal communities have been traditionally used as indicators of stream health, the potential of biogeochemical indicators (e.g. rates of decomposition, microbial activity, or N and C mineralisation) have not been fully explored. Biogeochemical measures of stream health offer a fundamental ‘bottom-up’ assessment of system function, in contrast to higher-order response measures e.g. macroinvertebrate composition. However, before such biogeochemical indicators of stream health can be adequately derived, we first require baseline studies, such as presented in this thesis, to define key biogeochemical processes, their rates and spatio-temporal heterogeneity.

1.5 PROJECT AIMS

This thesis provides the first detailed investigation of the role of flooding in biogeochemical cycling of three major elements (N, P, and C) in the soils and sediments of intermittent small streams, their associated riparian zones and floodplains, within the Australian drylands. My study focused on the spatio-temporal variation of different nutrient fractions in relation to riparian vegetation communities, topography and seasonal water and substrate availability. I sought to address the following integrative questions in this thesis:

1. How does flooding affect soil C, N and P patterns across the stream landscape?
2. How do microbial activity and community profiles, and N and C mineralisation change in response to water and substrate availability?
3. What are the interrelationships between benthic algae, nutrient availability and microbial communities in channel beds?

Briefly, Chapter 2 provides an overview of the study region - the Pilbara - including climate, geology and soils, vegetation, catchments and management issues. Original experiments conducted as part of this research project are then detailed in the following five chapters. Chapter 3 addresses biogeochemical patterns for the entire stream landscape (floodplain, riparian zone, banks and channels), through field-based examination of spatio-temporal dynamics in C and nutrient cycling and microbial

dynamics at Barnett Creek. Chapter 4 further explores these concepts in terms of finer-scale patterns in channel bed sediments. To resolve further detail in N processes in response to water availability, a lab-based incubation study examining potential N mineralisation in saturated Pilbara soils is presented in Chapter 5. A further lab-based incubation study, considering C and N mineralisation, microbial activity and community profiles responses to rewetting and substrate availability in Pilbara soils is detailed in Chapter 6. The interrelationships between benthic algae, nutrient availability and microbial communities in channel sediments are addressed in Chapter 7, using field observations from the second study site at Ratty Springs on Pirraburadoo Creek. Lastly, Chapter 8 provides a final synthesis of this research project including implications, limitations and further possible steps.

CHAPTER 2

The Pilbara Region

2.1 OVERVIEW

The setting for this thesis is the Pilbara region (Fig. 2.1), located in the northwest of Western Australia, about 1750 km north of Perth, and encompassing an area of > 508,000 km² (Department of Local Government & Regional Development, 2006). Extending from the Indian Ocean in the west and north to the Great Sandy Desert in the east and Ashburton River in the south, the Pilbara can be separated into three distinct geographical formations: a vast coastal plain, inland ranges and an arid desert region continuing into central Australia (Pilbara Development Commission, 2006b). The region has moderately high relief, with the Hamersley Range being the highest range (average 900 m asl) in the State, and Mt. Meharry as the highest peak at 1251 m (Bureau of Meteorology, 2006a; Pilbara Development Commission, 2006b). The Pilbara constitutes a distinct bioregion under the Interim Biogeographic Regionalisation for Australia (IBRA) categorisation with four bio-subregions – the Chichester, Fortescue Plains, Hamersley and Roebourne (Department of Conservation and Land Management, 2002; Environment Australia, 2000; Thackway & Cresswell, 1995).

Two sites within the inland ranges of the central Pilbara were the focus of field studies for this thesis. Both of these sites were located on small, intermittent streams within the Hamersley Ranges, and the Hamersley bio-subregion (Fig. 2.1). The first site was Barnett Creek on Hamersley Station and 14 km north-west of Tom Price township. The second site was at Ratty Springs on Pirraburadoo Creek, situated on a mining lease currently held by Pilbara Iron Pty Ltd, approximately 13 km west of Paraburadoo township. Ratty Springs is about 100 km south of Barnett Creek (Fig. 2.1). These sites are discussed in detail in Section 2.8.

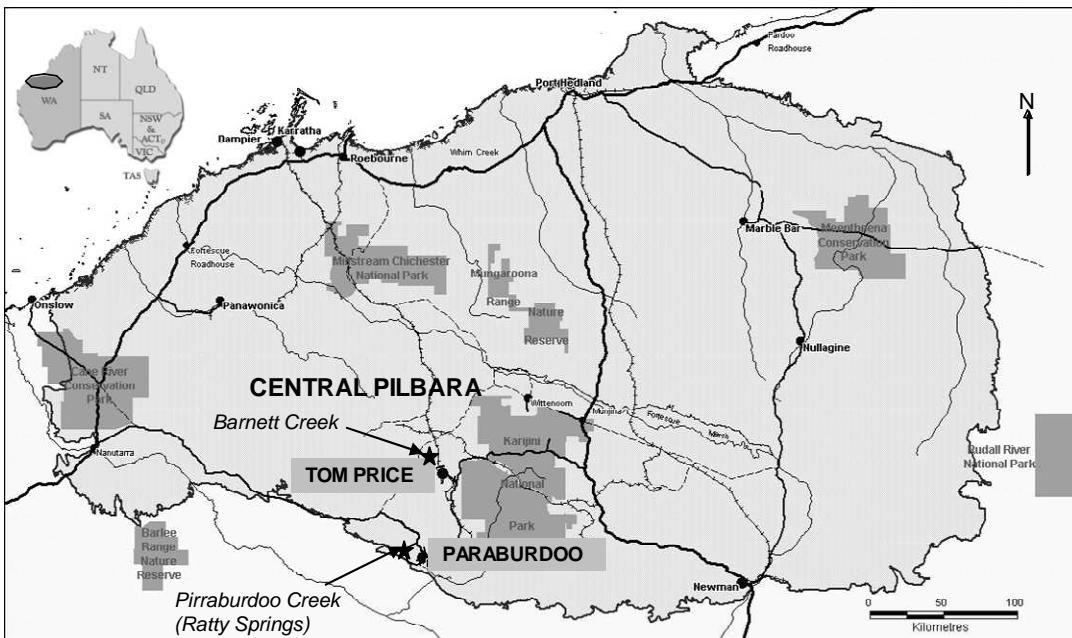


Fig. 2.1 Location of the central Pilbara region in north-west Australia. Locations of Barnett Creek and Pirraburadoo Creek (Ratty Springs) study sites indicated by arrows. Modified from Cookson *et al.* (2006).

2.2 CLIMATE

The climate of the Pilbara region is semi-arid and typical of the arid tropics elsewhere. It is characterised by hot summers with irregular thunderstorms and cyclones, and mild, dry winters (Payne *et al.*, 1988). Maximum winter temperatures generally range between 15-25 °C, whereas summer maximum temperatures inland average 26-40 °C, but can regularly exceed 40 °C for long periods, particularly in the east Pilbara (Bureau of Meteorology, 2007a). Maximum summer temperatures in the coastal Pilbara are typically 5 °C lower than those inland (Bureau of Meteorology, 2006a). Typical monthly temperatures and rainfall for the central Pilbara (Wittenoom; 22.24 °S, 118.34 °E) are given in Fig. 2.2. Rainfall (average ~340 mm yr⁻¹) is loosely bimodal and extremely variable both among seasons and between years, with most rainfall resulting from decaying summer cyclones moving south from the Indian Ocean in the January-March period (Bentley *et al.*, 1999; Department of Water, 2004; Pringle *et al.*, 1990). Coefficients of variation for annual rainfall are typically 40-70 % (Department of Water, 2004).

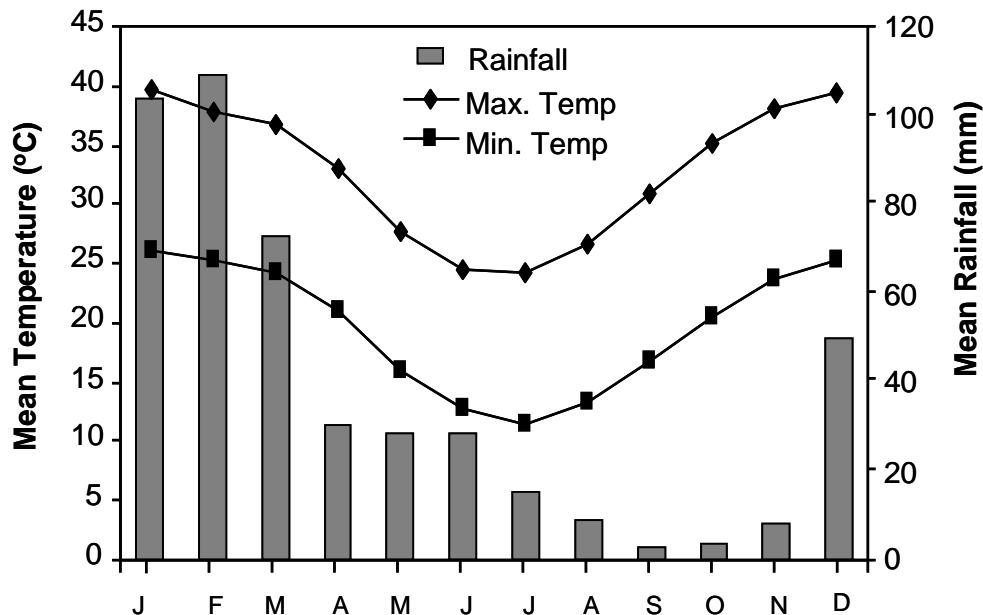


Fig. 2.2 Long-term monthly averages for temperature and rainfall for the central Pilbara, 1949 - 2007 (Bureau of Meteorology, 2007b). Bureau of Meterology, Site: # 005026 - Wittenoom, 22.24 °S, 118.34 °E.

The Pilbara region has a long-term average of four cyclones a year, contributing to episodes of heavy rain and flooding (Commonwealth of Australia, 2000). There were three significant cyclones impacting central Pilbara districts during the study period of January 2004 – August 2006: namely Cyclones Monty (February-March 2004; 150-300 mm rainfall), Clare (January 2006; 100-200 mm rainfall) and Glenda (March 2006; ~200 mm rainfall). Associated rain caused significant regional flooding in the central Pilbara during these periods (Bureau of Meteorology, 2006b, c, d). Floods also cause erosion and significant damage to infrastructure and private property (Mitchell & Leighton, 1997). In the first three months of 1980, Cyclones Amy, Dean and Enid resulted in over \$25 million worth of combined property damage, when rainfall in excess of 600 mm fell in some areas of the eastern Pilbara, causing severe regional flooding (Commonwealth of Australia, 2007b).

Evaporation greatly exceeds rainfall in the Pilbara region (Fig. 2.2), and pan evaporation on Hamersley Station is typically between 100-150 mm month⁻¹ during winter, and 350 - 400 mm month⁻¹ during summer (Landman, 2001). Radiation at the soil surface is often between 150-350 W m⁻², resulting in soil surface temperatures that are frequently ≥ 40 °C in summer (Landman, 2001).

2.3 GEOLOGY, GEOMORPHOLOGY AND SOILS

The geology of the central Pilbara is complex, and includes some of the oldest exposed rock deposits in the world, consisting of interbedded Archaean (2.5 to 3.8 bya) basalt, sandstone and dacite, overlain by eroded early Proterozoic (1.6 to 2.5 bya) sandstones and shales (Western Australian Geological Survey, 2006). The ranges form part of the Pilbara craton which has been exposed since the Palaeozoic (248 to 544 mya). This section of the craton is comprised of the metasedimentary Hamersley Ranges and the predominantly volcanic Chichester Ranges in the north (Trendall, 1990). The ranges overlay Archaean greenstones and granites that outcrop in the northeast. Extensive deposits of late Archaean (2.5 to 3.0 bya) banded iron ore formation (BIF) and shale formations are distributed throughout the Pilbara (Western Australian Geological Survey, 2006).

Pilbara soils are varied and highly weathered, and often include alluvial clays derived from basalt, with surface gravel of jaspilite (interbedded jasper and iron oxides) and quartz (Beard, 1975). A regolith of fine red sand blankets much of the eastern half of the region, and the vadose zone is typically very thin (Trendall, 1990). Duricrusts (thin, hard surface layers) are evident in many areas, with well-developed ferricretes, silcretes and calcretes (Hocking & Cockbain, 1990; Killick *et al.*, 2001). Soil classes in the central Pilbara are typically Ferralsols (deep, strongly weathered soils with a chemically poor, but physically stable subsoil), Regasols (soils with very limited development) or Calcisols (soils with accumulation of secondary calcium carbonates; World Reference Base for Soil Resources, 2003). The N and P contents of soils across the Pilbara are generally very low, due to formation from nutrient-poor parent material and successive weathering and leaching over many millions of years (Twidale, 1994). Total soil N of less than 0.07% and available P of less than 0.004% have been recorded in previous nutrient studies in the Pilbara (Ford *et al.*, 2007; Islam *et al.*, 1999). Indeed, Pilbara soils often have mean concentrations of N and P that are less than half those in soils of comparable aridity occurring elsewhere around the world (Bentley *et al.*, 1999).

2.4 VEGETATION

The study area lies within the Pilbara Botanical District, which is part of the Eremaean Botanical Province (Beard & Sprenger, 1984). In comparison to the South-West and Northern (Kimberley Region) Botanical Provinces that form the remainder of the Western Australian land area, Eremaean flora is not highly endemic (11 % of taxa) as it exhibits overlap with pan-Australian, central desert flora (Beard *et al.*, 2000). Nonetheless, the flora of the Pilbara is quite diverse, with > 1700 documented plant species, representing an overlap between northern tropical and inland, arid species (Western Australian Herbarium, 2008). Recently, the Pilbara ('Hamersley-Pilbara') was also listed as one of 15 National Biodiversity Hotspots, due to its provision of habitat for a number of threatened and endemic species and communities by the Department of Environment, Water, Heritage and the Arts (DEWHA; 2008). The Pilbara Region Biological Survey was conducted from 2002-2007 in 800 study sites throughout the region, and audited all occurring flora and fauna (Department of Environment and Conservation, 2008a). The final survey report (due for publication in 2009), is expected to detail a further significant increase in the known species richness for the region.

The study area in the central Pilbara includes the Fortescue (Hamersley Plateau subunit) and Ashburton (Ashburton Valley subunit) botanical districts (Beard, 1975). These subunits are divided by a climatically controlled vegetation boundary known as the *Acacia - Triodia* line that represents the transition from the northerly Eremaean vegetation dominated by *Triodia* steppe, to a southern-species, *Acacia* - dominated scrub and low woodland typical of the Gascoyne and Murchison Regions (Beard, 1975). On the Hamersley Plateau, the vegetation is broadly classified as tree steppe, dominated by *Eucalyptus brevifolia* – *Triodia wiseana* with small mallee *Eucalyptus gamophylla* in the ranges, and joined by *Eucalyptus kingsmillii* and *Callitris columellaris* on mountain summits. Riverine woodland contains scattered elements of *Eucalyptus camaldulensis*, *Eucalyptus microtheca*, *Acacia pruinocarpa*, *Acacia tumida*, *Eremophila longifolia* and various herbs, over *Triodia pungens* on lower slopes. Valley plains were mapped by Beard (1975) as mulga formation (*Acacia aneura* low woodland) over tussock grasses, while basalt hills are a “mosaic of *Acacia aneura* low woodland and *Acacia pyrifolia* - *Triodia* shrub steppe” (Beard, 1975). In the Ashburton Valley, the main river channels are lined by *Eucalyptus camaldulensis*, with *Melaleuca leucadendra*, *Acacia citrinoviridis* and *Acacia coriacea* on the river flats (Beard, 1975). Loam flats support

scrub of *Acacia victoriae*, *Acacia sclerosperma* and *Acacia wanyu* over smaller shrubs such as *Senna artemisioides* ssp. x *artemisioides*., while local clay flats and shingle plains are considered comparatively ‘poorly vegetated’ (Beard, 1975).

Key vegetation types, their spatial extent and retention status since European settlement are listed for Western Australia by Shepherd *et al.* (2002), using remote sensing data referenced against vegetation communities described by previous ground surveys (e.g. Beard). More recent vegetational information for the Pilbara has been collected in numerous small biological surveys (Department of Environment and Conservation, 2008b), performed on a local scale and in an *ad hoc* manner as part of the reporting process for development approvals. As such, no comprehensive, regional vegetation mapping has been attempted for the Pilbara since the work of Beard in the 1970s.

2.5 LAND USE AND ECONOMY

Pastoralism has been a major land use in the Pilbara since the 1800’s; however, mining activities have increased in spatial extent and economic importance over the last 50 years. Regardless, pastoral land use by extensive grazing still accounts for > 70 % of total land area in the Pilbara, with nature conservation and indigenous use areas representing > 20 % of the total area, and minimal use (particularly mining) accounting for the remaining areas (DEWHA, 2007). Today, the economy of the Pilbara is dominated by mining (mainly iron ore) and petroleum industries (North-West Shelf & Barrow Island), which contribute > 60 % of the value of total production for Western Australia (Pilbara Development Commission, 2006a). Total gross regional product is ~ AUD\$7 billion, contributed mainly by mining, with smaller contributions from the tourism, fishing, salt production and pastoralism industries (Department of Local Government and Regional Development, 2008; Pilbara Development Commission, 2006a). The permanent resident population of the Pilbara is approximately 39,000, however fly-in / fly-out (FIFO) workers contribute an additional large and fluctuating population (Chamber of Minerals and Energy, 2005).

2.6 HYDROLOGY AND STREAMS

2.6.1 Surface water

Three major catchments drain the Pilbara region: the Ashburton, Fortescue and De Grey (Fig. 2.3), the last of which shares a major boundary with the catchments of the Great Sandy Desert to the east (Halse *et al.*, 2002). The two study sites for this research were both located within the Ashburton catchment. The Fortescue and Ashburton Rivers collectively form extensive floodplains, draining either side of the Hamersley Ranges, while the Robe, Yule and De Grey Rivers extend as broad deltas from the highlands toward the Indian Ocean (Reeves *et al.*, 2007). Numerous other minor rivers also traverse the region.

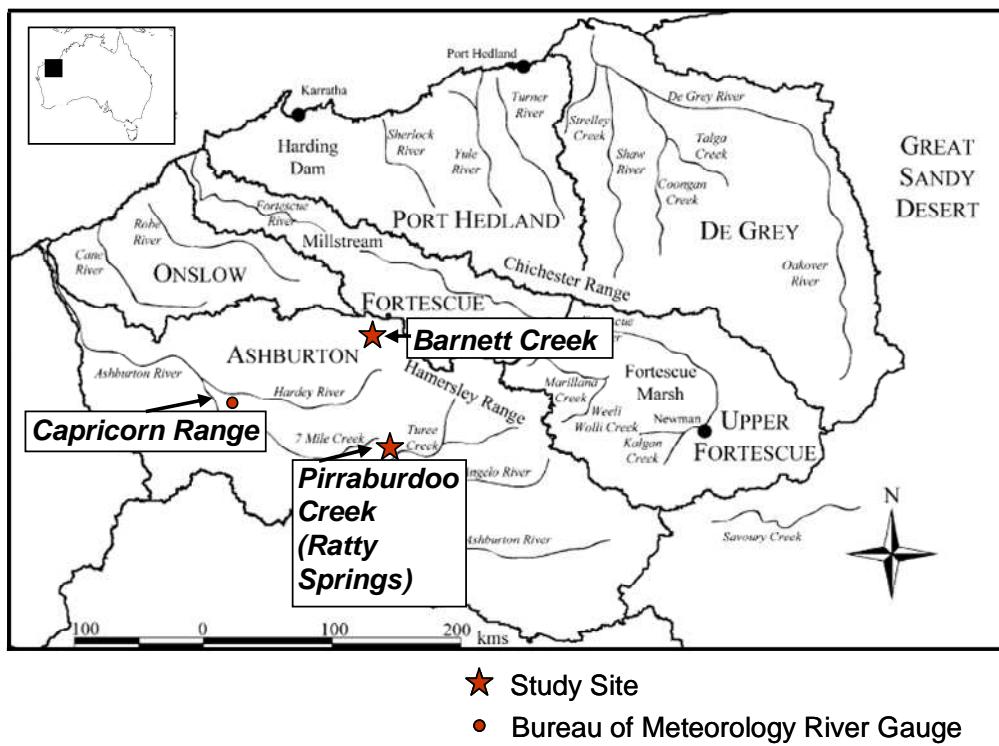


Fig. 2.3 The major catchments of the Pilbara region (modified from Reeves *et al.*, 2007), with project study sites and Bureau of Meteorology river gauge station (Capricorn Range).

Pilbara rivers drain the uplands of the Hamersley, Ophthalmia, Chichester and associated inland ranges, and are generally fresh with well-defined courses (Department of Environment and Conservation, 2004). These rivers flow through extensive floodplains in their lower courses, whereas upper courses may traverse deep gorges

created by regional uplift of the Hamersley plateau. In general, the three main river catchments are considered to be relatively undisturbed and in good health (Environmental Protection Authority, 2006; Halse *et al.*, 2002). Concentrations of dissolved nutrients in these natural waters are low (e.g. $<0.6\text{ mg L}^{-1}$ total N and $<0.01\text{ mg L}^{-1}$ total reactive P); however, redistribution of floodplain materials after floods may temporarily increase nutrient loadings (Kay *et al.*, 1999).

There is minimal information on the chemistry and biology of surface waters in the Pilbara, and this is particularly true for small streams. With the exception of a few aquatic macroinvertebrate and stygofauna studies (Kay *et al.*, 1999; Reeves *et al.*, 2007; Smith *et al.*, 1999), there are no peer-reviewed published studies of Pilbara streams, and few other studies considering aspects of other ecosystems in the Pilbara. Most information has been collected on a regional scale by government departments, or in piecemeal manner by industry as part of development approvals or environmental impact monitoring.

Typically, surface water is scarce in the Pilbara, and all rivers present are ephemeral and support surface flow only occasionally, primarily existing as disconnected pools or completely dry courses for considerable periods (Department of Water, 2004). Any persistent surface water is largely restricted to drainage lines or pools supported by natural springs (Reeves *et al.*, 2007). In nearly 50 % of years there is no or little streamflow in northern Pilbara rivers, with limited winter streamflow typical of southern and western rivers (Department of Water, 2004). Hence, zero surface flow is the ‘norm’, and not an indicator of drought. After heavy rains, rivers flood and often reconnect with their floodplains. In general, the Pilbara region is one of hydrologic extremes, with droughts of more than three years duration common for rivers that may subsequently flood and produce flow rates equivalent or greater than the annual flow rates of the major permanent rivers of other continents (Department of Water, 2004).

2.6.2 Groundwater

Generally, Pilbara groundwater is fresh, with salinity ranging from $200\text{--}1500\text{ mg L}^{-1}$, and is bicarbonate-dominated. Some waters with high sodium chloride concentrations are found in the coastal and arid eastern margins (Reeves *et al.*, 2007). Regional groundwater also tends to be low in dissolved nutrients (Department of Environment

and Conservation, 2003). There are three significant aquifer types in the Pilbara region: i) unconsolidated sedimentary aquifers, including recent valley-fill alluvium and colluvium, and coastal deposits; ii) chemically deposited calcretes and pisolithes within Tertiary drainage channels; and iii) fractured-rock dolomite, banded-iron formations and granite, which form local aquifers (Johnson & Wright, 2001). The majority of recharge is contributed by cyclonic rains, with a component of seepage from major waterways into aquifers during times of peak flow, and groundwater generally flows from the interior ranges towards the coast (Reeves *et al.*, 2007). In coastal aquifers, there may be significant interaction between surface water and groundwater (Department of Water, 2004), though in the majority of the Pilbara, there exist only localised interactions at natural springs, particularly in karstic areas (Johnson & Wright, 2001). Groundwater information for the majority of the Pilbara region is still lacking.

2.6.3 Riparian zones

Riparian environments in the Pilbara, and their associated floodplains or uplands, largely remain undescribed. In general, floodplain rivers and streams in the Pilbara may follow complex, sinuous and anastomosing courses (Plate 2.1), ensuring that riparian zones are variable in width, and often much more extensive than the riparian zones of more temperate streams (Storey *et al.*, 2001). Floods often move significant amounts of material to down-slope locations and along drainage lines, contributing to debris piles within the riparian zone and channel (Baynes *et al.*, 2005), as well as altering surface topography (Mitchell & Leighton, 1997). Rocky areas in the central Pilbara may have considerable topographic relief, leading to gravity-induced debris flow and rock falls into the stream system (Baynes *et al.*, 2005).



Plate 2.1 Aerial photograph of the main channel of the Ashburton River south of Mt Stuart, central Pilbara (22.5431 S, 116.1192 E), showing meandering, anastomosing morphology (Google, 2007).

As in other dryland environments, riparian communities in the Pilbara tend to be hot spots for plant diversity in the broader landscape (Rangelands WA, 2004), and provide habitat and resources for fauna. Rivers and creeks in the Pilbara are generally lined with eucalypts, particularly *Eucalyptus camaldulensis* and *E. victrix*, which often form groves around permanent pools (Beard, 1975). On minor channels and broader reaches of watercourses, these eucalypts are mixed with patchy scrub dominated by *Acacia* and *Melaleuca* spp. In contrast, the floodplain environments are a mosaic of plant communities ranging from grass savannah to tree and shrub savannah with *Acacia xiphophylla* and an understorey of annual grasses and spinifex (Beard, 1975). The transition between riparian environments and their associated floodplain and uplands (Plate 2.2) tends to be rather abrupt in the Pilbara, and watercourses are highly visible in the landscape due to the clustering of taller trees.

2.6.4 Stream and water management

Pilbara streams are affected by groundwater abstraction and pumping, recreational use, livestock trampling and grazing. They are also subject to invasion by a number of introduced plant species (Grice, 2006; Smith *et al.*, 1999; Water and Rivers Commission, 2001), particularly *Cenchrus ciliaris* L., *Cynodon dactylon* (L.) Pers., *Vachellia farnesiana* (L.) Wight & Arn., and *Acetosa vesicaria* (L.) A.Love (*pers. obs.*). In general, the effects of these pressures intensify during the frequent and long dry periods (Halse *et al.*, 2002). Due to these threatening processes, all major ephemeral watercourses in the Hamersley bioregion are considered to be ‘ecosystems at risk’ with a status of Vulnerable (Kendrick, 2002).

As the Pilbara region is developed further for mining and, to a lesser extent, agriculture and tourism, demands on available groundwater will increase. Indeed, expectations are that water use will triple in the Pilbara region over the next 25 years (Department of Water, 2007). Abstraction of groundwater has the potential to negatively impact groundwater-dependent ecosystems through lowering of the water table, and river pool and spring ecosystems in the Pilbara are particularly vulnerable to such hydrologic changes (Hatton & Evans, 1998). Where water tables decline, riparian health may decline through lack of available water (Masini, 1988), and groundwater-dwelling endemics such as stygofauna may be negatively affected (Gregory, 2006; Reeves *et al.*, 2007). Conversely, any local rise in water tables may also cause riparian decline through waterlogging (Francis, 2006).

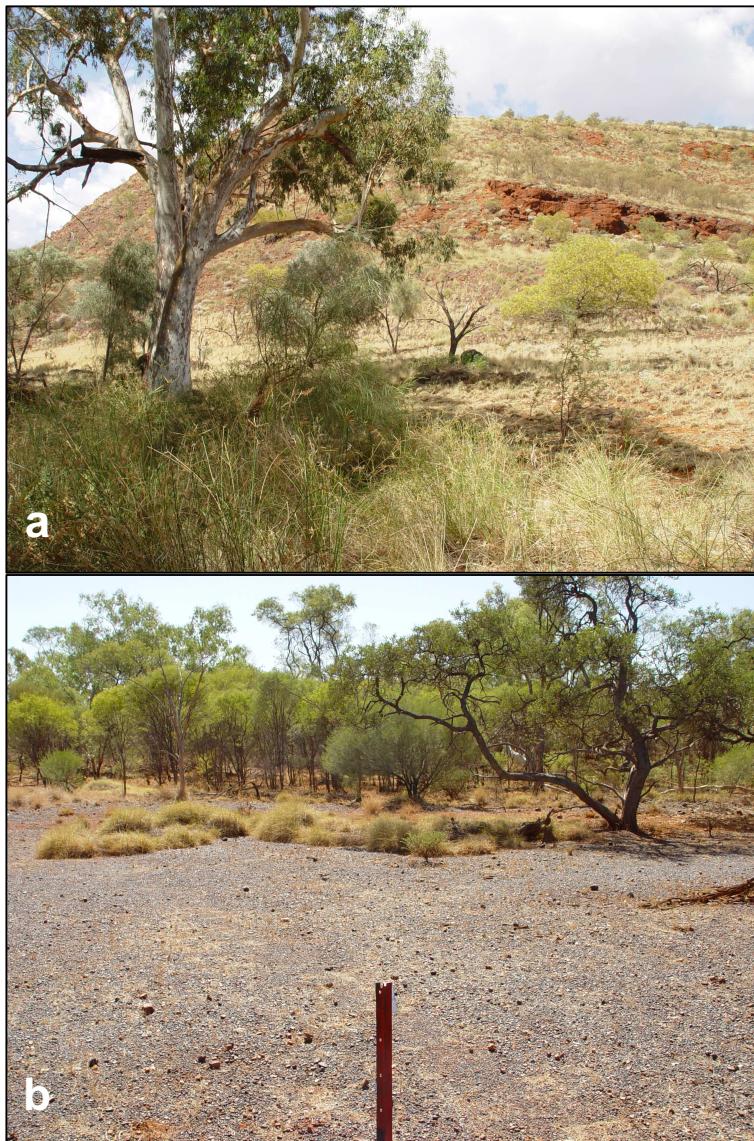


Plate 2.2 Landscape transitions in Pilbara streams, between a) riparian zone and rocky uplands at Pirraburadoo Creek, and b) between the riparian zone (background woodland) and floodplain (foreground grassland) with spinifex and lateritic gravel at Barnett Creek.

2.7 CLIMATE CHANGE

Mean temperatures have increased between 0.10-0.15 °C every 10 years between 1910 and 2006 in north-west Australia (Commonwealth of Australia, 2007a), and from 1900 to 2006, rainfall also increased by 5-10 mm every 10 years in the region (Commonwealth of Australia, 2007c). However other data suggest that, since 1980, conditions have been cooler in the Pilbara than anytime in the previous 80 years (Hennessy *et al.*, 1999; Suppiah, 2004). Stable isotope analysis of tree rings by Cullen

and Grierson (2007) has also indicated that summers in the Pilbara have become cooler and more humid since 1955. These inferred changes in climate correspond to a measured increase in rainfall since 1980 in north-west Australia associated with a greater intensity of tropical cyclones (Plummer *et al.*, 1999).

Although the vegetation of semi-arid and arid regions is adapted to short-term fluctuations in climatic conditions, long-term changes in climate variability are likely to have significant impacts on individual species (e.g. Cullen & Grierson, 2007), ecosystem processes and community composition (Pittock, 2003). Over the next century, rainfall in dryland regions of Australia is expected to become even more variable (Hughes, 2003). There remains considerable uncertainty as to the natural long-term climate cycles in dryland Australia (Pittock, 2003), which also hampers efforts to predict future climate change and their impacts. This uncertainty reflects the relative lack of long-term (>100 years) climate records for regions inland of the heavily populated coastal areas (Bureau of Meteorology, 2001).

2.8 STUDY SITES

2.8.1 Barnett Creek

The study site at Barnett Creek (50570457 E, 7511289 N) – an unregulated intermittent tributary of the Ashburton River - is located on Hamersley Station 14 km north-west of Tom Price township at 620 m elevation (Fig 2.1, Plate 2.3a). Barnett Creek forms a braided, anabranching pattern typical of many dryland rivers in lowland, unconstrained settings (Thoms *et al.*, 2006) and drains a catchment area of approximately 3000 km². The creek has a gravel and cobble channel bed, loam to loamy-sand riparian zone, and sandy floodplain capped with lateritic gravel and calcrete outcrops. Soils and sediments are moderately alkaline (pH 7.9). The study site encompasses a 500 m reach of the creek, including one main channel and one anabranch, extending ~20 m into the surrounding floodplain on each side. Banks range from 1-2 m high, with channel widths up to 14 m.

Annual rainfall in the Tom Price area is highly variable, ranging from 69 to 800 mm in the 80 years of records from Hamersley Station homestead (Bennett & Adams, 1999). While Barnett Creek is not gauged, total monthly discharge varies from no flow to

>1050 GL in the Ashburton River main channel at Capricorn Range (Australian Bureau of Meteorology Station #706209; WA Department of Water *unpubl. data*), ~100 km downstream of the study site (Fig. 2.3). Large river discharges usually follow intense summer cyclones, and water can persist in tributaries for > three months after such events. Flow at Capricorn Range was zero for approximately one-third of all months between 1972 and 2006, with a mean flow of 29 GL, ranging from 0 to 1050 GL with CV=370 % (WA Department of Water, *unpubl. data*; Fig. 2.4). During interflood periods, depth to groundwater at Barnett Creek is typically ~20 m within the channel and riparian zone and ~ 40 m in the floodplain (Landman, 2001).

Barnett Creek lies within the Fortescue Botanical District and Hamersley Plateau physiographic unit as defined by Beard (1975). The local area has small bands of *Eucalyptus brevifolia* and *Triodia wiseana* in a broader matrix of *Acacia aneura*, *A. pyrifolia*, *Triodia basedowii* and *T. pungens* (Beard, 1975). At Barnett Creek, floodplain vegetation is dominated by *Triodia* hummock grasses, small chenopods and *Eremophila* spp. shrubs, while the riparian zone is vegetated by often dense stands of *Acacia citrinoviridis*, with *Eucalyptus victrix* and *E. camaldulensis* lining channel banks. Barnett Creek is subject to limited grazing and informal recreational usage (picnicking) but is otherwise relatively undisturbed.

2.8.2 Pirraburadoo Creek

The second study site at Ratty Springs (50555077 E, 7433596 N) is located 14 km west of Paraburadoo township (Fig. 2.1). Ratty Springs is part of Pirraburadoo Creek (Plate 2.3b), an intermittent and unregulated tributary of the Ashburton River, and is loosely constrained in a 60-100 m wide valley by ~20 m high ironstone hills, at an elevation of 390 m asl. Pirraburadoo Creek drains a catchment of approximately 5000 km² in area. At Ratty Springs, the creek is a network of small (up to 5 m wide) channels divided by vegetated banks. Pirraburadoo Creek floods typically once every 2-5 years, usually between December and March (Bureau of Meteorology, 2008). As for Barnett Creek, data for Capricorn Range (zero flow for approximately one-third of all months) provides an approximation of long-term flow variation (Fig. 2.4).

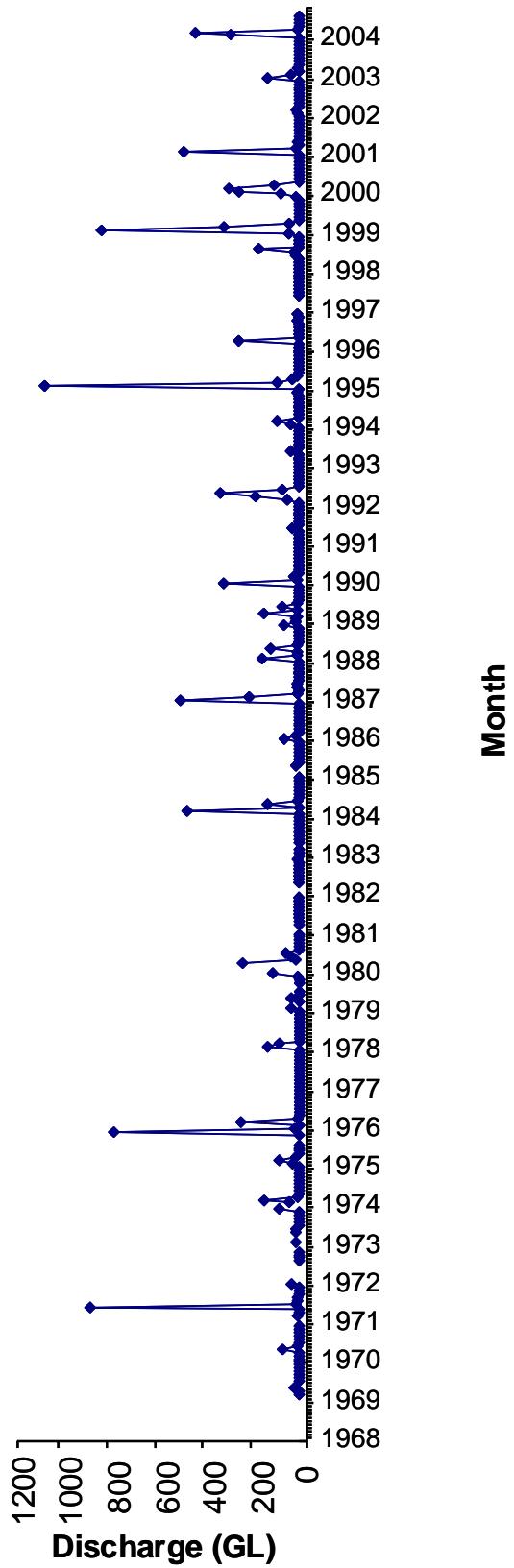


Fig. 2.4 Hydrograph of Ashburton River discharge at Capricorn Range, 1968-2004.

Pirraburadoo Creek is in the Ashburton Valley vegetation unit of the Ashburton Botanical District (Beard, 1975). The local area west of Paraburadoo was mapped by Beard (1975) as Snappy Gum (*Eucalyptus brevifolia*) and spinifex (*Triodia wiseana*), intergrading with Snakewood (*Acacia xiphophylla*) and other mixed wattles, *Acacia aneura* shrubland and teatree (*Melaleuca* spp.). Riparian vegetation at the study site has an evergreen overstorey dominated by *Eucalyptus victrix*, *Acacia citrinoviridis*, *Senna* spp. and *Melaleuca glomerata*, with an understorey dominated by sedges (*Cyperus* spp.), grasses such as *Eriachne mucronata* and *Cymbopogon ambiguus*, and small forbs (e.g. *Sida* and *Solanum* spp.). *Acacia aneura* and *Triodia pungens* dominate on surrounding hills.

Ratty Springs occurs above a rock bar, which acts as a “reservoir wall” for groundwater in the creek aquifer, causing groundwater levels to rise and connect into the lower reaches of the creek aquifer (Rathbone, 2005). The creek flows over poorly sorted alluvial sediments (10-15 m thick), with calcrete lenses (~1 m thick) present in the subsurface and exposed at creek margins (Resource and Environmental Management & Ensis, 2007). Surface sediments are mildly alkaline (pH 8.5), and consist of lateritic gravels and sands in upland areas, grading to sandy-loams in the riparian zone and gravel-topped sands in stream beds (see Chapter 7). Bulk density of surface soils (<5 cm depth) are typically high (~1.41 gm⁻³), reflecting a composition of heavy sands with intermixed gravels. Fine soil fractions (<2 mm) are almost pure sand (>98 %), with a small clay fraction.

The Barnett and Pirraburadoo study sites were selected to be representative of small, unregulated and intermittent watercourses in the central Pilbara region. This was based primarily on appraisal of landform and dominant vegetation communities (mapping and descriptions of Beard, 1975; Shepherd *et al.*, 2002), as well as the regional knowledge of long-term Pilbara researchers (P.F. Grierson and M.A. Adams).

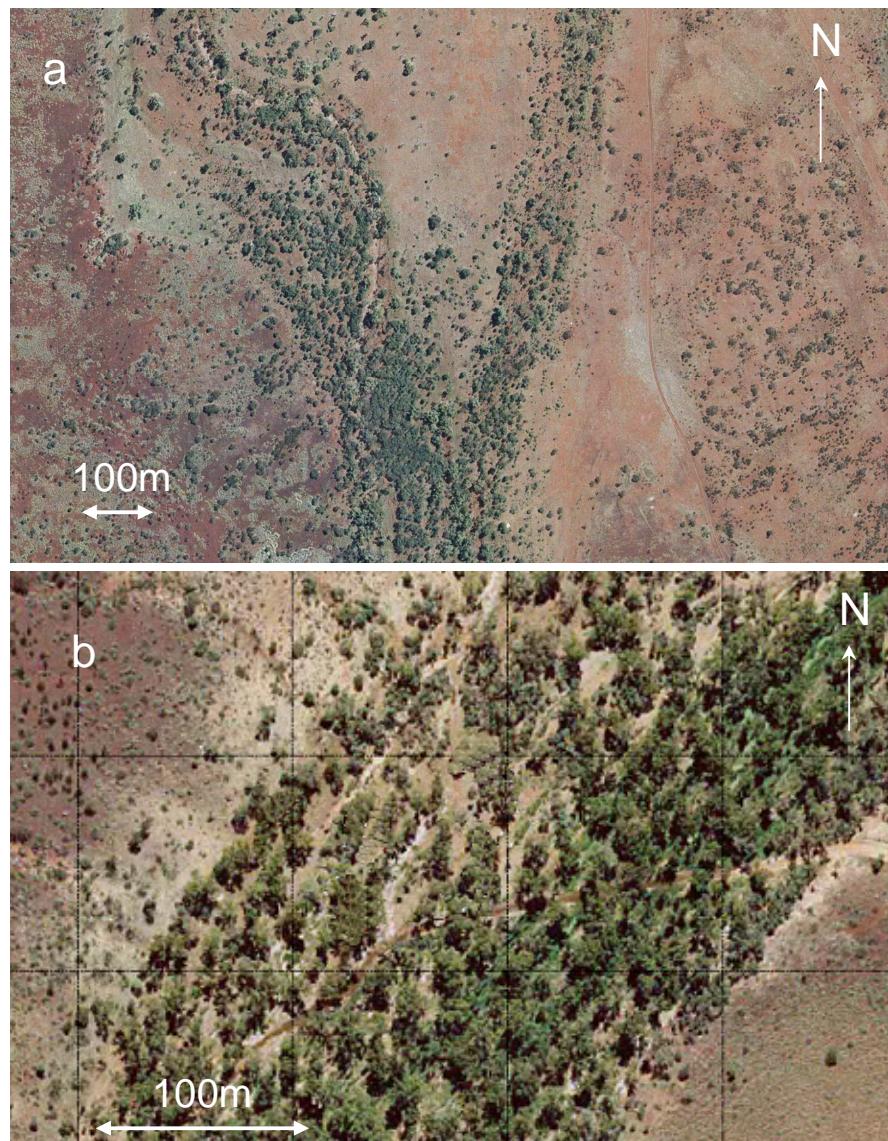


Plate 2.3 Aerial photographs of the study sites at (a) Barnett Creek (Landgate, 2007) and (b) Ratty Springs on Pirraburadoo Creek (Resource and Environmental Management & Ensis, 2007).

CHAPTER 3

Biogeochemical Patterns in Cross-Stream Toposequences at Barnett Creek

3.1 INTRODUCTION

Dryland stream systems, and particularly their associated riparian zones, are an important nutrient ‘hot spot’ within the broader landscape, supporting retention of water and nutrients and key biogeochemical transformations, including N fixation and OM decomposition (Harms & Grimm, 2008; Jacobs *et al.*, 2007; Lamontagne *et al.*, 2006; Schade *et al.*, 2005). Patch dynamics in streams have been considered primarily from the perspective of habitat provision (Lake, 2000; Pringle *et al.*, 1988), while studies of soil heterogeneity in semi-arid lands have tended to focus on non-lotic systems such as grasslands and shrublands (Schlesinger *et al.*, 1996; Tongway & Ludwig, 2005). The biogeochemistry of intermittent rivers and their associated riparian zones remain largely unstudied, likely due to the remote and unpredictable nature of these systems, and our existing knowledge has been derived primarily from systems in the south-west United States (e.g. Fisher *et al.*, 2001; Grimm *et al.*, 1981). Regardless, the amount of available nutrients in dryland soils is expected to be closely tied to rainfall pulses - owing to the tight coupling of mineralisation processes and soil moisture (Austin *et al.*, 2004; Belnap *et al.*, 2005; Ford *et al.*, 2007).

Vegetation, edaphic conditions and topography change considerably across stream landscapes, from the floodplains (or uplands) to the riparian zone and active channels. Nutrients may be exchanged laterally between floodplains, riparian zones, banks and channel beds, or longitudinally between stream reaches, depending on the size and direction of hydrological flows in the landscape. Concordant with these exchanges, nutrient hot spots and cold spots migrate spatio-temporally in the stream landscape. Vertical nutrient

exchanges are also significant in dryland streams elsewhere (e.g. Dent *et al.*, 2007), but are likely to be of less relevance to non-spring fed streams in sandy areas of inland Australia, where the nutrient content of groundwater is low and where groundwater only occurs at considerable depth.

Spatially, biota and resources in stream landscapes may appear patchy or gradational across multiple or hierarchical scales, or scale-dependence may be unobvious (Fisher *et al.*, 1998; Wright & Li, 2002). At smaller scales (10^0 - 10^2 metres) variability in soil texture and porosity and in the composition and activity of microbial communities contribute strongly to nutrient spatial heterogeneity (Bechtold & Naiman, 2006; Housman *et al.*, 2007). Topography and surface roughness in particular influence many processes at the soil surface (Hauer *et al.*, 2001; Lockaby *et al.*, 1996; Stoeckel & Miller-Goodman, 2001). For example, topographic depressions may accumulate OM, nutrients and microbial biomass (Belnap *et al.*, 2005; Harms & Grimm, 2008) and hence be ‘primed’ to act as biogeochemical hot spots after moisture pulses (Gallardo & Schlesinger, 1992), supporting relatively greater microbial activity and nutrient transformation. Conversely, harsh resource-poor patches (e.g. an indurated, unvegetated surface) may create a biogeochemical cold spot in the landscape (*sensu* Fisher & Welter, 2005), where nutrient transformations and microbial activity are inhibited. Surface topography of stream landscapes is frequently altered by disturbances such as flooding (Hauer *et al.*, 2001), influencing hot spot dynamics by redistributing biota and resources. Consequently, determining the interactions between precipitation events, soil surface and textural characteristics, and microbial and nutrient dynamics is essential to producing rigorous mechanistic models for ecosystem biogeochemistry (Schwinning *et al.*, 2004), particularly for dryland regions.

I sought to identify biogeochemical hot spots within an intermittent stream landscape (channels, banks, riparian zone and floodplain) during both flood and interflood periods. Soils were sampled at Barnett Creek (Section 2.8.1) over a three-year period that included a major flood. I sought to determine the effects of moisture availability, topography and landscape position, including four landscape positions (channels, banks, riparian zone and floodplain), on spatio-temporal patterns of soil nutrients (N, P), C, and microbes (biomass and community composition). I hypothesised that increased moisture availability (flooding)

would reduce spatial heterogeneity of available nutrients and microbial biomass in the landscape. Furthermore, I expected that this heterogeneity would be greatest in the riparian zone relative to other landscape positions, and that nutrients and microbial biomass would be greater in areas with greater microtopography (cm-scale). Finally, I considered observed patterns in the context of meso-scale ecosystem function (nutrient availability and microbial activity) of intermittent streams, and the development and loss of biogeochemical hot spots through flood-drought dynamics.

3.2 METHODS

3.2.1 Study period

Field studies were conducted at Barnett Creek (Section 2.8.1). During the study period from July 2004 to March 2006, Barnett Creek only flowed once (between December 2005 and March 2006; the ‘flood period’), when the local catchment received an unusually large amount of rain (522 mm, i.e. 1.5 times the yearly average in 3 months) (Fig. 3.1; Bureau of Meteorology, 2007). After recession of flood waters, base flow depth in channels was ~ 10–20 cm for 1–2 mo. Barnett Creek is ungauged; however, total discharge of the main channel of the Ashburton River during December 2005 and March 2006 was over 1000 million m³, reflective of severe regional flooding (Fig. 3.1; Department of Water, 2008). For the remainder of the study period, both before and after flooding (the ‘interflood period’), Barnett Creek remained dry. Prior to the study period, the most recent recorded flow was in February–March 2004. Consequently, sampling was undertaken in three periods – July 2004 (early interflood), August 2005 (late interflood) and March 2006 (flood).

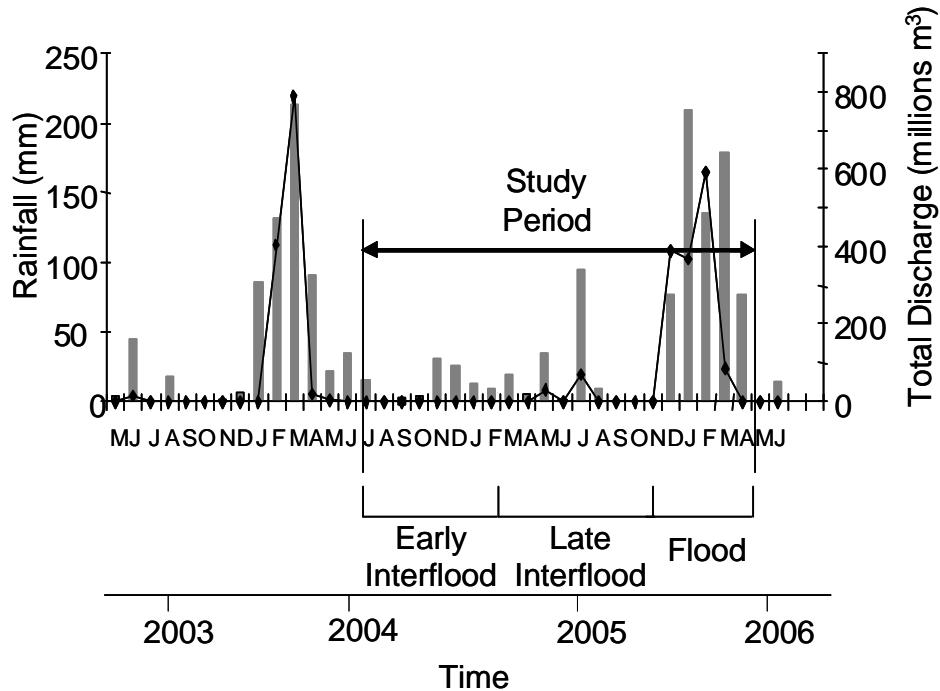


Fig. 3.1 Monthly rainfall at Tom Price, Western Australia, and total monthly discharge for the Ashburton River (main channel) during the study period. (Bureau of Meteorology, 2008; Department of Water, 2008).

3.2.2 Stream toposequences

The study site encompassed a ~ 500 m stream reach, covering an area of ~ 20 ha. Three cross-channel transects (Transects 1, 2 and 3) were established across the main channel of Barnett Creek and an anabranch (Fig. 3.2). All transects incorporated 25 m of the floodplain on either side of the creek, the two channels and the entire associated riparian zone (Fig. 3.3). Transects were parallel to each other, 20 m wide, 200 m apart and increased in length downstream (Transect 1= 224 m, Transect 2= 292 m, and Transect 3=386 m) owing to increasing distance between the main channel and anabranch. Metal pickets were placed at the ends and every 50 m along the three transects. All pickets and sampling locations from all sampling times were geo-referenced by Global Positioning System (GPS; Magellan eXplorist 210, San Dimas, United States).

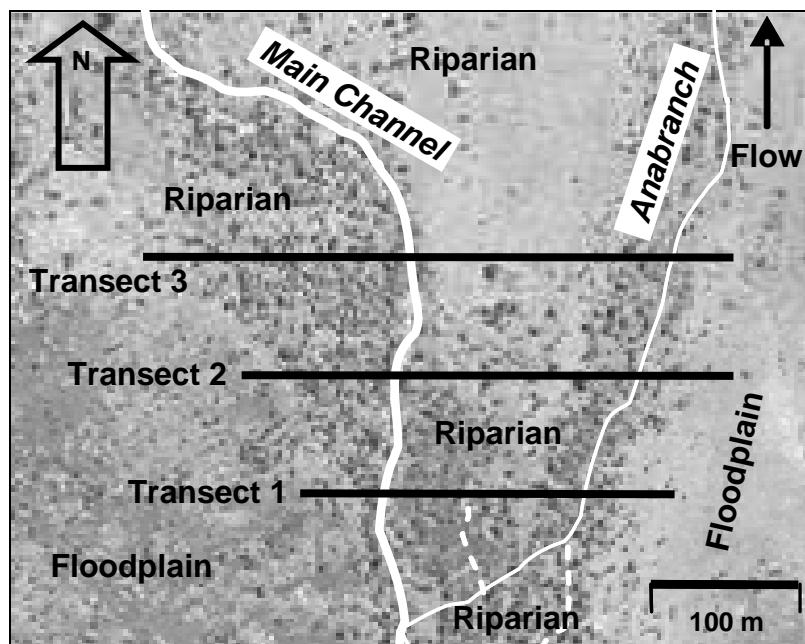


Fig. 3.2 Location of the three toposequence transects (Transects 1, 2 and 3) at Barnett Creek.

The sampled area was divided into four main landscape positions based on functional and vegetative characteristics: channel, bank, riparian and floodplain (Table 3.1; Plate 3.1). Banks were defined as raised alluvial deposits of ≤ 2 m width, lining channels. Transitions between adjacent landscape positions tended to be abrupt and easily recognisable in the field. The transition from floodplain to riparian zones was marked by a change from low scrubland to low woodland / forest dominated by *Eucalyptus* spp. and *Acacia citrinoviridis*, a potentially N-fixing species (Sprent, 2001). The riparian zone was further delineated into three community types (Table 3.1; Fig. 3.3): i) *Eucalyptus* open woodland, ii) *Eucalyptus* closed woodland (typically lining channels), and iii) *Acacia citrinoviridis* thicket. *Eucalyptus* woodland was dominated by *E. camaldulensis* and *E. victrix*. Hence, a total of six landscape positions were considered. Vegetation on banks shared overstorey vegetation with *Eucalyptus* closed woodland, with greater ground cover by annual forbs. Floodplain vegetation was dominated by soft spinifex (*Triodia pungens*), interspersed with chenopods, *Eremophila* spp. shrubs and *Hakea lorea* ssp. *loreia* trees.

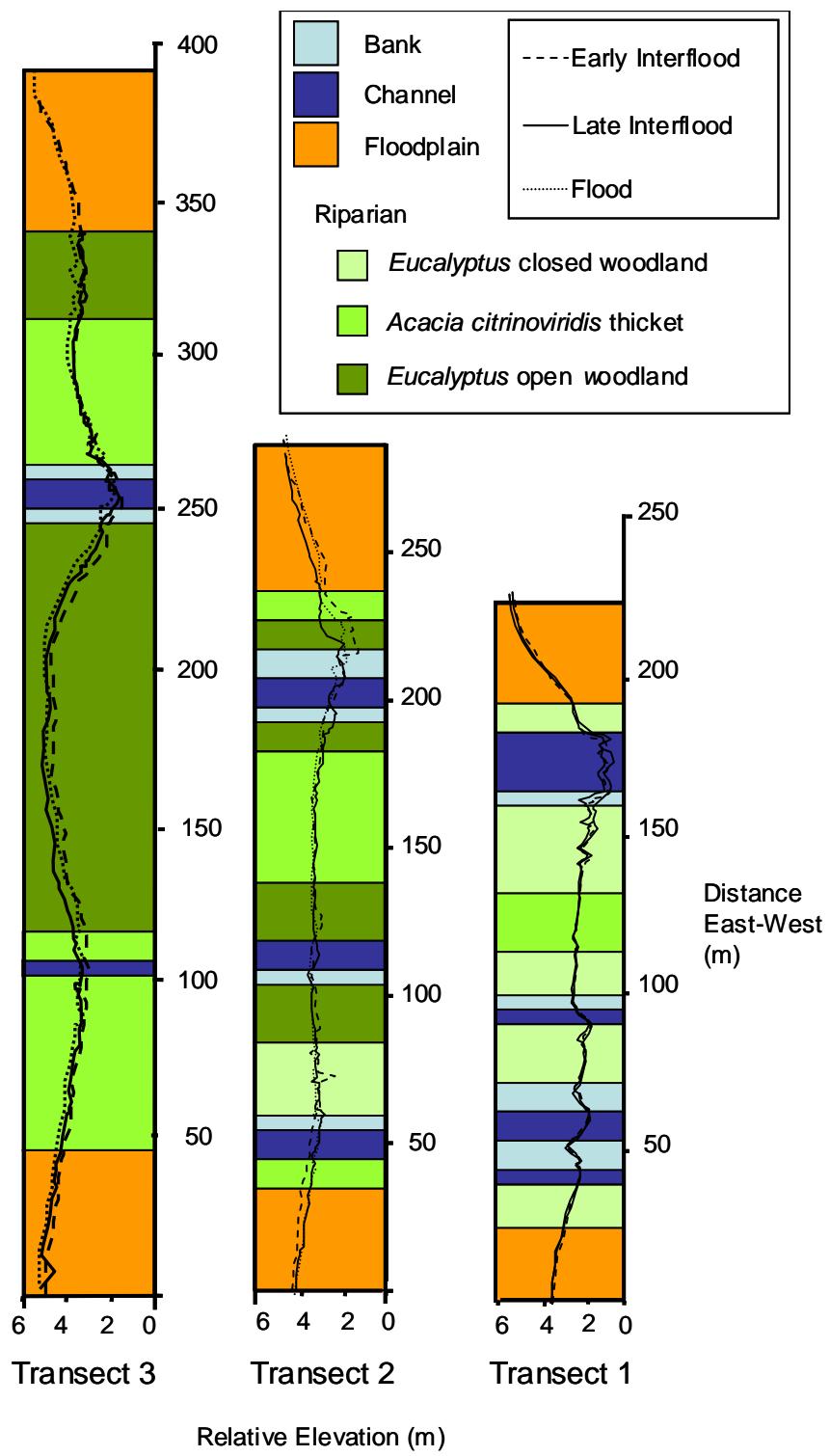


Fig. 3.3 Relative elevation across Barnett Creek toposequence transects (Transects 1, 2 and 3) in early and late interflood, and flood periods.

Table 3.1 Vegetation classification and general soil properties at different landscape positions at Barnett Creek. Data are means with SE in parentheses.

| Landscape Position | Muir (1977) Vegetation Classification | pH | Soil Type | Sand (%) | Clay (%) | Silt (%) | BD (g cm ⁻³) | |
|--------------------|---|-----------------------------|----------------|-----------------|------------------|-----------------|-----------------------------|----------------|
| Bank | Mid-dense low woodland | 7.66 (0.30) | Loam | 59.96 (0.84) | 15.95 (6.69) | 24.09 (7.08) | 1.33 (0.45) | |
| Channel | n / a | 7.88 (0.28) | Sand | 95.18 (3.85) | 4.74 (3.89) | 0.08 (0.20) | 1.70 (0.58) | |
| Floodplain | Sparse low scrub | 7.76 (0.76) | Loamy- Sand | 77.76 (2.58) | 9.79 (1.76) | 12.45 (0.87) | 1.83 (0.13) | |
| | <i>Eucalyptus</i> open woodland | Sparse open low woodland | 8.00 (0.08) | Loam | 60.64 (10.05) | 17.60 (0.53) | 21.76 (9.52) | 0.67 (0.32) |
| Riparian | <i>Eucalyptus</i> closed woodland | Mid-dense low woodland | 7.97 (0.14) | Loam | 57.31 (1.27) | 17.62 (8.34) | 25.07 (7.13) | 1.04 (0.11) |
| | <i>Acacia</i> <i>citrinoviridis</i> thicket | Mid-dense low forest | 7.48 (0.32) | Loam | 70.53 (11.96) | 15.03 (9.73) | 14.44 (13.73) | 0.80 (0.51) |

Soil sampling was stratified by landscape position and randomised between each landscape transition. Randomisation was performed for each transect using two numbers - a lateral distance (nearest m within each landscape transition) and a longitudinal distance (nearest m perpendicular north / south of the transect midline). At each sampling time, sufficient samples were taken from each landscape position to ensure an equal number of replicates among landscape position (corresponding replicates for each analysis type are provided where relevant).

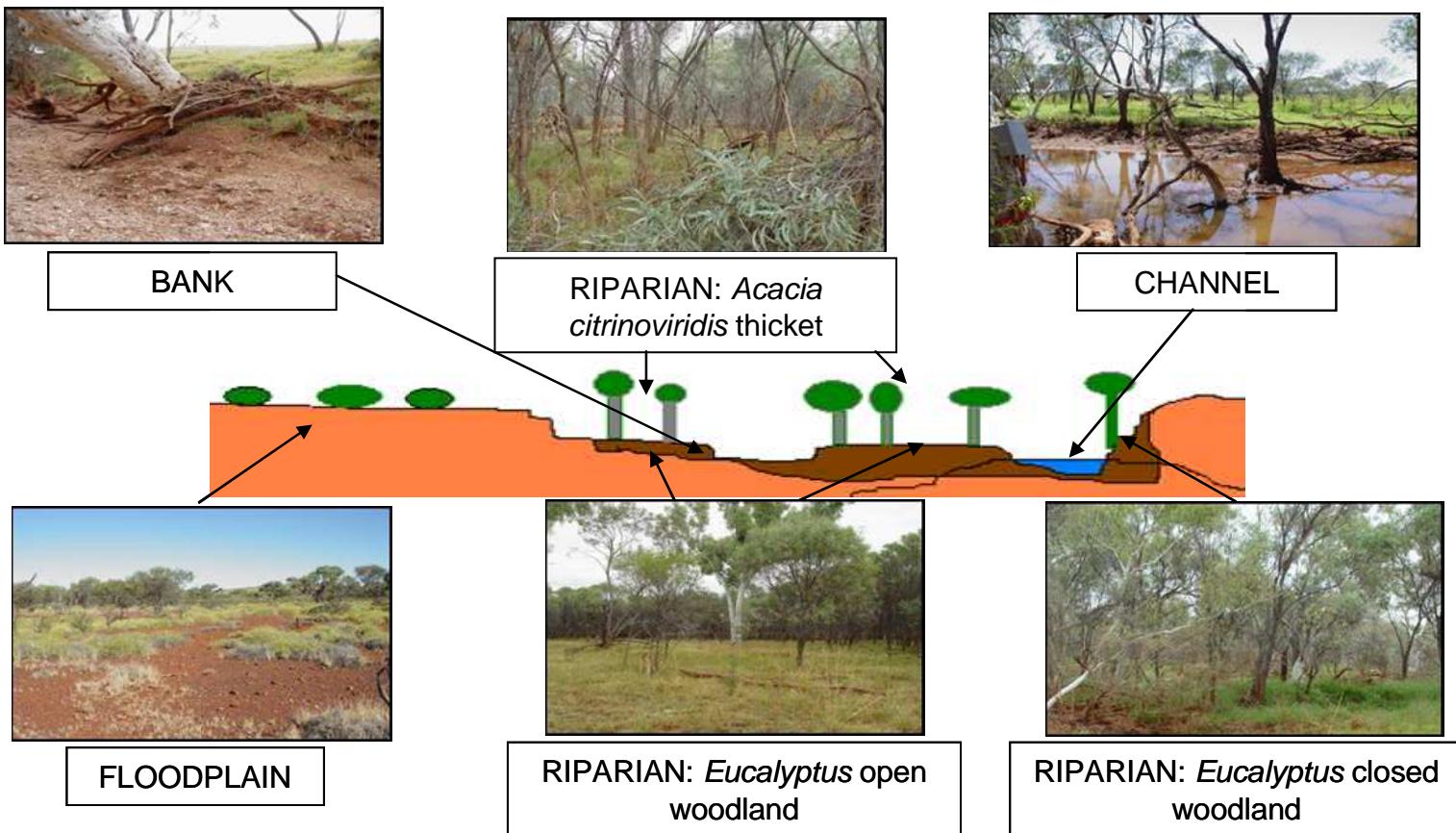


Plate 3.1 Representative photographs of landscape positions at Barnett Creek.

3.2.3 Characterisation of soil physical properties

Bulk density of surface soils (0-5 cm depth) was determined using the core method (diameter 8 cm) to collect 292 cm³ samples from each landscape position in November 2005 ($n=5$). The unsieved soils were dried at 100 °C and bulk density calculated as the oven dry weight of soil divided by soil volume, and adjusted for the presence of rocks and large gravel (Cresswell & Hamilton, 2002). Soil samples (~500 g; 0-2 cm depth; $n=5$) were also collected from each landscape position and subjected to particle size analysis using a method modified from Day (1965). Samples were pre-treated with repeated additions of 1 M HCl and centrifuging to remove dissolved carbonates. Determined fractions of clay, silt and sand were used to categorise soils into textural classes (Marshall, 1947).

3.2.4 Soil and sediment nutrient analysis

To characterise nutrient patterns and identify possible biogeochemical hot and cold spots, soil samples (~100 g; 0-2 cm depth) were collected from each landscape position, sieved to <2 mm in the field, and later analysed for nutrients. Field sieving was sufficient to extract the fine soil portion, and any soil clods were broken by hand to ensure even sieving. Soil samples were stored in individual zip-locked plastic bags and transported in eskies (wet samples), or in woven polyethylene bags (dry samples) for 10-30 hours before storage at 4 °C. Gravimetric soil moisture content (%) was determined after drying a 5 g soil subsample at 100 °C for three days. pH was measured on a subset of soil samples ($n=5$; 1:1 sample: deionised water). Soils were also analysed for total N and C content (%; $n=7$), and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰), using an automated N / C Analyser-Mass Spectrometer consisting of a Roboprep connected with a Tracermass Isotope Ratio Spectrometer (Europa Scientific Ltd, Crewe, UK). All samples were standardised against a secondary reference of radish collegiate (3.167 % N; $\delta^{15}\text{N}$ 5.71 ‰; 41.51 % C; $\delta^{13}\text{C}$ -28.61 ‰) that was subsequently standardised against primary analytical standards (IAEA, Vienna). Accuracy was measured as 0.07 % and precision as 0.03 %.

Labile NH₄-N and NO₃-N were extracted by shaking 5 g soil ($n=20$) in 50 mL of cold 1 M KCl for 1 h (Rayment & Higginson, 1992), and filtering using Whatman filter paper #40

(Whatman, Brentford, Middlesex, UK). Samples were stored at 4 °C until analysis within four weeks. Concentrations of NH₄-N and NO₃-N were analysed on a Technicon Autoanalyzer (Technicon Instruments, N.Y, USA). Labile inorganic P (OH-P_i) was extracted by shaking 10 g soil (*n*=20) in 50 mL of 0.1 M NaOH for 16 h and then filtering (Bentley *et al.*, 1999). An acidified extract was analysed for OH-P_i using a modified ascorbic acid method (Kuo, 1996) and analysed at 880 nm using a UV-1601 UV-visible spectrophotometer (Shimadzu, Kyoto, Japan). Total labile P (OH-P_T; *n*=20) was extracted by subjecting a subsample of the original extract to H₂SO₄ / H₂O₂ digest and analysed by the same method used for OH-P_i. Organic P (OH-P_o; *n*=20) was calculated as OH-P_T minus OH-P_i. Oxidisable organic C (OC) was determined for soils (*n*=7; 0.5-2 g) from each landscape position using the Walkley-Black method (Nelson & Sommers, 1996).

3.2.5 Microbial biomass and community composition

Extra soil samples (~15 g; *n*=15) were collected from the six landscape positions to assess microbial biomass and community composition by PLFA. Soil samples were sieved to <2 mm in the field, transported on ice and stored at -20 °C in the dark until freeze-drying within one week of initial collection. PLFAs were extracted from freeze-dried soils (~5 g) using a modified one-phase extraction technique as described by Zelles and Bai (1993). The fatty acids (FAs) and their derivatives were analysed on a Shimadzu GC-17A (Shimadzu, Kyoto, Japan) Gas Chromatograph using flame ionisation detection (FID), with settings as detailed by Ford *et al.* (2007). Fatty-acid methyl-esters (FAME) abundances were determined by the peak area and height, and extraction efficiency by the internal standard peak area. The concentration of each fatty acid was determined relative to the internal standard and calculated using the following formula (1):

$$\mu\text{g individual fatty acid g}^{-1} \text{ soil} = (\text{P}_{\text{FAME}} \times \text{ng Std}) / (\text{P}_{\text{ISTD}} \times \text{dilution} \times W) \quad (1)$$

where P_{FAME} and P_{ISTD} were the peaks of each fatty acid and internal standard respectively, ng Std is the concentration of the internal standard (ng μL^{-1} solvent), and *W* is the dry weight cm^{-3} of soil for extraction. Diversity (no. PLFAs g^{-1} dry weight) for each sample was estimated by the number of fatty acids identified by retention time, including the reference

set: 9:0, 10:0, 11:0, 10:00-2OH, 10:0-3OH, 12:0, 13:0, 14:0, 14:0-2OH, 14: 0-3OH, 15:0, 16:0, 16:0-2OH, 17:0, 18:0, 19:0, and 20:0.

3.2.6 Landscape topography

Relative elevation was measured along the three transects using an optical theodolite (Autolevel PAL-5C, Sokkia, Rydalmere, Australia) and a 4 m telescopic levelling rod (TN 14, Geo Fennel, Baunatal, Germany). Density of sampling points was sufficient to capture small (~5 mm) changes in elevation, resulting in an average of 107 points for Transect 1, 124 points for Transect 2, and 165 points for Transect 3 being assessed at each sampling time. Relative elevation was calibrated against elevation at the fixed start point of each transect at 0 m east (E) for each sampling time. Vertical and horizontal resolution was to the nearest cm, and higher values of relative elevation therefore correspond to rises while lower values represented depressions. Change in relative elevation was assessed by comparison of elevation against distance for the three sampling times. Random roughness (the standard deviation of elevation from a plane across an area, after oriented roughness has been accounted for) was quantified by fitting a linear curve to the topography profile of each transect, and calculating the standard deviation of the absolute value residuals between this curve and the observed height readings (Currence & Lovely, 1970). Hence, relative elevation was only meaningfully comparable for individual transects (not between transects) across the study period, while random roughness could be compared both between transects and sampling times.

3.2.7 Data analyses

Unless otherwise noted, *P* values included in text are based on two-factor (hydroperiod and landscape position) ANOVA (Genstat 7.0, VSN International 2001, Hemel Hempstead, UK). Data for ANOVA were subjected to square root or fourth root transformation where appropriate. Microbial community data (by PLFA) were transformed to presence-absence data in Primer 6 (Primer-E Ltd 2006, Plymouth, UK), then a resemblance matrix using Bray Curtis similarities for one-way analysis by ANOSIM with 999 permutations. One-way SIMPER tests (cut-off of 90 % for low contributions) and MDS plots (minimum stress of

0.01; 25 restarts) were also produced using Primer to identify sensitive microbial groups (by fatty acid) and examine microbial community heterogeneity in response to flooding and landscape position. Relationships between PLFA profiles, topography and soil variables were analysed using non-parametric multivariate multiple regression (DISTLM and DISTLM-forward) based on Bray-Curtis dissimilarities of untransformed data (Anderson, 2001).

Spatio-temporal patchiness in soil and microbial variables was examined using prediction maps prepared using ordinary kriging in ArcMap 9.1 (ESRI 2005, Redlands, USA). Weightings are obtained through analysis of statistical variation using semivariogram modelling in ArcMap. As data were collected in 20 m wide line transects 200 m apart, prediction maps were produced as kriging strips for each transect rather than as a continuous field. Cross-validation was performed using the difference between mean observed ($O_{\bar{b}a}$) and predicted ($P_{\bar{b}a}$) values and between observed (s_o) and predicted (s_p) standard deviation, and prediction accuracy was assessed by root mean square error (RMSE).

3.3 RESULTS

3.3.1 Variation in soil physical characteristics and topography

All riparian and bank soils were classified as loams, while floodplain soils were classified as loamy-sands and channel sediments as pure sands (>95 % sand; Table 3.1). Bulk density was significantly greater in bank, channel and floodplain soils ($>1 \text{ g cm}^{-3}$) than in riparian soils ($\leq 1 \text{ g cm}^{-3}$; $P < 0.05$). Soil pH were slightly alkaline (pH 7.8), and consistent over the study period. Relative elevation along transects was similar during the interflood period and after flooding, although more variable in the anabranch transect (Transect 1) than for the main channel Transects 2 and 3 ($P < 0.0001$; Fig. 3.3). Transect 1 also had greater random roughness (0.83 m) than Transects 2 and 3 (0.53 m). Random roughness generally increased (+0.27 m) during the interflood period, declined after flooding (-0.22 m), and varied among landscape positions, being greatest in floodplains and *Eucalyptus* closed woodlands, and least in banks and *A. citrinoviridis* thickets.

3.3.2 Changes in soil nutrients in relation to hydroperiod and landscape zone

Moisture content (%) was consistent from early to late interflood, and doubled in soils after flooding (6.7 to 11.8 %; $P<0.0001$; Figs 3.4a and 3.5a). Moisture contents varied along transects and were ranked by ANOVA: bank > channel > *Eucalyptus* closed woodland > *A. citrinoviridis* thicket = *Eucalyptus* open woodland > floodplain for all sampling times ($P<0.0001$; Fig. 3.5a). Kriging prediction mapping of soil moisture showed that only a few patches within channels and the southern riparian zone retained significant soil moisture by the early and early interflood (Fig. 3.4a). After flooding, soil moisture was mostly high but heterogeneously distributed (CV increased from 58 to 72 %), with floodplain areas now comparatively dry (Fig. 3.4a).

Total soil N (%) was similar across sampling times; however floodplain soils had only half as much N as other landscape positions ($P<0.0001$; Fig. 3.5f). Soil $\text{NO}_3\text{-N}$ (mg kg^{-1}) increased three-fold between the early and late interflood (3.74 to 9.75 mg kg^{-1} ; Fig. 3.5b) except in channel sediments; however this accumulated $\text{NO}_3\text{-N}$ subsequently decreased after flooding when $\text{NO}_3\text{-N}$ distributions were more homogeneous in the stream landscape ($P<0.0001$; Fig. 3.4b). $\text{NO}_3\text{-N}$ accumulated during the interflood primarily in the central and northern parts of the riparian zone and proximal floodplain (Fig. 3.4b). Indeed, bank and riparian soils had much higher $\text{NO}_3\text{-N}$ content – averaging 60-80 % greater than channel sediments, and >100 % greater than floodplain soils ($P<0.0001$; Fig. 3.5c). The three riparian community types had similar concentrations of $\text{NO}_3\text{-N}$ in interflood and flood periods. Kriging prediction maps considerably reduced variation in $\text{NO}_3\text{-N}$, so true patchiness is greater than indicated by interpolation (Fig. 3.4b).

In contrast to soil $\text{NO}_3\text{-N}$, soil $\text{NH}_4\text{-N}$ remained the same during the interflood period, but more than halved after flooding ($P<0.0001$; Fig. 3.5c) from 3.75 (SE 0.29) to 1.50 mg kg^{-1} (SE 0.18). $\text{NH}_4\text{-N}$ was 25 % greater in surface (0-2 cm) soils than deeper (2-10 cm) soils ($P<0.0001$). During the interflood, bank and *Eucalyptus* closed woodland positions were hot spots for $\text{NH}_4\text{-N}$ in the stream landscape ($P<0.05$; Figs 3.4c and 3.5c). However, after flooding, soils from *Eucalyptus* open woodlands had twice the $\text{NH}_4\text{-N}$ content of all other soils (Fig. 3.5d). The late interflood concentration of $\text{NH}_4\text{-N}$ was distributed as a large hot

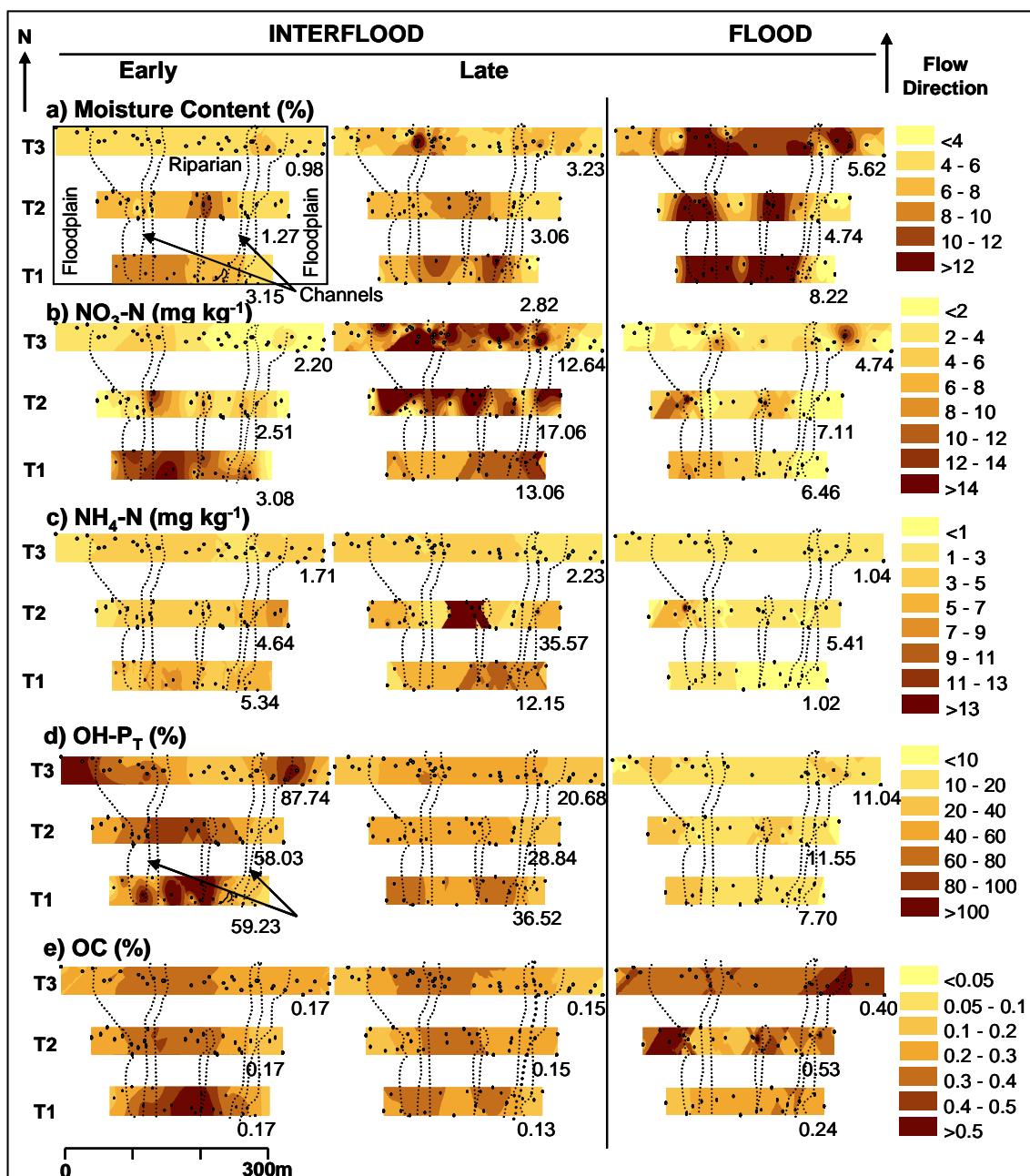


Fig. 3.4 Interpolation prediction maps for toposequence transects (Transects 1 [T1], 2 [T2], and 3 [T3]) from ordinary kriging for selected soil variables (a-e), in early and late interflood, and flood periods. Boundaries of main landscape positions indicated in 3.4 and transects aligned as per true relative spatial location. Prediction error provided below each map as root mean square error (RMSE). Dots indicate sample locations.

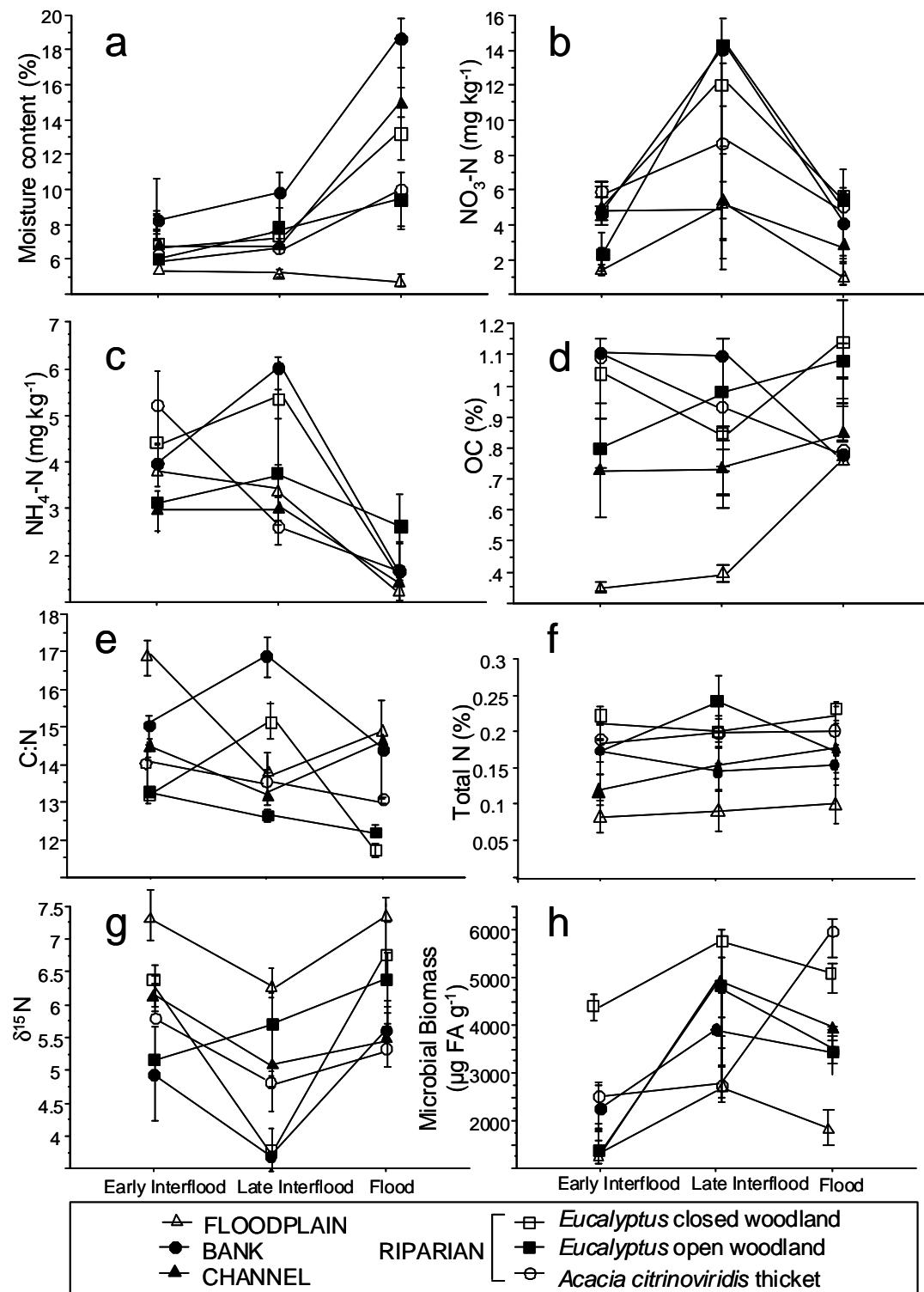


Fig. 3.5 Soil variables and microbial biomass means plots in early and late interflood and flood periods, by landscape position.

spot within the central riparian zone (Fig. 3.4c), where *Eucalyptus* open woodland is dominant (Fig. 3.3). Indeed, mean concentrations of NH₄-N were greatest in *Eucalyptus* open woodland soils (5.06, SE 0.54; $P<0.05$).

OH-P_T progressively decreased in all landscape positions ($P<0.0001$; Fig. 3.4d), amounting to an approximate loss of ~50 µg g⁻¹, or 75 % of P in surface soils in the stream reach over the study period. The distribution of OH-P_T also became more homogeneous over this period (CV decreased from 145 to 75 %; Fig. 3.4d). Increased homogeneity was consistent amongst landscape positions, and as OH-P_i remained unchanged during the study period, the decline was attributable to a reduction in the OH-P_o soil fraction ($P<0.0001$). Floodplain soils had considerably less OH-P_T (both OH-P_i and OH-P_o) than other soils ($P<0.0001$). Samples with higher inorganic C (carbonates; approximated as total C minus OC) also tended to have greater OH-P_T ($R^2=0.29$, $P<0.001$). Soil N:P ratios were four- to five-fold higher in the interflood period than after flooding ($P<0.0001$), yet were similar among all landscape positions.

Total C (%) was similar amongst sampling times, and amongst all landscape positions except for floodplain soils where concentrations were ~50 % lower ($P<0.0001$). Likewise, OC (%) was similar across the study period, and followed a pattern of bank = riparian > channel > floodplain amongst landscape positions ($P<0.0001$; Figs 3.4e and 3.5d). No difference was observed for soil OC between the three riparian community types, for each of the three sampling times (Fig. 3.5d). Floodplain soils had at least half the OC concentration of other soils, while channel sediments had ~20-30 % less (Fig. 3.5d). Patchiness of OC decreased slightly during the interflood (% CV decreased from 56 to 53 %), then increased again (CV = 69 %) after flooding (Fig. 3.4d). OC hot spots were located in riparian areas during the interflood, while hot spots occurred in both the floodplain and riparian zones after flooding (Fig. 3.4d). C:N ratios were similar in interflood and flood periods, and significantly less in riparian soils than in other soils across the study period ($P<0.01$; Fig. 3.5e). However, mean C:N ratios between landscape positions only varied between 13 (*Eucalyptus* closed woodland) and 15 (floodplain).

Floodplain soils were enriched in $\delta^{15}\text{N}$ ($\delta^{15}\text{N}=6.90 \text{‰}$, SE 0.29) relative to other soils (5.51 ‰, SE 0.22; $P<0.0001$; Fig. 3.5g). Floodplain soils were also enriched in $\delta^{13}\text{C}$ ($\delta^{13}\text{C}=-17.49 \text{‰}$, SE 0.53) compared to soils from other landscape positions (-21.25 ‰, SE 0.37; $P<0.0001$). Abundances of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ did not differ during the study period or between riparian community types.

3.3.3 Dynamics of microbial biomass and community composition

Soil microbial biomass (Fig. 3.5h) in late interflood (4023.7; SE 433.9) and flood samples (3742.7; SE 362.4) was twice that of samples collected in the early interflood (1800.3, SE 261.3; $P<0.0001$). Floodplain soils had at least half the microbial biomass of other landscape positions ($P<0.05$), and *Eucalyptus* closed woodland had 40 % greater microbial biomass than any other landscape position, including other riparian community types ($P<0.05$; Fig. 3.5h). Microbial community profiles were similar between sampling times (ANOSIM $R<0.03$), and riparian, channel/bank, and floodplain communities overlapped (ANOSIM $R=0.47$; Fig. 3.6). Riparian microbial profiles were very similar (average 62.38 %; ANOSIM $R<0.22$) to each other, while profiles from the other landscape positions (particular floodplain profiles) appeared much less defined (Fig. 3.6). SIMPER analysis indicated that four fatty acids (retention times 14.53, 14.42, 14.68 and 11.90 min) consistently contributed slightly more (each FA >2 % contribution of total, out of 163 PLFAs) to the dissimilarity between profiles from different landscape positions. In particular, two fatty acids (15.53 and 14.42 min) contributed most (each >6 % contribution of total variation by SIMPER analysis) to differences between riparian and non-riparian groups. A total of 163 PLFAs were defined by retention time, and microbial diversity (number of #FAs g⁻¹ soil) was similar across all sample times and landscape positions.

3.3.4 Multivariate relationships between topography, nutrients and microbial communities

Microbial biomass was positively correlated with soil moisture, NO₃-N availability, total N, OC and the soil C:N ratio (Table 3.2). Soil OC, total N and C were all positively correlated with moisture. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ soil signatures were positively correlated with relative elevation, while total C and microbial biomass were negatively correlated with relative

elevation (Table 3.2). Hence, soil samples taken at higher positions in the landscape were relatively enriched in ^{15}N and ^{13}C , and depleted in total C and microbial biomass. The majority (65 %) of significant correlations also withstood Bonferroni correction (Table 3.2). Multivariate multiple regression (DISTLM-forward) showed that OH-P_o, NO₃-N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ explained significant ($P<0.05$) proportions of the variance in microbial community composition when modelled individually (Table 3.3). However, the overall sequential model (DISTLM) explained only a small amount (~14 %) of the total variance in microbial community composition.

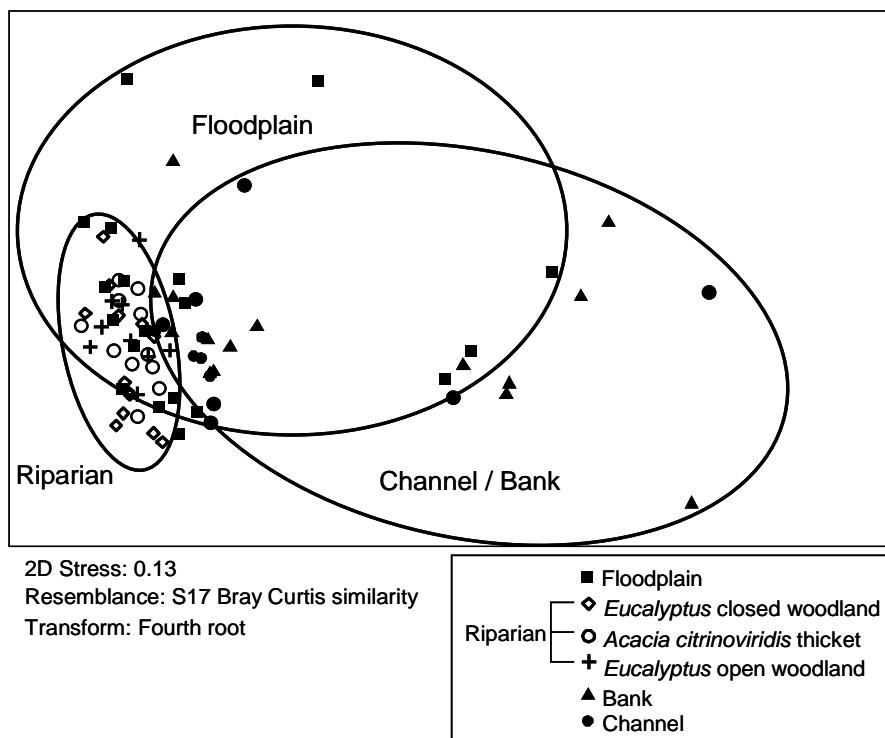


Fig. 3.6 MDS plot of microbial community profiles for floodplains, channels, banks and riparian (grouped community types) zones.

3.4 DISCUSSION

3.4.1 Effects of flooding on biogeochemical hot spots

I sought to identify and describe the dynamics of biogeochemical hot spots in toposequences at Barnett Creek, in the semi-arid Pilbara region. As hypothesised, flooding

reduced (or at least maintained) the spatial heterogeneity of biogeochemical soil patches (nutrient availability and microbial communities) across the stream landscape. A homogenising effect of flooding on nutrient distributions has been identified in studies of North American arid streams (e.g. Dent & Grimm, 1999). Conversely, flooding increased within-site variability in microbial communities in an Australian semi-permanent stream (Rees *et al.*, 2006). In my study, there was a specific increase in patchiness of NO₃-N from early to late interflood at Barnett Creek, most likely due to continued accrual of plant litter coupled with water limitations to NO₃-N uptake. Floodplain soils contained very little OM until after flooding, when OM content was comparable with other landscape positions, likely owing to ‘top-dressing’ of floodplain soils with flood-borne nutrients that in turn may stimulate primary production (Junk *et al.*, 1989).

OH-P_T progressively decreased over the study period, due solely to a reduction in OH-P_o. It is difficult to say whether this indicates that P is being locally ‘lost’ (e.g. by downstream export), or by mineralisation and uptake. Samples with higher inorganic C (carbonates) had greater OH-P_T ($R^2=0.29$; $P<0.001$), hence outcrops of calcrete bedrock at Barnett Creek may influence P patchiness through ion binding (Lajtha & Schlesinger, 1988). More than likely, the small pools of P typically available in Pilbara soils (Bennett & Adams, 2001) will vary considerably in relation to unpredictable weathering and precipitation events, and be sensitive to exhaustion, with long time frames for replenishment.

Interestingly, microbial biomass was similar in the late interflood and after flooding, despite low soil moisture during the interflood (5-8 %). Modest winter rains such as occurred during the late interflood (Fig. 3.1) may have stimulated microbial activity as much as, or more than, large floods (Austin *et al.*, 2004; Belnap *et al.*, 2005; Cui & Caldwell, 1997; Huxman *et al.*, 2004). Steinberger *et al.* (1999) found that PLFA biomass did not respond to precipitation events in very arid sites in the Judean Desert, and even increased during the dry period - similar to the increase observed during the interflood in this study. It is possible that such microbial responses, well-suited to sites with extremely low rainfall, are equally suited to sites susceptible to very unpredictable rainfall.

Table 3.2 Correlation for microbial biomass, relative elevation and soil nutrient variables. * = $P<0.05$, ^B= $P<0.005$ (Bonferroni-corrected).

| | Relative Elevation | Moisture (%) | NO ₃ -N (mg kg ⁻¹) | NH ₄ -N (mg kg ⁻¹) | OH-P _i (μg g ⁻¹) | OH-P _o (μg g ⁻¹) | Total N (%) | Total C (%) | δ ¹⁵ N (‰) | δ ¹³ C (‰) | C:N | OC (%) |
|---|--------------------|-------------------|---|---|---|---|--------------------|--------------------|-----------------------|-----------------------|--------------------|-------------------|
| Relative Elevation | | | | | | | | | | | | |
| Moisture (%) | -0.10 | | | | | | | | | | | |
| NO ₃ -N (mg kg ⁻¹) | -0.11 | 0.10 | | | | | | | | | | |
| NH ₄ -N (mg kg ⁻¹) | -0.01 | -0.08 | ^B 0.56 | | | | | | | | | |
| OH-P _i (μg g ⁻¹) | 0.07 | -0.07 | -0.05 | -0.07 | | | | | | | | |
| OH-P _o (μg g ⁻¹) | 0.07 | -0.18 | 0.05 | 0.07 | 0.14 | | | | | | | |
| Total N (%) | -0.16 | *0.28 | ^B 0.38 | 0.15 | -0.04 | 0.21 | | | | | | |
| Total C (%) | *-0.19 | *0.28 | *0.35 | 0.13 | -0.06 | 0.21 | ^B 0.98 | | | | | |
| δ ¹⁵ N (‰) | *0.20 | -0.24 | -0.29 | -0.14 | 0.13 | 0.15 | ^B -0.37 | ^B -0.41 | | | | |
| δ ¹³ C (‰) | *0.25 | -0.27 | -0.22 | -0.05 | -0.19 | -0.13 | ^B -0.47 | ^B -0.47 | 0.65 | | | |
| C:N | 0.060 | -0.10 | -0.19 | -0.10 | -0.12 | -0.14 | ^B -0.41 | -0.26 | 0.05 | *0.36 | | |
| OC (%) | -0.16 | ^B 0.42 | ^B 0.39 | 0.19 | -0.10 | 0.12 | ^B 0.79 | ^B 0.79 | ^B -0.46 | ^B -0.53 | -0.53 | |
| Microbial Biomass (μg FA g ⁻¹) | ^B -0.35 | *0.30 | *0.30 | 0.17 | -0.23 | -0.12 | ^B 0.41 | 0.36 | -0.12 | -0.10 | ^B -0.37 | ^B 0.39 |

Table 3.3 Multivariate multiple regression analysis of selected soil properties against microbial community composition. Numbers given are pseudo-*F* values (*F*), *P*-values (*P*) and the proportion of variance (variance) explained by each variable.

| Variable | <i>F</i> | <i>P</i> | Variance (%) |
|--|----------|----------|--------------|
| OH-P _o ($\mu\text{g g}^{-1}$) | 5.42 | 0.00 | 6 |
| $\delta^{15}\text{N}$ (‰) | 2.79 | 0.01 | 5 |
| $\delta^{13}\text{C}$ (‰) | 1.91 | 0.07 | 4 |
| NO ₃ -N (mg kg^{-1}) | 2.63 | 0.02 | 3 |
| C:N | 1.48 | 0.15 | 3 |
| Total N (%) | 1.01 | 0.38 | 2 |
| Total C (%) | 1.34 | 0.21 | 2 |
| Moisture (%) | 1.53 | 0.13 | 2 |
| Relative Elevation (m) | 1.09 | 0.31 | 1 |
| OC (%) | 0.72 | 0.64 | 1 |
| OH-P _i ($\mu\text{g g}^{-1}$) | 0.75 | 0.44 | 1 |
| NH ₄ -N (mg kg^{-1}) | 0.36 | 0.86 | <1 |

3.4.2 Landscape position effects on biogeochemical hot spots

In general, the riparian zone was a hot spot, and floodplains a relative cold spot, for soil NO₃-N and OC within the landscape, regardless of hydroperiod. Such differences are unsurprising, as others have previously shown that riparian zones act as storage sites for NO₃-N and OM in dryland landscapes, largely due to higher levels of productivity (Jacobs *et al.*, 2007; Lamontagne *et al.*, 2006; Schade *et al.*, 2005). Soils from the floodplains were also persistently enriched in ¹⁵N, consistent with greater denitrification (Bedard-Haughn *et al.*, 2003). Indeed, as there was no correlation between total N and ¹⁵N for floodplain soils (*P*=0.19; cf. overall correlations in Table 3.2), we might assume enhanced denitrification or a lack of *in situ* N-fixation processes (Hogberg, 1997), compared to the riparian zones where leguminous *Acacia* spp. are abundant.

Across the interflood and flood periods, bank soils retained moisture more readily than all other soils and sediments (from any other landscape position), and had significantly greater concentrations of OC. However, banks did not support greater soil microbial biomass (Fig. 3.5h). The banks of Pilbara streams often accumulate woody debris, and indeed soil C:N ratios were greater along banks than in channel beds. Poor substrate quality (i.e. coarser substrates) appears the most likely explanation for reduced microbial activity in bank soils (cf. Ford *et al.*, 2007 for Pilbara grassland soils).

Surprisingly, non-riparian soils and sediments had much more divergent microbial profiles than riparian soils. Given the biogeochemical complexity of the riparian zone shown here and elsewhere (Jacobs *et al.*, 2007; Naiman *et al.*, 2005), it was expected that microbial community composition would be similarly complex. However, channel and floodplain environments may offer comparatively harsher habitats (e.g. due to xeric conditions, induration or scour) for microbes in comparison to riparian communities. As such, suitable microhabitats for microbes in floodplains and channels may be spatially isolated, with very different physiochemical characteristics, and hence capable of supporting distinctly different microbial groups. For example, microbial communities persisting in inhospitable environments, such as deep sea vents and geothermal springs, are taxonomically distinctive, and occupy unique and isolated biogeochemical niches (Rothschild & Mancinelli, 2001).

While PLFA profiles are highly valuable in quantification of the living microbial biomass, such profiles are yet to be proven to equate directly to functional or taxonomic diversity (Marschner, 2007). Further work using enzymatic or DNA studies could therefore help test some of the ideas discussed above pertaining to landscape-scale divergence in microbial communities subject to environmental stress. For example, Rees *et al.* (2006) used terminal-restriction fragment length polymorphism (T-RFLP) techniques in channel sediments from an intermittent stream, to show diverging responses to drought by microbial communities from different hydrological microsites. Similarly, Bossio and Scow (1995) tested the significance of flooding and C availability for microbes using substrate utilisation patterns, and observed an increase in microbial respiration after coupled C inputs and flooding.

The three riparian community types were biogeochemically consistent across the study period, despite differences in species composition and canopy cover (Table 3.1). Hence, biogeochemical boundaries did not coincide with riparian vegetation boundaries. In terms of N availability, this is surprising given the dominance of a potentially N-fixing species (*Acacia citrinoviridis*) in one of the three riparian community types. OC availability also did not correspond to structural changes, such as canopy cover. Higher canopy cover in dryland riparian forests can prevent water loss through evaporation and increase substrate availability for microbes through litterfall (Schade & Hobbie, 2005). The results of this study contrast with other riparian forests, where vegetation composition and structure dictate soil and nutrient processes (Haycock & Pinay, 1993; Tabacchi *et al.*, 1998). The pervasiveness of poor litter quality and probable P limitation (see Section 2.3) may limit overall microbial activity in the riparian zone, regardless of flooding or the relative high availability of OM, or inorganic N.

3.4.3 Biogeochemical hot spots in relation to topography

Contrary to my hypotheses, most nutrients were not significantly correlated to landscape topography (relative elevation). As discussed earlier, topographic depressions can accumulate organic materials and nutrients, and retain moisture, creating favourable biogeochemical microhabitats. While microbial biomass was greater in areas of lower relative elevation at Barnett Creek, soil inorganic N and P, moisture and OC were unaffected by relative elevation (Table 3.2). Small depressions (mm to cm) therefore did not appear to offer a more suitable microhabitat for soil microbes, though these microhabitats may still afford other benefits not considered in this study, such as refuge from scour or solar radiation.

Relative elevation of the three transects remained unchanged during the study period, indicating minimal broad-scale geomorphic change in the stream landscape. In comparison, random roughness of all transects increased during the interflood, possibly due to accumulation of locally produced but undecomposed OM such as leaf litter, bark and CWD. Flooding reduced random roughness, indicating homogenisation of small-scale microtopography. The scouring and depositional effects of floods are well-documented

(Bull & Kirkby, 2002), but the role of primary production in generating surface microtopography during interflood periods has received less attention. Unlike their permanent counterparts, intermittent streams have the opportunity to accumulate large quantities of locally produced riparian debris, such as CWD, between infrequent flood periods. Litter from Australian native species such as eucalypts is known for its resistance to decomposition (Boulton, 1991), and this debris accumulation may be responsible for a number of significant differences between biogeochemical dynamics in Australian intermittent streams and those elsewhere.

3.4.4 Conclusion

This study demonstrates that soil topography has lower correlation to nutrient and microbial patterns at Barnett Creek than hydroperiod or landscape position. While I considered one stream system across one flood, long-term (multi-decadal) and multi-scale experiments may be necessary to fully describe the spatio-temporal variation inherent in Pilbara intermittent streams. Follow-up experiments could further elucidate the mechanisms controlling biogeochemical hot spots in the intermittent stream landscape, particularly the persistence and migration of such patches.

CHAPTER 4

Small-Scale Biogeochemical Patterns in Channel Sediments at Barnett Creek

4.1 INTRODUCTION

Channel sediments are important sites for microbially mediated transformation of nutrients in stream landscapes (Jones & Holmes, 1996). P and / or N may be limiting to microbes and algae in most aquatic environments, however such limitations may vary spatio-temporally, even on small (<cm) scales (Lewis *et al.*, 2007; Manzoni *et al.*, 2008; Steinman & Mulholland, 1996; Vitousek & Howarth, 1991). Nutrient availability in sediments is influenced strongly by the physiochemical characteristics of those sediments (Kirk, 2004; Wagener *et al.*, 1998). In semi-arid environments, mobilisation and transformation of key nutrients is particularly dependent on the distribution of moisture and OM (Ford *et al.*, 2007) and system-wide disturbances such as flooding (Austin *et al.*, 2004). Channels may be composed of numerous components including pools, riffles, runs, shoals and organic debris which in turn may influence nutrient mobilisation and transformation in sediments. Channel sediments in dryland intermittent streams are unique in that they may effectively function as terrestrial soils during frequent dry periods. However, few studies have considered biogeochemical changes at small scales (mm to cm) in channel sediments of intermittent streams. Smaller scales are likely to have greater biological meaning for microbial communities than larger scales, as most microbial interactions and physiochemical differences between adjoining microsites occur at small scales (Franklin *et al.*, 2002).

Microbes tend to congregate on interfaces, such as the sediment-water interface, and flourish under suitable conditions, sometimes forming dense biofilms capable of complex biogeochemical activity (Lock, 1993). Indeed, microbial biomass and activity in surface sediments is likely to be several magnitudes greater than at depth (Fierer *et al.*, 2003). Channel components such as woody debris (see Appendix A), rocks, bars,

scours, and litter packs, create microhabitats that can favour microbial activity, dependent on their physiochemical properties (Tank & Dodds, 2003).

Anabranch channels are a common element of floodplain rivers in semi-arid Australia, and may be particularly significant sites for storage, transformation and export of macronutrients moving longitudinally or laterally in the stream landscape (Thoms & Sheldon, 2000). Connected to the main river channel after floods, anabranches subsequently dry and disconnect during low flow or drought periods. Compared to main channels, anabranches have lower flow velocities and often accumulate leaf litter and other OM from upstream sources or adjacent vegetation (McGuiness *et al.*, 2002). While a few studies have considered food webs and carbon sources in anabranch channels and other backwaters associated with larger rivers (e.g. Bunn & Boon, 1993; McGuiness *et al.*, 2002) less is known about the biogeochemistry of these branches in comparison to processes in main river or stream channels. On a catchment scale, the networks of anabranches and other backwaters may contribute as much or more than main channel environments to total productivity and nutrient transformation, due to their greater spatial extent (Knighton & Nanson, 1997).

For terrestrial environments, topography affects the patchiness of soil variables such as moisture and OM (Florinsky *et al.*, 2002; Florinsky *et al.*, 2004). However, our understanding of topographic controls within stream beds is less clear. In streams, especially intermittent streams, floods modify topography and habitats, stimulate nutrient processes, and alter biota (Giller, 1996; Puckridge *et al.*, 2000). Such changes are significant at multiple scales, but have typically been considered at the reach scale or greater. Few studies have considered flood-induced changes at smaller scales in stream beds, particularly changes in biogeochemical patchiness that have relevance for local productivity and for improving large-scale models of biogeochemical process.

Severe floods can move large quantities of sediment, dramatically altering the morphology of semi-arid channels, disrupting within-channel vegetation and sediment structure, and redistributing organic materials (Bull & Kirkby, 2002a; Pettit & Naiman, 2005). Anastomosed streams can be reconfigured by high flow (Huggenberger *et al.*, 1998), though this may be of less significance for infrequently flooded channels that are stabilised by vegetation, such as typify much of dryland Australia (Tooth & Nanson, 2000). Infrequent flooding encourages soil formation and the encroachment of riparian

vegetation into the channel (Huggenberger *et al.*, 1998) that, in turn, increases resistance to geomorphic change. When coupled with the relatively long periods of physical stability during frequent drought periods, it is unsurprising that intermittent streams in dryland Australia are often viewed as being in a long-term static equilibrium (Bull & Kirkby, 2002b). Their resistance to change contrasts with typical views of rivers as process-response systems, freely adjusting their channel topography and structure in response to changes in flow and sediment regimes (Thoms *et al.*, 2006).

Few studies have quantified the spatio-temporal patterns of nutrients in stream bed sediments of intermittent streams during both droughts and floods (for one exception see Dent & Grimm, 1999). Consequently, most of the available information on nutrient processes in periodically submerged sediments has been inferred from studies of wetlands (e.g. Sanchez-Carrillo & Alvarez-Cobelas, 2001) or rice paddies (e.g. Keeney & Sahrawat, 1986), rather than studies of lotic systems. Lotic systems, and particularly flood-prone intermittent streams, may be subject to much greater physical forces than lentic environments such as lakes or wetlands, which presumably alter sediment topography and nutrient distributions. Understanding these interrelationships is integral to elucidating mechanisms controlling long-term biogeochemical function of intermittent streams.

The objectives of this study were to determine the small-scale (mm to cm) patterns of nutrients (N, P), C and microbial communities in channel sediments of Barnett Creek. Specifically, I sought to consider the relative correlation of i) physical factors (microtopography) ii) channel type (main or anabranch) and hydroperiod (early and late interflood, and flood period) to microbial biomass and community structure and availability of inorganic N, labile P and OC in sediments. I hypothesised that nutrient availability and microbial biomass and diversity would be greatest in areas of the stream bed with lower relative elevation (e.g. holes or scours) and higher random roughness, as it was expected that these areas would have greater retention of moisture and nutrients. I also hypothesised that nutrient availability and microbial biomass and diversity would be greater in the anabranch rather than main channel, due to lower flow velocities in anabranch channels and greater retention of both allochthonous and autochthonous materials. Lastly, it was expected that flooding would decrease surface roughness and small-scale spatial heterogeneity in nutrient availability and microbial communities, particularly in high-energy main channels rather than anabranches.

4.2 METHODS

4.2.1 Study site

Field experiments were conducted at Barnett Creek (Section 2.8.1). Rainfall and catchment river discharge data for the study period (July 2004 to March 2006) are provided in Section 3.2.1. A 200-m reach of the stream was sampled, encompassing the main channel and one anabranch. Channel width was between 7-14 m, with banks 0.2 – 2 m high. Three 50-m transects were established along the centre of the stream bed (Fig. 4.1), oriented parallel to stream banks and flow. Transects were marked at either end with permanent metal stakes geo-referenced by GPS (Magellan eXplorist 210, San Dimas, United States), for repeated topography measurements and sediment sampling. One transect (Transect A) was positioned in the anabranch, and the other two (Transects B and C) placed in the main channel. The anabranch was situated approximately 1 m higher in the landscape and was more narrow and densely vegetated than the main channel, with scattered piles of CWD (see Appendix A). In contrast, Transect C was in a broad gravel section of the main channel, with low canopy cover from riparian eucalypts and minimal surface debris. Transect B was intermediate between the other two transects for these characteristics. Photographs of the anabranch and main channel areas during an interflood period are presented in Plate 4.1. Unless otherwise specified, measurements were replicated along each channel transect at three sampling times - July 2004 (early interflood), August 2005 (late interflood) and March 2006 (flood).

4.2.2 Measurement of channel microtopography

Stream bed microtopography was described using methods detailed in Section 3.2.6. Relative elevation was measured every 0.5 m, or at shorter intervals where topographic change ≥ 5 mm was evident. Sediment texture was classified (August 2005) at 1 m intervals into four substrate categories – ‘poorly sorted’ (fine sand to cobbles >64 mm diameter), ‘fine-medium’ (gravel < 10 mm diameter), ‘medium-coarse’ (gravel > 10 mm diameter) and ‘clay crust’. Change in relative elevation between sampling periods was quantified by subtracting point elevations for each transect from the same point measurement made in following sampling times. Random roughness was also quantified following methods detailed in Section 3.2.6.



Plate 4.1 Typical anabranch (a) and main channel (b) environments at Barnett Creek, during an interflood period.

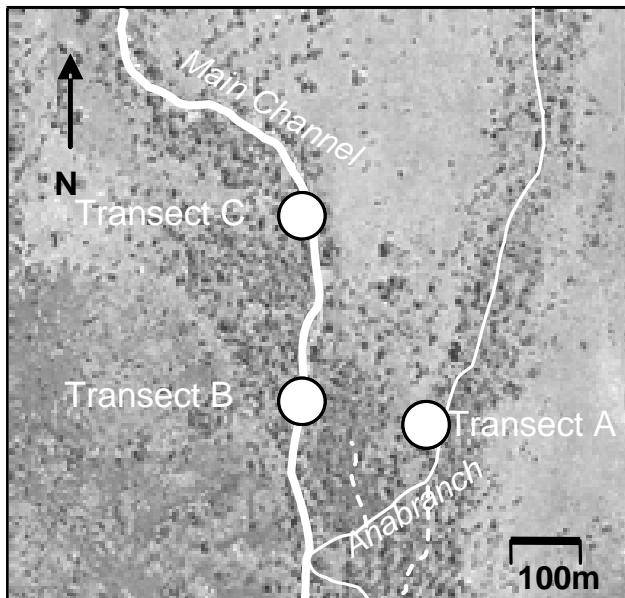


Fig. 4.1 Location of sampled channel bed transects (Transects A, B and C) at Barnett Creek. Flood flow is from south to north.

4.2.3 Sediment nutrient and microbial analyses

Sediments were at ten randomly selected positions within a 2 m strip either side of each transect line. Sediments were collected from three depths: 0-2, 2-5 and 5-10 cm, using a hand trowel and sieved to <2 mm in the field. A total of 30 sediment samples were taken at each sample time from each transect. A minimum of 300 g of sediment (to allow sufficient quantity for all soil tests) was collected for each sample and stored at 4 °C until nutrient analyses within four weeks. Sediment moisture was determined shortly after collection for each sample by gravimetric analysis, after oven drying at 110 °C for 48 h. NO₃-N, NH₄-N, OH-P_i, OH-P_T, OH-P_o, OC, total N, total C, δ¹⁵N and δ¹³C were analysed according to methods detailed in Section 3.2.4. PLFA was used to compare sediment microbial profiles, using ten sediment samples (~15 g each; 0-2 cm depth) from each sampling time and transect. Samples were analysed according to methods detailed in Section 3.2.5. As noted in Section 3.3.1, pH of Barnett Creek sediments averages ~7.8, and did not vary significantly during the study period.

4.2.4 Data analyses

To examine changes in nutrient patchiness, interpolation prediction maps were created by ordinary kriging in ArcMap 9.1 following the methods detailed in Section 3.2.7.

Unless otherwise noted, P values included in text are based on two-factor fixed (hydroperiod and channel type) ANOVA with Fisher's LSD post-hoc test for groupings (Genstat 2001, VSN International, Hemel Hempstead, UK). Data were transformed with square root or fourth root transformation where appropriate, before ANOVA. Microbial community data were analysed using the methods detailed in Section 3.2.7.

4.3 RESULTS

4.3.1 Channel dynamics and microtopography

Poorly sorted sediments dominated in the main channel (60-90 % by area), with sections of fine-medium gravel (< 10 mm diameter). In contrast, anabranch sediments were 51 % (by area) clay crust, with large sections of fine-medium gravel. Small (typically <0.1 m) changes in topography were observed in main and anabranch transects (Fig. 4.2). From early to late interflood, there was a significant increase in relative elevation in the anabranch (+0.09 m, SE 0.04, $P<0.01$). Relative elevation did not change significantly along this transect after flooding, or in the main channel transects during the study period. Overall, random roughness of stream beds was a third higher in the anabranch transect (random roughness=0.074 m), than in the main channel transects (overall random roughness=0.056 m; Table 4.1). Transect B showed the greatest temporal change in random roughness, which more than doubled after flooding.

4.3.2 Channel type and hydroperiod effects on sediment variables

Moisture content of sediments increased five-fold after flooding from 2.61 % (SE 1.45) in the early interflood and 3.67 % (SE 0.98) in the late interflood to 12.51 % (SE 0.41) after flooding ($P<0.0001$). The slight increase from early to late interflood was consistent with the occurrence of light winter rains during this time. In general, sediment moisture content was consistently low in all interflood samples, but quite variable in samples from the flood period (Table 4.2). Sediment moisture content increased significantly between 0-2 cm and 2-5 cm depths ($P<0.05$), but was similar between 2-5 cm and 5-10 cm depths (*data not shown*). Sediment moisture was noticeably patchier in Transects A and B than Transect C (Fig. 4.2).

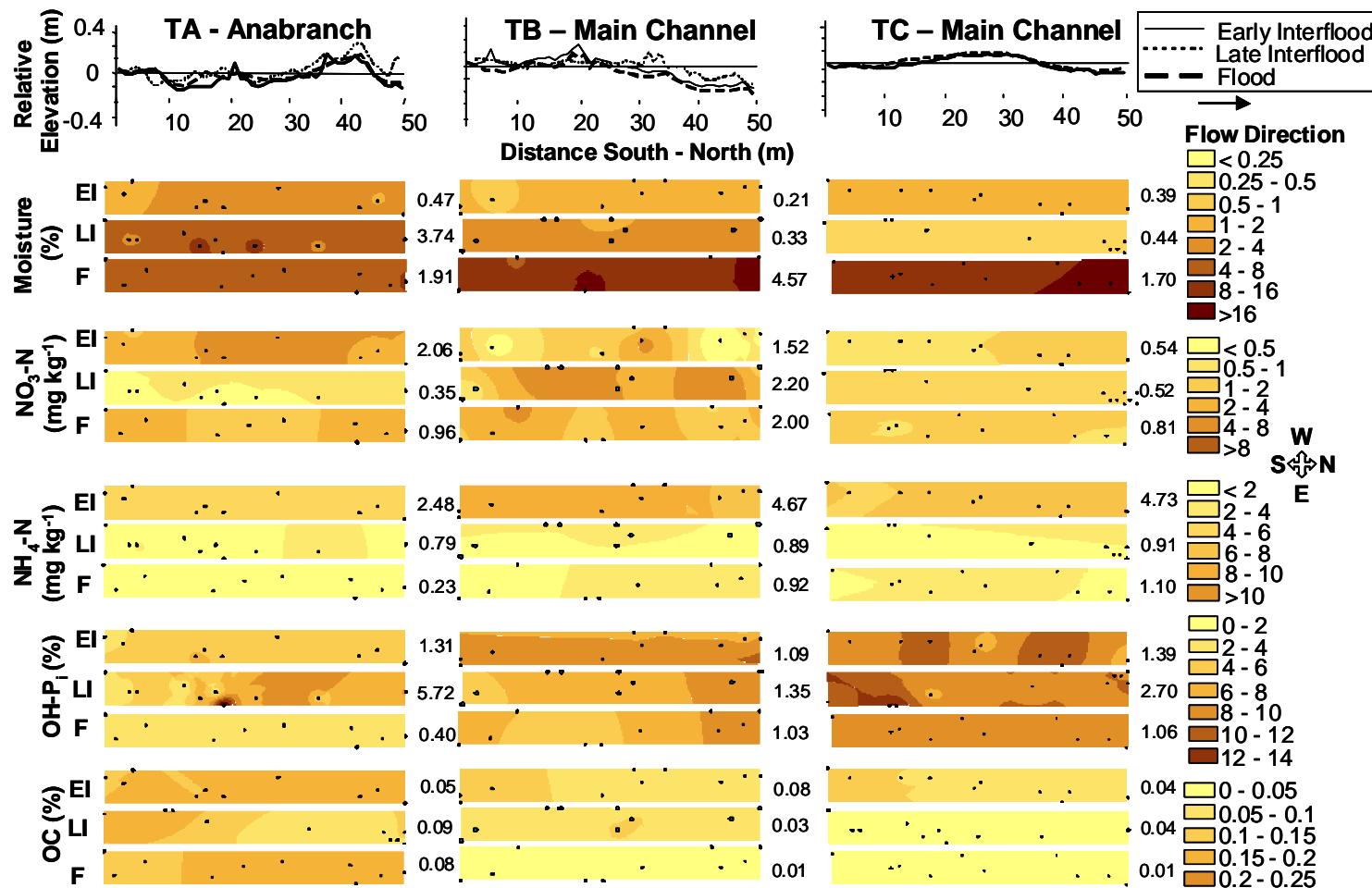


Fig. 4.2 Relative elevation of channel transects with ordinary kriging maps for selected sediment variables. Prediction error (at right of maps) as root mean square error (RMSE). EI= Early interflood, LI= Late interflood, and F=Flood.

Table 4.1 Comparison of physical, nutrient and microbial variables for anabanch and main channel environments. Significance is by ANOVA.

| | Anabanch (Transect A) | | | Main Channel (Transects B & C) | | | Significance | |
|---|--------------------------|-------|-------|-----------------------------------|-------|-------|--------------|---------|
| | Mean | CV | SE | Mean | CV | SE | F | P |
| Random Roughness (m) | 0.108 | 0.69 | 0.007 | 0.083 | 0.64 | 0.004 | 0.55 | 0.576 |
| Moisture (%) | 5.15 | 0.79 | 0.47 | 4.89 | 1.25 | 0.50 | 5.56 | 0.019 |
| OC (%) | 0.49 | 0.38 | 0.04 | 0.25 | 0.66 | 0.02 | 34.1 | <0.001 |
| Total N (%) | 0.098 | 0.35 | 0.01 | 0.056 | 0.58 | 0.01 | 11.7 | 0.002 |
| OH-P _i (µg g ⁻¹ sediment) | 5.04 | 0.79 | 0.46 | 8.78 | 0.29 | 0.21 | 74.1 | <0.0001 |
| δ ¹³ C (‰) | -19.71 | -0.11 | 0.67 | -22.06 | -0.07 | 0.28 | 14.6 | 0.0005 |
| N:P | 931.82 | 0.48 | 142.5 | 475.12 | 0.65 | 60.83 | 12.1 | 0.001 |
| Microbial Biomass (ng FA g ⁻¹ sediment) | 1946.37 | 0.56 | 164.0 | 1023.28 | 0.48 | 43.98 | 74.1 | <0.0001 |

Total N of sediments was significantly reduced after flooding ($P<0.0001$), decreasing from ~ 0.08 % to 0.05 % (Table 4.2). At all sampling times, sediment samples from the anabanch contained significantly more total N ($P<0.05$; Table 4.1). This difference was most pronounced after flooding, where the anabanch had almost twice as much total N as the main channel. Sediment NO₃-N increased from ~1.2 mg kg⁻¹ during the interflood to 2.05 mg kg⁻¹ sediment after flooding ($P<0.05$), and was significantly lower in Transect C than other transects ($P<0.05$). NO₃-N was also patchier in Transects A and B in comparison with Transect C (Fig. 4.2). NO₃-N decreased between 0-2 and 2-5 cm depths ($P<0.01$), but was similar between 2-5 and 5-10 cm depths (*data not shown*). In contrast to NO₃-N, sediment NH₄-N decreased ($P<0.01$) during the interflood and after flooding, from 7.52 (SE 0.97) to 1.91 mg kg⁻¹ sediment (SE 0.77; Table 4.2). NH₄-N concentrations were similar in the first 5 cm depth of sediment, then increased significantly in the 5-10 cm range ($P<0.05$; *data not shown*). Sediment total C (1.04, SE 0.09) was similar among all time periods (Table 4.2) and among different transects. Sediment OC decreased significantly in the main channel after flooding ($P<0.0001$), however remained unchanged in the anabanch. Hot spots of OC (>0.2 %) were present in the anabanch transect, while distributions were more homogeneous (generally 0–0.1 %) in main channel transects (Fig. 4.2).

Table 4.2 Sediment moisture and nutrients of stream bed sediments during early and late interflood, and flood periods. Flooding effect is by ANOVA.

| | Interflood | | | | | | Flood | | | Flooding Effect | | |
|---|------------|-------|------|-------|--------|------|-------|-------|------|-----------------|------|-----|
| | Early | | | Late | | | | | | | | |
| | Mean | CV | SE | Mean | CV | SE | Mean | CV | SE | P-value | F | df |
| Moisture (%) | 2.61 | 1.45 | 0.40 | 3.67 | 0.98 | 0.38 | 12.51 | 0.41 | 0.77 | <0.0001 | 98.0 | 222 |
| NO ₃ -N (mg kg ⁻¹) | 2.01 | 1.03 | 0.22 | 4.33 | 2.22 | 1.02 | 2.05 | 0.71 | 0.22 | 0.03 | 3.59 | 219 |
| NH ₄ -N (mg kg ⁻¹) | 7.52 | 0.97 | 0.77 | 2.33 | 2.05 | 0.50 | 1.91 | 0.77 | 0.23 | <0.0001 | 24.6 | 221 |
| OH-P _i (μg g ⁻¹) | 7.68 | 0.37 | 0.30 | 7.78 | 0.53 | 0.44 | 6.72 | 0.51 | 0.52 | 0.23 | 1.50 | 222 |
| OH-P _T (μg g ⁻¹) | 13.64 | 0.45 | 0.64 | 14.30 | 0.81 | 1.23 | 7.61 | 0.55 | 0.62 | <0.0001 | 10.4 | 195 |
| OC (%) | 0.34 | 0.53 | 0.03 | 0.37 | 0.55 | 0.04 | 0.22 | 1.04 | 0.06 | 0.007 | 5.26 | 71 |
| Total N (%) | 0.078 | 0.50 | 0.01 | 0.081 | 0.33 | 0.01 | 0.047 | 0.75 | 0.04 | 0.015 | 4.77 | 34 |
| Total C (%) | 1.07 | 0.39 | 0.11 | 1.17 | 0.44 | 0.17 | 0.87 | 0.62 | 0.15 | 0.34 | 1.11 | 34 |
| δ ¹⁵ N (‰) | 4.65 | 0.17 | 0.21 | 4.71 | 0.26 | 0.41 | 6.19 | 0.44 | 0.75 | 0.001 | 8.05 | 34 |
| δ ¹³ C (‰) | -21.4 | -0.06 | 0.37 | -22.6 | -0.039 | 0.30 | -20.5 | -0.13 | 0.71 | 0.046 | 3.39 | 34 |
| C:N | 14.4 | 0.15 | 0.57 | 14.2 | 0.10 | 0.47 | 22.8 | 0.74 | 4.67 | 0.073 | 2.84 | 34 |

OH-P_T decreased significantly in stream bed sediments after flooding ($P<0.0001$) - declining from 14.30 (SE 0.81) in the late interflood to 7.61 $\mu\text{g g}^{-1}$ sediment after flooding (SE 0.55; Table 4.2). OH-P_T was significantly greater in samples from Transect C than from the other transects ($P<0.0001$), and greatest in surface 0-2 cm sediments while similar in deeper sediments ($P<0.05$). OH-P_i was similar among the hydroperiods (Table 4.2), and generally increased Transect C>Transect B>Transect A. However, flooding appeared to have a homogenising effect on patchiness of OH-P_i (Fig. 4.2). No depth effect on OH-P_i was evident. Concomitant with the change in OH-P_T, OH-P_o decreased significantly after flooding ($P<0.0001$), from 0.79 $\mu\text{g g}^{-1}$ sediment in the late interflood to 0.10 $\mu\text{g g}^{-1}$ sediment during the flood period, and was similar

between sediments from different depths. OH-P_o generally increased Transect A>Transect C>Transect B.

Sediment C:N ratios (mean 16:1) were similar before and after flooding (Table 4.2), and between the anabranch and main channel transects. Sediment N:P ratios were also similar among periods, averaging 135:1, however anabranch samples had significantly higher ratios (mean 932:1) than main channel samples (mean 475:1; $P<0.01$). Sediment samples from the flood period were enriched in ^{15}N in comparison to early and late interflood samples ($P<0.0001$) – increasing from 4.71 ‰ (SE 0.26) in the late interflood to 6.19 ‰ (SE 0.44) after flooding (Table 4.2). Sediment $\delta^{13}\text{C}$ values did not change significantly during the study period, however anabranch samples were significantly less enriched in ^{13}C (-19.71 ‰, SE -0.11) than the main channel sediments (-22.06 ‰, SE -0.07; $P<0.0001$; Table 4.1).

4.3.3 Channel type and hydroperiod effects on microbial communities

After flooding, microbial biomass almost halved, from an average of ~1550 ng FA g⁻¹ sediment during the interflood period to 878 ng FA g⁻¹ sediment (SE 98.37, $P<0.001$; Fig. 4.3). Transect C sediment samples had lower microbial biomass than Transect A ($P<0.01$), while Transect B samples were intermediate (Fig. 4.3). Samples from different collection times had similar microbial profiles based on presence-absence data for the 17 fatty acids recorded (ANOSIM, $P=0.805$). The main channel transects had significantly different microbial profiles from each other (ANOSIM, $P<0.05$) - a dissimilarity that was contributed by, more or less equally, over ten of the tested fatty acids (SIMPER, average dissimilarity 37.32). The anabranch transect had a profile intermediate between those of the two main channel transects. However, MDS plots of microbial community profiles (by fatty acid) indicated no clear separation between samples collected in different periods or from different transects.

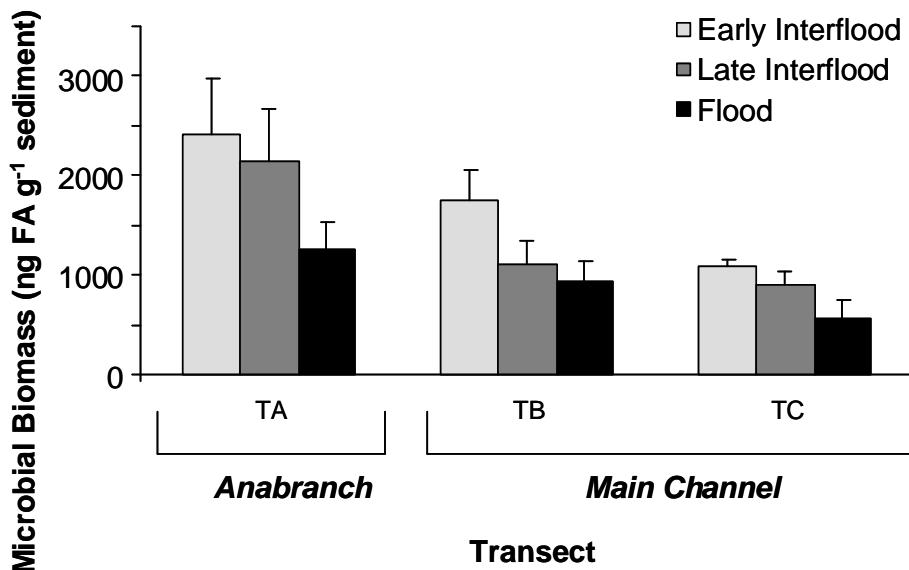


Fig. 4.3 Microbial biomass (phospholipid fatty acids) from anabanch (Transect A) and main channel (Transects B and C) sediments in early and late interflood, and flood periods. Error bars indicate standard error.

4.3.4 Relationship between microtopography and sediment variables

Microbial biomass was negatively correlated to relative elevation, while NO₃-N was positively correlated to relative elevation (Table 4.3). No other sediment variables were significantly correlated to relative elevation. Microbial biomass was also positively correlated to OC, and gravimetric sediment moisture was negatively correlated to OC and positively correlated to C:N. Sediment moisture and NO₃-N were also more patchy in transects with higher random roughness (Transects A and B; Fig. 4.2).

Table 4.3 Pearson correlation coefficients for measured sediment variables in stream bed sediments. * $=P<0.05$, ** $=P<0.01$, *** $=P<0.001$, ^B indicates significance after Bonferroni correction.

| | Relative Elevation | Moisture | NO ₃ -N | NH ₄ -N | OH-P _i | OC | δ ¹⁵ N | δ ¹³ C | C:N |
|--|--------------------|----------------------|--------------------|--------------------|-----------------------|---------------------|---------------------|-------------------|-------|
| Moisture (%) | -0.02 | | | | | | | | |
| NO ₃ -N (mg kg ⁻¹) | 0.49* | -0.22 | | | | | | | |
| NH ₄ -N (mg kg ⁻¹) | -0.01 | -0.40 | -0.17 | | | | | | |
| OH-P _i (μg g ⁻¹) | -0.09 | 0.18 | -0.27 | 0.89 | | | | | |
| OC (%) | -0.26 | ^B -0.57** | 0.02 | 0.10 | -0.10 | | | | |
| δ ¹⁵ N (‰) | -0.24 | 0.33 | -0.01 | -0.17 | -0.18 | 0.03 | | | |
| δ ¹³ C (‰) | -0.05 | -0.03 | -0.08 | -0.16 | ^B -0.67*** | 0.14 | ^B 0.50** | | |
| C:N | -0.11 | 0.49* | -0.08 | -0.16 | 0.21 | -0.41 | -0.01 | -0.37 | |
| Microbial Biomass (μg FA g ⁻¹) | -0.41* | -0.40 | -0.12 | 0.04 | -0.28 | ^B 0.54** | 0.06 | 0.32 | -0.27 |

4.4 DISCUSSION

4.4.1 Channel dynamics over the hydroperiod

Microtopography (relative elevation and random roughness) of stream beds at Barnett Creek varied little over the study period, despite severe flooding. So, contrary to hypotheses, flooding did not alter along-channel microtopography by scouring sediments and accumulated, locally produced materials/debris. While this study measured central channel (as opposed to channel edge) topography, the kinetic energy of semi-arid rivers in flood is readily observed, and a single flood may cause erosion to ~ 2 m depth and deposit over 0.5 m of sediment in ephemeral channel beds (Hooke & Mant, 2000). The results of my study instead lend support to the theory of dryland rivers being resistant to geomorphic change, existing in a static equilibrium (Bull & Kirkby, 2002b). Surface gravel can produce an armoured channel (*sensu* Wilcock & DeTemple,

2005), capable of withstanding erosion during floods, and an anabranching structure has been shown to be hydraulically efficient in allowing large discharges to move long distances through low gradient basins (Knighton & Nanson, 1994; Nanson & Knighton, 1996). Severe flooding, as typical of the Pilbara, can transport significant quantities of materials downstream by inhibiting the deposition and incorporation of materials into gravel beds, that would otherwise be deposited in smaller flow events (Poff *et al.*, 1997). Such a system would be more dependent on local production and nutrient turnover, than on transported materials.

Only $\text{NO}_3\text{-N}$ and microbial biomass were significantly correlated with relative elevation of the stream bed surface. $\text{NO}_3\text{-N}$ increased with greater relative elevation (rises) while microbial biomass increased with lower relative elevation (depressions). On a microscopic level (< 1 mm), microorganisms preferentially colonise areas of low relief (crevices, depressions, surface fissures) on sediment particles, where cells are protected from mechanical damage (Meyer-Reil, 1994). Stream bed depressions (e.g. pools) may provide a drought refuge in intermittent streams, allowing microbes to persist, probably in scour-resistant wetted biofilms around bed cobbles and gravel (Ashman & Puri, 2002; Battin, 2000; Davis *et al.*, 2002; Lisle & Hilton, 1992; Stanley *et al.*, 1997). Such persistence could promote the formation and maintenance of biogeochemical hot spots in the stream bed.

4.4.2 Role of channel type in channel dynamics and biogeochemistry

The anabranch channel displayed very different physical and chemical patterns to the main channel (Table 4.1). As discussed above, flow velocities in anabranches are often less than in main channels (McGuiness *et al.*, 2002), so these environments favour deposition of materials and retention of nutrients. Indeed, the anabranch at Barnett Creek had finer sediments, greater random roughness, greater nutrient concentrations (OC, total N, OH-P_i) and microbial biomass than the main channel transects. These results support my original hypotheses concerning differences between channel types (Section 4.1). The patchiness of OC and microbial biomass was also notably greater in the anabranch. Riparian zones are known hot spots of biogeochemical activity within semi-arid landscapes (Jacobs *et al.*, 2007). This study suggests that contributions of anabranch channels may at least rival activity in vegetated riparian zones due to greater water availability during and after flow events. Estimations of riparian productivity

should therefore also account for the contributions of semi-vegetation anabanches and backwaters incorporated in the riparian zone.

4.4.3 Influence of hydroperiod on sediment biogeochemistry

Flooding reduced availability of key nutrients and microbial biomass in channel sediments (as seen at larger scales for the entire stream landscape in Chapter 3), which is surprising given that increased water availability is considered the primary trigger for nutrient transformation and release in dryland streams (Austin *et al.*, 2004). However, rewetting of very dry soils and sediments can produce short-lived flushes of decomposition and mineralisation (Cabrera, 1993; McComb & Qiu, 1998), which can be difficult to observe via routine sampling. Similarly, microbial populations may peak quickly after rewetting and decline as available nutrients are consumed (Ford *et al.*, 2007). Furthermore, flood pulses of different sizes and frequency can elicit different biogeochemical responses, such as differing sediment affinity for P and coupling-decoupling of nitrification-denitrification zones (Baldwin & Mitchell, 2000). However, observations for my study were necessarily restricted to one flow event during the study period, owing to the infrequency of flooding at Barnett Creek.

Surprisingly, there was no change in microbial community profiles after flooding, consistent with observations from Chapter 3, where severe flooding had no influence on microbial profiles across the stream landscape. As hypothesised, flooding reduced spatial heterogeneity (% CV) in most bioavailable nutrients, including NO₃-N and NH₄-N, yet increased heterogeneity in OC (Table 4.2). As sections of stream bed are re-connected by water flow, biogeochemical hot spots may become spatially ‘stretched’ across the bed surface. On a regional basis, Pilbara groundwater tends generally to be low in dissolved nutrients (Department of Environment and Conservation, 2003), so subsurface flowpaths are expected to contribute little to the biogeochemistry of surface sediments, in contrast to studies in streams elsewhere. For example, at Sycamore Creek in Arizona, subsurface respiration is strongly linked to vertical down welling of N-rich OM (Jones *et al.*, 1995), while in Grape Vine Canyon Stream, Nevada, three different groundwater sources discharge varying amounts of NO₃-N into stream sediments (Jones, 2002).

4.4.4 Conclusions

The results of this study suggest that stream bed microtopography is fairly static and may be less important as a control of nutrient distribution in the study reach than channel type or hydrologic period. Nutrients and microbial biomass were greater in sediments in the anabranch rather than main channel environments, indicating that the former may be a hot spot of biogeochemical activity. Contributions of anabranch channels may at least rival activity in vegetated riparian zones due to greater water availability during and after flow events. Accordingly, it is suggested that future studies of stream bed biogeochemistry should distinguish the responses and contributions of the diversity of channel types present, even at equivalent positions along the stream network hierarchy (headwaters to outlet).

CHAPTER 5

Nitrogen Mineralisation Potential in Saturated Soils and Sediments

5.1 INTRODUCTION

N availability plays a significant role in determining overall ecosystem productivity. Where N is limiting, particularly in dryland regions, rainfall or flood pulses can mobilise otherwise inaccessible forms of N by stimulating decomposition and mineralisation processes (Fisher *et al.*, 1987). In comparison to other nutrients, there is a high probability of losses of N from ecosystems after infrequent disturbances such as flooding, clearing and fire (Caldwell *et al.*, 2002; Groffman & Tiedje, 1988; Matson & Vitousek, 1981). Quantification of N mineralisation potential can therefore assist in formulating suitable models for predicting such changes in N pools.

Intermittent streams in semi-arid regions can experience long periods of little or no flow, punctuated by floods that deliver vast quantities of water and materials both to and through these systems (Reid, 2002). These flood pulses may result either from local rainfall events, or from distant rainfall occurring upstream in the catchment. The drying-rewetting pulse produces a rapid flush of labile nutrients and stimulates microbial activity, in a biogeochemical ‘hot moment’ (*sensu* McClain *et al.*, 2003). Indeed, rapid soil microbial responses to increased moisture availability may result in almost instantaneous N mineralisation, followed by shifts in the C:N ratios of microbially available substrates, and an offset between nutrient immobilisation and mineralisation (Ford *et al.*, 2007; Sparling *et al.*, 1995). In more extreme environments, including semi-arid, inland Australia, microbial activity and mineralisation flushes may last for as little as a few days or weeks against prolonged periods (often years) of drought and severe resource limitation (Ford *et al.*, 2007). Such rapid changes are difficult to

observe in the field given the large spatio-temporal variability and remote nature of these environments.

Many studies have emphasised the importance of temperature as a primary, and possibly rate-controlling, factor in N mineralisation potential. However, for more or less constantly warm environments, temperature is less likely to be of significance than moisture availability in controlling nutrient mineralisation (Grierson *et al.*, 1998). Our understanding of N cycling processes during sustained inundation (i.e. after a intense or prolonged wetting event) is also largely limited to studies in systems such as wetlands (Venterink *et al.*, 2002) or managed paddy fields (Roelcke *et al.*, 2002). In contrast, there have been few studies of the dynamics of N mineralisation in response to rewetting in lotic and unregulated systems, particularly in semi-arid and arid environments (cf. work on N limitation and uptake in desert streams by N.B. Grimm and S.G. Fisher e.g. Grimm & Fisher, 1986). A natural river landscape is typically composed of a complex of channel beds, riparian vegetation, and floodplain (or other upland) environments. These landscape units are subject to very different geomorphic and hydrologic processes, which influence the sorting and weathering of their soils and sediments, creating a mosaic of soils of different textures and composition (Ward *et al.*, 2002). During floods, these landscape units reconnect, allowing for lateral exchange of particulate and dissolved N (Welter *et al.*, 2005). The relative N mineralisation potential of these units may be an important factor in determining which areas become sources or sinks for N during flooding.

Riparian zones represent hot spots for N transformation within the broader landscape (Naiman & Decamps, 1997), and particularly in dryland landscapes. Soil texture and composition, especially the availability of suitable OM, strongly influence N cycling in many systems, such as alluvial forests (Pinay *et al.*, 1995), shortgrass steppes (Schimel *et al.*, 1985), desert ecosystems (Schlesinger *et al.*, 1996) and temperate pasture (Hassink, 1994). Fine-textured soils, such as those found in riparian zones, tend to have higher water-holding capacity and more labile C and N than coarser-textured soils, and often show a much greater flush of N mineralisation in response to rewetting (Sala *et al.*, 1988). The magnitudes of flood pulses in lotic systems may also be greatly modified by soil texture (Loik *et al.*, 2004), as coarse-textured and OM-poor soils tend to have reduced water-holding capacities and faster rates of infiltration than fine-textured, OM-rich soils. However, the interactive effects of soil saturation (in response to flood

pulses) and soil characteristics (bulk density, texture and OM content) on N mineralisation are poorly quantified for most systems, and may have great significance for understanding nutrient cycling processes in highly weathered and resource-limited environments such as those of inland Australia.

Several studies have provided models for N mineralisation potential, and laboratory incubations have improved our understanding of N mineralisation kinetics and overall N cycling. Kinetic models allow us to predict net mineralisation and specify how rates change over time (Cabrera, 1993; Ford *et al.*, 2007; Grierson *et al.*, 1998). While a number of studies have indicated that the initial flush of N mineralisation after rewetting follows first-order kinetics (Cabrera, 1993; Ford *et al.*, 2007), the emphasis has been on single soil types, and we lack studies of N mineralisation that integrate spatial differences across stream (and other) landscapes, where substrates vary greatly in composition and texture, from soils to gravel sediments (cf. Bechtold & Naiman, 2006).

This study examined the N mineralisation potential of soils and sediments in a floodplain-riparian-channel toposequence at Barnett Creek. The objectives were to: (i) characterise differences in N mineralisation potential across a toposequence of soils and riparian community types and (ii) model N mineralisation potential across a range of water potentials that simulated conditions after heavy rains and / or flooding. I hypothesised that N mineralisation rates would follow first-order kinetics during laboratory incubations and that soil characteristics (landscape position) and flood pulse size (as reflected in the water potential of the soil after rewetting) would be of equal importance in controlling N mineralisation potential. I also expected that the N mineralisation pulse would be greatest in riparian soils that were fine-grained and OM-rich, and least in floodplain soils and coarse sediments that are OM-poor.

5.2 METHODS

5.2.1 Soil collection

In August 2005, soils were collected at Barnett Creek from the three channel-riparian-floodplain transects detailed in Chapter 3 (Section 3.2.5; Fig. 3.2). Soil collections were made during a typical dry period; the previous flood (and hence river flow) was ~20 months prior to sampling. Soil was collected from the four main topographic divisions

at Barnett Creek: channel, bank, riparian zone and floodplain. To consider possible differences in N mineralisation associated with variation in canopy cover, presence of leguminous species, and soil OM content, the riparian zone was further divided into the three distinct community types – *Eucalyptus* open woodland, *Eucalyptus* closed woodland and *Acacia citrinoviridis* thicket – resulting in a total of six landscape positions including banks, channels and floodplains (Table 3.1). Vegetation classifications after Muir (1977) are provided in Table 3.1, and dominant species for each landscape position are discussed in Section 3.2.2.

Soil collection was stratified for landscape position and randomised between each landscape transition. Randomisation was performed for each transect using two numbers - a lateral distance (nearest m within each landscape transition) and a longitudinal distance (nearest m perpendicular north / south of the transect midline). At each sampling time, enough samples were taken from each landscape position to ensure an equal number of replicates ($n=30$ by landscape position). Soils were collected from the top 0-2 cm of the soil profile, as most biological activity is expected to be concentrated in the upper surface soils in semi-arid systems (Bennett & Adams, 1999). Soils were sieved to <2 mm in the field and air-dried. Gravimetric moisture contents of soils were <2 % at collection.

General soil physical and chemical characteristics (0-5 cm depth) for each landscape position were determined from additional soils samples collected in August 2005. Bulk density and particle size analyses were performed as per methods in Section 3.2.3 ($n=8$). Soil OC content and pH were also determined following methods detailed in Section 3.2.4 ($n=8$). Typical physical and chemical soil characteristics for landscape positions at the study site are given in Table 3.1.

5.2.2 Moisture retention curves

Repacked soil cores were used to determine soil moisture retention curves using the ceramic pressure plate method, with equilibration at four water potentials: -0.1, -10, -100, and -1500 kPa (Cresswell & Hamilton, 2002). Three individual soil samples from each of the six landscape positions were tested across the four water potentials. Previous studies of other Pilbara soils have demonstrated that changes in gravimetric water content are most rapid between 0 and -500 kPa (Ford *et al.*, 2007), and microbial

activity is generally impaired at potentials more negative than -1000 kPa (Zak *et al.*, 1999). The inflection point of a moisture retention curve reflects the greatest change in water matric potential and therefore microbial activity. Based on the moisture retention curve for each landscape position, four water potentials were selected to encompass inflection point of each of the six curves and categorised as ‘Low’, ‘Moderate’, ‘High’ and ‘Very High’ (full) saturation (Table 5.1). Based on site observations, a Low saturation treatment corresponded to a light rain in the catchment, Moderate saturation to a heavy rain, High saturation to a flood, and Very High saturation to successive flooding events resulting in near complete soil saturation. Applied water potentials for each saturation treatment thus differed among the six landscape positions, to reflect the ranges of soil moisture potentially most sensitive to transitions in microbial activity and concomitant N mineralisation. Corresponding estimates of water-filled pore space (% WFPS) for each saturation treatment are also provided (Table 5.1), and were calculated using the following formula (1):

$$\% \text{ WFPS} = [P_W \times (D_B / S_t)] \times 100 \quad (\text{Gardner, 1994}) \quad (2)$$

where P_W is gravimetric water content ([g water / g dry soil] \times 100), D_B is bulk density (g cm^{-3}), S_t is total porosity ($[1-(D_B / \text{particle density})] \times 100$) and particle density is 2.65 g cm^{-3} .

5.2.3 N mineralisation potential

N mineralisation potential of soil from each of the six landscape positions was tested by incubation at 40°C for 504 h (21 d) for each of the saturation – landscape position combinations described previously ($n=5$). One extra soil for each landscape position was also included as a control, i.e. unwetted.

Air-dry soil (150 g total) was placed into uncapped, cylindrical glass jars (395 mL volume) and placed in the dark in an incubation unit at 40°C for 48 h to equilibrate (Ford *et al.*, 2007). This temperature was chosen to replicate the Pilbara summer season, which is when heavy rainfall is greatest due to cyclone activity. Optimal temperatures for N mineralisation also often corresponds to the average summer temperature of the given soil (Grundmann *et al.*, 1995).

Table 5.1

Saturation treatments and corresponding water matric potentials (ψ ; -kPa) and water-free pore space (WFPS; %) for incubated soils and sediments from each landscape position at Barnett Creek, Australia. Exponential relationship between gravimetric soil moisture (P_W) and ψ provided, with corresponding R^2 value ($n=3$).

| | | Landscape Position | | | | | | | |
|----------------------|---------------|-------------------------------|----------|-------------------------------|------------|---------------------------------|--------|-------------------------------|-----------------------------------|
| Saturation Treatment | | Bank | | Channel | Floodplain | <i>Eucalyptus</i> open woodland | | Riparian thicket | <i>Eucalyptus</i> closed woodland |
| | | ψ (-kPa) | WFPS (%) | | | | | | |
| Low | ψ (-kPa) | -436.31 | | -460.20 | | -994.62 | | -616.03 | |
| | WFPS (%) | | 45.39 | | 23.71 | | 50.14 | | 11.66 |
| Moderate | ψ (-kPa) | | -36.69 | | -25.68 | | -71.59 | | -36.19 |
| | WFPS (%) | | | 66.75 | | 42.68 | | 72.28 | |
| High | ψ (-kPa) | | | -6.17 | | -4.22 | | -11.07 | |
| | WFPS (%) | | | | 88.11 | | 61.65 | | 89.28 |
| Very High | ψ (-kPa) | | | | -1.53 | | -1.13 | | -2.60 |
| | WFPS (%) | | | | | >100.00 | | | |
| $P_W = a\psi^b$ | | $P_W = -43.697\psi^{-0.1525}$ | | $P_W = -17.431\psi^{-0.2036}$ | | $P_W = -28.966\psi^{-0.1542}$ | | $P_W = -36.353\psi^{-0.1643}$ | |
| R^2 | | 0.97 | | 0.85 | | 0.96 | | 0.95 | |
| | | | | | | | | 0.98 | |
| | | | | | | | | 0.98 | |

After the 48 h equilibration period, soils were wetted slowly (monitored gravimetrically) by direct surface application of MilliQ water to reach the relevant saturation point (Table 5.1). Soil jars were weighed daily for a period of three weeks and additional water added where necessary to maintain soils at constant saturation. No additional substrate was added, to ensure patterns of N mineralisation reflected field capabilities, and soils were not allowed to free-drain, so as to mimic a sustained flood.

5.2.4 Soil chemical analyses

Soil samples were collected from incubation jars at nine sampling times: prewetting ($t=0$ h), then at 1, 2, 8, 24, 48, 168, 336, and 504 h after rewetting. A total of 7 g soil was taken at each sampling point: 2 g for determination of soil gravimetric moisture content and 5 g for estimation of inorganic N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$). Soil moisture, $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ were determined according to methods detailed in Section 3.2.4. Net N mineralisation was estimated as the difference between the final and initial inorganic N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) content for a given time period. N mineralisation potential was calculated as the total amount of inorganic N accumulated during the incubation period (e.g. Hart *et al.*, 1994).

5.2.5 Data analyses

The amounts of N mineralised in each jar were described as a function of time (t in h) from the start of the incubation by subtracting the inorganic N at the start of the incubation (prewetting) from that measured at each sampling. Non-linear regression (NONLIN procedure, SAS Institute, 1989) was used to fit mineralisation models to the mean values of the five replicates of each treatment. The model offering the best description of the data was assessed based on R^2 values and the residual sum of squares (RSS) left unexplained by the regression. For generalised models of N mineralisation, the models that gave the best description of mineralisation kinetics were applied to treatment means for each factorial group (saturation treatment x landscape position) i.e., simple linear regressions were used to describe the relationship between predicted and observed values. Saturation treatment and landscape position effects on the net amount of N mineralised and rate constants were examined by two-way factorial analysis of variance (ANOVA) in StatView 5.0 (SAS Institute Inc, 1998). Correlations between soil

characteristics (bulk density, soil texture and OC) and the net amount of N mineralised were also performed in StatView with Fisher's test for P -values.

5.3 RESULTS

5.3.1 Moisture retention curves

Moisture retention curves for soils from Barnett Creek fitted well to the power relationship $P_W = 22.77 \psi^{-0.099} + b$ ($R^2 \sim 0.90$), where b equalled P_W at $t=0$ h. While all curves fitted a basic power function, inflection points, corresponding to the most sensitive part of the curve (Fig. 5.1 – dotted area), differed among landscape positions. At ambient (0 kPa) pressure, riparian soils held the most moisture (up to 45 % gravimetric) while floodplain soils held only 28 % and channel sediments held 25 %. Riparian soils still had 13 % gravimetric moisture content at the greatest tested matric potential (-1500 kPa), while channel sediments had only 4 %. In general, moisture retention curves were similar for soils from *Eucalyptus* open woodland and *A. citrinoviridis* thickets (Fig. 5.1). Moisture retention curves for soils from *Eucalyptus* closed woodland and bank soils were also not significantly different. Consequently, four moisture retention curves: (i) channel, (ii) floodplain, (iii) bank / *Eucalyptus* closed woodland and, (iv) *Eucalyptus* open woodland / *A. citrinoviridis* thicket soils (Table 5.1) were used to convert moisture contents of incubated soils to equivalent water potentials (kPa).

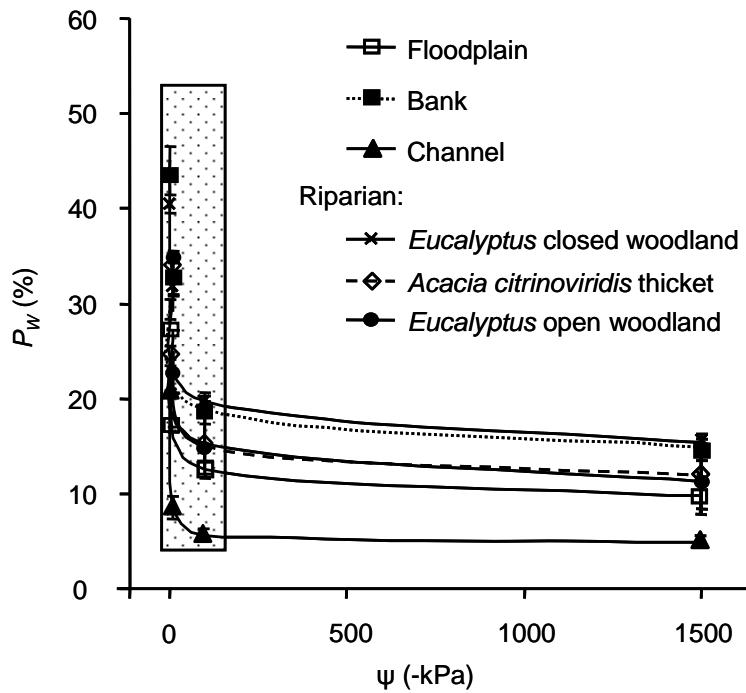


Fig. 5.1 Soil moisture retention curves for Barnett Creek surface soils and channel sediments (0–2 cm depth) by landscape position. Dotted area indicates section of greatest change in soil moisture (including curve inflection points). Error bars indicate SE ($n=3$). P_w = gravimetric soil moisture, ψ = water matric potential.

5.3.2 Relative effects of saturation treatment and landscape position on N mineralisation

N mineralisation potential was significantly different among landscape positions ($P<0.01$; Fig. 5.2a). The total amount of mineralised N was greatest in riparian soils (29.30 mg kg^{-1} , SE 1.11), which was $>50\%$ greater than channel sediments and floodplain soils, and 30 % greater than bank soils. There was no difference in total amounts of mineralised N among the three riparian community types ($P=0.16$). Total amounts of N mineralised in channel sediments were relatively consistent across replicates, particularly in comparison with riparian soils. Across all saturation treatments, riparian soils produced the greatest flush in mineralisation upon rewetting – more than 70 % of the total amount of mineralised N accumulated within the first 48 h following rewetting. In the same period, bank and floodplain soils accumulated less than half, and channels sediments less than one-quarter, of their respective total amounts of mineral N. There was no interaction between saturation treatment and landscape position ($P=0.43$), and N was mostly immobilised between 336 and 504 h. Table 5.2 summarises the results for all treatments. Bulk density was significantly negatively

correlated ($R^2=-0.34$, $P<0.01$) and percent clay ($R^2=0.39$, $P<0.01$) and percent silt ($R^2=0.37$, $P<0.01$) were significantly positively correlated with net amounts of mineralised N. However, OC was not significantly correlated with net N mineralisation ($R^2=0.26$, $P=0.05$).

Total amounts of mineralised N (N_1) were similar across the four saturation treatments ($P=0.44$; Fig. 5.2b). However, mineralisation rates were initially (≤ 48 h) faster in the Very High treatment compared to other soils. The first 48 h after rewetting accounted for >90 % of the total amount of mineralised N in this treatment. In Low, Moderate and High saturation treatments, <60 % of the corresponding totals were mineralised in the same period (Table 5.2). As expected, N mineralisation rates in control (dried and unwetted) soils were negligible.

Total amounts of $\text{NO}_3\text{-N}$ (*data not shown*) were 60 % greater in soils subjected to Moderate saturation (mean 9.23 mg kg^{-1} soil, SE 2.87) than Low (5.67 mg kg^{-1} , SE 1.77) or High (6.51 mg kg^{-1} , SE 2.99) saturation, while $\text{NO}_3\text{-N}$ was lost in the Very High treatment (-1.07 mg kg^{-1} , SE 0.83). Net immobilisation of $\text{NH}_4\text{-N}$ occurred in all saturation treatments by the conclusion of the incubation at 504 h (mean -1.42 mg kg^{-1} , SE 0.42; *data not shown*).

5.3.3 N mineralisation kinetics

Rates of N mineralisation after rewetting followed first-order kinetics in 22 out of the 24 treatment groups (Table 5.2). N mineralisation in floodplain soils closely followed first-order kinetics (all groups $R^2>0.80$). Soils from *A. citrinoviridis* thickets showed the poorest fit to a first order model (all groups $R^2<0.75$). Across all landscape positions, the best fit among saturation treatments to a first-order model was in the Low treatment (mean $R^2=0.85$).

Table 5.2

Amount of N released due to rewetting (N_1), its rate constant of mineralisation (k_1), as function of time (h). SE = standard error, RSS = residual sum of squares. ^a indicates that mineralisation could not be explained using first-order kinetics.

| Landscape Position | Saturation Treatment | N_1 ($\mu\text{g N g}^{-1}$) | SE | k_1 (h^{-1}) | SE | R^2 | RSS | |
|---------------------------------|--------------------------------------|----------------------------------|-------|---------------------------|--------|--------|--------|--------|
| Bank | Low | 30.49 | 2.59 | 0.028 | 0.009 | 0.91 | 129.78 | |
| | Moderate | 15.48 | 2.99 | 0.038 | 0.026 | 0.73 | 85.77 | |
| | High | 9.85 | 4.19 | 0.025 | 0.039 | 0.66 | 42.22 | |
| | Very High | 28.97 | 0.04 | 0.036 | 0.020 | 0.73 | 358.49 | |
| Channel | Low | 133.64 ^a | 0.00 | 0.000 | 0.000 | 0.04 | 83.44 | |
| | Moderate | 18.35 | 4.61 | 0.006 | 0.004 | 0.80 | 80.76 | |
| | High | 12.65 | 2.64 | 0.135 | 0.122 | 0.78 | 51.66 | |
| | Very High | 6.28 | 0.88 | 0.852 | 0.665 | 0.83 | 5.26 | |
| Floodplain | Low | 8.65 | 0.54 | 0.399 | 0.133 | 0.88 | 10.48 | |
| | Moderate | 22.90 | 1.98 | 0.013 | 0.004 | 0.95 | 39.15 | |
| | High | 13.90 | 2.69 | 0.008 | 0.005 | 0.87 | 33.08 | |
| | Very High | 13.01 | 1.61 | 0.041 | 0.020 | 0.81 | 50.95 | |
| <i>Eucalyptus</i> open woodland | Low | 48.03 | 3.04 | 0.037 | 0.009 | 0.96 | 156.63 | |
| | Moderate | 38.97 | 7.04 | 0.059 | 0.047 | 0.84 | 332.27 | |
| | High | 26.26 ^a | 6.91 | 0.173 | 0.238 | 0.35 | 414.84 | |
| | Very High | 21.08 | 4.21 | 0.056 | 0.047 | 0.73 | 109.96 | |
| Riparian | <i>Acacia citrinoviridis</i> thicket | Low | 16.35 | 2.90 | 0.534 | 0.500 | 0.63 | 97.89 |
| | <i>Eucalyptus</i> closed woodland | Moderate | 26.68 | 5.70 | 0.091 | 0.094 | 0.76 | 238.33 |
| | | High | 25.39 | 3.97 | 0.023 | 0.014 | 0.74 | 260.53 |
| | | Very High | 23.51 | 3.13 | 0.064 | 0.0378 | 0.74 | 220.34 |
| | <i>Eucalyptus</i> closed woodland | Low | 30.96 | 3.70 | 0.019 | 0.0085 | 0.86 | 204.69 |
| | Moderate | 39.21 | 4.92 | 0.033 | 0.0158 | 0.80 | 467.52 | |
| | High | 25.33 | 7.04 | 0.008 | 0.0074 | 0.66 | 293.44 | |
| | Very High | 30.28 | 2.45 | 0.067 | 0.0246 | 0.91 | 133.20 | |

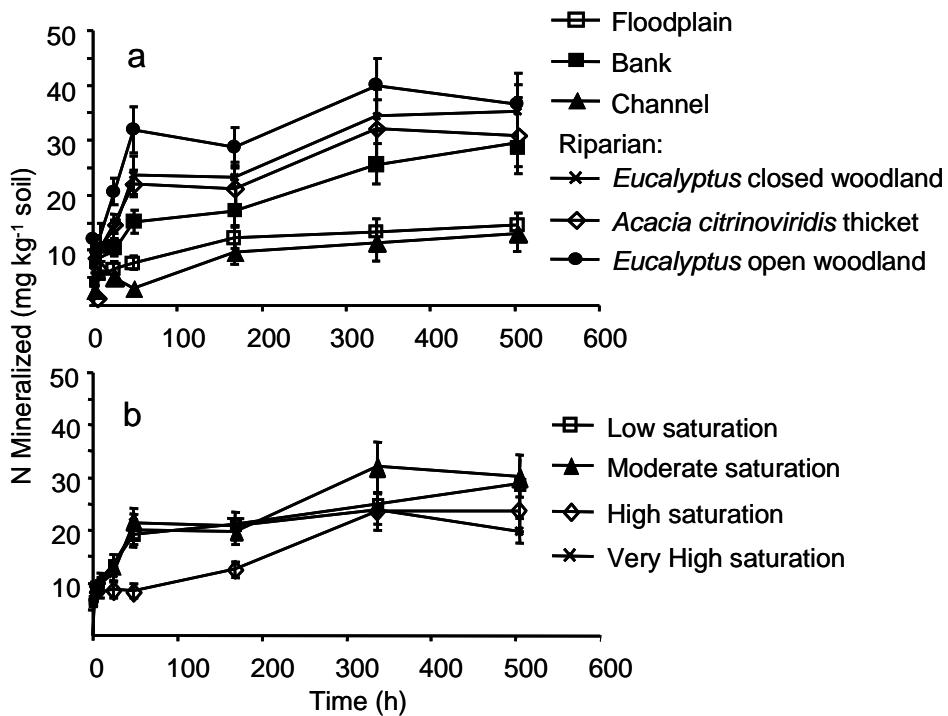


Fig. 5.2 Total amounts of N mineralised in rewetted surface soils and channel sediments (0-2 cm depth) from Barnett Creek by a) landscape position ($n=20$), and b) saturation treatment ($n=30$). Error bars indicate SE.

Rate constants (k_1) were variable between treatments, ranging from $0.006 - 0.85 \text{ h}^{-1}$ (Table 5.2). Rates constants for Moderate and High saturation treatments were five-fold less than those for Low and Very High treatments (ANOVA $P<0.0001$). Among landscape positions, rate constants were three- to ten-fold greater for channel, floodplain and *A. citrinoviridis* thickets than for other soils (ANOVA $P<0.0001$; Table 5.2). Channel sediments in particular had relatively large rate constants (0.33 h^{-1} , SE 0.08; Table 5.2).

5.4 DISCUSSION

It was originally hypothesised that landscape position (soil characteristics) and flood pulse size (soil saturation) would be of equal importance in controlling N mineralisation potential across the stream toposequences. However, it is clear from the results that landscape position plays a greater role in determining N mineralisation rates at Barnett Creek. The saturation treatments applied encompassed a wide range of water potentials (-1 to $< -900 \text{ kPa}$), so it is perhaps surprising that a flood pulse control (saturation level

effect) was not observed. The saturation levels chosen here reflect the likely differences among landscape positions to rainfall or flood conditions in the field. However, the relative insensitivity of N mineralisation to the different saturation might be partly explained by the resilience of the microbial community. Microbes in these semi-arid soils are likely well-adapted to utilise even modest increases in soil moisture (see Huxman *et al.*, 2004), such that there is a N mineralisation flush regardless of the size of the flood pulse. In comparison to vascular plants, that may require events of a minimum size or seasonal timing, microbes and microbial processes can be stimulated by even small (<2 mm) amounts of precipitation (Belnap *et al.*, 2005; Cui & Caldwell, 1997). Another possible explanation for the insignificance of saturation level in this experiment is that the small pool of labile substrates was quickly exhausted after rewetting. However, that net mineralisation continued until 336 h (14 d) tends to counter this explanation.

The results indicate that N will continue to be mineralised under sustained flooding conditions across the stream landscape, even in soils that are fully saturated. While N can be mineralised under both aerobic and anaerobic conditions, chemical shifts in flooded soils can often inhibit decomposition (Olk *et al.*, 2007). The decline in the net amount of mineralised N towards the end of the incubation period was not greater in the Very High treatment (full saturation), contrasting with other studies in semi-arid soils indicating that N removal through denitrification is pervasive in flooded soils (e.g. Aulakh *et al.*, 2000). Indeed, N mineralisation proceeded almost twice as fast in the Very High treatment in comparison to other treatments during the first 48 h following rewetting.

The N mineralisation pulse was greatest in riparian soils, and least in channel sediments and floodplain soils, as hypothesised. Total amounts of mineralised N in channel sediments and floodplain soils were 50 % less than in riparian soils. The differences in N mineralised among landscape positions supports other observations in semi-arid systems, where coarse-textured (floodplain) soils with lower total N had small, rapid cycling N pools, while finer-textured (riparian) soils had a larger, longer turnover (Bechtold & Naiman, 2006). The results also demonstrated a positive correlation between the net amount of N mineralised and fine soil texture (% silt, % clay), yet a negative correlation for bulk density, which agrees with other studies (Reich *et al.*, 1997). As OC content was not significantly correlated with the net amount of N

mineralised, OM quality may be more important in stimulating N transformation at Barnett Creek.

Interestingly, similar N mineralisation potential was observed among the three riparian community types - despite obvious differences in dominant vegetation, and canopy cover and therefore (presumably) differences in litter quantity and quality. N-fixing plants in riparian forests may contribute large amounts of N-rich organic matter (Decamps, 1993). *Acacia citrinoviridis* is a nodulating woody legume (Sprent, 2001); however riparian soils collected from where *A. citrinoviridis* was dominant had similar initial (pre-wetting) N and total amounts of N mineralised during incubation. The similar N mineralisation potential observed among riparian community types supports previous studies suggesting that landscape position (edaphic factors) is of greater importance in controlling N mineralisation than the associated vegetation community (Reich *et al.*, 1997). The riparian zone at the study site may act as a single contiguous hot spot for N mineralisation, without much internal variation, within an otherwise N-limited, semi-arid landscape. For management of riparian forests, this would suggest that retention of native riparian vegetation, regardless of forest structure or species composition, may assist in maintaining necessary N processes within the landscape.

Incubation studies can be very helpful in predicting field N mineralisation. However, artefacts such as sieving disturbance and pre-drying of soils may influence apparent N mineralisation potential by increasing the size of the mineralisation flush upon rewetting (Fierer & Schimel, 2002; Sierra, 1997). Channel and floodplain soil profiles in particular can often have large gravel inclusions (this was true of Barnett Creek), while these inclusions are more limited in riparian soils. It can therefore be expected that the *in situ* N mineralisation flush of channel sediments and floodplain soils is likely to be lower on a volumetric basis than estimated here. Pilbara soils are generally extremely dry (< 5 % gravimetric water content) except after rains or floods. However, soils used in this experiment held <2 % water when collected, so it is unlikely that air-drying soils before rewetting had any effect on rates of N mineralisation.

Given the similar N mineralisation potential across saturation treatments, it is expected that the N mineralisation flush would be similar regardless of whether the system was subject to light rains, heavy rains, a flood or successive floods. A sustained flood period (> 336 h) resulting from successive floods, would support microbial N immobilisation

and therefore ultimately limit N availability for terrestrial and aquatic biota. However, in terms of lateral exchanges between floodplain, riparian, bank and channel environments, the size and duration of the flood pulse is likely to affect the direction and magnitude of N exchanges, due to overbank flow. Storms generate runoff and lead to hydrologic redistribution and export of materials, including N (Schlesinger *et al.*, 2000), and their individual characteristics may vary N retention and export patterns (Welter *et al.*, 2005). During light or heavy rains or single floods (equivalent respectively to my Low, Moderate, High saturation treatments), directional sheet flow from adjacent or upstream terrestrial environments to stream water and sediments transports significant quantities of dissolved and particulate N (Grimm, 1992; Hornung & Reynolds, 1995). During major flooding (Very High saturation treatment), overbank flow allows for N transfer in the opposite direction, from the channel, bank and riparian environments to the floodplain. Hence while the size of the flood pulse was insignificant in this study for determining the N mineralisation potential, pulse size will still have consequences for where N mineralised is transported in the landscape, and subsequent local productivity.

Successive floods resulting in an overbank flow (Very High saturation treatment) and long periods of soil saturation may stimulate floodplain productivity, by supplying the products of N mineralisation formed in channel and (particularly) riparian environments. Less intense flood pulses would have the opposite effect, removing N mineralised from the floodplain and elevating productivity in the riparian and particularly in the channel environments. The distance that runoff travels (flowpath length) and the length of the dry period preceding flooding will also affect the concentrations of inorganic N received by different landscape positions (Welter *et al.*, 2005). Downstream transport and upwelling exchanges from groundwater and hyporheic sediments are other possibly important pathways for N exchange not accounted for in this study (Dent *et al.*, 2001; Valett *et al.*, 1997).

In conclusion, N mineralisation rates of soils and sediments from Barnett Creek followed first-order kinetics, and landscape position was a strong control of N mineralisation potential, while flood pulse size, as measured by soil saturation, was not significant. Greatest mineralisation was observed in riparian soils, but did not differ among riparian community types. Riparian soils also had the greatest mineralisation flush with over 70 % of the total amount of mineralised N accumulating within the first

48 h of rewetting. In conclusion, in semi-arid stream systems adapted to prolonged drought, N mineralisation potential is more likely to be controlled by soil characteristics than the size of the incident flood pulse. However, pulse size is still likely to play an important role in subsequent redistribution of mineralised N within the stream landscape.

CHAPTER 6

Rewetting-Drying and Litter Addition Influences Carbon and Nitrogen Mineralisation and Microbial Communities in Soils and Sediments

6.1 INTRODUCTION

In contrast to more mesic systems, the functional relationships between N and C mineralisation, water pulses and ecosystem dynamics for intermittent streams in dryland environments are not well understood (Bechtold & Naiman, 2006; Collins *et al.*, 2008; Fierer & Schimel, 2002). During infrequent floods, dry channel beds are inundated with substantial volumes of floodwater for days or weeks, and subsequent overland and overbank flow may stimulate productivity in adjacent riparian zones and floodplains (Baldwin & Mitchell, 2000; Junk *et al.*, 1989). Low relief in many semi-arid landscapes, including in Australia, generates a complex of anastomosing channels and riparia (Section 2.6.3, Plate 2.1). The subsequent differences in the quantity and quality of OM inputs, soil texture, and water retention across the stream landscape thus creates a stratified mosaic of potential microbial substrates (Chapters 3 & 5; Pringle *et al.*, 1988; Thoms & Sheldon, 2000). In addition, the extent and duration of any flood pulse is a likely major control on which ecosystem components and processes are active and to what degree (Cable & Huxman, 2004).

Post-flooding, drying of soils and sediments may cause divergence in mineralisation potential across the stream landscape as local substrate availability and physiochemical characteristics increase in importance. Substrate quantity, rather than substrate quality or microbial community composition, may be a primary control in determining N and C process rates in regions where OM inputs are low and soils are intrinsically nutrient-poor (Cookson *et al.*, 2006; Ford *et al.*, 2007). While there is an increasing interest in the influence of rewetting on nutrient release and microbial responses in dry soils (e.g.

Fierer & Schimel, 2002; Grierson *et al.*, 1998; Miller *et al.*, 2005), most of these studies have focussed on upland ecosystems. Relatively few studies have examined semi-arid stream landscapes, such that a quantitative and mechanistic understanding of mineralisation in these systems is lacking.

Microbes play an essential role in N and C cycling, and facilitate maintenance of pools of bioavailable nutrients in terrestrial ecosystems (Section 1.3.1; Balser & Firestone, 2005; Gallardo & Schlesinger, 1995). The relationship between water availability and microbial processes in soils and sediments is complex, and varies according to soil texture, moisture retention, porosity, OM content, pH and depth (Goncalves & Carlyle, 1994; Leiros *et al.*, 1999; Rodrigo *et al.*, 1997). In semi-arid systems, microbial activity is particularly affected by changes in moisture availability, and rewetting may cause large and rapid increases in the rate of microbial respiration and nutrient mineralisation (Collins *et al.*, 2008; Fierer & Schimel, 2002; Kieft *et al.*, 1987; Lund & Gorksoyr, 1980; Orchard & Cook, 1983; Sparling *et al.*, 1995). In contrast, full saturation of soils usually limits the activity of obligate aerobic microbes, and favours other processes such as denitrification and ammonification (Groffman & Tiedje, 1991; Zhang & Wienhold, 2002). During drying, several interrelated mechanisms cause a decrease in microbial activity, including reduced diffusion of soluble substrates and lowered microbial mobility, and direct physiological effects on microbial growth (Paul *et al.*, 2003). Regardless of other factors, microbial respiration is expected to be greatly reduced at soil water potentials less than -1000 kPa (Fierer *et al.*, 2003; Ford *et al.*, 2007; Zak *et al.*, 1999). While responses of microbes to drying vary by taxon, declining substrate and water availability is likely to favour fewer taxa, and microbial community profiles may therefore converge among soils and sediments in different parts of any given landscape.

The objective of this study was to quantify microbial responses and N and C mineralisation for rewetted-dried (cf. continual saturation in Chapter 5) soils and sediments from Barnett Creek. In particular, my aim was to quantify the relative roles of three factors: water availability, substrate availability and position in the stream landscape, on microbial communities and N and C mineralisation. It was hypothesised that: i) mineralisation and microbial variables (biomass, activity, diversity, community structure) are regulated equally by water availability, substrate availability and landscape position; ii) riparian soils will have greater rates of N and C transformation

and microbial activity in response to rewetting in comparison to floodplain soils and channel sediments; iii) mineralisation and microbial activity will be reduced under saturated (100 % gravimetric moisture content in free-draining soils) conditions, but increased under moderate (50 % gravimetric moisture content in free-draining soils) saturation; and iv) onset of substrate limitation would be rapid in unamended soils and sediments during incubation, owing to their naturally low content of available nutrients.

6.2 METHODS

6.2.1 Field sampling design

The three channel-riparian-floodplain transects (Section 3.2.2; Fig. 3.2) established for field studies at Barnett Creek (Fig. 2.1) were re-sampled for this experiment. Soils and sediments were collected in August 2006 at randomly selected points along the three transects, with 20 sample points for each of three landscape positions (channel, riparian and floodplain). At each sampling point, approximately 500 g of soil or sediment was collected from the top 0-2 cm of the profile, which was then sieved to < 2 mm in the field, and air-dried. General soil properties for each of the landscape positions are provided in Table 3.1.

6.2.2 Soil moisture retention, saturation treatments and water-filled pore space

Using the moisture retention curves developed for the N mineralisation potential experiment (Section 5.2.2; Fig. 5.1), the 100 % and 50 % saturation points were identified for each of the three landscape positions. 100 % saturation was defined as the maximum gravimetric moisture content (%) achieved in the free-draining soils and sediments after rewetting, with 50 % saturation defined as half this value (Table 6.1). At Barnett Creek, these saturation levels would correspond to a major flood and moderate rains, respectively. Equivalent matric potentials (kPa) were calculated using the moisture retention curves, and water-filled pore space (% WFPS) using Formula 2 (Section 5.2.2). WFPS is considered to reflect the water status of relevance to microbiological processes in soil (Linn & Doran, 1984; Scott *et al.*, 1996). Full (100 %) saturation corresponded to over 100 % WFPS in channel sediments and floodplain soils, and ~40 % WFPS in riparian soils (Table 6.1).

Table 6.1 Saturation treatments (%) and corresponding gravimetric soil moisture (%), water matric potentials (-kPa) and water-filled pore space (%) for incubated soils from each landscape position at Barnett Creek. Exponential relationship between gravimetric soil moisture and matric potential provided, with corresponding R^2 value.

| Gravimetric Soil Moisture (%) | | | |
|-----------------------------------|-------------------------|-------------------------|-------------------------|
| Water Saturation | Channel | Floodplain | Riparian |
| Zero (Prewetting) | 0 | 0 | 0 |
| 50 % | 12 | 14 | 17 |
| 100 % | 24 | 28 | 34 |
| Water Potential (ψ ; -kPa) | | | |
| Zero (Prewetting) | <-50000 | <-50000 | <-50000 |
| 50 % | -6.26 | -111.62 | -177.18 |
| 100 % | -0.21 | -1.25 | -2.28 |
| Water-Filled Pore Space (WFPS; %) | | | |
| Zero (Prewetting) | 0 | 0 | 0 |
| 50 % | 56.91 | 82.80 | 20.91 |
| 100 % | 113.81 | 165.59 | 41.81 |
| Matric Potential -kPa | | | |
| (x) / Gravimetric Soil | $y = 17.431x^{-0.2036}$ | $y = 28.966x^{-0.1542}$ | $y = 38.761x^{-0.1592}$ |
| Moisture % (y) | | | |
| R^2 | 0.85 | 0.96 | 0.9095 |

6.2.3 Laboratory incubation for mineralisation

Air-dry soils and sediments (340 g) from each of three landscape positions were rewetted under vacuum to two different saturation points – 50 % and 100 % saturation ($n=5$) and then incubated in 500 mL Mason jars fitted with Sun bio-filter sheets with 8 mm diameter, 0.2 μm filter disks to ensure maintenance of aerobic conditions. To assess if carbon supply was limiting during the experiment, half of the samples were amended with 5.25 g of ground *Eucalyptus* leaf litter (total N ~1 %, total C ~47 %) collected as fresh litter from the site. *Eucalyptus* litter dominates total litter fall at Barnett Creek. The amount of leaf litter added was the equivalent to accumulation (g C per unit area) over 2.5 yr of litter fall (by dry weight g m^{-2}) in a similar small stream in the central Pilbara (see Chapter 7).

Jars were capped and placed in the dark in an incubation unit at 40 °C (typical daytime temperature during the summer cyclone season in the Pilbara) for 2 d to equilibrate. Caps were fitted with a 1 cm diameter Suba-Seal stopper (Crown Scientific, Minto, NSW, Australia), and sealed between lid edges and jar with parafilm during incubation. After the two-day equilibration period, soils and sediments were wetted slowly by direct surface application of MilliQ water, until determined by weighing to have reached the relevant saturation point. Soils and sediments were subsequently allowed to dry over a period of two weeks without further water addition. Jars were uncapped daily to prevent anoxic conditions developing and to allow water vapour to escape.

At six sampling times – prewetting ($t=0$ h), 8 h, 24 h, 48 h, then at 7 d and 14 d – a 5 g soil sample was extracted for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ analysis by cold extraction with 1 M KCl (Mulvaney, 1996). A further 1 g of soil was extracted and weighed at each sampling time, then oven dried at 100-110 °C before re-weighing for gravimetric moisture (Gardner, 1994). Extra samples were taken at four sampling times (prewetting, 24 h, 7 d and 14 d) for estimation of OC (using 1-2 g) by the Walkley-Black method (Nelson & Sommers, 1996), total N and C (<1 g) by mass spectroscopy (See Section 3.2.4 for methods), and microbial biomass (5 g) by phospholipid fatty acid analysis (See Section 3.2.5 for methods; Zelles & Bai, 1993).

6.2.4 CO_2 efflux following rewetting

Treatment structure for CO_2 headspace measurement was identical to Mason jar incubations for mineralisation. Approximately 30 g of air-dry soil or sediment was placed in a Falcon filter unit (150 mL, #7103) assembled as described by Nadelhoffer (1990) and incubated at 40 °C for 14 d ($n=5$). Before sealing, the rim of the unit was coated with silicone lubricant to ensure a gas-tight seal then wrapped in parafilm. Measurements were taken at six times: prewetting ($t=0$ h), 8 h, 24 h, 48 h and at 7 d and 14 d to coincide with the mineralisation experiment. CO_2 measurements were taken using a needle inserted into the Suba-Seal stopper of each unit. A sample of 0.25-10 mL of air was extracted and injected into an Infra-Red Gas Analyser (LI-COR, Inc. Lincoln, Nebraska) for analysis of CO_2 content against a standard curve prepared using CO_2 gas (cylinder 4.9 % by volume). CO_2 accumulation (cumulative microbial respiration [CMR]), was then calculated using the number of hours since the last re-capping of the units. After each headspace sampling, units were uncapped and allowed to equilibrate

with ambient air conditions before re-capping and sealing with parafilm. CO₂ efflux was used as an estimate of microbial activity and C mineralisation.

6.2.5 Data analyses

Repeated measures of ANOVA was used to examine the main effects (landscape position, saturation, substrate amendment) of rewetting-drying on net N and C mineralisation, and microbial biomass, microbial (CO₂ efflux) and diversity (PLFAs). ANOVA was also used to compare water potential, inorganic N, OC, C:N, total N, total C, δ¹⁵N, δ¹³C, microbial biomass, activity and diversity between the start (0 h) and finish (14 d) of the incubation (StatView Version 5.0; SAS Institute Inc, Cary, USA). Data were square root, fourth root or eighth root transformed, where necessary, to improve homogeneity of variances. Pearson's correlation coefficients were used to describe relationships between variables, using the correlation matrix procedure by list-wise deletion in StatView Version 5.0. Given the anticipated relevance of % WFPS for microbial function, microbial activity was also correlated and regressed (simple linear regression, StatView 5.0) against % WFPS.

The amounts of N mineralised for each landscape position, saturation and substrate treatment were described as a function of time (t , h) from the start of the incubation by subtracting the inorganic N at the start of the incubation from that measured at each sampling. Non-linear regression (NONLIN procedure 1989, SAS Institute, Cary, USA) was used to fit mineralisation models to the mean value of the five replicates of each treatment. The model offering the best description of the data was based on R^2 values and the residual sum of squares (RSS) left unexplained by the regression, with the final model used being either a zero order: $N_{\text{min}} = k_0 t$, or first order: $N_{\text{min}} = N_i(1 - e^{-k_1 t})$; where N_{min} is the cumulative net N mineralised; P_i is the pool of mineralisable N made available; k_1 = rate constant of mineralisation of N_i ; and t = time (Cabrera, 1993). Simple linear regressions were used to describe the relationship between predicted and observed, with the final model explaining >85 % of the variance. Differences in microbial community structure among landscape positions, saturation and substrate treatments, as well as changes during the incubation, were examined by multivariate analysis of PLFA data (see Section 3.2.7 for method details).

6.3 RESULTS

6.3.1 Moisture profiles during incubation

All soils and sediments held similar amounts of water before rewetting ($P=0.09$; mean 1.01 %). Moisture content was still significantly greater at the conclusion of the incubation at 14 d than before rewetting ($P<0.0001$), despite substantial drying of soils from ~40 % gravimetric moisture at rewetting to 2.18 % at 14 d. Over the 14 d incubation, profiles of water loss were similar between landscape positions and between substrate treatments. After 7 d, water content was still three times greater in the 100 % saturation treatment than in 50 % group, but there was no significant difference in water content between treatment groups by 14 d ($P=0.10$).

6.3.2 Nitrogen mineralisation

Initial concentrations of $\text{NO}_3\text{-N}$ did not differ among landscape positions, substrate or saturation treatments, and averaged 1.90 mg kg^{-1} (Table 6.2). After 14 d of incubation, overall $\text{NO}_3\text{-N}$ concentrations were greater than before rewetting ($P<0.05$), and 20 times greater ($P<0.0001$) in unamended soils and sediments (25.57 mg kg^{-1}) than in those amended with *Eucalyptus* litter (1.31 mg kg^{-1} ; Table 6.2). Soils and sediments from different landscape positions and saturation treatments had similar $\text{NO}_3\text{-N}$ concentrations after 14 d.

Table 6.2 Change in chemistry of Barnett Creek soils between start ($t=0$ h) and finish ($t=14$ d) of incubation. N=no substrate amendment, S=substrate amendment. 50 % =50 % saturation treatment, 100 % =100 % saturation treatment. Means ($n=5$) with SE in parentheses.

| t (d) | | Channel | | | | Floodplain | | | | Riparian | | | |
|--|----|----------------|----------------|----------------|----------------|----------------|---------------|----------------|----------------|-----------------|----------------|----------------|----------------|
| | | N 50 % | N 100 % | S 50 % | S 100 % | N 50 % | N 100 % | S 50 % | S 100 % | N 50 % | N 100 % | S 50 % | S 100 % |
| $\text{NO}_3\text{-N}$ (mg kg^{-1}) | 0 | 2.9 (0.8) | 2.4 (1.0) | 2.1 (0.8) | 2.2 (0.7) | 1.2 (0.3) | 1.4 (0.3) | 1.0 (0.1) | 1.4 (0.2) | 2.3 (0.7) | 2.7 (0.8) | 1.0 (0.2) | 3.0 (1.0) |
| | 14 | 19.6 (4.5) | 21.8 (2.2) | 4.2 (3.9) | 0.5 (0.2) | 9.6 (3.8) | 22.6 (10.9) | 0.8 (0.3) | 0.4 (0.1) | 38.3 (8.8) | 41.5 (8.4) | 0.8 (0.3) | 1.1 (0.6) |
| $\text{NH}_4\text{-N}$ (mg kg^{-1}) | 0 | 3.2 (0.4) | 1.9 (0.2) | 1.9 (0.1) | 2.6 (0.3) | 1.9 (0.2) | 2.0 (0.1) | 2.1 (0.4) | 2.8 (0.4) | 3.1 (0.50) | 4.1 (0.4) | 3.5 (0.4) | 3.1 (0.5) |
| | 14 | 1.3 (0.4) | 0.8 (0.3) | 0.5 (0.1) | 0.5 (0.2) | 1.9 (0.5) | 1.5 (0.5) | 1.5 (0.5) | 0.4 (0.0) | 1.9 (0.6) | 3.1 (1.2) | 1.7 (0.7) | 1.4 (0.5) |
| Total C (%) | 0 | 0.9 (0.3) | 0.6 (0.1) | 1.1 (0.3) | 1.5 (0.4) | 0.3 (0.0) | 0.6 (0.3) | 2.1 (0.4) | 2.5 (0.5) | 5.3 (0.8) | 4.6 (0.5) | 6.0 (0.5) | 5.7 (0.6) |
| | 14 | 0.9 (0.3) | 0.6 (0.1) | 1.4 (0.3) | 1.4 (0.4) | 0.4 (0.1) | 0.9 (0.4) | 1.7 (0.3) | 1.6 (0.2) | 1.9 (0.5) | 1.4 (0.2) | 3.1 (0.3) | 3.0 (0.3) |
| Total N (%) | 0 | 0.03 (0.02) | 0.01 (0.01) | 0.02 (0.01) | 0.04 (0.03) | 0.02 (0.002) | 0.03 (0.12) | 0.04 (0.003) | 0.06 (0.01) | 0.12 (0.02) | 0.13 (0.03) | 0.21 (0.06) | 0.14 (0.02) |
| | 14 | 0.05 (0.04) | 0.02 (0.01) | 0.03 (0.02) | 0.05 (0.05) | 0.03 (0.00) | 0.04 (0.01) | 0.05 (0.01) | 0.05 (0.00) | 0.14 (0.04) | 0.12 (0.02) | 0.16 (0.03) | 0.16 (0.03) |
| OC (%) | 0 | 0.3 (0.1) | 0.1 (0.1) | 0.3 (0.1) | 0.3 (0.1) | 0.1 (0.0) | 0.1 (0.1) | 0.4 (0.1) | 0.5 (0.1) | 0.3 (0.1) | 0.3 (0.1) | 1.2 (0.2) | 0.8 (0.2) |
| | 14 | 0.1 (0.1) | 0.1 (0.0) | 0.3 (0.1) | 0.3 (0.2) | 0.1 (0.0) | 0.3 (0.2) | 0.4 (0.1) | 0.3 (0.1) | 0.6 (0.2) | 0.5 (0.1) | 0.6 (0.1) | 0.5 (0.1) |
| C:N | 0 | 48.5 (21.8) | 97.7 (34.0) | 55.5 (15.2) | 81.0 (21.3) | 14.6 (1.5) | 18.3 (3.4) | 54.9 (7.1) | 45.4 (5.6) | 50.3 (14.3) | 46.0 (12.1) | 36.6 (11.0) | 48.8 (18.8) |
| | 14 | 22.5 (3.1) | 22.8 (0.8) | 41.4 (4.3) | 46.1 (16.0) | 15.1 (3.3) | 18.0 (4.6) | 40.1 (8.12) | 31.2 (4.3) | 13.3 (1.0) | 12.7 (1.3) | 21.2 (2.4) | 22.3 (6.6) |
| $\delta^{15}\text{N}$ (‰) | 0 | 6.1 (1.0) | 6.6 (0.5) | 6.0 (0.6) | 7.2 (0.1) | 6.6 (0.2) | 7.3 (1.0) | 7.0 (0.5) | 8.0 (0.4) | 2.3 (0.3) | 2.2 (0.4) | 4.5 (1.0) | 2.8 (0.3) |
| | 14 | 6.2 (0.5) | 4.9 (0.5) | 6.1 (0.5) | 7.0 (0.2) | 6.9 (0.2) | 6.9 (1.0) | 5.4 (1.2) | 8.0 (0.4) | 6.5 (0.6) | 3.7 (0.7) | 6.3 (0.4) | 6.4 (0.7) |
| $\delta^{13}\text{C}$ (‰) | 0 | -18.8 (1.4) | -21.1 (2.9) | -21.8 (1.4) | -25.1 (0.4) | -22.3 (0.9) | -19.0 (3.0) | -23.9 (1.9) | -22.2 (2.0) | -21.2 (1.5) | -19.4 (1.2) | -23.8 (0.6) | -22.2 (1.6) |
| | 14 | -19.4 (1.1) | -20.8 (1.5) | -24.2 (1.4) | -23.3 (1.2) | -22.2 (1.0) | -18.8 (3.6) | -25.6 (0.8) | -22.4 (2.0) | -20.4 (0.7) | -21.6 (0.9) | -23.1 (0.3) | -23.0 (0.4) |
| Microbial Biomass (ng FA g^{-1} soil) | 0 | 804.2 (417.0) | 1303.1 (95.2) | 1201.0 (258.8) | 1339.5 (432.1) | 378.3 (123.9) | 533.3 (60.3) | 1754.6 (889.5) | 1780.6 (348.8) | 2428.6 (1127.9) | 2143.6 (453.0) | 2402.6 (449.9) | 2182.5 (748.6) |
| | 14 | 1357.8 (302.7) | 1910.6 (677.9) | 2207.3 (699.6) | 3003.5 (456.6) | 1241.0 (243.4) | 749.9 (161.6) | 2022.8 (323.0) | 2489.5 (753.9) | 3413.8 (532.1) | 3480.2 (936.5) | 2366.9 (151.4) | 2844.4 (891.3) |

In contrast to $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ concentrations halved from 2.69 mg kg^{-1} after rewetting to 1.36 mg kg^{-1} at 14 d ($P<0.0001$; Table 6.2). Soil $\text{NH}_4\text{-N}$ was initially similar among substrate and saturation treatments, however riparian soils had greater initial concentrations of $\text{NH}_4\text{-N}$ (3.48 mg kg^{-1}) than channel (2.41 mg kg^{-1}) or floodplain (2.19 mg kg^{-1}) soils ($P<0.0001$). After 14 d, $\text{NH}_4\text{-N}$ concentrations in unamended samples (1.74 mg kg^{-1}) were almost twice than in samples amended with *Eucalyptus* litter (0.99 mg kg^{-1} ; $P<0.01$; Table 6.2). $\text{NH}_4\text{-N}$ concentrations were also significantly different among landscape positions at 14 d ($P<0.0001$), but similar between saturation treatments.

Rates of net N mineralisation ($\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$) averaged $1.88 \text{ mg N kg}^{-1} \text{ d}^{-1}$ across 14 d, and N mineralisation rates in substrate-amended soils and sediments ($0.73 \text{ mg N kg}^{-1} \text{ d}^{-1}$) were only one-third that of unamended soils and sediments ($3.04 \text{ mg N kg}^{-1} \text{ d}^{-1}$; $P<0.0001$). As a result, the net amount of N mineralised in unamended soils and sediments was four times that of amended soils and sediments (Fig. 6.1). Overall rates were similar between saturation treatments and among landscape positions. Of the total amount of N mineralised during the incubation, about 67 % was produced in the first 7 d across all samples (Fig. 6.1). For substrate-amended soils and sediments, this value was about 80 %, compared to 65 % for unamended soils and sediments. More than 90 % of N mineralised in soils and sediments subject to the 50 % saturation treatment accumulated within the first 7 d of incubation, compared to only 48 % in the full (100 %) saturation treatment. Even though soils had only ~2 % gravimetric moisture (equivalent to water potentials $> -1,500 \text{ kPa}$) at the end of the experiment, N was still being mineralised (Fig. 6.2).

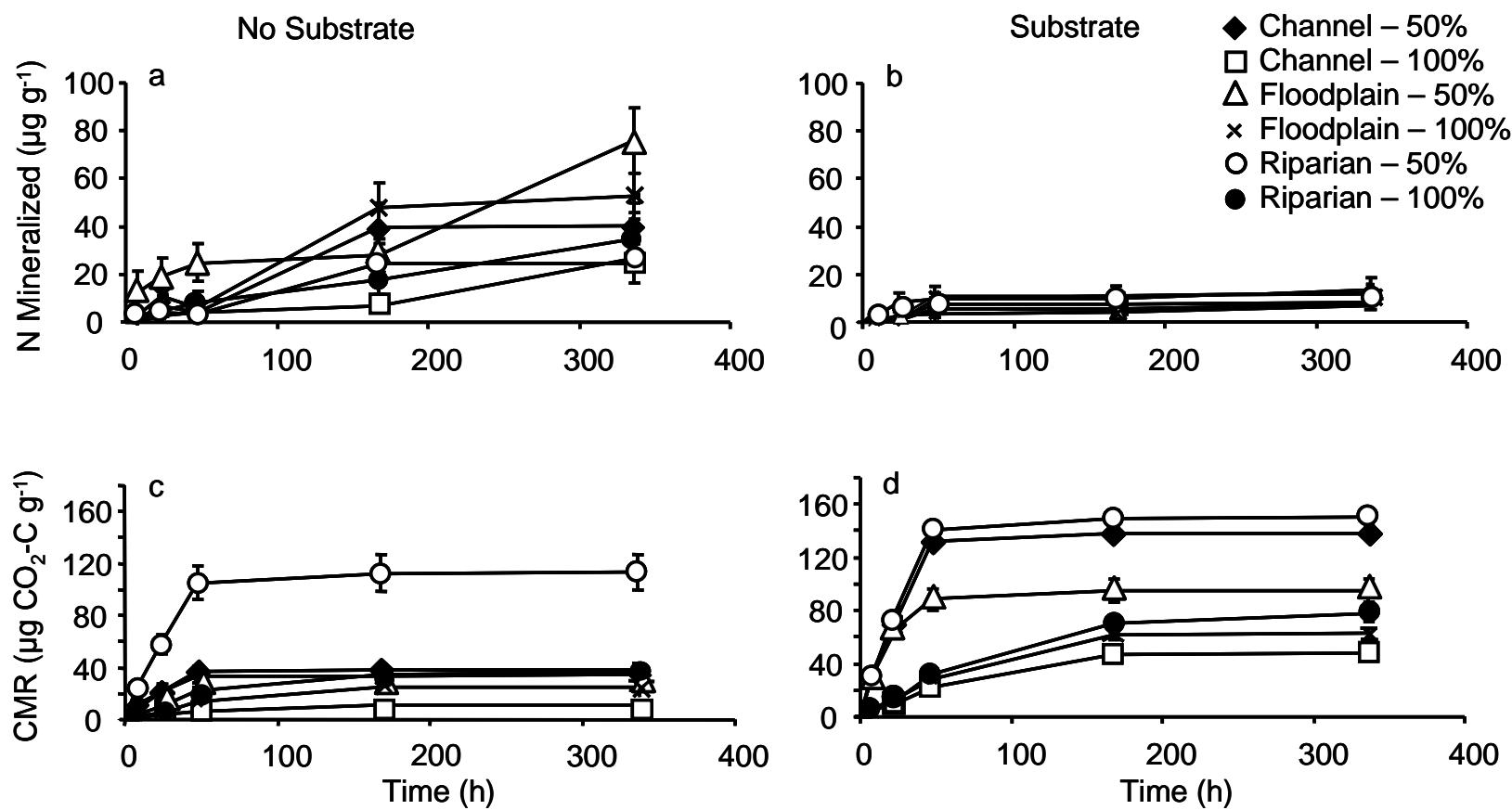


Fig. 6.1 Nitrogen and carbon mineralisation in substrate-amended and unamended Pilbara soils in response to soil rewetting and drying, expressed as time (h): (a, b) net N mineralised; and (c, d) cumulative microbial respiration (CMR).

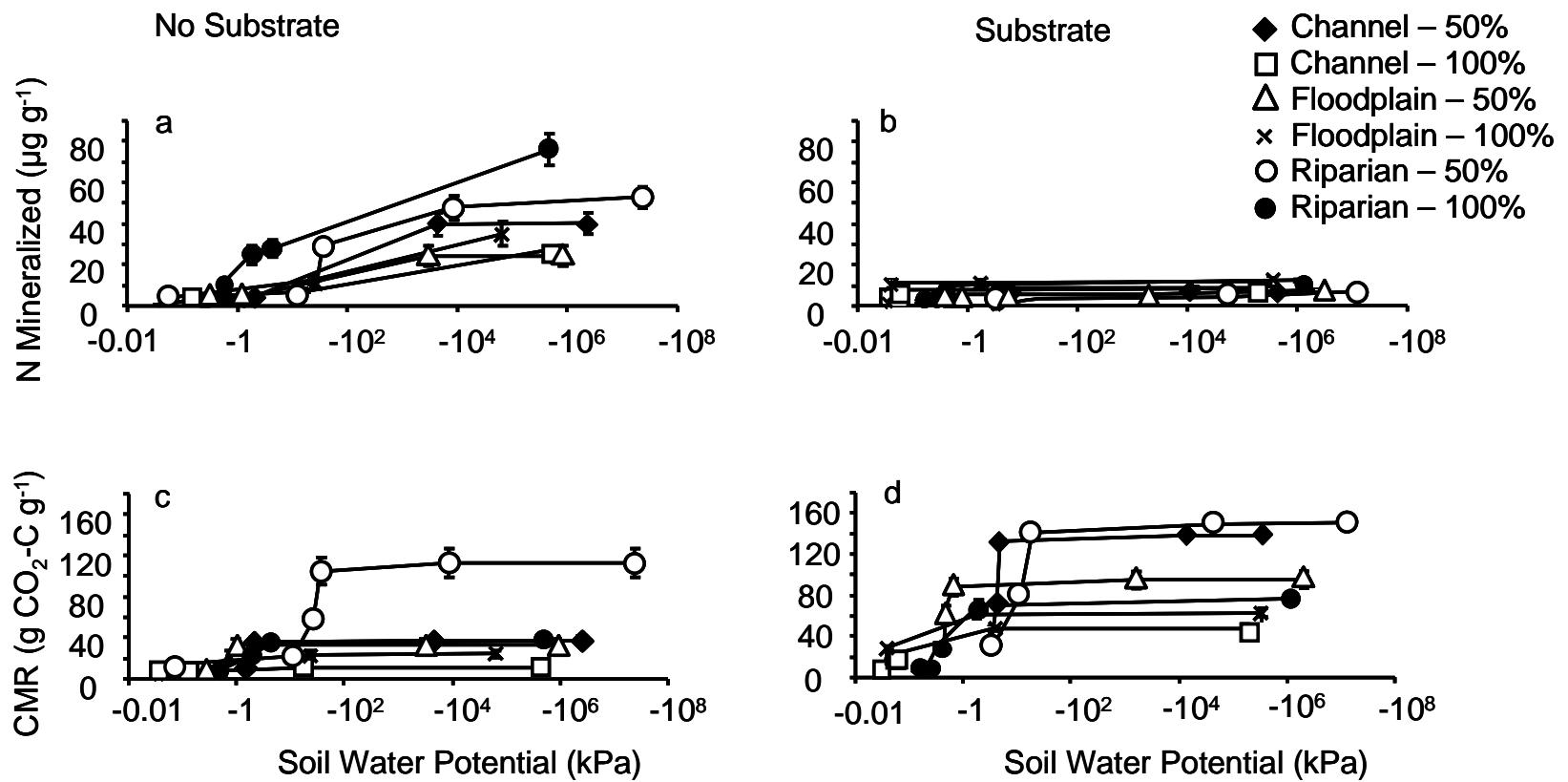


Fig. 6.2 Nitrogen and carbon mineralisation in substrate-amended and unamended Pilbara soils in response to soil rewetting and drying, expressed as water potential (kPa): (a, b) net N mineralised; and (c, d) cumulative microbial respiration (CMR).

The kinetics of N mineralisation after rewetting followed either zero-order or first-order kinetics (Table 6.3). Soils and sediments that were 100 % saturated with no litter-amendment fit a zero-order model, while the remaining treatment combinations fit a first-order model. Mineralisation rate constants (k) were an order of magnitude higher in substrate-amended soils and sediments, however the amount of N released due to rewetting (N_I) was three to ten-fold higher in unamended than substrate-amended soils and sediments (Table 6.3).

6.3.3 Total N and C content, OC & stable isotopes

Total N (mean 0.07 %) did not change over the course of the experiment, and was similar initially between all saturation and amendment treatments. However, riparian soils always had significantly greater total N than channel sediments or floodplain soils throughout the experiment ($P<0.0001$; Table 6.2). Soils were enriched in $\delta^{15}\text{N}$, with values between 0.14 and 9.72 ‰, and were similar before rewetting and at 14 d ($P=0.09$; mean 5.15 ‰). However, immediately after rewetting (0 to 8 h), $\delta^{15}\text{N}$ values were initially depleted to ~2 ‰ ($P<0.0001$), before becoming more enriched to prewetting levels for the remainder of the incubation period. Hence, rapid nitrification of the N pool following rewetting may have caused initial discrimination against the lighter N isotope. $\delta^{15}\text{N}$ of soils and sediments did not differ among substrate or saturation treatments (Table 6.2). In contrast, riparian soils were relatively more depleted in $\delta^{15}\text{N}$ (2.92 ‰; $P<0.0001$) before rewetting compared to channel sediments (6.48 ‰) and floodplain soils (7.23 ‰; Table 6.2). Riparian soils were 50 % more enriched in $\delta^{15}\text{N}$ after rewetting (0 to 1 d) while channel sediments and floodplain soils were 50 % more depleted during this time.

Table 6.3 Generalised models of nitrogen mineralisation with parameter estimates and statistics for soils from different landscape positions at Barnett Creek. N=no substrate amendment, S=substrate amendment. 50 % =50 % saturation treatment, 100 % =100 % saturation treatment.

| Landscape Position | Substrate | Saturation | R^2 | First-Order Model ^a | | | Zero-Order Model ^b | | |
|--------------------|-----------|------------|-------|------------------------------------|------------------------------------|-----------|-------------------------------|-------------------------------|-----------|
| | | | | Parameter N_1 (Asymptotic SE) | Parameter k_1 (Asymptotic SE) | Prob> F | R^2 | Parameter estimates (k_0) | Prob> F |
| Channel | N | 50 | 0.925 | 48.99 (13.81) | 0.006 (0.004) | 0.0022 | 0.831 | 0.133 | 0.0113 |
| | N | 100 | 0.923 | 366.25 [#] (366.25) | 0.0002 [#] (0.0002) | 0.0021 | 0.926 | 0.074 | 0.0021 |
| | S | 50 | 0.861 | 13.21 (2.76) | 0.01 (0.007) | 0.0077 | 0.756 | 0.040 | 0.0245 |
| | S | 100 | 0.897 | 8.22 (1.17) | 0.02 (0.01) | 0.0041 | 0.595 | 0.023 | 0.0724 |
| Floodplain | N | 50 | 0.935 | 29.08 (6.82) | 0.007 (0.004) | 0.0016 | 0.831 | 0.08 | 0.0114 |
| | N | 100 | 0.992 | 79.45 (38.94) | 0.002 (0.001) | <0.0001 | 0.992 | 0.100 | <0.0001 |
| | S | 50 | 0.881 | 7.12 (1.19) | 0.01 (0.01) | 0.0056 | 0.739 | 0.022 | 0.0281 |
| | S | 100 | 0.886 | 11.76 (1.74) | 0.02 (0.01) | 0.0051 | 0.564 | 0.032 | 0.0853 |
| Riparian | N | 50 | 0.943 | 63.66 (15.31) | 0.006 (0.003) | 0.0012 | 0.869 | 0.168 | 0.0068 |
| | N | 100 | 0.892 | 270.33 (963.07) | 0.0009 (0.004) | 0.0046 | 0.902 | 0.188 | 0.0037 |
| | S | 50 | 0.878 | 6.19 (0.96) | 0.02 (0.007) | 0.0059 | 0.821 | 0.019 | 0.0129 |
| | S | 100 | 0.977 | 11.52 (0.59) | 0.04 (0.007) | 0.0002 | 0.544 | 0.028 | 0.0945 |

^aFirst-order model: $N_{\text{min}} = N_1(1 - e^{-k_1 t})$; N_{min} = cumulative net N mineralised; P_1 = pool of mineralisable N made available; k_1 = rate constant of mineralisation of N_1 ; t = time.

^bZero-order model: $N_{\text{min}} = k_0 t$; N_{min} = cumulative net N mineralised; k_0 = rate constant of mineralisation; and t = time.

[#] SAS iterations did not converge.

Across all treatments, total C decreased from 2.59 to 1.51 % during the experiment ($P<0.05$; Table 6.2), within 7 d after rewetting. Total C did not differ with saturation level. Substrate amendment doubled total C (0.95 % to 2.05 %), and this difference was maintained from rewetting to 14 d (Table 6.2). Total C was initially four to five times greater in riparian soils (5.42 %) than in floodplain soils (1.36 %) and channel sediments (1.01 %). $\delta^{13}\text{C}$ values of soils were between -8.07 and -27.88 ‰, but did not change throughout the incubation. Unsurprisingly, soils amended with *Eucalyptus* litter were more depleted in ^{13}C (-23.15 ‰) than unamended soils (-20.29 ‰; Table 6.2). Among all soils, OC content did not change after rewetting (mean 0.39 %). Riparian soils had three times more OC initially than channel or floodplain soils, and riparian soils also had at least two to three times more OC at each sampling time during the incubation ($P<0.0001$; Table 6.2). Saturation treatment soils had similar OC before rewetting, and at each sampling time thereafter. Substrate amendment more than doubled OC content in soil samples (0.20 % to 0.57 %; $P<0.0001$; Table 6.2).

Soil and sediment C:N ratios decreased significantly during the incubation, from 50 before wetting, to 26 at 14 d ($P<0.001$; Table 6.2); reflecting the decrease in total C of soils. Substrate-amended soils had a C:N of 27 compared to 46 for unamended soils ($P<0.0001$), commensurate with the relatively high N content of the *Eucalyptus* litter in amended soils. Overall initial C:N of soils and sediments did not differ among landscape positions or saturation treatments.

6.3.4 Microbial biomass, respiration & diversity

Microbial biomass increased by one-third during the incubation ($P<0.01$), occurring mainly when soils were rewet (between 0 and 1 d) when biomass increased from 1500 to 2200 ng FA g⁻¹. Microbial biomass continued to increase between 7 and 14 d, when biomass was 50 % higher (2257 ng FA g⁻¹; $P<0.001$; Table 6.2) than before prewetting (1521 ng FA g⁻¹). Before rewetting, microbial biomass was similar across substrate and saturation treatments, however riparian soils had twice the microbial biomass (2289 ng FA g⁻¹; $P<0.01$; Table 6.2) of channel (1162 ng FA g⁻¹) or floodplain soils (1112 ng FA g⁻¹). Microbial biomass remained significantly higher in riparian soils in comparison to soils and sediments from other landscape positions (regardless of treatment) throughout the incubation ($P<0.0001$, Table 6.2).

Microbial activity (measured as CO₂ efflux) across all treatments was 6.96 µg CO₂-C g⁻¹ initially and increased to 10.63 µg CO₂-C g⁻¹ after rewetting (Fig. 6.1). Similar microbial activity was observed amongst samples before rewetting, and activity did not differ among landscape positions. CMR in substrate-amended soils and sediments was twice that of non-amended soils across the incubation period ($P<0.0001$; Fig. 6.1), and up to three times greater in soils wetted to 50 % saturation compared to those at 100 % saturation ($P<0.0001$). Microbial respiration was negligible at water potentials lower than -1000 kPa (Fig. 6.2). CO₂: total C significantly ($P<0.01$) increased over the 14 d incubation, while CO₂: microbial biomass (PLFA) remained unchanged ($P=0.45$).

Microbial diversity (number of PLFAs g⁻¹) was similar before rewetting and at the conclusion of the experiment ($P=0.13$). A slight increase in mean microbial diversity occurred after rewetting ($P<0.05$), from 7.84 to 9.79 PLFAs g⁻¹; however, diversity declined thereafter to prewetting levels. Microbial diversity was similar before rewetting among landscape positions, and in soils allocated to saturation and substrate treatments. Microbial community composition (by PLFAs) did not differ among landscape positions, saturation, or with substrate addition, and did not change over time (all ANOSIM $R\sim0.05$), and no discrete groupings were discernable in MDS. The ubiquitous fatty acids 16:0 and 18:0 (Cavigelli *et al.*, 1995; Salomonova *et al.*, 2003) contributed the most biomass by sample.

6.3.5 Interrelationships between soil and microbial variables

NO₃-N was positively correlated with NH₄-N, and negatively correlated with OC, δ¹⁵N and C:N (Table 6.4). NH₄-N was therefore negatively correlated with δ¹⁵N, and microbial biomass was positively correlated with total N and OC. Neither microbial biomass nor any of the tested soil variables was correlated with soil matric potential. Microbial activity (µg CO₂ h⁻¹) was positively correlated with % WFPS ($P<0.0001$); however, this relationship was not linear ($R^2=0.082$), with significantly higher activity between 20-40 % WFPS. Analysis by multivariate multiple regression showed that total N, δ¹⁵N and water potential explained significant ($P<0.05$) proportions of the variance in microbial community composition when modelled individually (Table 6.5). However, a sequential model explained only 9 % of the variation in microbial community composition, suggesting that other factors additional to those measured were influencing microbial communities.

Table 6.4 Pearson correlation coefficients of microbial biomass and soil variables.

| | NO ₃ -N | NH ₄ -N | Total N | Total C | OC | δ ¹⁵ N | δ ¹³ C | C:N | ψH ₂ O |
|--|--------------------|--------------------|---------|---------|--------|-------------------|-------------------|--------|-------------------|
| NO ₃ -N (mg kg ⁻¹) | | | | | | | | | |
| NH ₄ -N (mg kg ⁻¹) | | †0.588 | | | | | | | |
| Total N (%) | -0.081 | 0.414 | | | | | | | |
| Total C (%) | -0.476 | -0.030 | 0.454 | | | | | | |
| OC (%) | †-0.518 | 0.085 | †0.777 | †0.656 | | | | | |
| δ ¹⁵ N (‰) | †-0.619 | †-0.607 | 0.153 | 0.381 | 0.215 | | | | |
| δ ¹³ C (‰) | 0.310 | -0.128 | 0.071 | -0.215 | -0.243 | 0.229 | | | |
| C:N | †-0.575 | -0.381 | -0.208 | †0.716 | 0.153 | 0.486 | -0.269 | | |
| ψH ₂ O | 0.044 | -0.223 | -0.353 | -0.426 | -0.470 | 0.243 | -0.008 | -0.133 | |
| Microbial Biomass (µg FA g ⁻¹) | | | | | | | | | |
| Biomass | -0.043 | 0.124 | †0.301 | 0.138 | †0.221 | -0.182 | 0.154 | 0.005 | 0.004 |

† Indicates significant correlations ($P \leq 0.05$)

Table 6.5 Relationship between selected soil properties and microbial community composition from individual multivariate multiple regression analysis.

| | F | P | Variance |
|---|------|--------|----------|
| NO ₃ -N (mg kg ⁻¹) | 1.55 | 0.13 | 0.010 |
| NH ₄ -N (mg kg ⁻¹) | 0.66 | 0.70 | 0.004 |
| Total N (%) | 7.68 | 0.0001 | 0.051 |
| Total C (%) | 1.28 | 0.22 | 0.008 |
| OC (%) | 0.93 | 0.47 | 0.006 |
| δ ¹⁵ N (‰) | 3.14 | 0.003 | 0.021 |
| δ ¹³ C (‰) | 0.94 | 0.46 | 0.006 |
| C:N | 0.58 | 0.80 | 0.004 |
| ψH ₂ O | 2.60 | 0.045 | 0.017 |

NB: Numbers given are pseudo-F values (F), P-values (P) and the proportion of variance (variance) explained by each variable.

6.4 DISCUSSION

There was a clear and rapid pulse response to rewetting in the soils and sediments from the study site. Microbial biomass increased three-fold within the first day following rewetting, and more than 60 % of the total N mineralised by the end of the incubation

had accumulated within the first 7 d. CMR of soils wetted to high (100 %) saturation was only one-third that of moderately wetted (50 % saturation) soils, and N mineralisation rates were similarly slower in these fully saturated soils. These results agree with the hypothesis that mineralisation and microbial activity would be reduced under full soil saturation. However, as drying progressed, the rate of N mineralisation increased in soils and sediments that were 100 % saturated, so that cumulative N mineralised was similar to 50 % saturated soils and sediments by the conclusion of the experiment. At 100 % saturation, unamended soils fit a zero-order model for N mineralisation (in comparison to all other groups, which fit a first-order model), confirming the lack of a discrete mineralisation flush for these soils, and that N mineralisation had not peaked at 14 d.

When soils are fully saturated, obligate aerobic organisms are greatly inhibited (Drew & Lynch, 1980). Hence in the stream landscape, a large flood pulse (similar to the 100 % saturation treatment) may mean a delayed and more prolonged mineralisation flush, while smaller pulses (similar to the 50 % saturation treatment) will stimulate immediate nutrient transformation and availability. This model partly concurs with general observations of microbial activity in response to varying pulse size in other arid and semi-arid systems (e.g. Collins *et al.*, 2008; Huxman *et al.*, 2004). The majority of rainfall events in the Pilbara region and central Australia are large pulse events, which contrasts with many Northern Hemisphere dryland systems (Cable & Huxman, 2004). The ‘slow-release’ patterns of mineralisation associated with these large pulse events and greater infiltration of water to the rhizosphere may favour plants competing with microbes for N and other nutrients that are otherwise rapidly released and immobilised by microbes during small pulse events. It is suggested that large water pulses may therefore be of greater importance in maintaining vegetation communities at Barnett Creek than small pulses.

Substrate amendment with ground *Eucalyptus* leaf litter had a clear inhibitory effect on N mineralisation in this experiment, while stimulating microbial activity (CMR), which agrees with previous studies considering the effects of *Eucalyptus* litter on mineralisation (Aggangan *et al.*, 1999). Like many Australian native trees and shrubs, eucalypts typically have leaves with a low N content, a thick waxy cuticle and high concentrations of tannins and lignins which can inhibit microbial colonisation (Bunn, 1988, b). As the N content of the leaves added in the experiment was <2 % and C:N

ratios were >30, net N immobilisation is expected (Palm & Sanchez, 1991; Paul *et al.*, 1996). *Eucalyptus* leaf litter decomposes slowly, resulting in the immobilisation and storage of significant amount of nutrients (especially N) in surface soil litter (Adams & Attiwill, 1986; Chander *et al.*, 1995). For eucalypts generally, litter fall is usually greatest during drier seasons (Attiwill & Adams, 1993). The same is true for northern Australia – litterfall is greatest when streams are not flowing (Williams, 2007), and litter quality may decline further during dry periods due to the terrestrial ageing process (Baldwin, 1999). When rains and flood commence, accumulated *Eucalyptus* litter seems likely to stimulate microbial activity, yet limit nutrient availability for primary producers due to microbial immobilisation. A longer dry season, with concomitant greater accumulation of *Eucalyptus* litter, may increase this stimulatory effect on microbial activity and subsequent nutrient immobilisation. However, local availability of litter of higher quality (e.g. from tussock grasses or leguminous *Acacia* spp. in the riparian zone) or transport of such material from upstream sources during floods may mitigate the immobilisation effects of *Eucalyptus* litter, and create a mosaic of soils with differing C:N values across the stream landscape.

Unexpectedly, riparian soils had similar rates of C and N mineralisation and microbial activity in response to rewetting as channel sediments and floodplain soils, despite the much greater total N, OC and microbial biomass observed in riparian soils before rewetting. However, CMR in unamended riparian soils wetted to 50 % saturation was three times greater than the other five treatment groups (Fig. 6.1c), and an effect was also noticeable in amended soils (Fig. 6.1d). Riparian soils at 50 % saturation had the lowest % WFPS (~20 %) after rewetting, suggesting that these conditions were optimal for microbial activity and C mineralisation in these Pilbara soils and sediments. This observation contrasts with other studies where aerobic microbial activity and N and C mineralisation were optimised between 50-60 % WFPS (de Neve & Hofman, 2002; Franzluebbers, 1999; Linn & Doran, 1984). Riparian soils were also depleted in ^{15}N , suggesting that N fixation by the leguminous tree *Acacia citrinoviridis*, may contribute significantly to N availability at Barnett Creek when soils are moist. There are no previous studies of N inputs from fixation in the Pilbara region, including for riparian zones, so the significance of these processes are unknown. In addition, a variety of free-living, N-fixing microorganisms are capable of surviving in soils of inland Australia and may contribute to overall N availability (Smith *et al.*, 1990).

Overall, the average rate of net N mineralisation ($1.88 \text{ mg N kg}^{-1} \text{ d}^{-1}$) was similar or higher than rates observed by other authors for rewetted arid and semi-arid soils. For example, Ford *et al.* (2007) recorded rates between 0.62 and $2.12 \text{ mg N kg}^{-1} \text{ d}^{-1}$ in Pilbara grassland soils, while Bechtold and Naiman (2006) observed rates between 0.13 and $0.26 \text{ mg N kg}^{-1} \text{ d}^{-1}$ for a stream toposequence in semi-arid South Africa. However, the CO_2 efflux in response to rewetting observed for the incubation of Barnett Creek soils (an increase of 50 % to $10.63 \mu\text{g CO}_2\text{-C g}^{-1}$) was considerably lower than that observed in similar studies. For instance, a CO_2 efflux $> 250 \mu\text{g CO}_2\text{-C g}^{-1}$ was observed by Zaady *et al.* (1996) in Negev Desert soils, while Sponseller (2007) observed a 300 % increase in efflux from rewetted soils in a Sonoran Desert upland.

N was still being mineralised at the conclusion of the experiment at 14 d, even though soils had dried considerably. Microbial biomass and activity were also significantly greater at 14 d than before rewetting, even though matric potentials at this time were more negative than - 1500 kPa . This persistence contrasts with other studies indicating - 1000 kPa as a critical point for microbial activity (e.g. Ford *et al.*, 2007; Zak *et al.*, 1999). Microbial groups adapted to extremes of water potential typical in soils and sediments of Australian semi-arid streams may persist at lower water availabilities, protected in biofilms on soil aggregates or clay particles (Chenu & Stotzky, 2002). Microbial community profiles by PLFA were very similar between treatment groups and throughout the incubation, though further work using other profiling techniques such as enzymatic analysis and sole source carbon utilisation (SSGU) analysis would be useful for discerning functional changes.

In conclusion, for large water pulses ($> 40 \text{ \% WFPS}$) the characteristics distinguishing soils and sediments from different landscape positions (e.g. bulk density, OM content) were much less important in controlling microbial activity than soil saturation. Contrary to the hypotheses, substrate limitation was not evident in unamended soils and sediments during the incubation, despite the inherent low nutrient status of Pilbara soils. Previous N mineralisation studies in Pilbara grasslands have indicated the importance of N and C limitation, and litter quantity over quality (Cookson *et al.*, 2006; Ford *et al.*, 2007). Similarly, C limitation has been observed in rewetted soils from other dryland regions, including arid uplands (Sponseller, 2007). However, stream ecosystems are more heterogeneous than grassland and many upland ecosystems in spatio-temporal distribution of soil, vegetation types and nutrients (including OM inputs). The

productivity of riparian forests ensures a greater quantity and variety of litter than available in upland or grassland settings. Hence, while the quantity of litter available may be sufficient to support mineralisation processes in intermittent Pilbara streams, the heterogeneity of litter sources may mean litter quality is highly variable and therefore more delimiting of microbial activity.

CHAPTER 7

Algal and Microbial Responses to Nutrient Availability and Severe Flooding at Pirraburadoo Creek

7.1 INTRODUCTION

Channel sediments of intermittent, dryland streams are subject to alternate periods of wetting and drying (Chapter 4; Austin *et al.*, 2004). Stream beds are heterogeneous environments possessing spatio-temporal patchiness on many scales (Hawkins *et al.*, 1993; Lake, 2000). Mesohabitats (e.g. pools, riffles, runs) are visually distinct, mesoscale (m scale) habitat patches (Beisel *et al.*, 1998), and that are of importance to invertebrates (Brunke *et al.*, 2001) algae (Mullner & Schagerl, 2003), and possibly microbial communities (Rees *et al.*, 2006; Sobczak & Burton, 1996). These habitat patches may be permanent or transient (Pringle *et al.*, 1988; Stanley *et al.*, 1997). On a catchment scale, channel sections can be viewed as arrays of shifting hydrogeomorphic patches, or functional process zones (FPZs) which differ in biocomplexity and nutrient dynamics (Thorp *et al.*, 2006).

Pools and runs are common in gravel-sand lowland rivers, with riffles more typical of elevated settings or in association with outcropping bedrock. In lowland rivers, pools are low energy environments (Jowett, 1993), which tend to accumulate OM, retain moisture and hence support food webs and nutrient transformations during dry periods (Davis *et al.*, 2002; Lisle & Hilton, 1992; Stanley *et al.*, 1997). In comparison, runs are higher energy environments (Jowett, 1993), which may function mainly to store and process smaller amounts of OM (e.g. leaf packs) and to transport nutrients rather than supporting the local processing and storage of nutrients likely for pool mesohabitats.

Microbes and benthic algae are often closely associated with stream sediments. In part this is due to their organisation in sessile communities, or biofilms, attached to sediment

particles or other substrates (Section 1.3; Fig. 1.7; Lock, 1993). Microbes play an essential role in stream sediments, facilitating the majority of biogeochemical processes, and benthic algae are likewise important as primary producers and indicators of nutrient availability and stream health (Fellows *et al.*, 2006; Horner *et al.*, 1990). Algae are also a significant source of energy for higher trophic levels in many streams, and can sequester inorganic nutrients and labile organics (Mulholland, 1996). Consequently, cycles of algal growth, senescence and sloughing during hydrological disturbances in intermittent river systems have significant implications for nutrient availability to other organisms (Townsend & Padovan, 2005).

Light is an important regulator of growth of benthic algae in many streams (Hill *et al.*, 1995). However, the largely aseasonal streams typical of dryland Australia are mostly lightly shaded and are instead ‘photo-saturated’. After light, models of gravel bed rivers suggest that hydrological factors are equally important as nutrients in controlling algal biomass (Biggs & Close, 1989; Grimm & Fisher, 1989), and that algae recover more quickly than microbes after flooding (Holmes *et al.*, 1998). OM availability and oxygen status are other important factors influencing microbial communities in sediments (Brune *et al.*, 2000; Claret & Boulton, 2003). During stream flow, upwelling of nutrients from the hyporheic zone may also enrich surface sediments with nutrients and promote growth (Dent *et al.*, 2007; Valett *et al.*, 1994), though these connections are lost during drought, when water tables fall (Lake, 2003; Packman & Salehin, 2003).

Both algae and microbes depend on N (excluding those biota capable of N fixation) and P availability. P is limiting in many freshwater ecosystems (Hecky & Kilham, 1988), and N may be equally or more limiting in others (Grimm & Fisher, 1986; Lohman *et al.*, 1991). However, nutrient limitation may vary considerably spatio-temporally in soils and sediments, even at very small (<cm) scales (Lewis *et al.*, 2007; Manzoni *et al.*, 2008). Algal stoichiometry, or nutrient status (C:N:P ratios), is a useful indicator of nutrient limitation (Kahlert, 2001), and litter ratios indicate the relative dominance of mineralisation versus immobilisation processes (Cross *et al.*, 2005). In accordance with resource limitation, it might be expected that both benthic algae and microbes will be inactive during drought periods and highly active and diverse after flooding in semi-arid Australian systems. These changes may be most pronounced in runs rather than in pool environments, given the more episodic nature of water availability and, presumably, nutrient availability in runs. Drying models for stream reaches indicate a reach-wide

convergence of biotic assemblages towards those typical of pond habitats (as riffle and run habitats shrink spatially) after successive and severe drought periods (Wood *et al.*, 1992). There is uncertain relevance of this model for most semi-arid Australian streams, which dry completely during drought and are consequently ecologically ‘reset’ from the perspective of stream biota (Boulton *et al.*, 1992).

This study considered the responses of benthic algae and microbial communities to nutrient availability and disturbance by hydroperiod (interflood / flood) across a single drought-flood cycle at Ratty Springs, on Pirraburadoo Creek (Section 2.8.2; Figs 2.1 & 7.1). Microbial activity (*in situ* CO₂ efflux) and community composition (by PLFA), benthic algal biomass and composition (genera-level), and nutrient (N and P) and C availability in sediments were all quantified. The overall aim of this study was to assess the responses of algal and microbes in pool and run habitat patches to the drought-flood cycle and nutrient availability. Specifically, it was hypothesised that: (i) algal and microbial communities would increase in biomass and activity in response to flooding, and be comparatively inactive during drought; (ii) algal stoichiometry would indicate both P and N limitation; and (iii) pools would support greater nutrient availability, microbial and algal diversity and growth than runs, particularly during drought. Finally, the results of this study are discussed in the context of the development and maintenance of stream bed habitat patches.

7.2 METHODS

7.2.1 Study site and patch selection

Sampling and field measurements were based at Ratty Springs on Pirraburadoo Creek (Section 2.8.2; Fig. 7.1) in November 2005 (interflood) and March 2006 (flood period). This study commenced some 22 months after the previous flood (Bureau of Meteorology, 2008), and Ratty Springs therefore supported only a few small, disconnected pools. Between January and March 2006, three successive cyclones contributed significant rainfall to the area (Fig. 7.1), causing flooding at Paraburadoo and elsewhere in the Pilbara. Given the lack of predictability of floods, sampling was necessarily opportunistic. The sampled stream reach was approximately 100 m in length, and included two channels (Fig. 7.2). Six patches of stream bed were sampled - three patches supporting persistent benthic algal growth in both wet and dry seasons

(pool mesohabitats; Plate 7.1a, b), and three patches only supporting growth in wet seasons (gravel run mesohabitats; Plate 7.1c, d). Patches were each approximately 30 m² in size, shaped to fit wholly within the stream bed to the bases of the adjacent banks (0.2 – 0.5 m high).

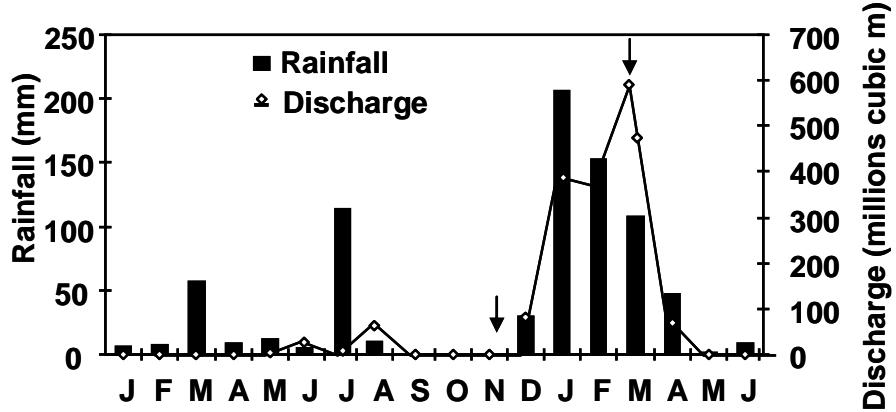


Fig. 7.1 Rainfall at Paraburadoo township and discharge in the Ashburton River (line graph; Capricorn Range monitoring station #706209) for January 2005 to June 2006 (Bureau of Meteorology, 2007; Department of Water, 2007). Arrows indicate sampling times.

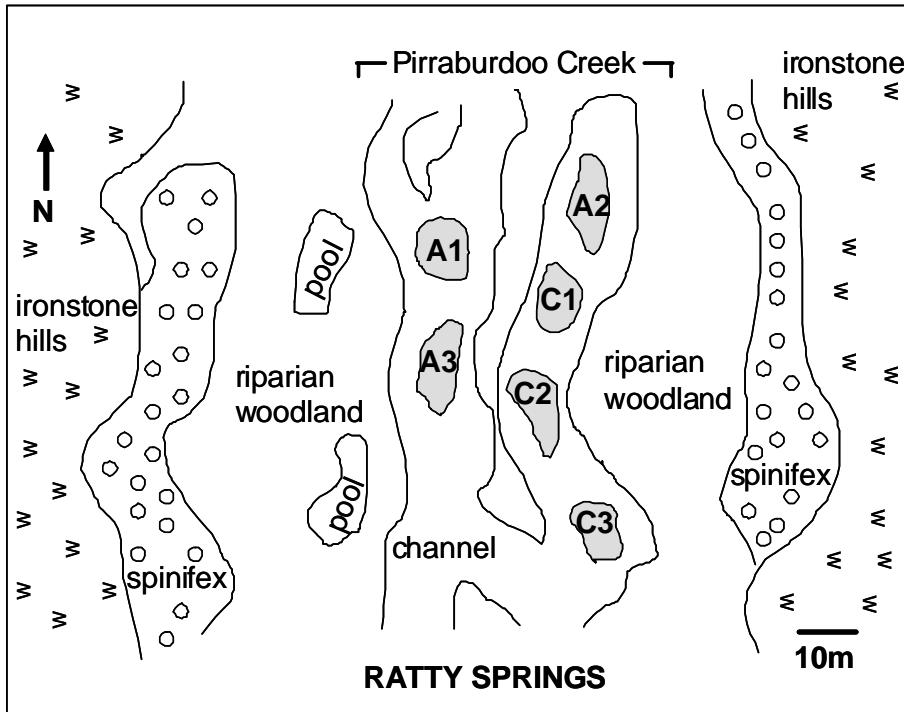


Fig. 7.2 Location of sampled pools (A1, A2, A3) and runs (C1, C2, C3) within the channel of Pirraburadoo Creek at Ratty Springs.

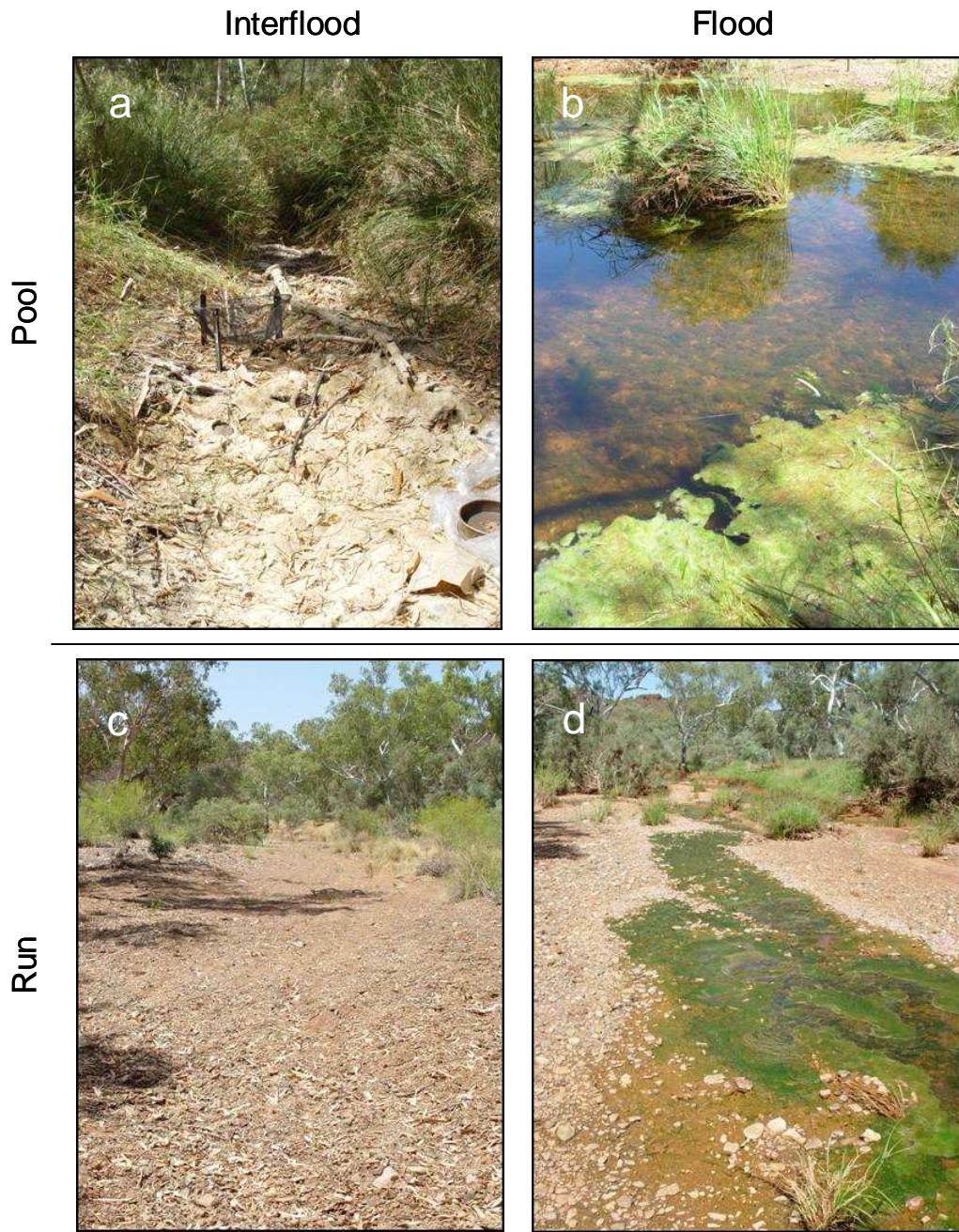


Plate 7.1 Algae in pool and run mesohabitats at Ratty Springs; a) pool in interflood, b) pool in flood period, c) run in interflood, d) run in flood period.

7.2.2 Nutrient availability and sediment characterisation

To determine nutrient availability in sediments, three cylindrical sediment cores (7.5 cm diameter x 5 cm depth) were taken from each patch at each sampling time ($n=9$). Cores were positioned randomly, and the sample volume was selected to provide a minimum mass for the chemical and microbial tests. Any surface litter or algal mat was removed,

and each sediment core then sieved to <2 mm in the field, prior to storing at 4 °C for chemical analyses. Water content was determined shortly after collection for each sample by gravimetric analysis, after oven drying at 110 °C for 48 h (Gardner, 1994). NO₃-N, NH₄-N, OH-P_T, OH-P_i and OH-P_o of sediments were analysed according to methods detailed in Section 3.2.4. OH-P_T content of algal and litter samples were also determined after H₂SO₄ / H₂O₂ digestion.

Oxidisable OC was determined for sediment samples (0.5-2 g) from each patch using the Walkley-Black method (Nelson & Sommers, 1996). Sediment, litter and algal samples were also analysed for total N and C content (%), and δ¹⁵N and δ¹³C (‰) using the methods detailed in Section 3.2.4. To compare the physical characteristics of pool and run mesohabitats, extra samples ($n=9$) were collected to determine bulk density and particle size classes (see Section 3.2.3 for method details).

7.2.3 Algal communities

Benthic algal biomass (dry weight) was measured at each sampling time, by randomly sampling six points ($n=18$; ~40 cm²) in each patch. Six additional samples of benthic algae were taken from each patch for determination of algal diversity and relative abundance by light microscopy ($n=18$). Algal genera were categorised (W. Hosja *pers. comm.*) as dominant (>40 % of sample by cell counts), co-dominant (10-40 %), present but not abundant (0-10 %) or undetected (0 %). Epiphytic genera were also noted, as their presence is one indication of a mature successional stage (Wetzel, 1996). Grab samples (100 mL; $n=9$) of overlying water (where present) were also collected and assessed for densities of cyanobacteria.

In a preliminary study to assist site selection, additional algal samples were also collected using the above methodology from a site on Weeli Wolli creek, ~ 70 km north of Newman. The algal inventory for these collections is provided separately as supplementary data in Appendix B.

7.2.4 Litter inputs and shading

To consider possible differences in shading over pools and runs, one canopy photograph was taken of overstorey vegetation (essentially *Eucalyptus* spp. trees) above each patch in March 2006 to estimate foliage projected cover ($n=3$). Given the relative height of the overstorey trees (>10 m) to patch size, a single photograph was sufficient to capture total cover over a respective patch, and seasonal cover changes were not expected given that eucalypt trees are evergreen. Photographs were taken using a 5.0 mega-pixel digital camera (Sony DSC-F717, Tokyo, Japan) mounted pointing upwards at 1 m above ground level, on a spirit-levelled tripod. Cover images were analysed in Adobe Photoshop 7.0 (Adobe Systems Inc., San Jose, California, USA) for foliage projective cover (f_f) using the following formula (3) (MacFarlane *et al.*, 2007):

$$f_f(\%) = 100 * (1 - \text{total gap pixels} / \text{total pixels}) \quad (3)$$

To compare nutrient inputs from litter between pool and run mesohabitats, direct litterfall to the stream bed was collected using circular litter traps (105 cm diameter x 20 cm depth, 15 cm elevation) constructed from a 2 mm nylon mesh, with one trap positioned over each patch. Litterfall was collected once, as accumulated litter over the summer growing season (November 2005 - January 2006). Further litterfall collections between March and August 2006 (the flood period) were disrupted by damage and upturning of traps by stray livestock. Samples of *in situ* litter (unconsolidated litter on the surface of the stream bed) were also collected at three random points, 40 cm² in area, within each patch in both November 2005 and March 2006. Litterfall and *in situ* litter samples were oven dried at 70 °C for 24 h (Walinga *et al.*, 1995), and then weighed for total litter mass. The dried litter was divided into (i) leaves, (ii) sticks, (iii) bark, and (iv) diaspores (seeds and fruits) to estimate weight contribution of each component. ‘Woody debris’ comprised all stick and bark fragments.

7.2.5 Microbial communities and activity

In order to profile microbial communities in sediments, three vials (~10 g each) of sieved (to 2 mm) sediment were randomly sampled from each study patch at both sampling times ($n=9$). Samples were analysed according to the methods detailed in Section 3.2.5. To identify broad microbial groups, sediment samples were re-extracted

using PLFA methods (as above) and the FAME fractions analysed on an Agilent 6890 / 5973 Gas Chromatography-Mass Spectrometer (GC-MS; Agilent, Santa Clara, California, USA). A 60 m x 0.25 mm x 0.25 µm ZB-5 (Phenomenex, Torrance, California, USA) capillary column was used. The GC was used in pulsed splitless mode with the oven temperature set for 70 °C to 1 min, then increased at a rate of 10 °C min⁻¹ to 150 °C, followed by 3 °C min⁻¹ to 300 °C, and finally held isothermal for 20 min. The helium carrier gas was maintained at a constant flow of 1.1 mL min⁻¹, and full scan (50-550Da) data were acquired. Other standard mass spectral conditions were applied including electron energy of 70 eV and source temperature of 230 °C. Product identifications were based on comparison to library mass spectra. Biomass was compared for five general indicator types – eubacteria: 15:0, 17:0, and i19:0; fungi: 18:2w6-9; sulphate-reducing bacteria: 13Me14:0, 12Me14:0; ubiquitous: 16:0, 18:0; and markers for bacterial nutrient status: 16:1w7c.

Microbial activity was estimated by measuring surface CO₂ efflux (net respiration) in the field using a CIRAS-1 portable differential CO₂ IRGA with a SRC-1 soil respiration chamber attachment (PP Systems, Amesbury, MA, USA). Diurnal measurements were taken at five random spatial points in each patch ($n=15$), in November 2005 and March 2006. Where benthic algal mats were present, respiration was measured above the surface mat and on the sediment surface directly beneath the mat. The soil respiration chamber used was not suitable for measurement on submerged sediments.

Surface CO₂ efflux was calculated using the following formula (4):

$$R = [(C_n - C_o) \times V] \times [T_n \times A] \quad (4)$$

where R is the surface respiration rate (efflux of CO₂ / unit area / unit time), C_o is the CO₂ concentration at time zero and C_n is the concentration at a time T_n later, A is the surface area of sediment, and V is the total respiration chamber volume (PP Systems, 1993).

7.2.6 Data analyses

Data were analysed using two fixed factors: time of collection (hydroperiod) and algal patch type (pool / run). ANOVA and correlation tests were performed in Statview 5.0

(SAS Institute, Cary, North Carolina, USA). Data were transformed where appropriate for ANOVA (square root or fourth root), and groups separated using Fishers PLSD post-hoc test. Samples were nested within patches for two-way ANOVA (balanced), except for algal nutrient data where a sequential one-way ANOVA was performed with Bonferroni-correction (Holm, 1979). PLFA microbial community data were analysed using multivariate techniques, including MDS and ANOSIM (square root transformation / Bray Curtis similarities) in Primer 6.1.5 (Primer-E, Plymouth, UK). Unless otherwise stipulated, *P* values provided in the text indicate significance by ANOVA.

7.3 RESULTS

7.3.1 Algal communities and stoichiometry

Benthic algal communities at Ratty Springs were dominated by the filamentous green macroalgae *Spirogyra* (Table 7.1). Pools supported a higher diversity and density of attached epiphytic diatoms (especially *Synedra*, *Eunotia*, *Gomphonema*, *Fragilaria*) in both interflood and flood conditions. Runs only supported benthic algae mats in the flood period (Plate 7.1d). Cyanobacteria were present in nearly all benthic mat samples, but were not abundant (Table 7.1). Densities of cyanobacteria in water samples were similarly low, averaging <16 cells mL^{-1} , across the two patch types. Biomass of benthic algae in pools decreased by 70 % after flooding from 137 to 41 g m^{-2} dry weight (Fig. 7.3). Meanwhile, in runs, algal biomass increased 400 % (from negligible to $\sim 400 \text{ g m}^{-2}$ dry weight) after flooding. Consequently, biomass of benthic algae showed a strong interaction between flooding influences and patch type ($P<0.0001$).

In contrast, total C (mean 22.00 %, SE 1.68) and N (mean 1.94 %, SE 0.22) of algal tissues were not significantly different between samples collected in the flood and interflood, or between pool and run mesohabitats (Table 7.2). Meanwhile, OH- P_T concentrations (mean 0.08 %, SE 0.01) in algal tissues were significantly lower in runs after flooding ($P<0.001$), yet unchanged in pools. Benthic algae had an average molar C:N:P ratio of 712:55:1 across all samples. However, N:P ratios in algal tissues were two to three times greater in runs under after flooding, compared to pools at either time (Table 7.2). Algae in runs were also significantly less enriched in ^{15}N and more depleted in ^{13}C than algae in pools (Fig. 7.4).

Table 7.1 Genera detected in algal mat samples from Ratty Springs, Pirraburadoo Creek.

| Group | Genus | Interflood | | Flood |
|------------------|--------------------------------|------------|------|-------|
| | | Pools | Runs | |
| Chlorophytes | <i>Spirogyra</i> | ■ | ■ | ■ |
| | <i>Oedogonium</i> | | | ○ |
| | <i>Scenedesmus</i> | | ○ | ○ |
| | <i>Pithophora</i> | ● | | |
| | <i>Cosmarium</i> | ○ | | |
| | <i>Rhizoclonium</i> | | ● | |
| | <i>Closterium</i> | | ○ | |
| Bacillariophytes | <i>Nitzschia</i> | | ○ | ○ |
| | <i>Navicula</i> | | ○ | ○ |
| | <i>Synedra</i> ^e | ● | ● | ○ |
| | <i>Fragilaria</i> ^e | ● | ● | ○ |
| | <i>Amphora</i> ^e | ○ | ○ | |
| | <i>Gomphonema</i> ^e | ● | ● | |
| | Pennate Diatoms ^e | ● | ○ | |
| | <i>Eunotia</i> ^e | ● | ● | ● |
| | <i>Gyrosigma</i> ^e | ○ | | |
| | <i>Cocconeis</i> | ○ | | |
| Cyanobacteria | <i>Oscillatoria</i> | ○ | ○ | ○ |
| | <i>Chroococcus</i> | ○ | | |
| | <i>Lyngbya</i> | ○ | | |
| Amoebae | <i>Arcella</i> | ○ | | |

■ dominant (>40 % of sample by cell counts) ●=co-dominant (10-40 %), ○=present but not abundant (0-10 %), blank=not detected (0 %). ^e=epiphytic.

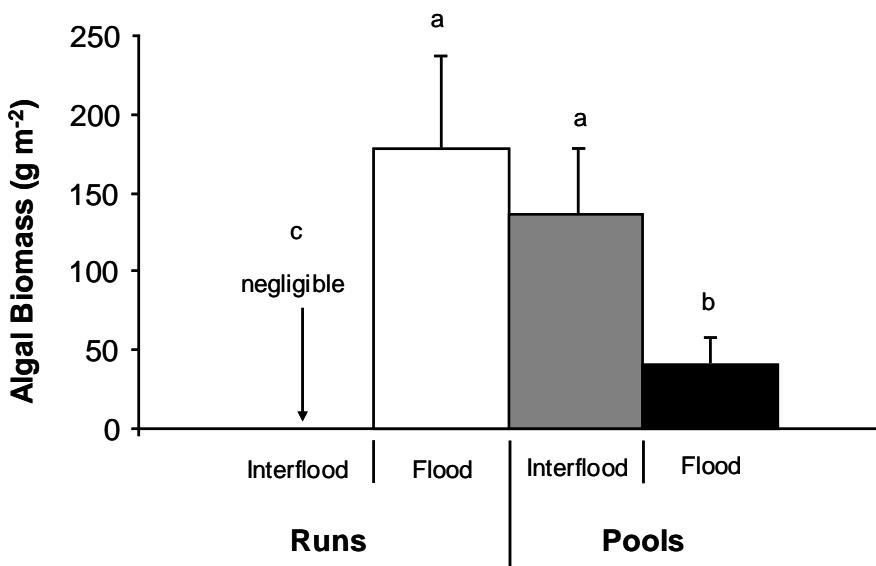


Fig. 7.3 Mass of benthic algae in pools and runs, in interflood and flood periods. SE indicated by error bars, post-hoc groupings by ‘a’, ‘b’ and ‘c’. $n=18$.

7.3.2 Litter contributions from streamside trees

Foliage projective cover from overstorey trees was ten times greater ($P<0.01$) over pools (Table 7.3), which was reflected in five times greater litterfall over these patches ($P<0.05$). However, the mass of *in situ* litter was not significantly different between patch types. Nutrient concentrations in litter did not differ among patches or between collection times, and litter typically consisted of 46 % C, 0.5 % N and 0.15 % P by mass (Table 7.3).

In situ litter was dominated by *Eucalyptus* leaves (64 %) and woody debris (24 %), with a small diaspore component (9 %). Similarly, nearly all *in situ* litter (89 %) in samples collected from runs was *Eucalyptus* leaves. By contrast, pools had only 48 % *Eucalyptus* leaves with a significant proportion of woody debris (37 %) and diaspore litter (14 %). Collected litterfall was composed almost entirely of *Eucalyptus* leaves (49 %) and woody debris (50 %), with a negligible diaspore component (<1 %). All litter samples had consistent $\delta^{13}\text{C}$ signatures of approximately -28.20 ‰, while $\delta^{15}\text{N}$ signatures were more variable, ranging from 3.82 to 10.69 ‰ (Fig. 7.4).

Table 7.2 Content of moisture and major nutrients in sediments and algal tissues, for pools and runs in interflood and flood periods. All values are means with SE given in parentheses ($n=9$). Post-hoc groupings indicated by ‘a’, ‘b’, ‘c’ and ‘d’.

| | Interflood | | Flood | | ANOVA (P -value) |
|---|---------------------------|--------------------------|---------------------------|---------------------------|--|
| | Run | Pool | Run | Pool | |
| ALGAE | | | | | |
| Total C (%) | n / a | 23.95 (3.92) | 20.47 (4.42) | 21.58 (13.25) | ns |
| Total N (%) | n / a | 2.12 (1.71) | 1.56 (0.41) | 2.16 (1.71) | ns |
| OH-P _T (%) | n / a | 0.08 (0.05) ^a | 0.04 (0.02) ^b | 0.12 (0.05) ^a | Patch Type (0.004) ^B |
| C:N:P (molar) | n / a | 750:57:1 | 1408:93:1 | 464:40:1 | n / a |
| SEDIMENT | | | | | |
| Moisture (%) | 0.51 (0.15) ^a | 1.44 (1.38) ^b | 15.33 (2.69) ^c | 16.97 (6.31) ^d | Time (<0.0001) ^B , Patch Type (0.0099) ^B |
| NO ₃ -N (mg kg ⁻¹) | 1.66 (2.86) ^a | 4.20 (1.37) ^b | 0.52 (0.28) ^a | 0.43 (0.20) ^a | Time x Patch Type (0.0025) ^B |
| NH ₄ -N (mg kg ⁻¹) | 4.30 (0.51) ^a | 4.39 (1.58) ^a | 4.03 (2.73) ^b | 2.66 (1.26) ^b | Time (0.037) |
| Total N (%) | 0.07 (0.10) ^a | 0.20 (0.13) ^b | 0.04 (0.03) ^a | 0.04 (0.04) ^a | Time x Patch Type (0.0049) ^B |
| OC (%) | 0.17 (0.11) ^a | 0.28 (0.13) ^a | 0.10 (0.09) ^b | 0.13 (0.01) ^b | Time (0.002) ^B |
| Total C (%) | 1.23 (1.30) ^a | 2.33 (1.04) ^b | 1.33 (0.59) ^a | 0.89 (0.64) ^a | Time x Patch Type (0.0064) ^B |
| C:N (molar) | 35:1 (13.56) ^a | 16:1 (4.41) ^b | 39:1 (12.47) ^a | 37:1 (18.30) ^a | Time (0.0019) ^B , Patch Type(0.0037) ^B |
| OH-Po (μg g ⁻¹) | 0.67 (0.73) ^a | 2.07 (1.34) ^b | 1.14 (0.67) ^a | 0.65 (0.58) ^a | ns |
| OH-P _i (μg g ⁻¹) | 2.34 (0.78) ^a | 4.44 (2.54) ^b | 1.65 (0.46) ^a | 2.45 (1.44) ^a | Time (0.0065) ^B , Patch Type (0.0111) |

^B Significant at Bonferroni-corrected significance level of $P<0.02$ for algal data and $P<0.01$ for sediment data.

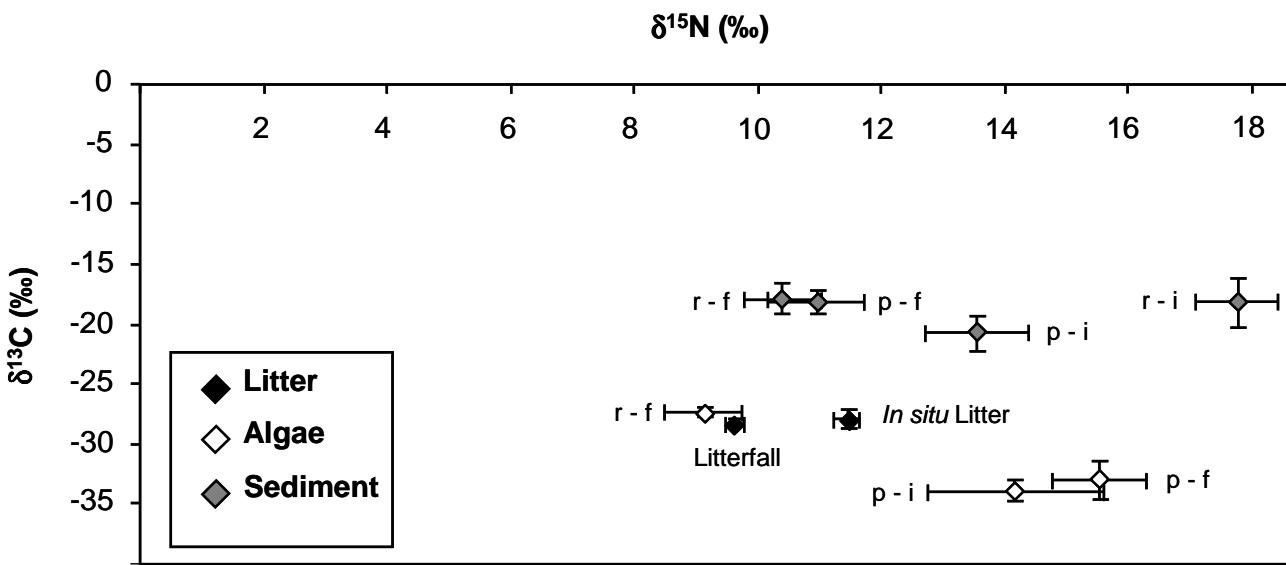


Fig. 7.4 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures for stream bed sediments, litter and benthic algae. SE indicated by error bars. i=interflood period, f=flood period, p=pool, r=run. $n=9$.

Table 7.3 Mass of *in situ* litter ($n=9$) and litterfall ($n=3$) between November 2005 and January 2006 at Ratty Springs (Pirraburadoo Creek). Foliage projective cover (FPC; %; $n=3$) over patches, and nutrient content of litter from pools and runs. All values are means with SE in parentheses. * $=P<0.05$, ** $=P<0.01$.

| | Pool | Run | | |
|----------------------------|-----------------------|----------------|-----------------------|---------------|
| FPC (%) | 53.84 (12.16)** | 5.08 (1.87) | | |
| | <i>In situ</i> Litter | Litterfall | <i>In situ</i> Litter | Litterfall |
| Mass (g m^{-2}) | 181.91 (44.50) | 174.85 (77.50) | 256.88 (97.24) | 34.49* (6.68) |
| Total C (%) | 45.18 (0.66) | 46.46 (1.18) | 46.57 (0.56) | 46.54 (0.90) |
| Total N (%) | 0.53 (0.03) | 0.43 (0.05) | 0.51 (0.02) | 0.52 (0.08) |
| OH-P _T (%) | 0.19 (0.03) | 0.12 (0.05) | 0.13 (0.006) | 0.16 (0.01) |
| C:N:P Molar Ratio | 691:6:1 | 1129:8:1 | 1045:9:1 | 848:8:1 |

7.3.3 Nutrient availability in sediments

Sediment physical characteristics (bulk density and particle size classification) were similar among patches and sampling times. Moisture content increased greatly after flooding ($P<0.001$), from about 1-2 % to over 15 % in both pools and runs. Patches were exposed to air during the interflood, and overlain by <10 cm of water (runs) and 20-40 cm of water (pools) after flooding (Plate 7.1b, d). Changes in nutrients in sediments were influenced by an interaction between collection time and patch type (Table 7.2). Sediments from pools after flooding had two to eight times greater NO₃-N, three to five times more total N, and two to three times more labile OH-P_i, OH-P_o, OC and total C than pools after flooding, or runs at any collection time ($P<0.05$). In particular, NO₃-N and OH-P_i concentrations more than halved in stream sediments after flooding.

Due to the higher total N (0.2 %) in pools before flooding, the sediment C:N ratio was 16:1, compared to all other patches, where sediment C:N was approximately 37:1 (Table 7.2). $\delta^{13}\text{C}$ signatures of stream sediments were approximately -19 ‰, and were similar between collection times and patch types (Fig. 7.4). Meanwhile, $\delta^{15}\text{N}$ signatures

were significantly less enriched after flooding ($P<0.01$) across all patches, decreasing from 15 to 11 % (Fig. 7.4).

7.3.4 Sediment microbial communities and activity

Sediment microbial biomass, as estimated by total PLFA, was more than twice as high in the interflood ($P<0.01$), but did not differ between patch types. Interflood microbial biomass was approximately 2138 ng FA g⁻¹, decreasing to 865 ng FA g⁻¹ after flooding. Microbial community composition (PLFAs) differed by hydroperiod (MDS stress=0.09; Fig. 7.5). Pairwise comparisons of patches before and after flooding indicated that runs in the interflood had significantly different PLFA profiles (ANOSIM, $R=0.184$, $P<0.05$). The subset of PLFA extracts analysed by GC-MS to target specific fatty acid indicators revealed consistent differences among groups. Eubacteria, fungi, sulphate-reducing bacteria and nutrient starvation (in bacteria) markers all contributed consistent amounts of fatty acids per gram of sediment between samples from different patch types and collection times (Fig. 7.6). The total mass of ubiquitous fatty acids (16:0 + 18:0) increased significantly after flooding in runs, yet decreased in pools ($P<0.05$). Specific markers used are detailed in the methods section of this paper. Simple microbial diversity (# identified FAs per sample) was similar across patch types and sampling times.

Surface CO₂ efflux was variable, ranging from -4.4 to 18.0 g CO₂ m⁻² hr⁻¹. Respiration from the mat surface was significantly lower than respiration on the stream bed surface ($P<0.05$), presumably reflecting greater photosynthetic activity. Likewise, measurements taken on the surface of algal mats after flooding were significantly lower ($P<0.001$) than CO₂ efflux from interflood (senescent) algae.

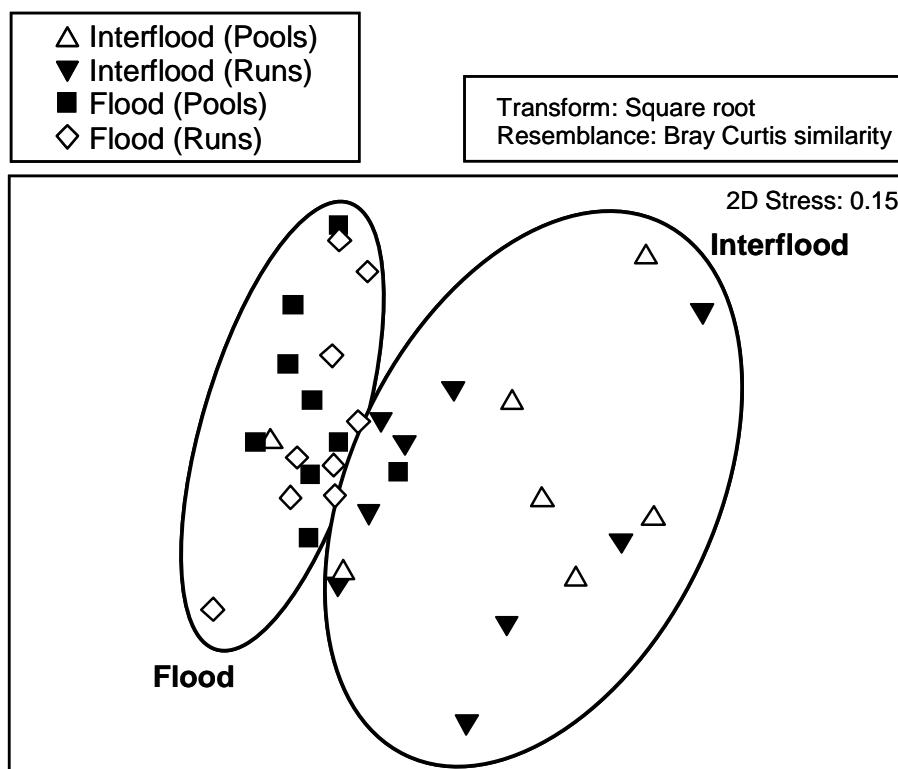


Fig. 7.5 MDS plot for sediment microbial communities (PLFAs).

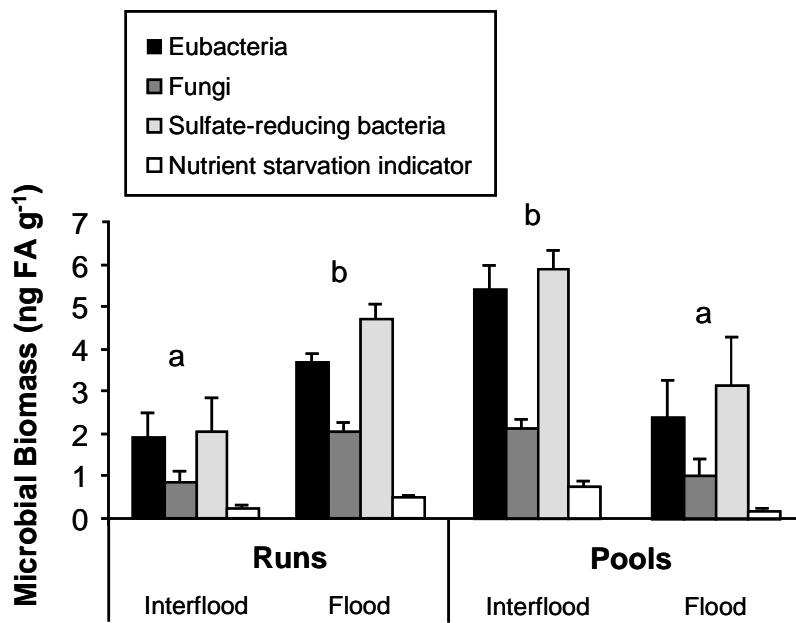


Fig. 7.6 Mass of selected microbial indicator groups (PLFAs) in pool and run sediments, during the flood and interflood periods. SE indicated by error bars, post-hoc groupings (by microbial indicator) using 'a', and 'b'. $n=9$.

Table 7.4 Pearson correlation coefficients for sediment moisture and nutrient variables, microbial and algal biomass in interflood and flood periods. *= $P<0.05$, **= $P<0.01$, ***= $P<0.001$. ^B indicates significance after Bonferroni correction.

| | Moisture (%) | NO ₃ -N (mg kg ⁻¹) | δ ¹⁵ N | δ ¹³ C | OC | OH-P _i | C:N | N:P | Microbial biomass |
|--|-----------------|--|----------------------|-------------------|-----------------------|----------------------|--------|--------|----------------------|
| Moisture (%) | | | | | | | | | |
| NO ₃ -N (mg kg ⁻¹) | | ^B -0.52** | | | | | | | |
| δ ¹⁵ N (‰) | 0.04 | | ^B 0.51** | | | | | | |
| δ ¹³ C (‰) | 0.24 | | -0.37* | -0.20 | | | | | |
| OC (%) | -0.30 | | ^B 0.63*** | 0.39* | ^B -0.54*** | | | | |
| OH-P _i (μg g ⁻¹) | -0.23 | | 0.39* | -0.01 | ^B -0.64*** | ^B 0.55*** | | | |
| C:N | 0.27 | | -0.37* | -0.001 | 0.36* | -0.42* | -0.38* | | |
| N:P | | ^B -0.54*** | ^B 0.67*** | 0.42* | ^B -0.42** | 0.62* | 0.32 | -0.40* | |
| Microbial biomass (ng FA g ⁻¹) | | -0.43* | 0.29 | -0.26 | -0.03 | 0.25 | 0.11 | -0.30 | 0.23 |
| Algal Biomass (g m ⁻²) | | 0.26 | 0.05 | 0.08 | -0.19 | 0.31 | 0.10 | 0.20 | -0.14 |
| | | | | | | | | | -0.12 |

7.3.5 Combined microbial, algal and nutrient effects

A correlation of selected chemical characteristics of sediments, microbial biomass and algal biomass indicated a significant negative correlation between sediment moisture content and NO₃-N, N:P and microbial biomass (Table 7.4). No further significant correlations were found for microbial or algal biomass.

7.4 DISCUSSION

Ratty Springs experienced one flood during the study period from November 2005 to March 2006. During the flood period, rainfall at Paraburadoo approached the long-term maximum average for each particular month (1971 to present). The flood observed was thus exceptional for the region, and was also preceded by a long drought (22 months). Hence this study documented a severe flood for Pirraburadoo Creek.

7.4.1 Algal responses to flooding

Benthic algae grew quickly in runs after flooding (from negligible to 400 g m⁻² biomass). Runs supported more than twice the algal growth (consisting primarily of *Spirogyra*) than in pools either before or after flooding. In contrast, algal biomass in pools decreased by 70 % after flooding, most likely due to initial flood scour effects (Biggs & Close, 1989) and subsequent light limitation in deeper (>30 cm water depth) sections. Light limitation would be exacerbated by shading from streamside trees, which tend to cluster around pools in the central Pilbara, resulting in the higher foliage projective cover observed for pools in this study. Benthic algae thrive in warm, shallow environments where oxygen and light are abundant (Stevenson, 1996), conditions prevalent in the runs of Pirraburadoo Creek after flooding.

Biomass dynamics of *Spirogyra* (the alga dominant at Ratty Springs) in northern Australia have been suggested to be strongly linked to hydrological disturbances and nutrient limitation (Townsend & Padovan, 2005). Based on nutrient analysis of benthic algal tissues, which revealed an average molar C:N:P of 715:55:1, it is clear that P availability is the major likely limitation to algal growth at Ratty Springs. These ratios substantially exceed the Redfield ratio of 106:16:1 typical of phytoplankton and benthic microalgae (Hillebrand & Sommer, 1999). Likewise, N and P concentrations in algal

tissues were much less than the threshold values of 11 % N and 0.5 % P that have been used elsewhere to infer nutrient limitation (Francoeur *et al.*, 1999). Even greater nutrient limitation in *Spirogyra* has been observed in northern Australia, with molar C:N:P ratios over 1400:99:1 (Townsend & Padovan, 2005), which is very similar to observed ratios in this study in runs after flooding. This result further supports findings by Townsend *et al.* (2008) that optimal ratios for macroalgae (*Spirogyra fluviatilis*) in northern Australia may routinely exceed the Redfield ratio, and that standards developed for microalgal stoichiometry require reconsideration before application to macroalgae. The use of nutrient-diffusing substrates (e.g. experiments of Tank & Dodds, 2003) in further studies could help identify and quantify the specific nutrient limitations present.

Benthic communities in pools contained a diversity of algal epiphytes regardless of hydroperiod (Table 7.1) – generally indicative of good nutrient availability and a mature successional stage (Wetzel, 1996). This contrasts with general theories developed for floodplain rivers, which regard flood-dominated systems as remaining in a consistently ‘immature’ and highly productive state of community development (Junk & Wantzen, 2003). The pools at Ratty Springs therefore represented a local, interflood store of nutrients in otherwise nutrient-poor landscape, when connectivity to upstream reaches or upland environments was weak or non-existent. While cyanobacteria were present in benthic samples from the study site, they did not occur in high densities despite the suitable light and temperature conditions after flooding, so N contributions from instream fixation are likely to be low (though dependent on cyanobacterial activity). Given the poor quality of the litter inputs, and low nutrient content of Pilbara soils in general (Cookson *et al.*, 2006), it is unsurprising that algae in Pirraburadoo Creek should be nutrient-limited. However the degree of P limitation is much greater than suggested by previous studies in the region (e.g. Bennett *et al.*, 2003) and elsewhere in Australia (Mosisch *et al.*, 1999).

In comparison to permanent streams, where a relatively predictable hydrological regime ensures factors such as light are more important than water availability in regulating algal growth (Hill, 1996), productivity in intermittent stream beds is expected to shift spatio-temporally depending on the current point in the flood-drought cycle (e.g. Bunn *et al.*, 2003; Grimm & Fisher, 1989). Open canopies are typical of many dryland streams subject to alternating disturbance from large floods and drought. When water is available, riparian shading is of minimal importance in comparison to nutrient

availability in influencing algal growth in such photosaturated streams (Mosisch *et al.*, 1999).

7.4.2 Sediment nutrient availability and stream function

During drought conditions, pools were nutrient hot spots within the stream bed environment, with significantly greater concentrations of NO₃-N, total N, labile OH-P_i OC and total C in stream sediments. As largely depositional environments, stream pools trap moisture, detritus and biota (Davis *et al.*, 2002; Lisle & Hilton, 1992; Stanley *et al.*, 1997) At Ratty Springs, pools received more litter than runs, which would also contribute to increased nutrient availability. Over time, continual cycles of accrual and decomposition of benthic algae in such pools are expected to enrich the underlying sediments, creating a persistent hot spot in the stream bed. Further studies could identify how long (seasons / years) these hot spots persist, and quantify their contribution to overall nutrient retention in the intermittent stream landscape. However, as little topographic change was noted at the Barnett Creek study site after severe flooding (Chapters 3 & 4), these pools are likely to be physically stable, and hence long-term nutrient hot spots. Furthermore, Pilbara groundwater and surface water tends generally to be low in dissolved nutrients (Halse *et al.*, 2002; Kay *et al.*, 1999), so variable subsurface flowpaths are expected to contribute less to the biogeochemistry of surface sediments than in streams elsewhere (e.g. Dent *et al.*, 2007).

After flooding, concentrations of all labile nutrients decreased in sediments from all stream bed patches, presumably due to uptake by benthic communities. As nutrient availability was similar in pool and run mesohabitats after flooding, the expectation that runs would act as a conduit for nutrients while pools would retain nutrients after floods was negated. The large decline in sediment total N after flooding (from ~0.13 to 0.04 %) may be attributed to denitrification in submerged sediments or algal uptake. Denitrification is less likely, as sediment ¹⁵N declined following flooding (Fig. 7.4), and denitrification would have resulted in enrichment by discrimination against the heavier ¹⁵N isotope (Hogberg *et al.*, 1995). Before flooding, the C:N ratio in pool sediments was 16:1 - favouring mineralisation processes based on the threshold value of 25:1 (e.g. Gundersen *et al.*, 1998), while all other patches in the flood and interflood periods had ratios greater than 35:1, favouring microbial immobilisation. Patchiness of nutrients and OC is expected to increase during extreme drought (Dahm *et al.*, 2003). The results of

the current study indicate that, during drought, patches diverge in chemistry and biogeochemical function, and subsequently converge during floods that re-establish flowpaths and redistribute nutrients and materials.

7.4.3 Microbial responses to flooding

Total microbial biomass (by PLFA) and activity (by CO₂ efflux) was greater before than after flooding, a result that contrasts with the experimental hypotheses (Section 7.1) and with previous studies in flooded soils and sediments (e.g. Belnap *et al.*, 2005; van Gestel *et al.*, 1992). Indeed, correlation analysis indicated a negative relationship between sediment moisture content and microbial biomass (Table 7.4). A rich crop of senescent algae in drying pools acting as a substrate for microbial decomposition might partially explain this result; however, no such substrate was available in runs after flooding and similarly high levels of microbial biomass were still observed in these patches. Sediment scouring and anaerobic conditions could also initially inhibit recovery of benthic microbial communities after flooding. For example, a recovery period of up to 60 d post-flood was required for parafluvial bacteria to achieve pre-flood densities in arid Sycamore Creek, Arizona (Holmes *et al.*, 1998). Substrates in pools and runs were similar - pure sand, with high bulk density - and hence normally well-drained. Anaerobic conditions were likely, as flooded sediments held 15-17 % moisture (gravimetric), which is close to full saturation (see Chapter 5).

Microbial community composition differed significantly by hydroperiod, though simple diversity (of fatty acids) was unchanged. Samples collected after flooding were much more similar to each other (based on MDS plot space) than were interflood samples (Fig. 7.5), which supports findings of Wood *et al.* (1992) of convergence among biotic assemblages after flooding. However, patterns in the three discernable microbial groups (eubacteria, fungi, sulphate-reduced bacteria) were identical (Fig. 7.5). This is surprising for fungi in particular, given their role as aerobes and tendency therefore to decline under waterlogged conditions (Bossio & Scow, 1997; van der Valk, 2006). Use of enzymatic or other functional microbial techniques could help further identify which groups were affected by flooding, and hence also the dependant biogeochemical pathways which were enhanced or restricted.

While the nutritional starvation marker (16:1w7c) measured for bacteria in sediments was similar before and after flooding, it remained at very low concentrations in samples analysed by PLFA (~0.77 % of total FA biomass). This contrasts with studies where values greater than 10 % were commonly observed for this marker (e.g. Potts *et al.*, 1987). This suggests that nutrient limitation in bacteria at Ratty Springs may be pervasive. To identify small changes in nutrient status in soils and sediments where nutrients are already severely limiting, the development of novel biomarkers may be required. In terms of nutrient sources, the strong ^{15}N enrichment (mean 14.9 ‰) of algal tissues from pools indicates a possible reliance on edaphic N sources, while algae growing in runs after flooding were less enriched (9.1 ‰), perhaps due to a greater contribution from dissolved inorganic N (DIN; Gu & Alexander, 1993). As temporary algal patches were largely associated with gravel runs while persistent patches occurred in pools habitats, relative differences in water flow and hence delivery of DIN may contribute to this result.

Microbes contribute to ecosystem function on a number of scales (Groffman & Bohlen, 1999), and can respond quickly to resource pulses – proliferating in microhabitats where physio-chemical conditions are temporally favourable. After an initial flush of nutrients post-flooding, microbial communities may have quickly reached nutrient limitation and then declined. This would partly explain the negative correlation observed between sediment moisture content and microbial biomass. While this study focussed primarily on general microbial responses to the flooding effect, a further examination of microbial dynamics at a hierarchy of spatio-temporal scales (and across a number of floods) would possibly help resolve key functional relationships.

CHAPTER 8

Synthesis

8.1 INTRODUCTION

This thesis provides the first detailed analysis of biogeochemical responses to flooding of intermittent streams both for the Pilbara region and broader dryland Australia. The main objectives of my research, as explored in the preceding chapters, were to: (1) quantify the effect of flooding on soil C, N and P patterns across the stream landscape; (2) examine changes in microbial activity and community profiles, and N and C mineralisation in response to water and substrate availability; and (3) determine the interrelationships between benthic algae, nutrient availability and microbial communities in channel beds.

In this concluding chapter, I briefly summarise the major findings of this thesis and discuss their relevance to the ecological functions and management of semi-arid intermittent streams. Finally, I consider the significance of these findings in the context of recent developments in the field of stream-riparian biogeochemistry, and provide some comments regarding future work.

The original conclusions of this thesis are summarised in Table 8.1 against the three main objectives.

Table 8.1 Synthesised original conclusions of this thesis for the biogeochemistry of soils and sediments in Pilbara stream landscapes.

Objective 1: To quantify the effect of flooding on soil C, N and P patterns across the stream landscape (Chapters 3 & 4)

| Conclusions |
|---|
| 1 Flooding reduces, or at least maintains, the spatial heterogeneity of biogeochemical patchiness (particularly bioavailable P and N, and microbial communities) across the stream landscape. |
| 2 Nitrate increases in patchiness during interflood periods, most likely due to continued accrual of plant litter coupled with water limitations to $\text{NO}_3\text{-N}$ uptake. |
| 3 Light rains, but not severe flooding, increase soil microbial biomass. |

- 4 Riparian zones are a hot spot for soil NO₃-N and OC.
- 5 Floodplains are a cold spot for soil NO₃-N and OC.
- 6 Banks retain more moisture than other landscape positions and are a hot spot for OC.
- 7 Soil microbial profiles (by PLFA) are not affected by severe flooding on a temporal scale of weeks to months.
- 8 Soil microbial profiles (by PLFA) in riparian zones are more uniform than for floodplain, channel or bank soils.
- 9 Different riparian community types in Pilbara streams are similar biogeochemically.
- 10 Soil microtopography is less important than flood period, or landscape position (zone or channel type) in influencing biogeochemical patchiness, though NO₃-N and microbial biomass are sensitive to small-scale changes in microtopography in channel beds.
- 11 Flooding removes small-scale soil microtopography in riparian, bank and floodplain zones, but not in channel beds.
- 12 Anabranch channels are biogeochemical hot spots, particularly for OC, total N, inorganic P and microbial biomass, in comparison to main channels.
- 13 Severe flooding generally reduces bioavailable nutrients and microbial biomass on a temporal scale of weeks to months.

Objective 2: To examine changes in microbial activity and community profiles, and N and C mineralisation in response to water and substrate availability (Chapters 5 & 6)

Conclusions

- 1 Dried Barnett Creek soils and sediments have a clear and rapid mineralisation flush in response to rewetting, except where soils are fully saturated.
- 2 Microbial biomass triples within 24 hours after rewetting.
- 3 Landscape position and hence soil characteristics are of greater importance in controlling N mineralisation potential than flood pulse size (soil saturation level), except for exceptionally large pulses resulting in >40 % WFPS.
- 4 N mineralisation and microbial activity will continue even when soils are fully saturated, though at a reduced rate.
- 5 The N mineralisation potential of riparian soils is 50 % higher than for floodplain soils or channel sediments, and riparian soils have the greatest mineralisation ‘flush’, though overall N (and C) mineralisation rates are similar between different landscape positions.
- 6 Riparian community type is not important in controlling N mineralisation potential.
- 7 N mineralisation in Barnett Creek soils and sediments follows first-order kinetics, except in fully saturated soils that are subsequently allowed to dry (zero-order kinetics).
- 8 Substrate limitation does not occur readily in rewetted soils and sediments.
- 9 Microbial profiles (by PLFA) vary little in rewetted incubated soils.
- 10 Microbial activity (and N mineralisation) can persist at soil matric potentials <-1500 kPa, lower than the -1000 kPa suggested by other studies.
- 11 Microbial activity and N mineralisation are optimal at ~20 % WFPS, lower than the 50-60 % WFPS suggested by other studies.
- 12 Amendment of soils and sediments with *Eucalyptus* spp. litter significantly inhibits N mineralisation while stimulating microbial activity.

Objective 3: To determine the interrelationships between benthic algae, nutrient availability and microbial communities in channel beds (Chapter 7)

Conclusions

- 1 P is very limiting and N moderately limiting to algae in typical Pilbara streams.
- 2 Pools are nutrient store (for NO₃-N, total N, labile OH-P_i organic and total C) during interflood periods, and a nutrient source after floods.
- 3 Gravel runs can support high algal productivity after floods.
- 4 Flooding decreases concentrations of labile nutrients in channel sediments.
- 5 Severe flooding decreases microbial biomass and causes convergence in microbial profiles (by PLFA) in channel sediments on a temporal scale of weeks to months.
- 6 Flooding reduces heterogeneity of nutrients in channel sediments.

8.2 SIGNIFICANCE OF THIS STUDY IN THE CONTEXT OF CURRENT RESEARCH IN STREAM AND SOIL BIOGEOCHEMISTRY

8.2.1 Comparison of the Pilbara study sites to dryland sites worldwide

This thesis considered two sites, Barnett Creek and Pirraburadoo Creek, in the central Pilbara – but how comparable are these sites, biogeochemically, for other systems worldwide? Nutrient availability is a key aspect of biogeochemical cycling. This thesis provides the first comparison of soil nutrient availability (inorganic N and P), OC and the C:N of organic matter between two study sites in semi-arid Australia (using soils information from all landscape positions and collections) and >13 other dryland sites worldwide (Figs 8.1 & 8.2; Tables 8.2 & 8.3).

The measured availability of inorganic N in soils and sediments of Barnett Creek and Pirraburadoo Creek were similar to, or slightly less than, that measured at most other dryland sites worldwide (Fig. 8.1a). In contrast, availability of inorganic P was clearly amongst the lowest recorded worldwide (Fig. 8.1b). Somewhat surprising were the generally similar concentrations of soil OC in Barnett Creek and Pirraburadoo Creek compared with other dryland sites (Fig. 8.2a; Table 8.2). Nevertheless, the generally low concentrations of total N ensured that C:N ratios at my two study creeks were greater than recorded at all comparison sites (Fig. 8.2b, Table 8.3), except for the Shy Oaks Field Station site in California (Vourlitis & Zorba, 2007).

Barnett Creek and Pirraburadoo Creek are thus positioned at the ‘low end’ of the spectrum of bioavailability of nutrients, even though such stream systems are hot spots in the landscape for nutrient availability and that the majority of the comparison sites were non-riparian (e.g. grassland or shrubland). The findings of this thesis therefore have the most relevance to Regosols, Calcisols and Ferrasols (see Section 2.3), which are frequently depleted in N, P and OM (e.g. most Australian and African soils).

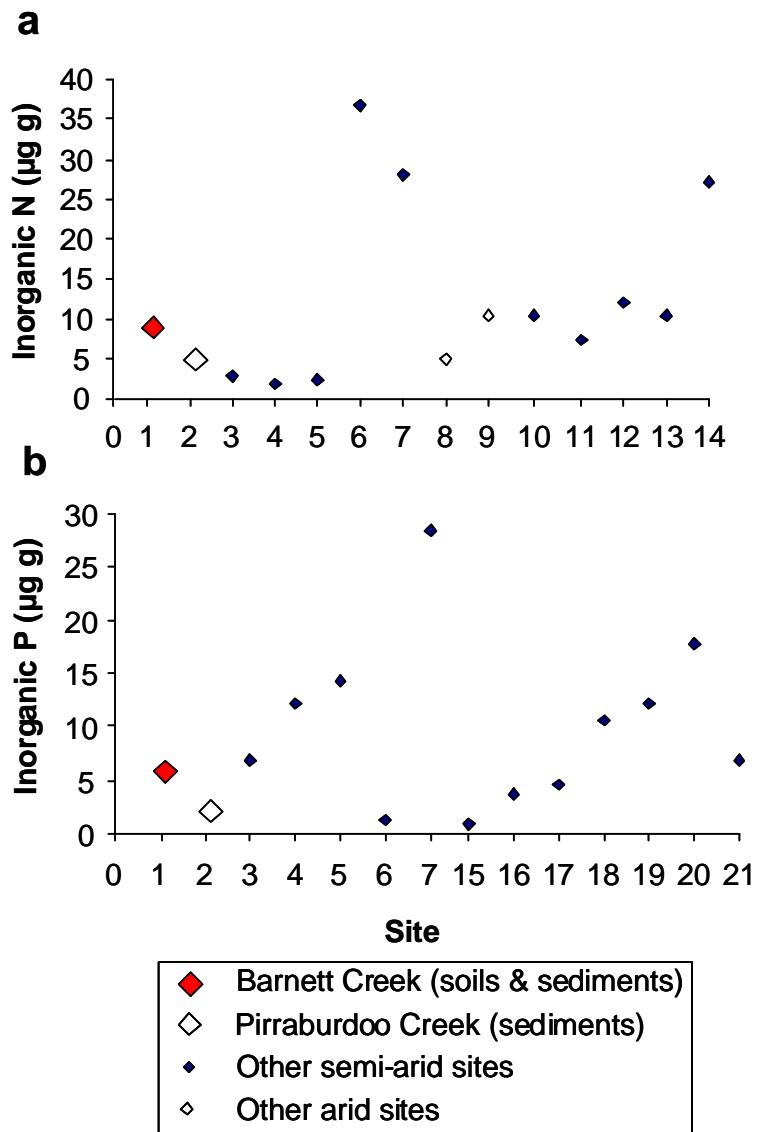


Fig. 8.1 Comparison of inorganic N and P between the two study sites (1: Barnett Creek, 2: Pirraburadoo Creek) and other dryland sites worldwide. Site descriptions and references are provided in Table 8.2.

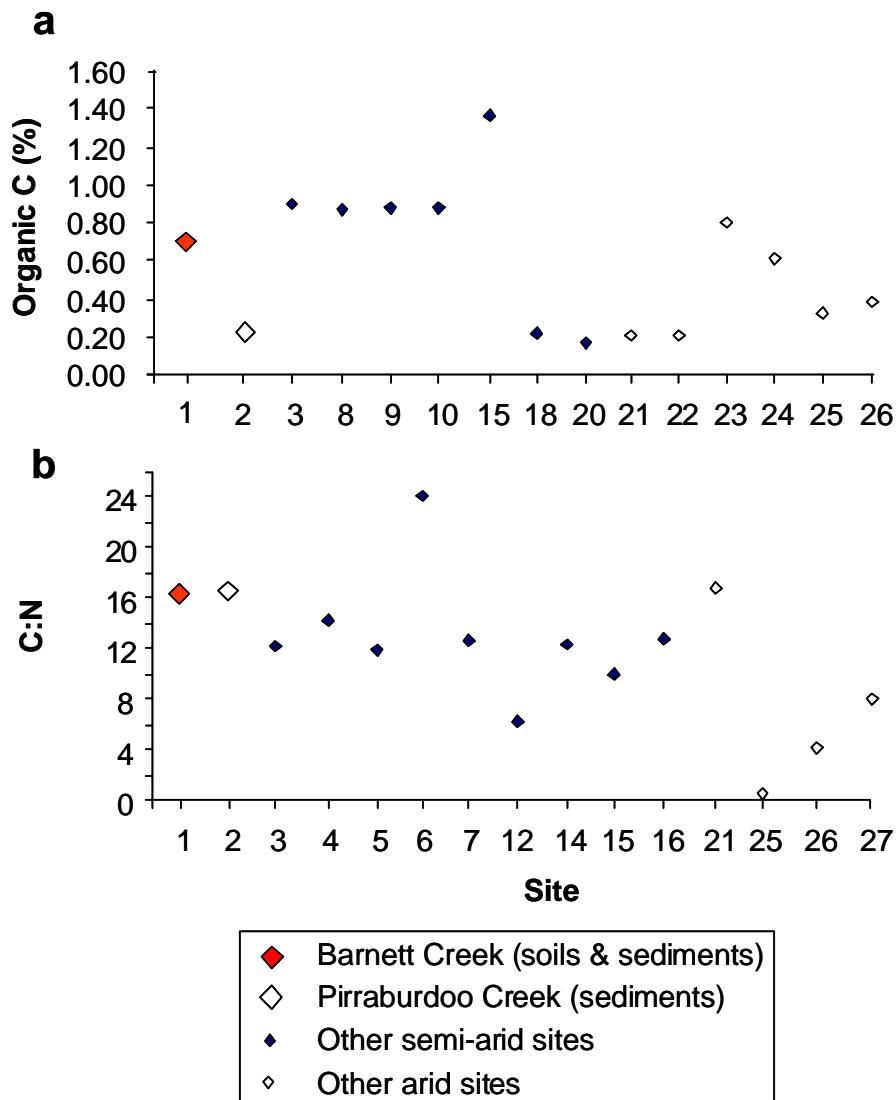


Fig. 8.2 Comparison of OC and C:N between the two study sites (1: Barnett Creek, 2: Pirraburadoo Creek) and other dryland sites worldwide. Site descriptions and references are provided in Table 8.3.

Table 8.2 Dryland sites compared for soil nutrients (inorganic N and P) in Fig. 8.1.[†]

| Site. | Site | Location | Reference |
|-------|--|-------------------------------|------------------------------------|
| 1. | Barnett Creek – semi-arid woodland | Pilbara, AUSTRALIA | This thesis |
| 2. | Pirraburadoo Creek – semi-arid channel | Pilbara, AUSTRALIA | This thesis |
| 3. | Hamersley Station – semi-arid grassland | Pilbara, AUSTRALIA | (Bennett <i>et al.</i> , 2003) |
| 4. | Narran River – semi-arid grassland | Queensland, AUSTRALIA | (Ogden <i>et al.</i> , 2002) |
| 5. | South Campus – semi-arid grassland | Colorado, USA | (Reed <i>et al.</i> , 2007) |
| 6. | Da Nangou – semi-arid shrubland | Shaanxi, CHINA | (Wang <i>et al.</i> , 2001) |
| 7. | IPA – semi-arid shrubland | Chapada do Araripe, BRAZIL | (Tiessen <i>et al.</i> , 1992) |
| 8. | Mojave Desert – arid scrubland | Nevada, USA | (Schaeffer <i>et al.</i> , 2003) |
| 9. | CAP LTER – arid scrubland | Arizona, USA | (Hope <i>et al.</i> , 2005) |
| 10. | Jim Wells – semi-arid mesquite woodland | Texas, USA | (Geesing <i>et al.</i> , 2000) |
| 11. | Kleberg – semi-arid mesquite woodland | Texas, USA | (Geesing <i>et al.</i> , 2000) |
| 12. | Atascosa (East) – semi-arid mesquite woodland | Texas, USA | (Geesing <i>et al.</i> , 2000) |
| 13. | La Copita – semi-arid grassland | Texas, USA | (McCulley <i>et al.</i> , 2004) |
| 14. | La Copita – semi-arid drainage woodland | Texas, USA | (McCulley <i>et al.</i> , 2004) |
| 15. | Ludhiana – semi-arid pasture | Punjab, INDIA | (Aulakh & Rasricha, 1991) |
| 16. | Santa Rita – semi-arid luvisol thorn forest | Pernambuco, BRAZIL | (Araujo <i>et al.</i> , 2004) |
| 17. | Santa Rita – semi-arid latosol thorn forest | Pernambuco, BRAZIL | (Araujo <i>et al.</i> , 2004) |
| 18. | Hunting National Reserve – semi-arid open shrubland | Malaga, SPAIN | (Carreira <i>et al.</i> , 1997) |
| 19. | Hunting National Reserve – semi-arid gorse scrubland | Malaga, SPAIN | (Carreira <i>et al.</i> , 1997) |
| 20. | Hunting National Reserve – semi-arid garrigue shrubland | Malaga, SPAIN | (Carreira <i>et al.</i> , 1997) |
| 21. | Sabie River – semi-arid woodland | Drakensbergs, SOUTH AFRICA | (Pettit & Naiman, 2005) |

[†] KCl-extracted inorganic N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) and NaOH-extracted P_i data were used where available. Data were from surface soils and control treatments, where applicable.

Table 8.3 Arid and semi-arid sites compared for OC and C:N in Fig. 8.2.[†]

| Site | Site | Location | Reference |
|--|------------------------------|-----------------------------------|-----------|
| 1. Barnett Creek – semi-arid woodland | Pilbara, AUSTRALIA | This thesis | |
| 2. Pirraburadoo Creek – semi-arid channel | Pilbara, AUSTRALIA | This thesis | |
| 3. Hamersley Station – semi-arid grassland | Pilbara, AUSTRALIA | (Bennett & Adams, 1999) | |
| 4. Santa Margarita - semi-arid shrubland | California, USA | (Vourlitis & Zorba, 2007) | |
| 5. Mottee Rimrock – semi-arid shrubland | California, USA | (Vourlitis & Zorba, 2007) | |
| 6. Shy Oaks – semi-arid shrubland | California, USA | (Vourlitis & Zorba, 2007) | |
| 7. San Dimas – semi-arid shrubland | California, USA | (Vourlitis & Zorba, 2007) | |
| 8. Da Nangou – semi-arid woodland | Shaanxi, CHINA | (Wang <i>et al.</i> , 2001) | |
| 9. Da Nangou – semi-arid shrubland | Shaanxi, CHINA | (Wang <i>et al.</i> , 2001) | |
| 10. Da Nangou – semi-arid grassland | Shaanxi, CHINA | (Wang <i>et al.</i> , 2001) | |
| 11. Charleville – semi-arid grassland | Queensland, AUSTRALIA | (Christie, 1981) | |
| 12. Sabie River – semi-arid woodland | Drakensberg, STH AFRICA | (Pettit & Naiman, 2005) | |
| 13. Makoba Range – semi-arid savannah | Kalahari Desert, BOTSWANA | (Doudill <i>et al.</i> , 1998) | |
| 14. Dry Chaco – semi-arid grassland | Cordoba, ARGENTINA | (Mazzarino <i>et al.</i> , 1991) | |
| 15. Rush Valley – semi-arid shrubland | Utah, USA | (Saetre & Stark, 2005) | |
| 16. Colorado Front Range – semi-arid grassland | Colorado, USA | (Reed <i>et al.</i> , 2007) | |
| 17. West Africa – semi-arid grasslands | WEST AFRICA | (Bationo <i>et al.</i> , 1997) | |
| 18. Niger Sahel – semi-arid shrubland | NIGER | (Wezel <i>et al.</i> , 2000) | |
| 19. IPA – semi-arid shrubland | Chapada do Araripe, BRAZIL | (Tiessen <i>et al.</i> , 1992) | |
| 20. Sadore – semi-arid grassland | Niger Sahel, NIGER | (West <i>et al.</i> , 1984) | |
| 21. Ludlow – arid shrubland | Mojave Desert, USA | (Ewing <i>et al.</i> , 2007) | |
| 22. Hoanib River – arid woodland | Khowarib, NAMIBIA | (Jacobson <i>et al.</i> , 2000) | |
| 23. Huab River – arid wetland | Opdraend, NAMIBIA | (Jacobson <i>et al.</i> , 2000) | |
| 24. Kuiseb River – arid woodland | Kuiseb District, NAMIBIA | (Jacobson <i>et al.</i> , 2000) | |
| 25. Jornada Experimental Range - arid grassland | Chihuahuan Desert, USA | (Gallardo & Schlesinger, 1992) | |
| 26. Jornada Experimental Range - arid shrubland | Chihuahuan Desert, USA | (Gallardo & Schlesinger, 1992) | |
| 27. Sycamore Creek – arid uplands | Sonoran Desert, USA | (Sponseller, 2007) | |
| 28. Harper's Well – arid woodland | Sonoran Desert, USA | (Shearer <i>et al.</i> , 1983) | |
| 29. Catavina – arid woodland | Sonoran Desert, MEXICO | (Shearer <i>et al.</i> , 1983) | |

[†] Data were from surface soils and control treatments, where applicable.

8.2.2 Small floods pulses are more important for microbial activity and nutrient availability than large flood pulses

There has been increased interest in recent years in the relationships between moisture availability and ecosystem processes in drylands (Puckridge *et al.*, 2000; Schwinnig *et al.*, 2004). This study has shown that small flood pulses can be of greater importance in stimulating biogeochemical transformations in stream landscapes than large flood pulses. This finding contrasts with the focus of other studies where large, rare floods are considered to be the major drivers for stream or river biogeochemistry and productivity (e.g. Bunn *et al.*, 2006; Junk *et al.*, 1989). For example, Bunn *et al.* (2006) distinguished between two flow types – ‘floods’ ($>20,000 \text{ ML day}^{-1}$ river flow) and ‘flow pulses’ ($2 - 20,000 \text{ ML day}^{-1}$ river flow) for the intermittent Cooper Creek system of central Australia. ‘Floods’ were less than half as frequent as ‘flow pulses’ in Cooper Creek; however floods were attributed with greater system-wide influence on productivity.

In contrast, my research has emphasised that, while large flood pulses may indeed cause overbank flow and stimulate plant growth and primary productivity in the surrounding landscape, microbial activity and nutrient release in intermittent streams appear to be stimulated most by small flood pulses. Hence, while increased productivity in the surrounding landscape will contribute to riparian productivity through allochthonous contributions of carbon and nutrients, small floods or ‘flow pulses’ (*sensu* Bunn *et al.*, 2006; Walker *et al.*, 1995) are of greater import to autochthonous productivity and maintenance of microbial activity in the stream landscape (see Chapters 3, 5 & 6).

As most precipitation events in drylands are small pulses $<3 \text{ mm}$ (Loik *et al.*, 2004), there is a clear adaptive advantage for microbes to successfully utilise small events rather than relying on less predictable, larger events. The greater frequency of small precipitation events could well ensure that their cumulative contributions to nutrient availability and transformation are even more significant. In contrast to microbes, woody vegetation (and many grasses and herbs) seems less likely to be able to utilise smaller pulses, and unable to access mineralised nutrients in otherwise extremely dry soils (Austin *et al.*, 2004). A possible classification of rainfall events in dryland ecosystems based on productivity responses is shown in Fig. 8.3. These responses are based on system-wide effects, where Vegetation Productivity Pulses (‘VPPs’),

correspond to larger floods that increase vegetation productivity across the landscape) while Microbial Productivity Pulses ('MPPs'), correspond to smaller rainfall events that stimulate microbial activity and plant productivity though only at a highly localised scale. VPPs would result in widespread nutrient uptake by vascular plants, biomass production, increased litterfall and hydrological connectivity between landscape positions. In contrast, MPPs would stimulate decomposition processes and help release of nutrients that will become available, after a lag-time, to vegetation during VPPs. Depending on the lag time between individual pulses, ecosystem responses could be either linear or stepped. Ultimately, the sequential behaviour and relative frequency of the two pulse types would greatly influence overall system biogeochemistry (see Chapter 3).

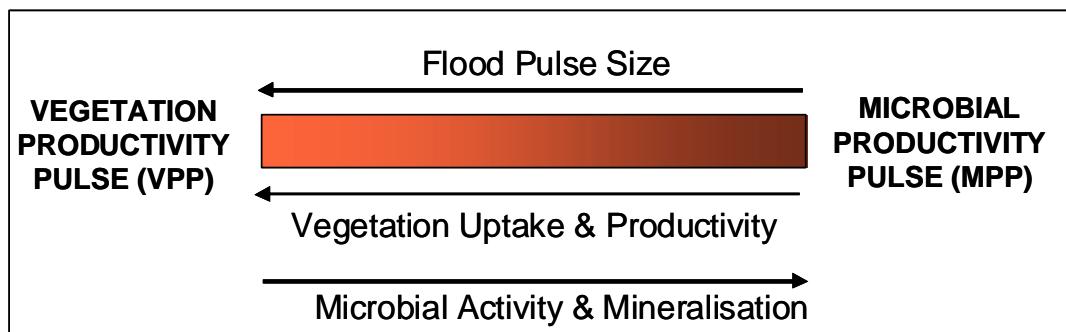


Fig. 8.3 A gradational scale for flood pulse types in dryland streams.

8.2.3 Severe flooding reduces nutrient patchiness in the stream landscape

An intriguingly consistent result of field studies at Barnett Creek and Pirraburadoo Creek was the reduction in nutrient patchiness and availability and microbial biomass after severe floods. A hydrological concept of ecosystem expansion and contraction for streams, with a strong emphasis on intermittent streams, was presented by Stanley *et al.* (1997). We might develop this model to include a hydrologically coupled expansion and contraction of soil biogeochemical potential across the stream landscape. Floods redistribute nutrients in the four dimensions of the stream landscape (Fig. 1.3). Severe flooding may initially stimulate microbial activity and nutrient release by expansion of favourable biogeochemical microsites to 'megsites'. However, over greater temporal scales, severe flooding has a homogenising effect in terms of contributing to nutrient depletion across the landscape, and also through uniform 'top-dressing' of the floodplain and riparian zone with flood-imported materials.

In contrast, as the interflood period progresses and soils and sediments continue to dry, microbial activity will depend upon the spatial coincidence of increasingly patchy moisture availability with suitable substrates for decomposition. Over time, isolated soil patches diverge in physiochemical behaviour, influenced by evaporation, smaller ‘top-up’ precipitation events, microbial community composition and substrate dynamics. Hence, stream ecosystem contraction during drying may actually support greater soil biogeochemical complexity in the wider stream landscape than the ecosystem expansion associated severe floods (see Chapter 3).

8.2.4 Microbial communities can function under hydrologic extremes

The results of this thesis showed that microbial activity (and N mineralisation) can persist at soil matric potentials <-1500 kPa (Fig. 6.2), which is significantly more negative than the -1000 kPa suggested by other studies (Fierer *et al.*, 2003; Ford *et al.*, 2007; Zak *et al.*, 1999). Furthermore, N mineralisation and microbial activity continued in soils that were fully saturated, albeit at a reduced rate (Fig. 5.2), which contrasts with studies indicating that N loss is dominant in flooded and waterlogged soils (e.g. Aulakh *et al.*, 2000; Keeney & Sahrawat, 1986). Hence, microbial communities in Pilbara soils and sediments were capable of functioning under conditions of both severe drought and severe flood.

Soil microbes in the Pilbara should, arguably, be considered extremophiles (*sensu* Rothschild & Mancinelli, 2001) as, while Pilbara rainfall ($\sim 340 \text{ mm yr}^{-1}$) is not so low as to be exceptional on a world scale, the unpredictability of that rainfall on an intra- and inter-annual scale (Bureau of Meteorology, 2008b) presents a particularly harsh environment for soil biota (particularly when combined with a highly weathered landscape dominated by rocky regolith). Extremophiles have traditionally been defined as organisms adapted to live outside the normal range of at least one environmental variable e.g. salinity, pH, moisture or temperature (Kristjansson & Hreggvidsson, 1995). This static definition should probably be extended to those organisms surviving in variable environments with rapid shifts in environmental conditions. For microbes, Pilbara soils and sediments offer microsites extreme in not only water variability, but also in surface temperatures and UV radiation and, occasionally, erosive forces of wind and water. While we currently know more about extinct Pilbara microorganisms in the fossil record (e.g. Banerjee *et al.*, 2006; Watanabe *et al.*, 2004), as opposed to extant

communities, Pilbara microbes presumably employ similar strategies to extremophiles elsewhere, such as specialised pigmentation or the formation of desiccation-resistant structures or protective cysts (Torsvik & Ovreas, 2008; Wynn-Williams *et al.*, 2002).

8.2.5 Gravel bed streams and their associated riparian-floodplain systems are geomorphically resistant

Floodplain rivers and streams in drylands are traditionally considered ‘process-response systems’, freely adjusting their channel dimensions and form in response to changes in flow and sediment regimes (Thoms *et al.*, 2006). However, my field studies at Barnett Creek demonstrated minimal changes in microtopography and no changes to larger-scale topography after severe floods. Dryland streams often support a large stable main channel, with variable anastomosing side channels to absorb excess stream flow. However, even anastomosing side channels at Barnett Creek remained geomorphically static during high flow (Chapter 4). Substrate size may be of greater importance than landscape setting or hydrologic regime in determining geomorphic responses to erosive forces. Indeed, gravel bed streams worldwide have been observed to have greater geomorphic stability than streams dominated by finer particles (Church, 2002).

The bed surface of most gravel streams is considerably coarser than the sub-surface or gravel load transported over it, and is usually referred to as an ‘armour’ or ‘pavement’ (Dietrich *et al.*, 1989). In the central Pilbara, ironstone gravel and cobble are pervasive in stream channels and floodplains and as surface and subsurface inclusions in riparian and bank soil profiles. Calcrete bedrock platforms are also common in Pilbara streams. While riparian stability has been considered in the context of the importance of vegetation and large woody debris (Bragg, 2000; Pettit & Naiman, 2005), the role of large rocky inclusions in stability of the riparian soil profile has not been explored. Overall, ironstone gravel and cobble may increase overall stream landscape stability in the Pilbara (and for streams in highly weathered settings elsewhere), by weighting soil profiles and protecting fine sediment from erosion, a mechanism previously observed in river channels (Church, 2002).

8.2.6 A conceptual model for linkages between algae, microbes, litter and water availability in stream beds

To draw together many of the elements discussed in Chapter 7 regarding coupled algal and microbial responses to flooding in stream beds at Pirraburadoo Creek, Fig. 8.4 links the above components (algal, microbes, litter and water availability) into a biogeochemical process model for run and pool environments during flood and interflood periods. This approach provides a useful framework for further consideration of the biogeochemical mechanisms involved in spatio-temporal responses of stream bed sediments and communities.

During the interflood (Figs 8.4a, b), channel sediments are moist in pools and dry in runs. Benthic algae communities have senesced in runs, but persist in some pools where they stimulate soil microbial communities with their decay products. Aerobic microbes are stimulated by increased O₂ availability, combined with the small remaining moisture available in the stream bed in pool environments. As substrate C:N values shift, sediments in pool environments become mineralisation loci, while run environments favour immobilisation. Vertical and downstream hydrologic connectivity has ceased by the interflood, and nutrient uptake by vegetation declines as sediments dry.

During flood periods (Figs 8.4c, d), sediments are saturated and peak nutrient uptake by vegetation from the channel bed occurs. Aerobic microbes decline as sediments become saturated and O₂ is limiting, while benthic algae expand in shallow, warm and highly insolated runs, though declining somewhat in pools as water depth increases. Groundwater and downstream connectivity is re-established, and the uptake of bioavailable nutrients means that sediment C:N ratios support only immobilisation processes in both stream pools and runs.

From this model we can conclude that biogeochemical flood-drought responses of sediments are complexly linked to stream bed heterogeneity, inputs from streamside vegetation and benthic algae.

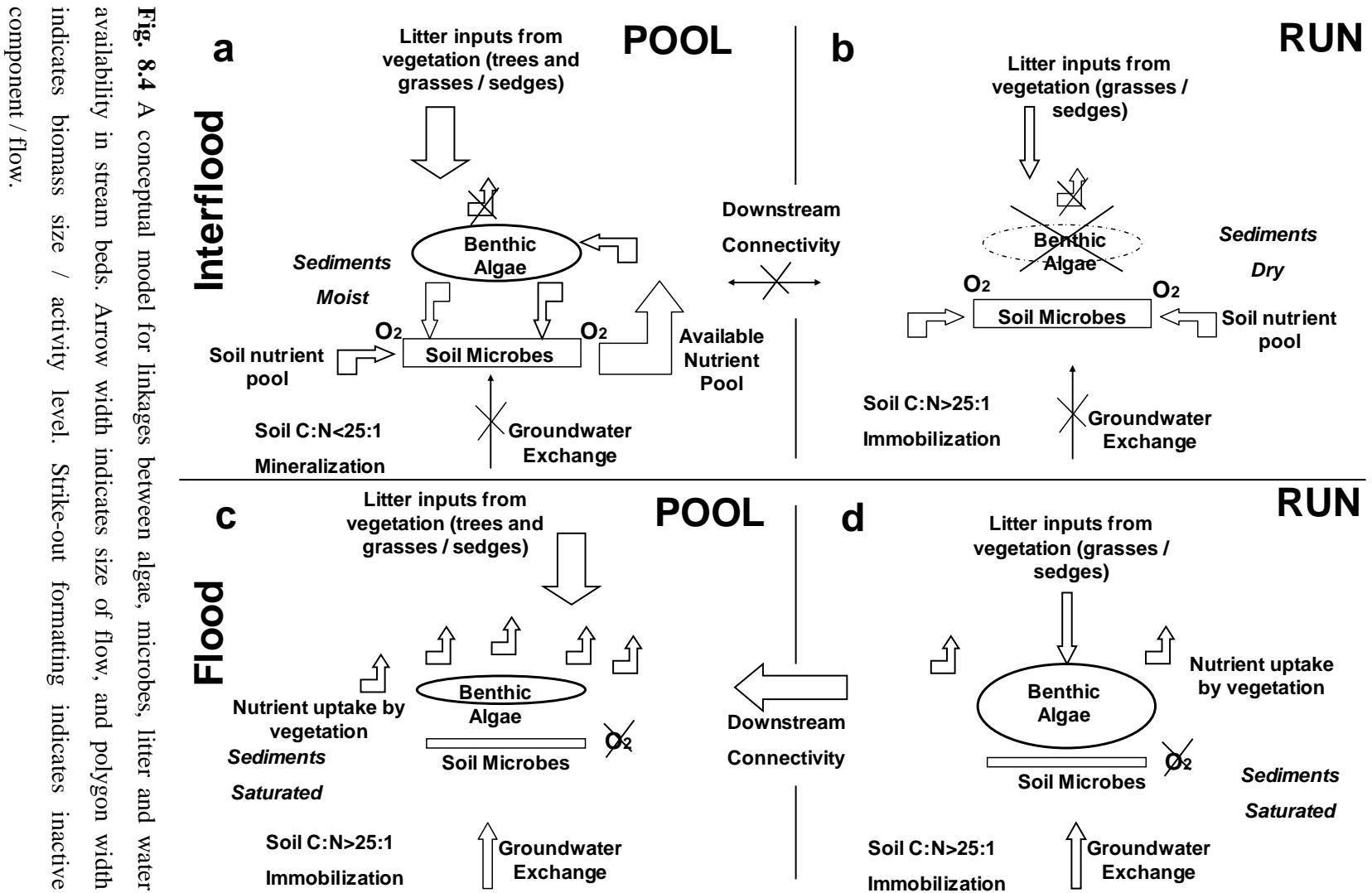


Fig. 8.4 A conceptual model for linkages between algae, microbes, litter and water availability in stream beds. Arrow width indicates size of flow, and polygon width indicates biomass size / activity level. Strike-out formatting indicates inactive component / flow.

8.2.7 Stream biogeochemical models developed from long-term research sites in arid and semi-arid zones

While this research has focused on streams in north-west Australia, cross-site syntheses allow for prediction of system responses based on readily observable ecosystem properties, and may provide the basis for the development of a ‘best practice’ guide for future monitoring and management of stream biogeochemical function. Here, I discuss formal and informal models developed for three long-term ecological research sites (both recognised LTER and ‘LTER-like’ sites) in other dryland (both warm and cold) catchments worldwide, in the context of the findings of this thesis. Long-term research sites provide the opportunity to develop integrated system models, and offer greater potential for advancing our understanding of ecosystem function. As it is not possible to explore the full suite of research conducted at these long-term sites, my discussion is limited to a number of key, interesting comparisons for each site. It is worth noting that the Ecosystems Research Group at UWA has been conducting ecosystem research on Hamersley Station in the central Pilbara since 1995. As such, this site is also, arguably, an LTER.

Sevilleta LTER – Rio Grande, USA

The Sevilleta LTER Program was established in 1988 to conduct research on ecological processes and responses to climate dynamics in a biome transition zone in central New Mexico. The study area is positioned at the nexus of the Chihuahuan Desert, Great Plains Shortgrass Steppe and Mogollon (Piñon-Juniper) Conifer Woodland in the southwest USA. The Sevilleta is strongly influenced by the El Niño Southern Oscillation, and therefore, like the Pilbara region, experiences major fluctuations in precipitation on semi- and multi-decadal time scales. Overall, research at the Sevilleta LTER has focused on the role of energy and water as limiting factors for ecological processes. Limnological sites include the Rio Grande and the various tributaries of this extensive river system grading from ephemeral to perennial streams. Specific stream studies have included landscape nutrient cycling (Kitchell *et al.*, 1999), litter decomposition (Ellis *et al.*, 1999), stream biogeochemical responses to drought (Dahm *et al.*, 2003), climate change - induced shifts in precipitation (Molles & Dahm, 1990), N availability (Follstad Shah & Dahm, 2008) and denitrification (Mulholland *et al.*, 2008).

Follstad Shah and Dahm (2008) recently considered changes in N availability in response to duration of experimental floods in the riparian forests of the middle Rio Grande. They concluded that for riparian soils in arid and semi-arid regions, floods promote both gains and losses of inorganic N in riparian soils, depending on the timing of the floods, the duration of inundation and the effects on quantity of leaf production. Long-duration inundation resulted in greater N losses via denitrification and greater stress to riparian vegetation along the Rio Grande. Rates of net N mineralisation were consistently greater at sites subjected to long interflood intervals (LIFI; ≥ 10 years) versus short interflood intervals (SIFI; 2-3 years).

Follstad Shah and Dahm (2008) also proposed a model of the effects of flood interval on N cycling that classified riparian forests into two types: SIFI Open System and LIFI Closed System. In a SIFI Open System, frequent floods slowed soil N accumulation due to regular flushing, decreased net N mineralisation and decreased N inputs from vegetation. In contrast, in a LIFI Closed System, less frequent floods induced increased soil N accumulation, with increased net N mineralisation and inputs from vegetation. I propose that for streams with irregular flood intervals, such as in the Pilbara, the model developed by Follstad Shah and Dahm (2008) may be modified to include spatio-temporal class shifts between an SIFI Open System and LIFI Closed System. My field studies in the Pilbara indicated patchy accumulation of inorganic N in riparian zones during the interflood (Chapter 3; Fig. 3.4). Depending on landscape topography and the severity of flooding, juxtaposed sections of the stream reach or riparian zone may operate as SIFI Open Systems and LIFI Closed Systems concurrently.

Drought provides an essential counterpoint to the effect of flooding on stream biogeochemistry. For example, Dahm *et al.* (2003) considered coupled biogeochemical and hydrological responses to drought on the spring-fed Rio Calaveras and Rio Grande Bosque, using long-term climate data to calculate drought severity indices. The authors provided a conceptual model of the effects of drought on the hydrology and biogeochemistry of the interface between surface waters and ground waters, whereby nutrient inputs to streams reflected the biogeochemistry of regional ground water. However, while useful for spring-fed streams, the emphasis on groundwater contributions to nutrient cycling has less relevance for truly intermittent streams such as those in the Pilbara and many regions elsewhere. In these intermittent streams, any

streamflow typically represents a perched surface expression of precipitation, before gradual removal by infiltration or evaporation.

Regardless, the drought model of Dahm *et al.* (2003) provides three potentially useful categories for drought - baseflow, moderate drought and extreme drought – that may be applied to other systems, including those of the Pilbara. During extreme drought in the streams considered by Dahm *et al.* (2003), surface discharge is minimal and nutrient distributions are patchy with little OC available for microbes. The authors concluded that key general attributes of drought were a decrease in stream discharge, reduced nutrient availability and contracted aquatic habitat. Based on my studies at Barnett Creek, drought may not signal reduced nutrient availability *per se* across the stream landscape. Drought periods at Barnett Creek still resulted in accumulation of inorganic nutrients, and flooding reduced nutrient concentrations (on a scale of weeks to months) at both Barnett Creek and Pirraburadoo Creek. While drought increased measured concentrations of available nutrients, these pools would be restricted in their availability to plants when soils and sediments are extremely dry. Upon rewetting, the spatial distribution of these accumulated nutrients would play a significant role in seeding biogeochemical hot spots during the flood season. Clearly, any refinement of coupled biogeochemical-hydrological drought models to include streams where groundwater inputs are less important than *in situ* production and downstream transport, should encompass drought-induced accumulations of available nutrients.

Studies of the role of flooding in leaf C:N:P stoichiometry indicated considerable spatio-temporal variation across the riparian-floodplain system of the Rio Grande on a reach-scale (Tibbets & Molles, 2005). These authors highlighted the role this variation would play in decomposition and food web processes. My Pilbara studies have indicated the importance of litter quality, rather than quantity, as a key factor controlling soil nutrient transformation (Figs 6.1 & 6.2). While previous studies in Pilbara grasslands have considered forage quality (e.g. Islam *et al.*, 1999), further study is still required to quantify the range of variation in litter quality across Pilbara stream landscapes. Understanding this variation would help elucidate the role of litter quality as a control of biogeochemical function in the stream system.

Sycamore Creek, Arizona, USA

While not part of the formal LTER network, Sycamore Creek in Arizona (arid Sonoran Desert) is considered an ‘LTER-like’ site, and has been extensively studied since the late 1970s. This research has included a number of key foci, specifically: N dynamics and limitation (Grimm & Petrone, 1997; Holmes *et al.*, 1996; Schade *et al.*, 2001), hyporheic zone biogeochemistry (Valett, 1993), parafluvial microbial dynamics (Holmes *et al.*, 1998), (periphyton dynamics (Grimm & Fisher, 1989), macroinvertebrate communities and food webs (Sanzone *et al.*, 2003), soil re-wetting responses (Heffernan & Sponseller, 2004; Sponseller, 2007) and regional land management issues (Grimm *et al.*, 2004).

The synthetic conceptual models derived from studies at Sycamore Creek are worth exploration. Firstly, Fisher *et al.* (2001) discussed the broad transition of stream ecology from a primarily ecosystem-based to landscape-based science, using transitions in research focus at Sycamore Creek as an example. This transition is likewise relevant to studies of Australian streams, which have also been traditionally confined to the wetted channel. More recently, researchers have incorporated the whole stream landscape, from channel to riparian zone and uplands (Fisher *et al.*, 2001). The benefits of the latter approach, particularly for comparisons of nutrient pools and processes over a range of spatio-temporal scales, have been asserted for many natural systems (Withers & Meentemeyer, 1999). While such a multi-scalar approach was beyond the scope of this thesis, my research findings would benefit considerably from further research using the hierarchical framework as proposed for Sycamore Creek (Fisher *et al.*, 1998; Fisher *et al.*, 2001). Fisher *et al.* (2001) also highlight a conceptual divide between those studies considering landscape ecology in the stream bed (as examined in Chapters 4 and 7 of this thesis) versus landscape ecology across the stream-riparian-upland system (as examined in Chapter 3 of this thesis). My Pilbara research is exceptional in this regard, and particularly for the Australian continent, by drawing together numerous studies of biogeochemical patterns both within the channel bed and the broader stream landscape.

Fisher *et al.* (2001) provide a conceptual model for N processing in desert catchments affected by precipitation pulses of varying size. Small pulses (small storms) ‘turn on’ upland hot spots for nutrient processing, while moderate pulses mobilise and transport water and nutrients to the network of intermittent channels. During large pulses (severe

storms) nutrients and water are transported rapidly to the largest order lotic or lentic system in the catchment, where nutrient retention may or may not occur. This model may add another interesting facet to my flood pulse model presented in Section 8.2.2, namely that stimulation or inhabitation of microbial activity and nutrient mineralisation should be considered on a catchment scale, to incorporate upstream-downstream spatial shifts in nutrient processing zones with changes in pulse size.

Holmes *et al.* (1998) investigated the impact of flash floods on microbial distribution and biogeochemistry in parafluvial sediments at Sycamore Creek. The authors found that algae recovered quickly after flooding but that the bacterial response was lagged, and that bacterial numbers actually declined immediately after flooding. Algal exudates sustained parafluvial metabolism in mid- to late-successional stages after flooding. These observations correspond favourably to the model presented in Fig. 8.4. Holmes *et al.* (1998) also suggested that, immediately post-flood, terrestrially-derived OM was of more importance to parafluvial communities than aquatic OM. The model given in Fig. 8.4 suggests that this relative importance of OM source may be spatially variable in the stream system, and depend more on stream bed geomorphology.

Sponseller (2007) examined soil responses to experimental re-wetting in soils at Sycamore Creek. As for my mineralisation experiments (Chapters 5 and 6), a rapid re-wetting response was observed in Sycamore Creek soils. Elevated CO₂ efflux only lasted 48 hr in the study by Sponseller (2007), which the author noted was in contrast to many other studies in a variety of ecosystems. This short-lived response was also observed in my Pilbara soils (Fig. 6.1), and may be a function of rapid evaporation and infiltration in sandy soils with typically low OM. Sponseller (2007) found no relationship between experimental storm size (flood pulse) and CO₂ efflux, and concluded that beyond a certain threshold for storm size, increased duration of moisture availability had little influence on microbial activity and subsequent C loss. Given the preponderance of small flood pulses (< 0.5 cm rainfall) in the Sycamore Creek system, Sponseller (2007) acknowledged that the majority of pulses would be too small to induce plant responses, yet sufficient to elicit optimal microbial activity at near maximum rates. This observation compares favourably to the model presented in Section 8.2.2, where small pulses (Microbial Productivity Pulses) dominated larger pulses (Vegetation Productivity Pulses) in their frequency and long-term incremental effect on system biogeochemistry.

McMurdo Dry Valleys LTER, Antarctica

An intriguing example of stream biogeochemical research from a *cold* dryland environment is offered by the McMurdo Dry Valleys LTER programme, an interdisciplinary study of aquatic and terrestrial ecosystems in ice-free high valleys in Antarctica (MCM-LTER, 2008). Unlike the hot arid and semi-arid systems of the Pilbara, Sonoran Desert or Sevilleta range, the dry valleys represent a cold desert, where temperature limitation of biological activity is common and vascular plants are absent. Despite its position as an end-member in the spectrum of ecosystems, stream research in Antarctica provides an intriguing opportunity to more closely examine the influence of physical forces on biogeochemical phenomena, and its soil biota is considered most similar to warm arid systems (Wall & Virginia, 1999). Like the Pilbara, the dry valleys experience long periods of limited precipitation with streams that flow for periods less than 10 weeks per year (McKnight *et al.*, 1999), and through geological settings highly weathered by abiotic forces. Interestingly, both the Pilbara and McMurdo dry valleys have been used as biogeophysical analogues for Mars research (Brown *et al.*, 2004; Liebert, 2001) because of the harshness of their habitats and the ongoing preponderance of physical forces (as opposed to biological ones) in shaping modern landscapes.

The McMurdo dry valleys support numerous ephemeral streams, as well as wetlands and lakes, and since 1993 considerable research has been conducted exploring the biogeochemical function of these systems. Key themes have included nutrient limitation and dynamics (Barrett *et al.*, 2007; McKnight *et al.*, 2004), soil spatial variation (Ho *et al.*, 1996), denitrification (Gooseff *et al.*, 2004), algal mat dynamics (Dana *et al.*, 1994), soil biodiversity (Bardgett *et al.*, 2001) and hydrological flowpaths (Gooseff *et al.*, 2003). Streams in the McMurdo dry valleys are hot spots of microbial and algal life in an otherwise barren landscape, and there are limited interactions with upland environments, and (obviously) no leaf litter inputs (McKnight *et al.*, 1999). Algal hot spots are found on stable stone pavements with limited exposure to sediment transport and scour. During long dry periods, these algae and associated microbial communities exist on stones in a desiccated cryptobiotic state that responds rapidly to renewed flow (McKnight *et al.*, 1999). So, as seen at Ratty Springs in this thesis (Chapter 7), where armoured gravel runs supported lush benthic growth after flooding, stable stone pavements may provide a physical refuge for benthic life in intermittent stream systems. This is particularly important for McMurdo streams, where the availability of inorganic

nutrients is regulated solely by benthic algae in the absence of vascular plants (Alger *et al.*, 1997; McKnight *et al.*, 2004).

Similar to my studies of Pilbara streams, access to low soil nutrients (particularly P) by microbes in the McMurdo dry valleys is limited primarily by the patchiness of soil moisture availability, which averages from ~1 % gravimetric in dry zones to 13 % under snow patches or glacial melt paths (Barrett *et al.*, 2007; Virginia & Wall, 1999). Physical forces are the most significant in influencing stream biogeochemistry, with the influence of biological processes constrained by first by water availability and secondarily by nutrient stoichiometry (Barrett *et al.*, 2007). As observed in my research, landscape position in the McMurdo dry valleys is an important control over nutrient availability and stoichiometry across the stream-terrestrial interface (Barrett *et al.*, 2007). Past climate and palaeo-drainage patterns continue to define present-day nutrient distributions in the dry valleys (Wall & Virginia, 1999). In the Pilbara, surface erosional, natural vegetational, and land use changes obscure part of these physical landscape ‘legacies’ (*sensu* Moorhead *et al.*, 1999); however, an extensive network of palaeo-drainage is still preserved in the subsurface and reflected by vegetation (Beard, 1973). Quantifying the influence of such landscape legacies on modern nutrient patterns would present an interesting further study.

8.3 IMPLICATIONS OF THIS STUDY FOR SOIL AND STREAM MANAGEMENT IN NORTH-WEST AUSTRALIA

8.3.1 Dewatering

Streams in the Pilbara are increasingly affected by groundwater abstraction and pumping, and it is expected that water use will triple in the Pilbara region within 25 years (Department of Water, 2007; see Section 2.6.4). Barnett Creek is currently unregulated and not subject to water abstraction. In contrast, Pirraburadoo Creek is unregulated, however sections of it have been dewatered since 2001 for mining activities (Resource and Environmental Management & Ensis, 2007). Dewatering lowers the water table, which may cause death of *Eucalyptus* spp. and *Melaleuca* spp. growing in association with the stream systems and which are variably dependant upon groundwater for survival during dry periods (Rathbone, 2005). The demise of riparian vegetation subsequently reduces canopy cover in and around streams, raises stream

temperatures and insolation (Davies-Colley & Quinn, 1998), and can reduce bank stability (Easson & Yarbrough, 2002). In spring-fed streams, vertical hydrologic inputs to surface soils may also cease if water tables are lowered, or may persist for a shorter time period after floods. However, the importance of vertical hydrologic exchanges for nutrient cycling in Pilbara streams is expected to be less than for streams elsewhere (see discussion Sections 4.4.3 & 7.4.2).

Biogeochemically, it is difficult to predict how dewatering activities may influence ecosystem function in Pilbara stream landscapes, as most previous studies on the environmental impacts of dewatering have focussed on primarily on the ecohydrology of particular tree species (e.g. Graham, 2001; Landman, 2001; Scott *et al.*, 1999) or the health of riparian vegetation communities (e.g. Webb & Leake, 2006), rather than specifically on soil or sediment processes. It is reasonable to assume that the decline of riparia caused by anthropogenic lowering of water tables would influence nutrient availability and transformation in semi-arid streams. For example, my field study at Pirraburadoo Creek and studies by others (e.g. Bunn *et al.*, 1998; Sabater *et al.*, 2000) indicate that algal growth will be favoured by stream channels with greater levels of insolation, hence removal of overstorey species should stimulate growth of algae and macrophytes. Lastly, my Barnett Creek field studies also indicated that banks are an interflood store and potential source of moisture and organic matter in the stream system. If bank stability was reduced, a system-wide decline in water and substrate availability could therefore occur.

8.3.2 Clearing and rehabilitation of riparian vegetation

Clearing of riparian vegetation for pastoral, mining development or urban purposes has been a common disturbance factor affecting streams in semi-arid Australia and elsewhere. As stock concentrate by water sources in drylands, riparian vegetation is also often heavily impacted by grazing, trampling and nutrient enrichment, and livestock also introduce and spread weed seed in the stream corridor (Kauffman & Krueger, 1984; Naiman *et al.*, 2005; Price & Lovett, 2002; Robertson & Rowling, 2000). Extensive land use means that waterways are rarely fenced from stock, unlike those in intensive land use zones. However, awareness by land managers of the importance of retention and rehabilitation of riparian vegetation has improved significantly in recent years. For example, since 1991 riparian forests have actually increased in spatial extent by 0.3 %

throughout Australia, slowly reversing through revegetation and protection the trend of rapid decline of riparian forests since European settlement (DEWHA, 2006).

Rehabilitation goals for degraded riparian zones have typically focused on restoration of the previous riparia, flood control, and water quality and bank stability improvement (Naiman *et al.*, 2005; Osborne & Kovacic, 2006; Wissmar & Beschta, 1998). Restoring soil and sediment biogeochemical function has rarely been a goal of such rehabilitation projects, as these characteristics are more difficult to quantify and we lack specific baselines for assessment of ‘biogeochemical health’. My research indicated that soil characteristics, rather than vegetation community composition, are of greater importance in influencing soil biogeochemical function. While vegetation community composition will influence soil retention and development in rehabilitated ecosystems (Schwendenmann, 2000), stream managers should appreciate that, where restoring biogeochemical function is a major goal during rehabilitation, a range of riparian plant species may be suitable for replanting. In heavily disturbed systems, without suitable remnant topsoil, imported surface soils may be necessary to seed the rehabilitated system with microbial communities and starter organic substrates. Such a programme of biogeochemical rehabilitation would ideally be coupled with strategies to improve geomorphic stability, techniques of which are already well-developed (de Waal *et al.*, 1999; Gore *et al.*, 1994). In general, the areas of biogeochemical health assessment and biogeochemical rehabilitation of stream landscapes offer considerable scope for both further basic and applied research.

Furthermore, my Pilbara studies have indicated that semi-arid riparian zones can be a hot spot for soil $\text{NO}_3\text{-N}$ and OC, and support large mineralisation flushes when water is available. Removal of riparian vegetation through clearing, or its degradation through other anthropogenic disturbance, will reduce the ability of the riparian zone to store $\text{NO}_3\text{-N}$ and OC, and alter the soil characteristics that support comparatively higher levels of N and C mineralisation. As a result, overall nutrient availability in the stream landscape would decline.

8.3.3 Climate change implications for biogeochemical cycling in north-west Australia

As discussed in Section 2.7, current models suggest that rainfall is increasing in magnitude and variability in the Pilbara (Commonwealth of Australia, 2007; Cullen & Grierson, 2007; Hughes, 2003). This trend is a departure from the wider climate change model accepted for many Australian ecosystems, where a progressively drier climate is expected particularly for southern Australia (Kershaw *et al.*, 2003). The inferred changes in Pilbara climate correspond to a measured increase in rainfall since 1980 in north-west Australia associated with a greater intensity of tropical cyclones (Plummer *et al.*, 1999). As the central Pilbara is dependent largely on cyclonic rainfall, an increase in the intensity of these systems would mean that cyclones would travel further inland and persist for longer periods (Bureau of Meteorology, 2008a; Kaplan & DeMaria, 1995). Hence, it is expected that the climate of the central Pilbara would change relative to present conditions much more markedly than coastal areas, and that intermittent streams in these areas would flow more frequently and possibly for longer periods.

An increase in the severity of floods induced by climate change may have a number of effects on stream systems such as Barnett Creek and Pirraburadoo Creek. My studies indicate that severe flooding removes small-scale soil microtopography in riparian, bank and floodplain zones, reduces bioavailable nutrients and microbial biomass and activity, and reduces biogeochemical patchiness (Chapters 3 & 4). Where floods increase in magnitude and duration, it might therefore be expected that Pilbara stream landscapes will become more internally homogenous, and that the bioavailability of P, N and C to both microbial and plant consumers may decline. Severe floods also cause greater erosion, which can remove OM deposits, CWD and nutrient-rich topsoils (Hooke & Mant, 2000; Pettit *et al.*, 2005). Riparian zones would lose their biogeochemical ‘stickiness’ for storage of nutrients, as microtopography and soil cohesiveness declines. Conversely, floodplains would receive greater and longer inundation by flood waters due to overbank flow, and receive greater quantities of transported nutrients and materials. Floodplain productivity may therefore be stimulated by an increase in flood severity induced by climate change, while riparian productivity may concurrently decline.

Previous studies of the effects of climate change on dryland streams have indicated that the flow permanence of lowland desert streams is likely to be highly sensitive to

changes in precipitation and runoff and net basin supply of water (Grimm *et al.*, 1997). Riparian zone recruitment and stability was considered to be highly sensitive to flow permanent and variation in precipitation and runoff on the temporal scale of tens to hundreds of years. In contrast, geomorphological structure of these desert streams was expected to be most dependant on precipitation and runoff on the scale of hundreds to thousands of years (Grimm *et al.*, 1997). Consequently, what is needed next is to extend primarily hydrological models for climate change such as this to models of soil biogeochemistry and ecosystem function.

8.4 FURTHER WORK

Our understanding of the role of flooding in the biogeochemistry of soils and sediments of semi-arid intermittent streams has been improved by this thesis. Given the experimental constraints associated with conducting multi-site field studies during a three-year window in a remote and climactically unpredictable location, there are logically further questions that have been prompted by this study. These questions include, in order of priority:

- Do the nutrient and microbial patterns observed persist over (i) multi-decadal scales, (ii) mega-spatial (larger landscape to regional) scales, (iii) different flood frequency-magnitude regimes, and (iv) different stream sizes?
- How do *in situ* (field) rates of N, P and C processes change over the flood-drought cycle in intermittent streams subject to severe flooding?
- What is the key pulse size and frequency for maintaining health of riparian vegetation in the Pilbara and soil microbial function?
- How is functional microbial diversity affected by severe flooding?
- What are the appropriate indicators for assessing biogeochemical health in stream landscapes and what techniques can we use to ensure biogeochemical rehabilitation of disturbed streams?
- How long do specific biogeochemical conditions persist at any one location in the stream landscape?
- What are the threshold characteristics that might shift basic biogeochemical conditions for N, P and C?
- How quickly do microbial community profiles respond and decline to flood pulses in intermittent streams?

- How important is litter quality in determining N mineralisation and microbial activity in soils and sediments from Pilbara streams, and how does the chemical composition of this litter change for different species, and vegetational communities?
- Which physiochemical characteristics of channel and floodplain environments are responsible for producing exceptional internal divergence in microbial community profiles?
- How do we relate $\delta^{15}\text{N}$ signatures to processes occurring at the stream ecosystem scale?
- What role does calcrete play in influencing soil nutrient availability in Pilbara streams?
- How do large and rocky inclusions quantitatively influence predicted N mineralisation in channel beds?
- How pervasive is P limitation in other Pilbara streams?

8.5 CONCLUSION

Stream biogeochemistry is a burgeoning field worldwide, and therefore it is reasonable to expect that many of the above existing gaps in our knowledge may be addressed in the near future. Intermittent streams in semi-arid regions are sensitive environments that are disproportionately affected by anthropogenic pressures such as pastoralism, land clearing and water extraction in comparison to streams in more mesic settings. Without appropriate ecological baselines to inform management and rehabilitation processes, the long term stability of these systems is indeterminate and insecure. This study has made a substantial contribution towards establishing one such baseline for soil biogeochemical function in semi-arid, intermittent streams.

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APPENDIX A

Assessment of Coarse Woody Debris and Soil Nutrient Enrichment

A.1 INTRODUCTION

Large nutrient deposits in the stream landscape in the form of coarse woody debris (CWD; Plate A.1), have become an increasingly important issue in stream and particularly riparian zone management (Erskine & Webb, 2003). Catastrophic flooding may cause mass input or removal of material in the form of CWD, from downed trees or branches, or downstream transport (Jacobson *et al.*, 1999). Accumulations of debris may act as nutrient “retention devices”, trapping leaves, sediment and small branches and modifying flow patterns (Winterbourn & Townsend, 1991). CWD can persist for considerable lengths of time - the average lifetime of CWD reported by Mackensen *et al.* (2003) for Australian species ranges from 11 to 54 years depending on timber durability, and very similar lifetimes were obtained by Brown *et al.* (1996) in Western Australia (from 13.6 years for *Corymbia calophylla* to 42.8 years for *Eucalyptus marginata* and 59.9 years for *Pinus pinaster*). Slow to decompose, CWD may be a C sink in the short run, as well as the substratum for many processes (Harmon *et al.*, 1986). CWD is a significant ecological component of many streams, both in Australia and elsewhere (Benke *et al.*, 1985), and often provides essential habitat for both aquatic and terrestrial organisms (Treadwell *et al.*, 1999).



Plate A.1 Coarse woody debris pile at Barnett Creek.

While CWD piles are known to provide relative moist, organic-rich microhabitats that are focal points for decomposition and secondary production (Jacobson *et al.*, 1999), little is known of how they enrich surrounding soils or contribute to nutrient patchiness in the channel and riparian zone. In this short study at Barnett Creek, soil nutrients (N, P) and C were measured at set distances from CWD piles, in order to investigate the biogeochemical influence of debris mounds on surrounding soils. It was hypothesised that soils close to the debris mound would be significantly enriched in nutrients and C, and that this enrichment would decrease proportionately with increasing distance.

A.2 METHODS

All field work was conducted at Barnett Creek (Fig. 2.1; Section 2.8.1) in November 2004.

A2.1 Definition of CWD

The minimum diameter for CWD in some studies is as small as 2.5 cm (Wei *et al.*, 1997), although many studies consider only larger material (>10 cm in diameter). For the purposes of this study, the diameter set by Wei *et al.* (1997) was used, so that dominant woody species present at Barnett Creek that only deposit CWD of small diameter (e.g. *Acacia citrinoviridis*) were not excluded.

A2.2 Description of CWD piles

Ten piles of CWD were randomly selected at Barnett Creek. Piles were described by measuring overall dimensions (to nearest cm), landscape position and dominant species composition (Table A.1). CWD piles were primarily located adjacent to channels either on the edge of the riparian zone or on channel banks (Table A.1).

Table A.1 Description of coarse woody debris piles.

| Pile No. | Estimated Volume (m ³) | Species Composition | Location Notes |
|----------|------------------------------------|--|----------------------|
| 1 | 7.9 | <i>A. citrinoviridis</i> | shallow channel edge |
| 2 | 5.2 | <i>A. citrinoviridis</i> | shallow channel edge |
| 3 | 2.5 | <i>A. citrinoviridis</i> <i>Eucalyptus</i> spp. | riparian zone |
| 4 | 10.2 | <i>A. citrinoviridis</i> | riparian zone |
| 5 | 2.1 | <i>A. citrinoviridis</i> | riparian zone |
| 6 | 10.8 | <i>A. citrinoviridis</i> <i>Eucalyptus</i> spp. | in main channel |
| 7 | 37.4 | <i>A. citrinoviridis</i> <i>Eucalyptus</i> spp. | in main channel |
| 8 | 16.7 | <i>A. citrinoviridis</i> | in main channel |
| 9 | 10.9 | <i>A. citrinoviridis</i> <i>Eucalyptus</i> spp. | on bank |
| 10 | 5.8 | <i>A. citrinoviridis</i> | on bank |

A2.3 Species-specific measurements

Wood in CWD piles at Barnett Creek was comprised of three main species: *Acacia citrinoviridis*, *Eucalyptus camaldulensis* and *E. victrix* (Table A.1). Wood from *E. camaldulensis* and *E. victrix* are not readily distinguishable in the field. Average wood density for *A. citrinoviridis* and *Eucalyptus* spp.) was calculated by weighing (to nearest 500 g) and measuring the dimensions (to nearest mm) of wood sections collected at Barnett Creek ($n=10$). In addition, decay stages for the two wood types (*Acacia / Eucalyptus*) were classified visually, to produce a field decay scale. Such classifications have assisted forest

managers elsewhere in rapid field assessments of forest health and structure (Robinson & Beschta, 1990)

A2.4 Soil sampling for nutrient analysis

At each CWD pile, three soil samples (~300 g) were taken at three distances (0.0, 0.1 and 1.0 m) from the base of the debris pile ($n=9$). The soil sample at 0.0 m was extracted from directly under the edge of the CWD pile. Sample points were randomised before sampling by use of three radially arranged chains (at 0.0, 0.1, and 1.0 m) with random selection of a 10 x 10 cm grid along each chain. Hence samples were in random directions from the pile, and were not based on flow direction. At each sample point, soils were collected from three depths: 0-2, 2-5 and 5-10 cm, using a hand trowel and sieved to <2 mm in the field. NO₃-N, NH₄-N, OH-P_i, OH-P_T, OH-P_o, OC, total N, total C, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were analysed according to methods detailed in Section 3.2.4.

A2.5 Data analysis

Data were analysed in ANOVA (Statview 5.0) using two fixed factors: distance from CWD pile and soil depth. Data were transformed where appropriate (square root transformation) and groups separated using Fishers PLSD post-hoc test.

A.3 RESULTS

A3.1 Composition of CWD piles

Average wood density for *A. citrinoviridis* was 560.6 kg m⁻³ (SE 67.3), and 1203.8 kg m⁻³ (SE 441.9) for *Eucalyptus* spp. The estimated volume of CWD piles at Barnett Creek was between 2.1 m³ and 37.4 m³, and all piles were dominated by *A. citrinoviridis* debris (Table A.1).

A3.2 Field scale for decay stages

Three decay stages were described for CWD at Barnett Creek. Four attributes were considered useful for visual description of decay stage for *Acacia* spp., with six attributes for *Eucalyptus* spp. (Table A.2).

Table A.2 Field scale for decay stage of *Acacia* and *Eucalyptus* coarse woody debris.

| Genus | Attribute | Decay Stage [†] | | |
|-------------------|-----------------------|--------------------------|---------|---------------|
| | | Stage 1 | Stage 2 | Stage 3 |
| <i>Acacia</i> | outer bark | ✓ | x | x |
| | lateral fragmentation | x | x | ✓ |
| | inner bark exposed | x | ✓ | ✓ |
| | lateral twigs | ✓ | x | x |
| | outer bark | ✓ | x | x |
| | lateral fragmentation | x | x | ✓ |
| <i>Eucalyptus</i> | inner bark exposed | x | ✓ | ✓ |
| | lateral twigs | ✓ | x | x |
| | cross-section | round | round | hemispherical |
| | texture | hard | hard | crumbling |

[†] x=absent, ✓=present

A3.3 Nutrient enrichment of soil by CWD piles

Soil moisture decreased significantly with increasing distance from CWD piles ($P<0.05$; Fig. A.1a), as did soil $\text{NO}_3\text{-N}$ ($P<0.001$; Fig. A.1b). Indeed, moisture content was 40 % greater and soil $\text{NO}_3\text{-N}$ concentrations were >100 % higher in soils under CWD piles than in soils 1 m distant (Fig. A.1). Change in $\text{NO}_3\text{-N}$ concentrations by distance from the CWD pile fit the power equation (5):

$$[\text{NO}_3\text{-N}] = 10.794 \times d^{-0.6893} \quad (5)$$

where $[\text{NO}_3\text{-N}]$ is the soil concentration of $\text{NO}_3\text{-N}$ (mg kg^{-1} soil) and d is the distance (m) from the base of the CWD pile ($R^2=0.95$).

Moisture increased significantly with soil depth ($P<0.0001$; Fig. A.1a), while concentrations of $\text{NH}_4\text{-N}$ decreased by 60 % between 0-2 cm and 2-5 cm depth (Fig. A.1c). Soil OH-P_i, OH-P_T, OH-P_o, OC, total N, total C, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ did not significantly change by depth or distance from CWD piles.

A.4 CONCLUSIONS

This short study has indicated that CWD piles may have an enrichment effect for $\text{NO}_3\text{-N}$ for local (<1 m distant) soils, and may enhance soil water availability. This would presumably stimulate local microbial activity and nutrient transformations during dry periods, when such processes may be water-limited. Where numerous CWD piles are present in the stream channel, banks and proximal riparian zone, such enrichment may increase the spatial patchiness of soil $\text{NO}_3\text{-N}$ and available moisture. During floods, leaching of these CWD piles may also contribute labile N laterally to other sections of the riparian zone and floodplain, or longitudinally to downstream reaches. Experimental removal and construction of CWD piles could support my observations of local soil enrichment, and quantify the contributions of CWD piles to the total stream N budget.

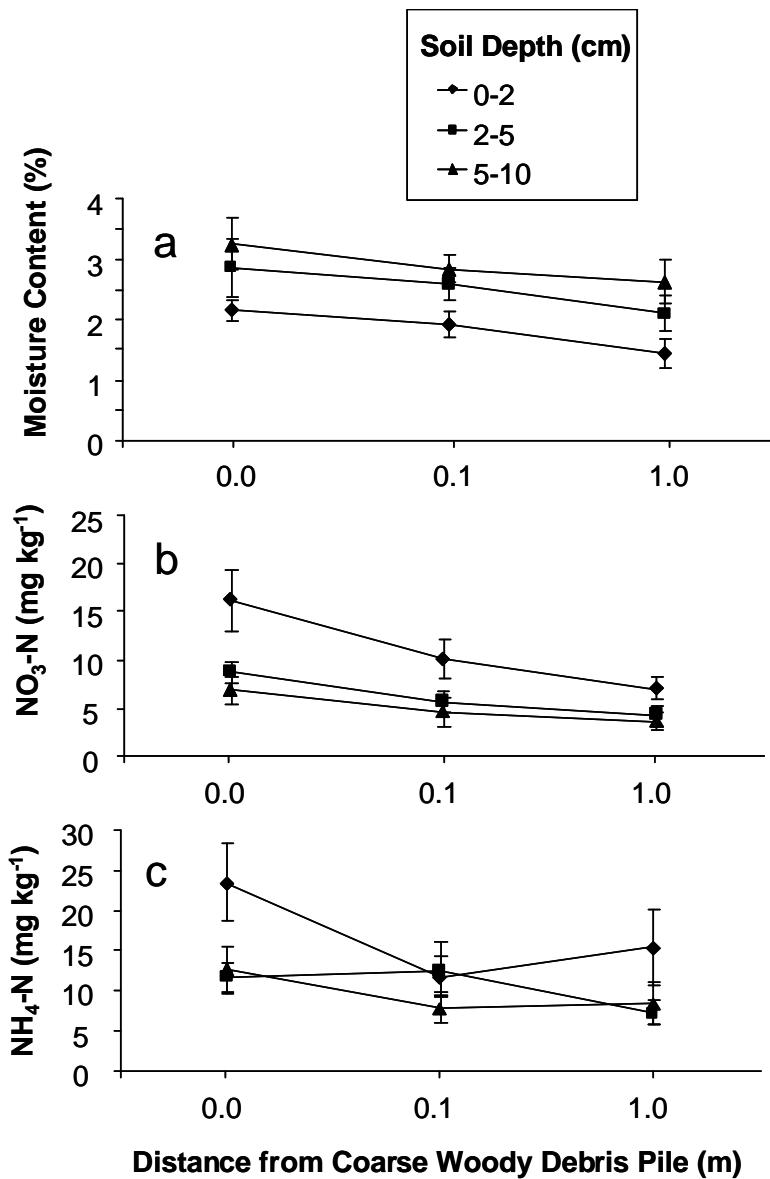


Fig. A.1 Soil enrichment near CWD piles.

Surprisingly, CWD piles did not seem to influence P, C, total N or $\text{NH}_4\text{-N}$ soil concentrations or stable isotope patterns. Given that CWD piles are mainly composed of C, local enrichment in C was expected. It is possible that the debris size mix and decay stage of individual CWD piles may be of greater importance in controlling any local nutrient enrichment.

APPENDIX B

Algal Mats at Weeli Wolli Springs

B.1 INTRODUCTION

A comprehensive inventory of algal diversity for the Pilbara bioregion is not currently available. As part of field studies conducted for this thesis, opportunistic sampling of benthic algal mats was undertaken at Weeli Wolli Creek. The purpose of this sampling was as a pilot study as part of the site selection for work presented in Chapter 7, and to provide first-time algal diversity information for this creek system. As a spring-fed system supporting endemic stygofauna (Reeves *et al.*, 2007), Weeli Wolli has attracted considerable environmental interest.

B.2 FIELD MEASUREMENTS

Field data were collected at Weeli Wolli Creek (Plate B.1a; 50727090 E, 7464800N) in the central Pilbara, ~70 km NW of Newman. Three samples (~40 cm²) of benthic algal mats (Plate B.1b) were taken from three different algal patches at Weeli Wolli Creek in November 2005 (*n*=9). Patches were defined as spatially discontinuous sections of algal mats contained wholly within the stream bed. Algal diversity and relative abundance was determined by light microscopy, and the genera present were categorised as dominant, co-dominant or present (but not abundant). Two grab samples (100 mL each) of creek water were also taken from the site, and examined for any additional planktonic algal groups.

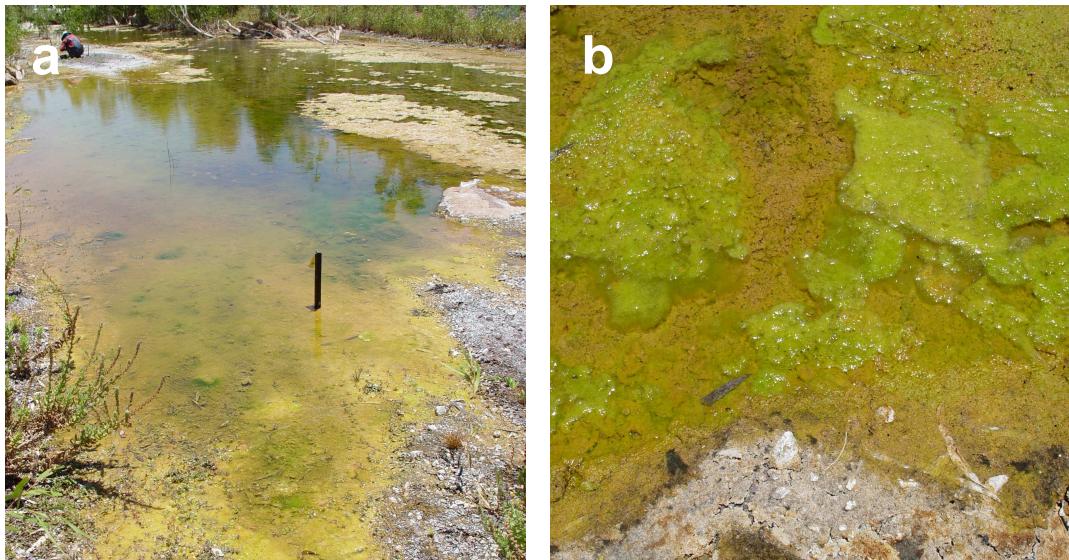


Plate B.1 Weeli Wollie Creek in November 2005 with creek pools (a) and algal mats (b).

B.3 ALGAL INVENTORY

Fifteen different genera were recorded in algal mat samples from the study site (Table B.1). The most common genera were *Zygnema* (Chlorophyta), *Mastogloia* (Bacillariophyta), *Amphora* (Bacillariophyta), *Pseudoanabaena* (Cyanophyta) and *Oscillatoria* (Cyanophyta). Water samples included the additional genera: *Netrium* (Chlorophyta), *Euastrum* (Chlorophyta) and *Fragilaria* (epiphytic diatom).

Table B.1 Genera detected in benthic algal mat samples from Weeli Wollie Creek.

| Group | Subgroup | Genus | Relative Abundance |
|------------------|------------|-----------------------|--------------------|
| Chlorophytes | | <i>Spirogyra</i> | Present |
| | | <i>Zygnea</i> | Abundant |
| | | <i>Cosmarium</i> | Present |
| Bacillariophytes | Planktonic | <i>Rhopalodia</i> | Present |
| | Benthic | <i>Cocconeis</i> | Present |
| | | <i>Hantzschia</i> | Present |
| | | <i>Navicula</i> | Present |
| | Epiphytic | <i>Mastogloia</i> | Dominant |
| | | <i>Amphora</i> | Abundant |
| | | <i>Synedra</i> | Present |
| Cyanobacteria | Planktonic | <i>Pseudoanabaena</i> | Abundant |
| | Benthic | <i>Anabaena</i> | Present |
| | | <i>Oscillatoria</i> | Abundant |
| | | <i>Chroococcus</i> | Present |
| Euglenophytes | | <i>Euglena</i> | Present |
| Others | Ciliates | | Present |