

Global change impacts on organic matter dynamics in stream ecosystems

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by

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Summary

1. With freshwater ecosystems worldwide at significant risk from global change, there is an urgent need to understand the processes involved and to develop adaptive responses. Riparian management might offer a means of increasing resilience to global change in headwaters, but evidence is scarce. This thesis investigates the potential effects of riparian management on the storage, processing and downstream export of resource subsidies – dominantly as terrestrial litter – that enter streams from the riparian zone.
2. In a large scale field study over four years, natural and experimental systems were used to test the hypothesis that riparian woodlands enhance stream ecosystem resilience to climatically mediated changes in flow regimes. Specific work included assessments of benthic organic matter stocks and export in contrasting catchments (broadleaf woodland, conifer plantations or sheep-grazed moorland), flow manipulations in mesocosms, and a large-scale field experiment simulating riparian broadleaved tree planting.
3. Standing stocks of particulate organic matter (POM) were influenced by flow regime, and declined following larger and longer flow-events, but event frequency had no apparent impact. Experimental data showed also that coarse fractions of POM in transport were significantly elevated in the early stages of simulated floods.
4. Despite flow effects on POM dynamics, streams bordered by broadleaves maintained consistently higher standing stocks of POM than conifer or moorland streams. Broadleaved streams also transported the highest concentrations of carbon in the form of high-quality FPOM. Leaf litter additions of stream channels did not reproduce these effects, possibly because the scale was insufficient to mimic real riparian woodlands.
5. While predicted flow changes under a warmer climate might affect the storage and flux of organic matter, riparian broadleaves are likely to mitigate these effects in stream ecosystems. This project illustrates the value of blending catchment-scale studies with field-based mesocosms to understanding complex global change processes.

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General Introduction

Human activity has profoundly altered exchanges of water, matter, organisms and energy in freshwater catchments with major consequences for water supply, biodiversity and environmental quality (Millennium Ecosystem Assessment 2005). Climate change and growing resource needs will increase pressure on freshwater ecosystems in future, but there is only fragmentary knowledge of the exact mechanisms through which freshwater ecosystems respond. Meanwhile, these ecosystems – among the Earth's major biodiversity hotspots – incur species extinction rates faster than any other (Strayer and Dudgeon 2010).

In a unique interface position between land and sea, freshwater ecosystems, and particularly headstreams, derive a critical part of their energy and matter from the riparian vegetation (Cummins 1974; Gregory *et al.* 1991; Naiman and Décamps 1997). Organic matter entering the freshwater ecosystem is either stored within the stream system as detritus or stream biota biomass, or exported via physical export and respiration (Fisher and Likens 1973). These energy inputs, termed 'riparian subsidies', play a pivotal role in regulating in-stream processes such as food web dynamics, secondary production and a range of ecosystem functions (Polis *et al.* 1997), which are all key processes that support major ecosystem services on which humans rely, such as clean water or fisheries (Millennium Ecosystem Assessment 2005).

Environmental factors such as land-use and climate change interact with these transfers of energy by altering the supply of organic matter, as well as the capacity of stream ecosystems to store and process these materials (Kominoski and Rosemond, 2012; Figure 1). In the UK, as in much of Europe, widespread changes in upland catchments have occurred over the 20th Century, largely due to the intensification of meat production and afforestation with conifer plantations (Simmons 2003; Reed *et al.* 2009). To add to these existing pressures, climate change in Northern Europe is expected to increase the intensity, duration and frequency of winter storms, with upland areas likely to be particularly hard hit (Birsan *et al.* 2005; Hannaford and Buys 2012). In headwater streams, these expected more frequent floods could potentially alter the structure and functioning of headwater streams, namely by depleting key basal resources (Kominoski and Rosemond 2012; Graça *et al.* 2015). These relationships are likely to be complex,

however, with climate interacting with channel structure and the riparian zone, making it difficult to identify underlying mechanisms.

Pressures stemming from the need to respond to global changes in climate patterns and growing human population needs are likely to alter riparian subsidies further, but current understanding of the role of riparian subsidies in supporting freshwater ecosystem processes is insufficient to guide decision making. Riparian vegetation is increasingly advocated as a management tool to protect water quality or regulate water temperature (Broadmeadow and Nisbet 2004; Abell *et al.* 2007; Ormerod 2009; Palmer *et al.* 2009; Seavy *et al.* 2009), but large scale evidence to support riparian management to deliver these and other ecosystem services is scarce.

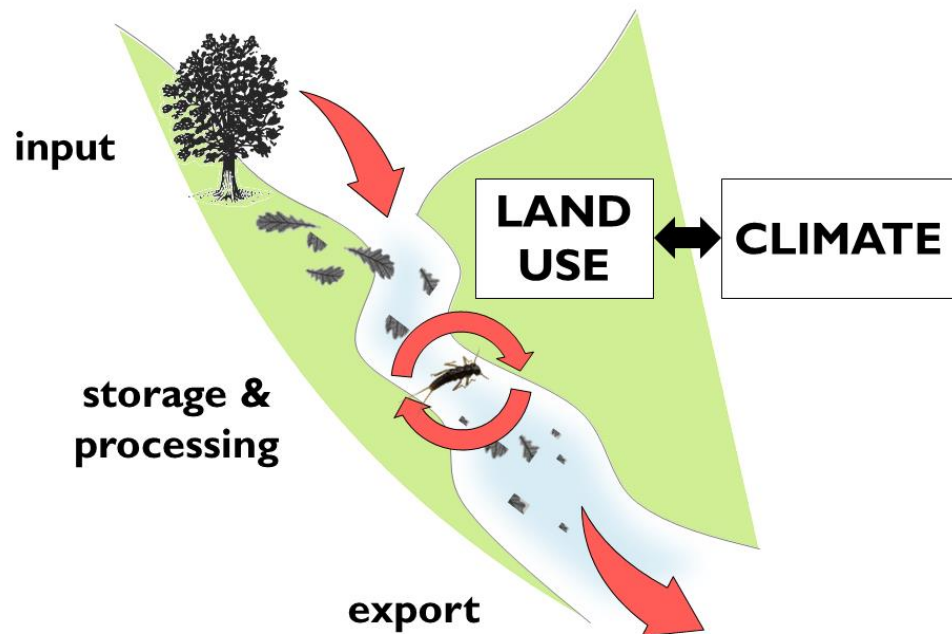


Figure 1. Schematic diagram of the process of energy flow through stream ecosystems, which could be altered by changes in land use and climate. Riparian subsidies provide key inputs of energy and nutrients to stream ecosystems, and are subsequently stored, processed and exported downstream.

Aims & Hypotheses

The main objective of this study is to understand the impact of land use and climate change on the fate of riparian subsidies in headwater streams. Using field-based, large-scale approaches, this study combines natural gradients and experimental methods to test the central hypothesis that **riparian woodlands enhance stream ecosystem resilience**.

More specifically, the following hypotheses are tested:

- ❖ **Climate change will reduce benthic organic matter resources in headwater streams due to increased organic matter export during high flow events** (Chapters 2, 3 and 4)
- ❖ **Streams bordered by riparian broadleaf woodlands support greater stocks of organic matter resources than those bordered by conifer plantations or moorland** (Chapters 2, 3 and 5)

The Llyn Brianne Stream Observatory (LBSO; www.llynbrianne-lter.org) offers the ideal setting to test these large-scale ecological questions. 35 years of ecological data on 14 replicated streams, with a range of land uses and water qualities typical of the UK uplands, provide the correlative power necessary for large scale analysis. In addition, a set of 12 mesocosm channels alongside these streams provides unique facilities for experiments to support the correlative observations.

CHAPTER 1: Literature review

As a background for the work presented in this thesis, a review is presented here of:

- (1) litter dynamics in streams (input, storage and export), and the biotic and abiotic factors that control these dynamics in terms of quantity, quality and timing; and
- (2) the interactive effects of land use and climate on litter dynamics, and the possible implications for energetic processes in stream ecosystems.

1.1 Litter dynamics

1.1.1 Inputs

Allochthonous inputs to streams occur as particulate or dissolved forms of organic matter. Coarse particulate organic matter (CPOM, >1mm) typically includes leaves, twigs, flowers and wood entering via direct litter fall or lateral pathways driven by wind or surface run-off (Cummins 1974). Fine particulate organic matter (FPOM, >0.5 μ m <1mm) is mainly generated from the breakdown of larger CPOM by physical and biological processes, though some also enters streams from adjacent terrestrial areas through windblow, surface runoff, bank erosion, groundwater and rainfall through the canopy (Cummins 1974). FPOM is also generated by flocculation of dissolved organic matter (DOM), which is generated from groundwater or leaching (Cummins 1974). The distinction by particle size relates to the types of consumers whose mode of feeding is adapted to the different physical states of organic matter (Cummins 1974; Cummins and Klug 1979). CPOM is consumed mainly by a group of invertebrates known as “shredders”, and FPOM is consumed by “collectors” and “filter-feeders” (Cummins 1974). The relative abundance of different types of producer and consumer organisms is therefore expected to change in response to the availability and character of organic matter inputs (Vannote *et al.* 1980).

Litter inputs play a pivotal role in the structure and function of stream ecosystems because they influence the quantity, quality and timing of energy and matter supply that support in-stream secondary production. Leaf litter is transported to streams by two major pathways: (1) direct deposition from overhead canopies (‘vertical input’), and (2) lateral movement (‘lateral input’) from the surrounding land. Many factors affect inputs, including the composition of riparian vegetation, slope and climate (see below). While it

is recognised that wood is also an important component of inputs, the direct contribution of wood to stream energy budgets is considered minimal because wood is highly resistant to breakdown (Webster and Benfield 1986). However, wood is indirectly important because it creates habitat for aquatic organisms and enhances leaf litter retention (Bilby and Likens 1980; Eggert *et al.* 2012). As such, wood will be considered here mainly in terms of its structural role in the retention and long-term storage of leaf litter (see Retention, storage & processing, below).

The production and species composition of riparian vegetation affects the quantity, quality and timing of leaf litter entering streams (Abelho 2001). Variations in the quantity of litter produced and subsequently entering streams differ between vegetation types; forested streams tend to provide much larger inputs of litter than non-forested streams (Webster *et al.* 1990; Benfield 1997). Different riparian species also vary in the quality of litter they produce, which is generally defined in terms of their palatability and assimilation by consumers, and therefore their breakdown rates. These characteristics include the abundance of essential nutrient elements (C:N:P), and presence of chemical inhibitors (Webster and Benfield 1986). For example, deciduous species supply more litter inputs of higher quality than coniferous species (Hart *et al.* 2013). The phenology of riparian vegetation affects the temporal dynamics of litter inputs. For example, temperate deciduous trees shed leaves in large pulses during autumn, which can account for up to 79% of total annual leaf fall (Abelho and Graça 1996). Conversely, coniferous or evergreen species will shed leaves throughout the year (González 2012).

Much of the UK uplands are characterised by open moorlands dominated by grasses consisting of *Molinia* and *Juncus* spp. (Simmons 2003). There have been no studies to date that have quantified the contribution and energetic importance of these types of allochthonous litter to moorland streams, however (Cariss and Dobson 1997). Moorland streams are considered to be more reliant on autochthonous production (Huryn *et al.* 2001), with invertebrate assemblages characterised by grazer species (Dobson and Cariss 1999). There is some evidence to suggest, however, that some grasses may provide an important food resource for shredders in open-canopy streams (Leberfinger *et al.* 2011), and can even limit autochthonous production where the degree of overhanging is sufficient (Menninger and Palmer 2007). Therefore, grass litter could provide an important subsidy to streams at least when in-stream primary productivity is limited (Huryn *et al.* 2001), though more research is needed.

While direct inputs can account for the majority of total inputs (Fisher and Likens 1973), lateral inputs (i.e. litter entering the stream from the catchment slopes via gravity, blow-in and water run-off) can contribute relatively significant amounts, with values reaching as much as a third of total inputs (Webster *et al.* 1999; Abelho 2001) and even exceeding direct inputs in some cases (Kochi *et al.* 2010). The relative proportions of direct and laterally transported litter entering streams may significantly influence in-stream community dynamics as a consequence of input quality and timing (Cummins *et al.* 1989). Laterally transported litter may be qualitatively important to consumers because of its higher nitrogen concentration than that of litter falling directly into the stream (Benson and Pearson 1993). In addition, lateral inputs may provide an important longer term replenishment of resources that may have been exported or consumed following autumn-winter pulses and high flows (Hart *et al.* 2013; Riedl *et al.* 2013).

The amount and relative contribution of direct and lateral inputs of litter depends on slope, distance from the shoreline, composition of riparian vegetation, and climate (Hart *et al.* 2013). Lateral contributions tend to increase with steeper slopes (Orndorff and Lang 1981; Selva *et al.* 2007; Leroux and Loreau 2008; Hart *et al.* 2013), but decrease with increasing distance from the shoreline (Gasith and Hosier 1976). Other factors such as the density and composition of ground vegetation can influence the rate of lateral movement. For example, Scarsbrook *et al.* (2001) suggested that ground vegetation such as tussock grass can act as barriers that reduce lateral inputs of litter. Hart *et al.* (2013) found that slope and the composition of the overstory vegetation was more important in regulating lateral transport than the density of understory vegetation, however, with the effect of slope being more pronounced in deciduous sites than conifer. Laterally transported litter in surface runoff may only occur in significant amounts during high storm events (Maridet *et al.* 1995) and these effects may increase with cumulative events (Naiman and Décamps 1997). Data on how proportions and contributions of direct and lateral inputs change through time are, however, scarce (but see Hart *et al.* 2013).

1.1.2 Retention, storage and processing

The retention and subsequent breakdown of litter inputs is an important process in stream ecosystems both in terms of energy flow and nutrient cycling (Giller and Malmqvist 1998). Benthic storage of organic matter provides a critical energetic and habitat resource for stream organisms and ultimately drives their production (Wallace *et al.* 1997; Wallace *et al.* 1999). The processing and conversion of retained litter into finer particles also

increases its availability and nutritional properties to different groups of organisms, both locally and further downstream (Giller and Malmqvist 1998). The relative amounts, quality and long-term storage of litter within a channel depend primarily on the retention capacity and hydrology of the stream, but also on the characteristics of the litter itself (Cordova *et al.* 2008; Hoover *et al.* 2010).

In low-order streams, the abundance of channel obstructions such as boulders and large wood can provide effective retention structures that enhance long-term storage of benthic litter and shredder biomass. For example, there have been multiple demonstrations of the important structural role of wood in retaining litter in such streams (e.g. Speaker *et al.* 1984; Dobson and Hildrew 1992; Wallace *et al.* 1995; Eggert *et al.* 2012). Current forest practices reduce inputs of wood to streams and hence their ability to retain litter because trees are felled before significant amounts of wood can enter (Dobson and Hildrew 1992; Wallace *et al.* 1995). As a result, shredder biomass has shown to be reduced in these streams (Dobson and Hildrew 1992; Eggert *et al.* 2012). Open grassland or moorland streams have a lower storage potential than forested streams because wood is generally sparse or absent (Cariss and Dobson 1997; Huryn *et al.* 2001). Litter retention also depends on the characteristics of the litter itself. For example, larger particles are more easily retained than smaller, more flexible types (e.g. Pretty and Dobson 2004a; Quinn *et al.* 2007). Very few studies have investigated factors affecting the retention of grass litter (but see Cariss and Dobson 1997), though Scarsbrook and Townsend (1994) suggested that tussock grass litter plays more of a role in stabilising the stream bed as opposed to providing refuge or food for invertebrates.

Litter retained in streams is gradually broken down into finer particles through a combination of physical and biological processes (Cummins 1974). The rate at which different types of litter are broken down largely depends on the interactions between the intrinsic chemical and physical properties of litter, the organisms involved in its decomposition, and environmental factors such as temperature, pH, nutrient concentrations and hydrology (Webster and Benfield 1986). Aquatic microbes, particularly hyphomycete fungi, play a pivotal role in the process of litter breakdown and mediate energy transfer to higher trophic levels (Suberkropp and Klug 1980). These microbes directly decompose leaf litter by converting it into their own biomass and releasing FPOM (Suberkropp and Klug 1980). Microbial activity also 'conditions' leaf litter, making it more nutritious (lower C:N ratio; Suberkropp *et al.* 1976), and more

palatable and readily assimilated by shredders (Benke *et al.* 1988). While most of the energy requirements of shredders come from leaf litter itself, extracellular enzymes from microbes may retain activity in the animal gut and enhance digestion (Benke *et al.* 1988). However, the poor quality of leaf litter means that shredders must process relatively large quantities to support their growth (Giller and Malmqvist 1998). Hence, the feeding activity of shredders, together with microbes, can be an important source of FPOM by increasing the rate of conversion of coarse material into smaller particles that are more easily entrained and transported downstream (Cuffney *et al.* 1990; Cushing *et al.* 1993).

The chemical properties of leaf litter influence the rate at which it is broken down. Leaves with high initial nitrogen and low lignin content, are broken down more rapidly than those with low nitrogen (Kaushik and Hynes 1971). For example, “slow” species such as oak leaves and conifer needles with high C:N ratios and lignin content have relatively slow breakdown rates, while “fast” species with a lower C:N ratio such as alder are processed relatively quickly (Petersen and Cummins 1974; Webster and Benfield 1986). Variation in the elemental composition of riparian organic matter inputs therefore may have important implications for stream functioning. However, other factors influence breakdown rates: low pH reduces litter processing rates (e.g. Dangles *et al.* 2004) by inhibiting microbial conditioning of leaf-litter, which reduces food quality and availability to shredder invertebrates (Larrañaga *et al.* 2010). Stream hydrology also affects breakdown by increasing physical fragmentation and downstream transport (Dewson *et al.* 2007; Cordova *et al.* 2008).

1.1.3 Export

Export of organic materials from upland streams represents the downstream flux of energy and matter that supports food webs in larger rivers (Vannote *et al.* 1980; Wipfli *et al.* 2007). Export also occurs in the form of emerging adult aquatic invertebrates, which support higher level organisms in adjacent terrestrial ecosystems (Nakano and Murakami 2001). Particulate organic matter export is determined by the interaction of availability, hydrologic variability, and retention mechanisms (Newbold *et al.* 2005). Finer particles are more easily entrained and transported downstream, and are more closely related to hydrology (Webster *et al.* 1987; Thomas *et al.* 2001).

On an annual basis, the major fraction of particulate material in transport is FPOM (Webster and Meyer 1997), however, the total amount and composition of exports vary

through time. In forested streams, for example, high availability of material coupled with higher discharge in autumn-winter months means that there is a greater total export of material by comparison with those in summer months (Eggert *et al.* 2012). Exports in autumn-winter months are dominated by CPOM, whereas in summer, exported material are comprised more of FPOM after material has been processed and fragmented into smaller particles by organisms (Webster *et al.* 1990; D. C. Richardson *et al.* 2009).

A vast proportion of annual budgets are exported during high discharge (e.g. storm runoff) events (Golladay *et al.* 1987; Wallace *et al.* 1995; Johnson *et al.* 2006), with some studies reporting 97% of annual exports occurring during storms (Newbold *et al.* 1997). However, the amount that is exported during storm events depends on its availability in the channel and ultimately from terrestrial sources (Webster *et al.* 1987). For example, Heartsill-Scalley *et al.* (2012) found that following a large hurricane, subsequent storms did not have as large an effect on litter export, implying that resources had become depleted (see also Eggert *et al.*, 2012). Timing of high discharge events could therefore be important in regulating organic matter export from temperate forested streams, particularly if they coincide with periods of peak litter inputs (Molinero and Pozo 2004; Sabater *et al.* 2008).

While CPOM typically makes up the majority of litter inputs, it generally represents only a small fraction (<4%) of total export (Wallace *et al.* 1995; Shibata *et al.* 2001; Johnson *et al.* 2006; Heartsill-Scalley *et al.* 2012; Eggert *et al.* 2012), with FPOM making up the largest proportion of export from streams (Webster and Meyer 1997; Colón-Gaud *et al.* 2008; Eggert *et al.* 2012). These differences have been attributed to the feeding activity of shredder invertebrates, which increase the rate of conversion of coarse benthic material into smaller particles (Cuffney *et al.* 1990; Cushing *et al.* 1993). Although filter feeder invertebrates can play an important role in removing FPOM from the water column (Voshell and Parker 1985), filter feeding activity is unlikely to regulate FPOM exports to downstream systems to the same extent as stream discharge, depth and POM concentration (Monaghan *et al.* 2001).

Riparian land use affects export from streams, by regulating the availability of benthic material and retention structures such as wood in streams, which increases benthic storage and reduces export in the long-term (Webster *et al.* 1990; Eggert *et al.* 2012). This could have important implications for productivity both locally and further downstream. For example, Wipfli & Musslewhite (2004) suggested that stream and riparian productivity

was higher with increasing alder density resulting in greater total exports of materials downstream. There are very few reports on export from open moorland streams, but those reported by Cariss & Dobson (1997) were very low by comparison with wooded sites, attributed to low input levels as opposed to low retention. In terms of quality, Young & Huryn (1997) reported that the quality of exports in grassland streams may be higher due to higher contributions of algae relative to terrestrial contributions by comparison with forested sites.

1.2 Effects of land use and climate

1.2.1 Land use

The UK uplands have a long history of land use change; during the mid-Holocene large areas of woodland were cleared by humans to create pasture (Simmons 2003; Holden *et al.* 2007). Years of traditional low-intensity agricultural practices have led to the development of the distinctive open moorland landscape that currently dominates the UK uplands (Holden *et al.* 2007). Large areas of the upland landscape are considered to be of high nature conservation value and are protected under national and/or international conservation designations (e.g. Sites of Special Scientific Interest (SSSIs), EU Habitats and Birds Directives; Burt *et al.* 2002). Changes in the way the UK uplands were managed over the 20th century, largely in response to socio-economic drivers, however, have led to widespread loss of habitat and degradation of the uplands (Haines-Young *et al.* 2003; Holden *et al.* 2007). These land-use changes include the intensification of sheep production and afforestation with coniferous plantations (Simmons 2003; Reed *et al.* 2009).

Agricultural intensification in the UK was largely ignited after the Second World War, when concerns for food security led to the introduction of government subsidies that encouraged farmers to increase the productivity of the uplands (Reed *et al.* 2009). This involved liming and fertiliser addition, land drainage, ploughing, conversion of native vegetation to provide improved pasture, and overgrazing (Simmons 2003). Sheep densities increased by up to 400% in some upland areas (Holden *et al.* 2007). This led to the degradation of upland soils in many parts of the UK due to changes in the chemical and physical conditions of the soils (Reed *et al.* 2009). As a result, there has been a general trend from more productive vegetation with high species diversity to large areas

dominated by less diverse and more aggressive species of lower agricultural value such as *Molinia* and *Nardus* spp. (Holden *et al.* 2007). Today, the reformed EU Common Agricultural Policy (CAP) decouples payments from production, and in response, sheep stocking numbers are declining rapidly across many parts of the UK uplands (Reed *et al.* 2009).

Widespread afforestation of open moorlands with coniferous plantations, mostly following the Second World War, to reduce reliance on imports, has also changed the face of uplands (Simmons 2003; Reed *et al.* 2009). Coniferous plantations alter the hydrology, water chemistry and temperature regime of upland streams (Ormerod *et al.* 1989; Weatherley and Ormerod 1990). As a result, many upland streams in the UK and elsewhere have suffered reductions in diversity and productivity (Ormerod *et al.* 1993; Friberg *et al.* 1997; Friberg 1997). In undisturbed open moorland streams, autochthonous production provides the primary energetic base for food webs (Huryn *et al.* 2001), whereas allochthonous inputs of litter are low (Cariss and Dobson 1997). However, conversion to conifer plantations reduces light intensity in these streams through heavy, permanent shading, which limits primary production (Friberg *et al.* 1997) and subsequently reduces the number of grazing invertebrates (Dobson and Cariss 1999). Conifer plantations also alter the quality and availability of litter in streams (Hoover *et al.* 2011). Conifer needles are of poor nutritional quality to stream organisms (Webster and Benfield 1986), though they may become more palatable to invertebrate consumers if they are retained on the stream bed for long enough to allow significant microbial conditioning (Pretty and Dobson 2004b). However, conifer needles are not easily retained because they are relatively small and inflexible (Pretty and Dobson 2004a; Cordova *et al.* 2008). Furthermore, intensive forestry practices reduce the retentiveness of conifer streams because trees are harvested before significant amounts of large wood can enter and provide effective retention structures (Dobson and Cariss 1999).

1.2.2 Climate change

The global hydrological cycle is expected to intensify in a warmer climate (Huntington 2006), resulting in a greater frequency and magnitude of extreme precipitation events and overall increases in variability (Bates *et al.* 2008). While regional effects are still uncertain, headwaters at higher latitudes and altitudes are already showing trends towards increasing discharge in winter (e.g. Birsan *et al.* 2005; Dixon *et al.* 2006; Hannaford and Buys 2012), shifts towards earlier spring snowmelt (Kormann *et al.* 2015), and faster rates

of warming (Hassan *et al.* 2005). Given the importance of hydrological and thermal regimes in regulating and energetic processes in streams, climate-driven changes are expected to have a strong effect on the structure and functioning of stream ecosystems through a combination of direct effects on the survival of sensitive species and indirect effects on basal resources. For example, a +1°C change to some Welsh upland streams could reduce spring abundances of stream invertebrates by as much as 21% (Durance and Ormerod 2007). These changes could reduce the capacity of consumers to process and utilise these resources to support their production (Friberg *et al.* 2009; Ferreira *et al.* 2010). However, understanding climate-driven changes in freshwaters is particularly complex because ecological processes are affected by local meteorological, hydrological and nutrient regimes, as well as indirect terrestrial impacts (Ball *et al.* 2010).

Warmer temperatures may alter the phenology of terrestrial plants, with predicted earlier leaf growth in spring (Schwartz *et al.* 2006) and delayed leaf abscission in autumn (Menzel *et al.* 2006). This would alter the timing of litter inputs to streams, which could in turn reduce the production of organisms whose life-histories reflect the temporal availability of resources (Cummins 1974). Increases in temperatures may stimulate microbial activity (Bärlocher *et al.* 2008) but inhibit invertebrate feeding (Friberg *et al.* 2009), resulting in increased microbial rather than invertebrate processing of litter (Kominoski and Rosemond 2012). Meanwhile, changes and increased variability in precipitation patterns and associated hydrology could also alter the availability and processing of organic matter in streams. Reduced flows in summer could reduce both physical and biological breakdown (Kominoski and Rosemond 2012) and promote the accumulation of benthic litter (Sabater *et al.* 2008). In contrast, greater frequencies and magnitude of high flow events in winter could reduce the availability of resources by accelerating physical breakdown and downstream transport of organic matter (Heartsill-Scalley *et al.* 2012; Eggert *et al.* 2012).

1.3 Knowledge gaps

Overall, the effects of expected changes in climate and land use indicate a greater temporal and spatial variability in the quantity and quality of food resources available to support the food web productivity in stream ecosystems. Questions remain, however, as to what effect these changes will have on the overall functioning and resilience of upland

streams under changing land-use and climate: What is the capacity of different consumers to adapt to shifts in the quantity, quality and timing of resources? How does riparian land-use and management serve to mitigate or exacerbate some of the negative effects of climate change on energetic processes in streams? For example, the effects of changes in hydrological and thermal regimes on stream organisms and processes could be exacerbated in intensively managed plantation streams, where productivity is already limited by the low retention and poor quality of litter (Dobson and Cariss 1999). In contrast, while forested riparian zones may reduce flood peaks to some degree (Bradshaw *et al.* 2007), the effects of hydrological extremes on energy flows could be mitigated in mixed broadleaved streams, by increasing the quantity, quality and diversity of litter, and enhanced retention in the long-term (Entekin *et al.* 2009; Eggert *et al.* 2012). Answering such questions on the effects of global changes on ecosystem structure and functioning, as well as the likely outcomes of management interventions to mitigate such effects, will require an improved understanding of the changes that are likely to occur at the base of the food web.

Organic matter dynamics have been a major focus in freshwater ecology for many decades (Tank *et al.* 2010). Yet, recent attempts to model them in relation to future climate or riparian management scenarios are still limited by gaps in empirical evidence and process-based understanding (e.g. J. S. Richardson *et al.* 2009; Acuña and Tockner 2010; Stenroth *et al.* 2014). Many factors interact to affect the input, storage and transport of organic matter in stream ecosystems (Sections 1.1 and 1.2). To date, most field-based studies on organic matter dynamics have, however, been limited to short temporal scales (~1 year, e.g. Abelho and Graça 1996; González and Pozo 1996; Cariss and Dobson 1997; Pozo *et al.* 1997), or small spatial scales (~ 1 study site e.g. Molinero and Pozo 2004; Mollá *et al.* 2006; Wallace *et al.* 2015). Long-term, field-based studies conducted over larger spatial scales are therefore needed to allow for stronger inference and inform land management decisions. Manipulative field experiments are also needed to identify causal relationships and gain mechanistic understanding of the impacts of land use and climatic changes on organic matter dynamics. For example, investigations on the effects of altered flow regimes on organic matter dynamics often focus on average changes (e.g. Dewson *et al.* 2007), highlighting the need for more studies on the effects extreme hydrological events (Dunne *et al.* 2004; Ledger *et al.* 2011; Stewart *et al.* 2013).

1.4 Conclusions

Headwater stream ecosystems are closely connected with their surroundings through a range of processes, making them highly sensitive to changes in catchment land use and climate. Managing these ecosystems to safeguard the many services they provide is key. While there are growing demands for increased tree cover in upland catchments and in riparian zones, for example to buffer against thermal and hydrological extremes, the potential for such management interventions to increase stream ecosystem resilience to future changes by enhancing the availability of basal resources, and ultimately food web stability and productivity is less well understood. Understanding what drives these processes is therefore crucial to enable informed management decisions in the face of global change.

CHAPTER 2: Interactive effects of riparian land cover and climate variability on detrital resource availability in headwater streams

2.0 Summary

1. Headwater streams are disproportionately vulnerable to the effects of global climate and land use change through altered fluxes of water, heat and organic matter. Changes in stream flow and thermal regimes are already occurring worldwide, and are likely to alter the availability of important detrital resources, which could have important consequences for the structure, functioning and stability of these ecosystems, the effects of which could extend far beyond their boundaries. The potential for riparian land cover to modify the effects of climate change on detrital resources in streams, however, is poorly understood.
2. This study assessed the effects of stream flow and thermal regime on the standing stocks of two important sources of detritus contrasting in structural complexity and lability – coarse and fine benthic particulate organic matter (CPOM and FPOM, respectively) – over four years in streams differing in riparian land cover types in central Wales, UK. Specifically, this study tested whether variations in CPOM and FPOM standing stocks were driven by certain aspects of the flow regime (i.e. magnitude, frequency, timing, duration, variability), and whether these effects varied among riparian land cover types.
3. The four-year study period captured significant seasonal and interannual variability in stream flow and temperature, including the wettest summer, the wettest winter, and the warmest autumn in Wales over the last 100 years. Standing stocks of CPOM and FPOM were linked with certain aspects of the flow regime, showing significant reductions with increased magnitude and duration of high flow events, with effects on FPOM being more pronounced overall. Despite these effects, POM availability remained consistently higher in streams with broadleaved riparian land cover than those with either coniferous or open-canopy moorland cover.
4. This study indicates that benthic POM, an important basal food resource in headwater streams, could be sensitive to future intensification of the hydrological cycle predicted under a warmer climate. Subsequent reductions in the abundance

and heterogeneity of detrital resources could have important indirect ecological effects, for example by disrupting energy fluxes to higher trophic levels and reducing ecosystem stability. Riparian broadleaves, however, could play an important role in supporting ecosystem stability by maintaining a greater abundance of detrital resources than both conifer plantation and open-canopy moorland streams, even if regional rainfall exceeds the upper limits of future climate projections.

2.1 Introduction

Climate change poses one of the biggest threats to global biodiversity and ecosystem functioning (IPCC 2014). Among the world's ecosystems, freshwaters are arguably the most vulnerable (Ormerod 2009), with many freshwater organisms being directly linked to thermal and hydrological regimes, having limited dispersal, and often subjected to additional stressors that exacerbate climatic effects (Woodward *et al.* 2010).

Headwater stream ecosystems (1st to 2nd order streams) are particularly sensitive to climate change due to their high surface to volume ratio and subsequent rapid response to atmospheric temperature and precipitation (Gomi *et al.* 2002; Caissie 2006). Headwaters at higher latitudes and altitudes are already showing trends towards increasing discharge in winter (Birsan *et al.* 2005; Dixon *et al.* 2006; Hannaford and Marsh 2006; Marsh and Dixon 2012), shifts towards earlier spring snowmelt (Kormann *et al.* 2015), and faster rates of warming (Hassan *et al.* 2005). Evidence of concomitant biological responses in headwaters is also emerging (Durance and Ormerod 2007), however the exact causes are rarely identified (Cahill *et al.* 2012) and are likely to arise from a complex set of mechanisms that include not only the direct physiological effects on individual taxa, but also indirect effects on organisms, processes and functions (e.g. Durance and Ormerod 2010). Given the value of headwater streams as biodiversity hotspots (Meyer *et al.* 2007; Finn *et al.* 2011), their wide-reaching effects in terms of water and organic matter supply to adjacent and downstream ecosystems (Wipfli *et al.* 2007; Battin *et al.* 2008), and their value as 'sentinel systems' (Perkins *et al.* 2010), the need to understand how they could respond to current and future climate change is acute.

One of the mechanisms by which climate change could affect ecosystem functioning in headwaters is by altering the availability of basal food resources, for example by

indirectly altering the amount and composition of food resources that are retained and subsequently made available for biological uptake (Verdonschot and van den Hoorn 2010; Kominoski and Rosemond 2012), or by causing phenological mismatches between consumers and resources (Durant *et al.* 2007). Like many ecosystems (Polis *et al.* 1997), headwaters are fuelled by inputs of resources from outside their boundaries, as well as by *in situ* primary production. In headwaters, these ‘resource subsidies’ are largely composed of terrestrial detritus, namely leaf litter from riparian vegetation, and there is increasing evidence that its availability could be sensitive to climate-induced changes in stream flow and thermal regimes. For example, expected warmer temperatures could affect basal resources by altering the seasonality and timing of leaf fall (Duputié *et al.* 2015; Sanpera-Calbet *et al.* 2016) and accelerating biological processing rates (Graça *et al.* 2015). Furthermore, a number of studies have shown that leaf litter retention decreases with increasing discharge (Speaker *et al.* 1984; Webster *et al.* 1987; Pretty and Dobson 2004a; Koljonen *et al.* 2012) and that the majority of annual export occurs during storm events (Webster *et al.* 1987; Johnson *et al.* 2006; D. C. Richardson *et al.* 2009; Eggert *et al.* 2012). These effects, coupled with expected increases in litter breakdown under warmer temperatures (Graça *et al.* 2015), suggest that these resources may become depleted with projected intensification of the hydrological cycle (Acuña and Tockner 2010; Heartsill-Scalley *et al.* 2012).

Changes in resource availability are likely to have important consequences for energy fluxes in stream ecosystems. In many ecosystems, the abundance, composition and timing of basal resources are an important driver of food web structure, productivity and dynamics (Polis *et al.* 1997). In particular, detritus is considered to play an important role in providing a heterogeneous resource and habitat for a diverse set of organisms (Moore *et al.* 2004), often increasing food chain length and ecosystem stability and persistence (Rooney *et al.* 2006). There is a wealth of evidence that demonstrates the importance of detritus in subsidising recipient food webs in forested headwater streams (e.g. Fisher and Likens 1973; Benke *et al.* 1984; Wallace *et al.* 1999; Wallace *et al.* 2015), and increasingly so in open-canopy streams, where detrital inputs are comparatively low (e.g. Menninger and Palmer 2007; Leberfinger *et al.* 2011; Dekar *et al.* 2012). The significance of detritus in headwaters is even reflected in the diversity of traits among aquatic invertebrates in response to the different forms and seasonality of detritus, with some that ‘shred’ leaf litter and other structurally complex materials, while others ‘collect’ or ‘filter’

the smaller, more labile particles of organic matter (Cummins *et al.* 1989). With the aid of microbes, these organisms play a key role in transferring the energy and nutrients derived from detritus to higher trophic levels. Changes in the availability of this resource is thus likely to impact a wide range of organisms by disrupting fluxes of energy that extend far beyond headwater boundaries (Wipfli *et al.* 2007; Richardson *et al.* 2010; Scharnweber *et al.* 2014; Jonsson *et al.* 2015).

Predicted land use changes in response to altered climate patterns and growing populations are likely to interact with climate impacts on basal resources in headwater streams. Changes in land use are already altering detritus inputs to streams and rivers worldwide (Kominoski and Rosemond 2012). However, different types of riparian land cover (e.g. grassland, deciduous woodland, conifer plantations) are likely to interact differently with climate fluctuations (Kominoski and Rosemond 2012). For example, forested streams are known to buffer streams against thermal (Broadmeadow *et al.* 2011; Garner *et al.* 2015) and hydrological (Robinson *et al.* 1991; Bradshaw *et al.* 2007) extremes, increase detritus retention through the presence of wood (Cariss and Dobson 1997; Eggert *et al.* 2012), and supply greater quantities of detritus to streams by comparison with open-canopy, grassland streams (Benfield 1997). The effects of flow and temperature can also depend on other factors that vary with riparian land cover type such as the type of detrital material (Hoover *et al.* 2010) and the leaf fall phenology of riparian vegetation relative to the timing of high flows (Abelho and Graça 1996; Molinero and Pozo 2004). Investigating the role of riparian land cover in regulating detritus availability in streams would improve our understanding not only of the mechanisms that underpin ecological responses to global climate and land use change, but also the potential role of riparian management in mitigating these effects (Thomas *et al.* 2016).

Aims & Hypotheses

This study tested whether riparian land cover could modify the effects of stream flow and thermal variability on the availability of benthic particulate organic matter (POM), an important detrital resource in headwater streams. To this end, monthly variations in benthic standing stocks of coarse and fine particulate organic matter (CPOM and FPOM, hereafter) were measured over four years in four pairs of headwater streams with contrasting riparian land cover types in central Wales, UK. Specifically, the following predictions were tested:

- (1) CPOM and FPOM standing stocks would be reduced with increased magnitude, duration and frequency of high flows;
- (2) the relationship between POM standing stocks and stream flow regime would vary with particle size (coarse, fine) and among riparian land cover types;
- (3) despite the interaction between flow regime and riparian land cover type, CPOM and FPOM standing stocks would be consistently greater in streams with broadleaved woodland cover by comparison with streams with conifer and moorland cover

2.2 Methods

2.2.1 Study sites

The study was conducted in eight 2nd to 3rd order streams, located in the headwaters of the Afon Tywi, within the Llyn Brianne Stream Observatory in central Wales, UK (52°8'N 3°45'W; Figure 2.1; see Durance & Ormerod (2007) for full site details). Regional climate is maritime and temperate, mean daily stream temperatures are between

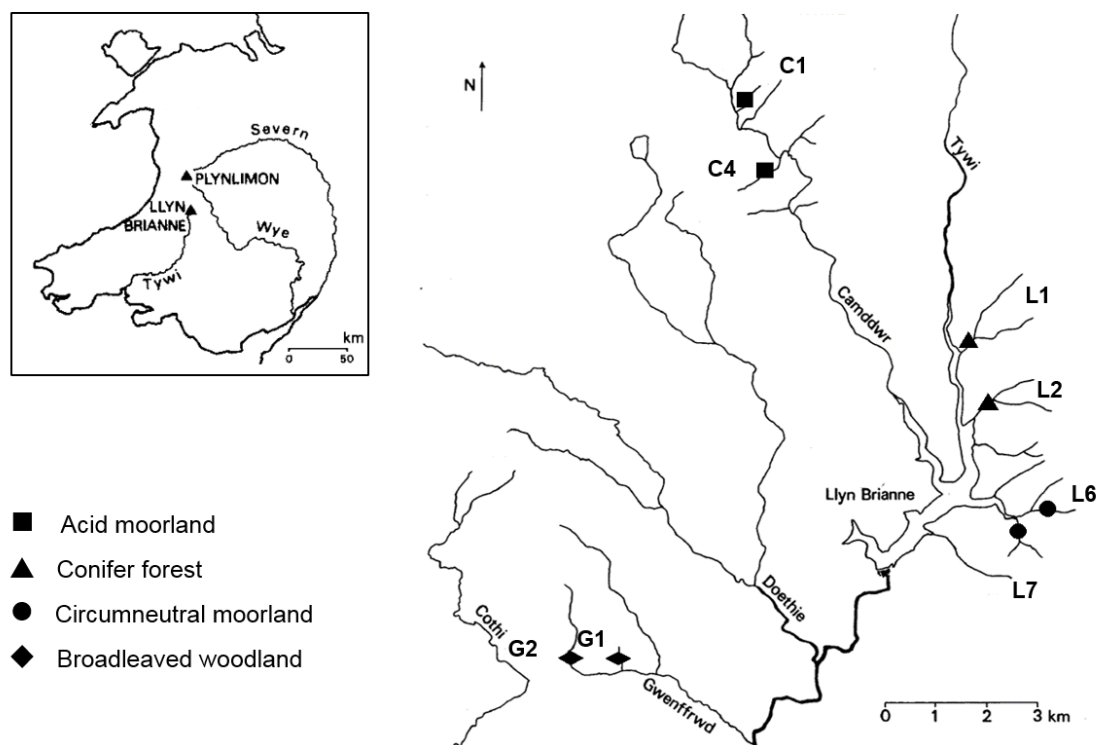


Figure 2.1. Map showing the locations of the eight streams surveyed as part of this study within the Llyn Brianne Stream Observatory in central Wales, UK. Major river systems are labelled. Images adapted from Edwards *et al.* (1990) and Broadmeadow and Nisbet (2002).

0-16°C and annual mean rainfall is approximately 1900 mm (Weatherley and Ormerod 1990). The sites were chosen to encompass the natural gradients in land cover that occur across upland catchments in the UK, and were categorised into four pairs according to riparian land cover (defined here as the dominant vegetation within 10 m of the stream bank): Broadleaved woodland (Bl; site codes 'G1' and 'G2'), conifer plantation (Co; site codes 'L1' and 'L2'), acid moorland (AM; site codes 'C1' and 'C4') and circumneutral moorland (CM; site codes 'L6' and 'L7'). Although acid and circumneutral moorland streams were similar in wider catchment land cover, riparian land cover (and therefore litter input (Isabelle Durance, *unpublished data*) is distinct as a result of historical reductions in livestock rates at the circumneutral moorland sites giving rise to increased cover of bracken with occasional mountain ash, willow and hawthorn in the riparian zones of these catchments. All study sites were located within ~ 10 km of each other ensuring that climatic conditions were similar throughout the study.

2.2.2 *Stream flow and temperature conditions*

Stream discharge ($\text{m}^3 \text{s}^{-1}$) was recorded at 15-minute intervals at one of the study sites, L1, over the duration of the study between November 2010 and September 2014 (data supplied by Natural Resource Wales; Station number 060S0589W) and was assumed to reflect flow conditions for all sites and wider hydro-climatic conditions. These assumptions were supported by (i) long-term observations of stream flow at several nearby catchments in mid-Wales that show similarities in flow regimes, despite differences in land cover (Conlan *et al.* 2007; Marc and Robinson 2007) and (ii) comparisons between stream flow measured at L1 and regional rainfall data (Figures 2.3 and 2.4).

Stream temperature was recorded using Onset Hobo water temperature recorders (Pro v2) at 15-minute intervals at all the sites, between November 2010 and March 2014. Recorders were placed in the margins of the streams and encased in drainage bricks to protect them from direct sunlight while allowing water throughput. Hobo loggers have a stated accuracy of 0.2°C, and this was confirmed by testing the loggers at 0 °C and 30 °C before deployment in the field. Since this study is focused on trends and all sites were highly correlated (all $R^2 > 98.4\%$ for daily temperature measures) temperature records from L1 were retained as representative for all sites. Since stream temperature records were not available between March to September 2014, stream temperature data were derived from the relationship between daily water temperature at L1 and daily water

temperature at the nearby site L2 using the linear relationship derived from the three previous years ($L1 \text{ Temperature} = 0.911(L2 \text{ Temperature}) + 0.901$; $R^2 = 98.7\%$).

2.2.3 Benthic sampling and laboratory methods

Five replicate samples of benthic organic matter ($n=5$) were collected using a randomly positioned Hess sampler (area 0.707 m^2 ; mesh aperture $500\mu\text{m}$; sampling depth 10-15 cm) at all sites approximately every 4-8 weeks between November 2010 and September 2014 ($n=36$ sampling occasions). In the first year of the study, sampling was constrained to one site per riparian land cover type. However, from October 2011 onwards, site replication was increased to two sites per land cover type. Samples were preserved on-site in 70% industrial methylated spirit (IMS; Fisher Scientific, UK) and transported to the laboratory for processing. All macroinvertebrates were separated from the leaf litter and preserved in 70% IMS. Leaf litter was thoroughly rinsed under tap water to remove sediment and separated into fine ($>0.5\text{mm} <2\text{mm}$; FPOM) and coarse ($>2\text{mm}$; CPOM) size fractions using graduated sieves (Endecotts Ltd., UK). Both size fractions of leaf litter were air-dried at room temperature and weighed to the nearest 0.01 g . Ash-free dry mass (AFDM) of all samples was estimated by combusting a subset ($n=160$) of all samples ($n=1250$) at 550°C for 5 h in a muffle furnace, and applying site-specific conversion factors to the air-dried mass. CPOM and FPOM were expressed in g AFDM m^{-2} .

2.2.4 Statistical analysis

To determine how different aspects of the stream flow and temperature regime affected POM standing stocks (Hypothesis 1), linear-mixed effects modelling was used to test the individual effect of each of 15 candidate flow variables and two candidate temperature variables (Table 2.1) on CPOM and FPOM standing stocks (while controlling for the effect of riparian land cover) using likelihood ratio tests with maximum likelihood estimation (Zuur *et al.* 2009). All flow variables were derived from 15-min discharge data recorded at L1, and included variables that characterised the magnitude, variability, frequency and duration of flows over the 30 days prior to each sampling occasion (after Clausen and Biggs 2000 and Olden and Poff 2003). Mean discharge for 0, 3, 7 and 14 days prior to each sampling occasion were also included to investigate whether the timing of flow events were important in explaining variations in CPOM and FPOM. The two temperature variables were derived from partially modelled daily mean, minimum and

Table 2.1. Summary and definitions of the temperature and flow variables used to characterise the antecedent conditions for each sampling occasion. Each variable represents the 30-day antecedent temperature and flow conditions of each sampling occasion (excluding M_A0d, M_A3d, M_A7d and M_A14d, which represent the sampling day, 3-, 7-, and 14-day antecedent flow conditions of each sampling occasion, respectively). Flow categories and abbreviations after Clausen and Biggs (2000); abbreviations after Olden and Poff (2003).

Category	Variable (unit)	Abbreviation	Definition
Average flow magnitude	Mean discharge (m ³ s ⁻¹)	M _A Q50, M _A 0d, M _A -3, M _A -7, M _A -14, M _A -30	Median (Q50) discharge and mean discharge of the 3-/7-/14-/30-day antecedent flow record
Magnitude of low flows	Low flow discharge (m ³ s ⁻¹)	M _L Q95	Discharge equalled or exceeded in 95% (Q95) of the 30-day antecedent flow record
Magnitude of high flows	High flow discharge (m ³ s ⁻¹)	M _H Q5	Discharge equalled or exceeded in 5% (Q5) of the 30-day antecedent flow record
Intensity of high flows	Mean high peak flow (m ³ s ⁻¹)	I _H Q5, I _H Q10, I _H Q25	Mean discharge during high flows above an upper threshold (thresholds = long-term Q5, Q10, Q25)
Flow variability	Coefficient of variation (%)	M _A CV	Standard deviation of 30-day antecedent flow/mean 30-day antecedent flow
Frequency of high flows	High flood pulse count (integer)	F _H Q25	Number of occurrences during which the magnitude of flow remains above an upper threshold (threshold = long-term Q25)
Duration of high flows	High flow duration (days)	D _H Q5, D _H Q10, D _H Q25	Number of days during which the magnitude of flow remains above an upper threshold (thresholds = long-term Q5, Q10, Q25)
Average temperature magnitude	Mean temperature (°C)	M _A T	Mean stream water temperature of the 30-day antecedent temperature record
Temperature variability	Daily temperature amplitude (°C)	M _A TR	Mean daily stream water temperature range of the 30-day antecedent temperature record

maximum stream temperature for L1 (see Section 2.2.2), and included the magnitude of mean daily stream temperature and mean daily stream temperature amplitude (after Dang *et al.* 2009) over the 30 days prior to each sampling occasion.

To determine how riparian land cover affected POM standing stocks (Hypothesis 2), and whether the effects of stream flow and/or temperature on POM standing stocks depended on riparian land cover (Hypothesis 3), one of each of the candidate flow and temperature variables that explained the most variation in POM standing stocks were selected to include in a global model, which was then refined using a backwards selection procedure. First, the flow and temperature variables were selected based on the initial models (from Hypothesis 1) that gave the lowest Akaike Information Criterion (AIC). Second, the least parsimonious model (Fixed effects: Riparian land cover type (LC); Temperature (T); Flow (F); and all two- and three-way interactions) was fitted, then non-significant terms were sequentially removed following a backwards selection procedure, selecting the models with the lowest Akaike Information Criterion (AIC) in each case until only significant terms remained (Zuur *et al.* 2009). Each model also included ‘site’ within ‘sampling occasion’ as a nested random effect to account for the possible inter-correlation of repeated samples within sites and within sampling occasions. The final optimal models were then re-fitted using restricted maximum likelihood (REML) estimation and validated by visual inspection of the distribution of the standardised residuals versus the fitted values and versus each explanatory variable, and of the distribution of the random effects (Zuur *et al.* 2009). Where necessary, response and explanatory variables were log or log+1 transformed prior to analysis to homogenise variances. All mixed models were fitted using the *lme* function in the *nlme* package (Pinheiro *et al.* 2013) in R (R Development Core Team. 2016).

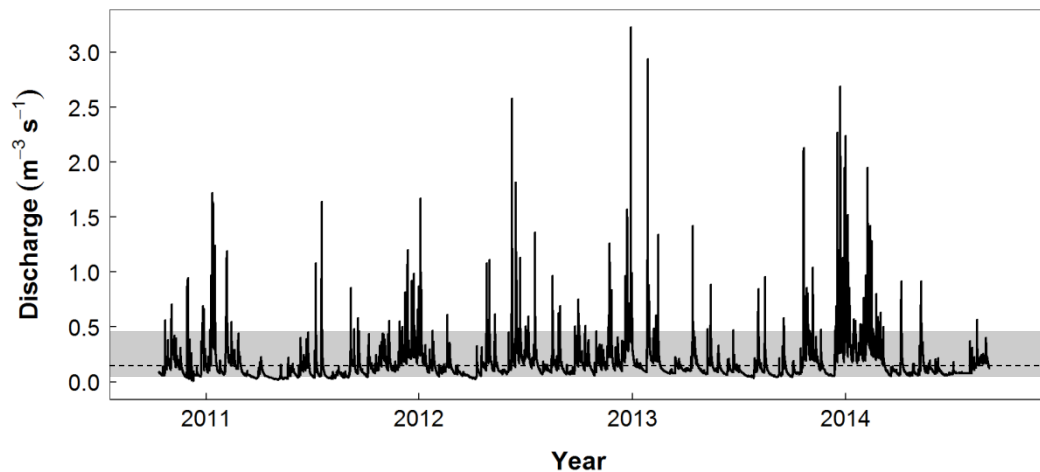
2.3 Results

2.3.1 Stream flow and temperature variation

Over the four-year study period, stream discharge at L1 ranged between 0.001 and 4.080 m³ s⁻¹ with an overall median of 0.120 m³ s⁻¹ (Figure 2.2a), while stream temperature ranged between 0 and 18.08 °C with a median of 8.31°C (Figure 2.2b). Seasonal anomalies in stream flow (Figure 2.3b) and temperature (Figure 2.3d) at L1 over the study period were similar to regional rainfall (Figure 2.3a) and air temperature (Figure 2.3c)

patterns, respectively, which in turn reflected historical inter-annual (Figures 2.3e, f) and seasonal (Figures 2.4a, b) variability. Years 1 and 3 were relatively cold and dry, while Years 2 and 4 were relatively warm and wet (Figures 2.3e, f). The two wet years notably included the warmest autumn (Year 2), the wettest summer (Year 2) and the wettest winter (Year 4) in Wales in the last 100 years (Figures 2.4a, b).

(a)



(b)

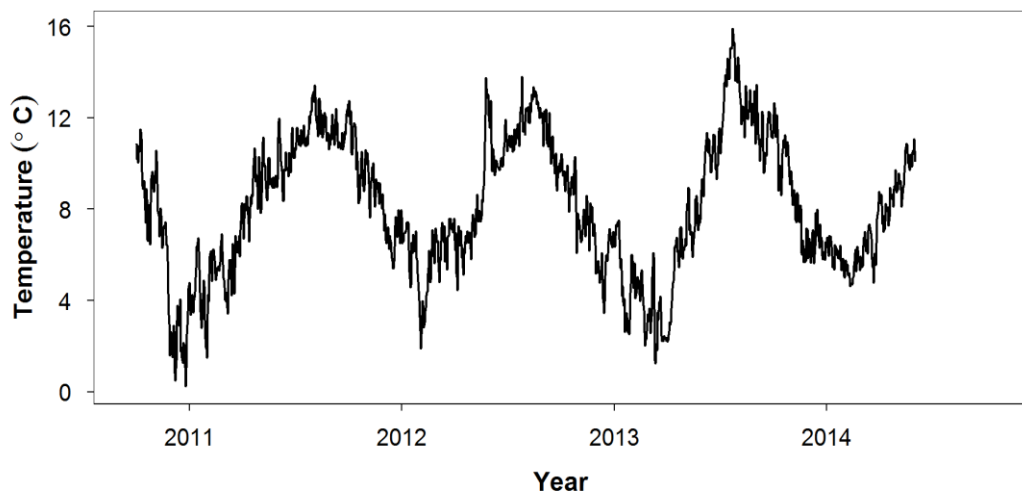


Figure 2.2. (a) 15-minute water discharge ($\text{m}^3 \text{s}^{-1}$) and (b) mean daily stream water temperature ($^{\circ}\text{C}$) recorded at study site L1 during the study period October 2010 to September 2014. Dashed line and shaded band, respectively, depict the overall mean and range of stream flows under which organic matter sampling took place. Discharge data provided by Natural Resources Wales (© Natural Resources Wales and database right). Temperature data provided by Isabelle Durance.

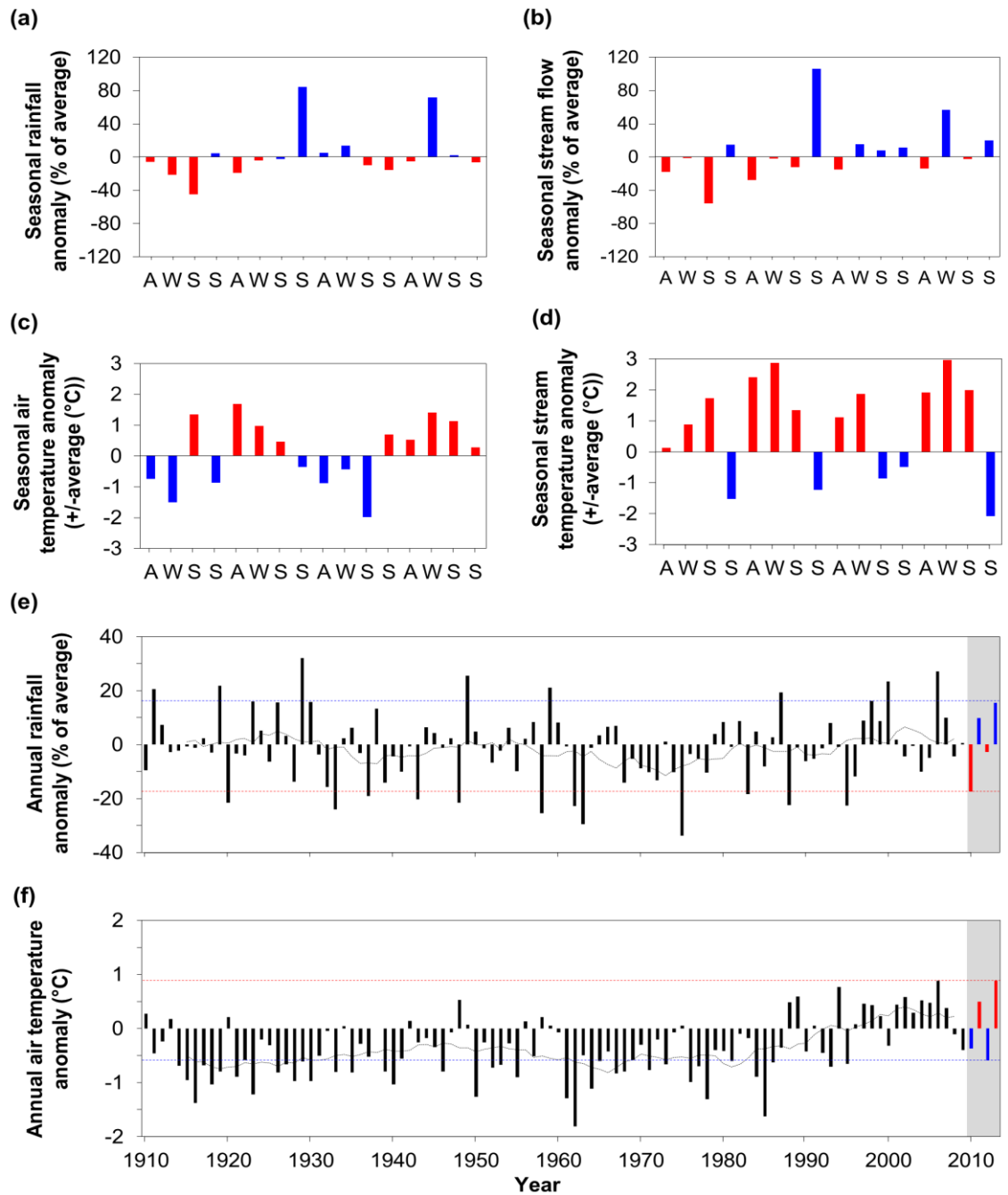


Figure 2.3. Climatic anomalies over the period 1910-2014 at the regional (Wales, UK) and local (study site L1, Llyn Brianne Stream Observatory, mid-Wales, UK) scale. Figures a-d show seasonal anomalies in (a) regional rainfall, (b) local stream flow, (c) regional air temperature and (d) local stream temperature, respectively, during the study period October 2010 to September 2014 (corresponding to the shaded areas in (e) and (f)). Seasonal anomalies represent differences in average seasonal temperature, rainfall or discharge from 1996-2010 averages. Seasonal averages are calculated using data over a 3-month period for Autumn (A; Sep-Oct-Nov), Winter (W; Dec-Jan-Feb), Spring (S; Mar-Apr-May) and Summer (S; Jun-Jul-Aug). Figures e-f show annual (=October-September) anomalies in regional (e) rainfall and (f) air temperature during 1910-2014. Blue and red dotted lines denote maximum and minimum values, respectively. Black dotted line denotes moving average (10-year). Regional rainfall and air temperature data provided by © UK Meteorological Office; L1 stream flow data provided by Natural Resources Wales; L1 stream temperature data provided by Isabelle Durance.

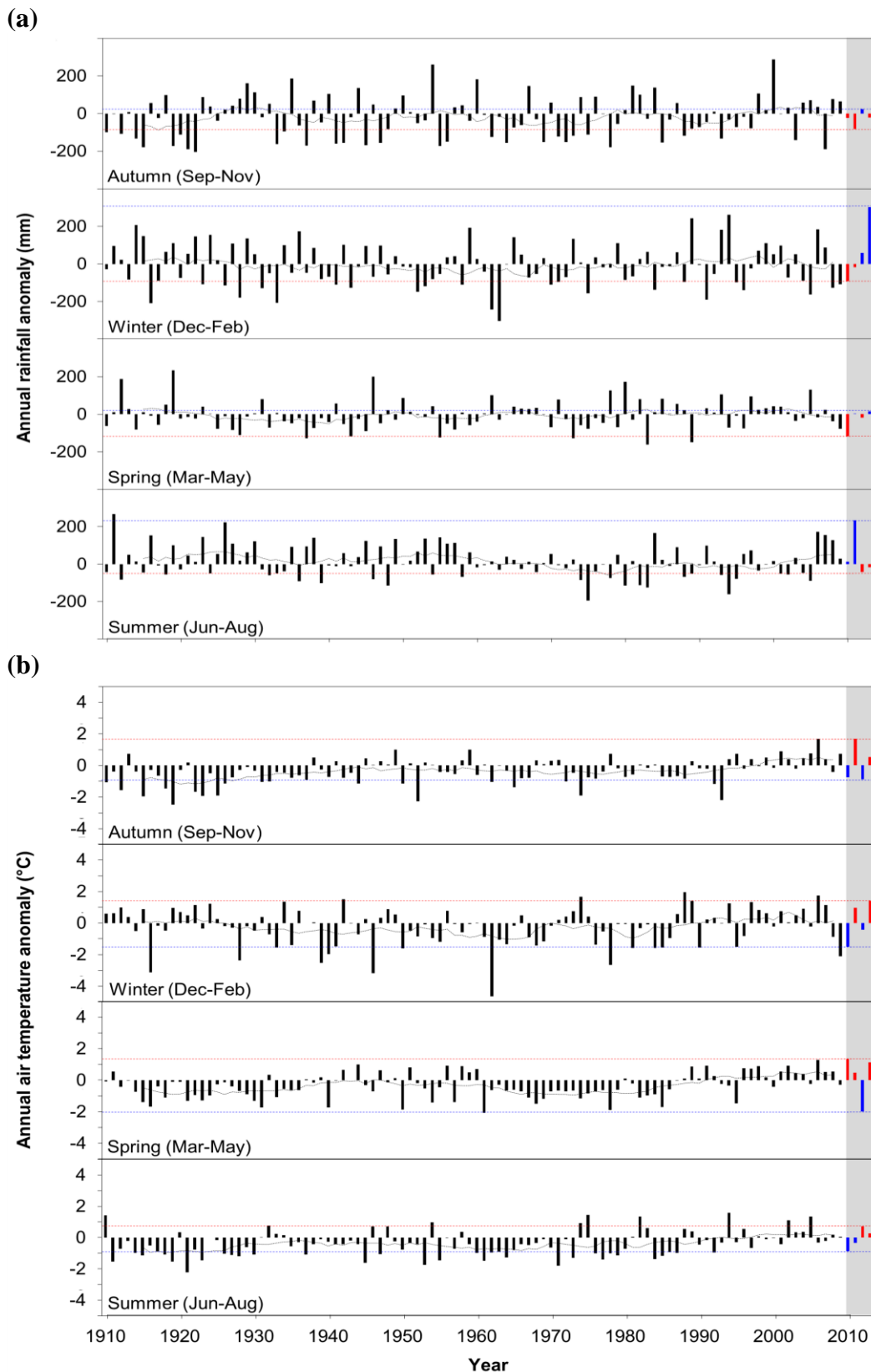


Figure 2.4. Seasonal anomalies in (a) rainfall and (b) air temperature in Wales (UK) over the period 1910-2014, highlighting maximum and minimum values (blue and red dotted lines, respectively) during the study period October 2010 to September 2014 (shaded area). Seasonal anomalies represent differences in average seasonal rainfall and temperature from 1981-2010 averages. © UK Meteorological Office.

2.3.2 Effects of flow and temperature regimes on CPOM and FPOM standing stocks

CPOM dominated the benthic POM pool in all sites throughout the study period, with values ranging between 0.02 and 428.10 g AFDM m⁻² (overall mean = 15.17 g AFDM m⁻²) while FPOM ranged between 0.04 and 49.89 g AFDM m⁻² (overall mean = 2.85 g AFDM m⁻²) (Figure 2.5). CPOM standing stocks were more variable both within and between sampling occasions by comparison with FPOM (Figure 2.5).

CPOM was significantly negatively associated with a number of the candidate flow variables, mostly those describing high flows (Table 2.2). Of the candidate flow variables considered, flow variability best explained variations in CPOM, as indicated by the steepest regression slope and the greatest reduction in model AIC values, with increased flow variability being significantly associated with reductions in CPOM. CPOM was also significantly reduced with increased flow maxima and with increased magnitude and duration of high flows. Variations in CPOM, however, were not significantly associated with the frequency of high flow events. CPOM was not significantly associated with magnitude of low or median flows, flow minima, or with mean discharge on the day of sampling. CPOM was weakly associated with mean discharge over longer (7-30 day) time scales, but was significantly associated with mean discharge over the 3 days prior to sampling. CPOM standing stocks were not significantly associated with the magnitude of mean daily temperatures or mean daily temperature amplitudes. Mean daily temperature did not significantly reduce model fit ($\Delta\text{AIC} < 2$), and was therefore used in subsequent analyses along with flow variability to test for possible interactions with riparian land cover.

FPOM was significantly negatively associated with most of the candidate flow variables that described high flows, with these effects being more pronounced overall by comparison with effects on CPOM, as indicated by the steeper regression slopes in all cases (Table 2.2). While CPOM was more closely associated with flow variability, variations in FPOM were best explained by the magnitude of high flows, with greater magnitudes of high flows being significantly associated with reductions in FPOM standing stocks. Similar effects were also observed with increased duration of high flows, flow maxima and with increased mean flows on the day of sampling and at longer (3- to 30-day) time scales. FPOM standing stocks were also reduced with increased flow variability and with increased magnitude of low and median flows, though these effects

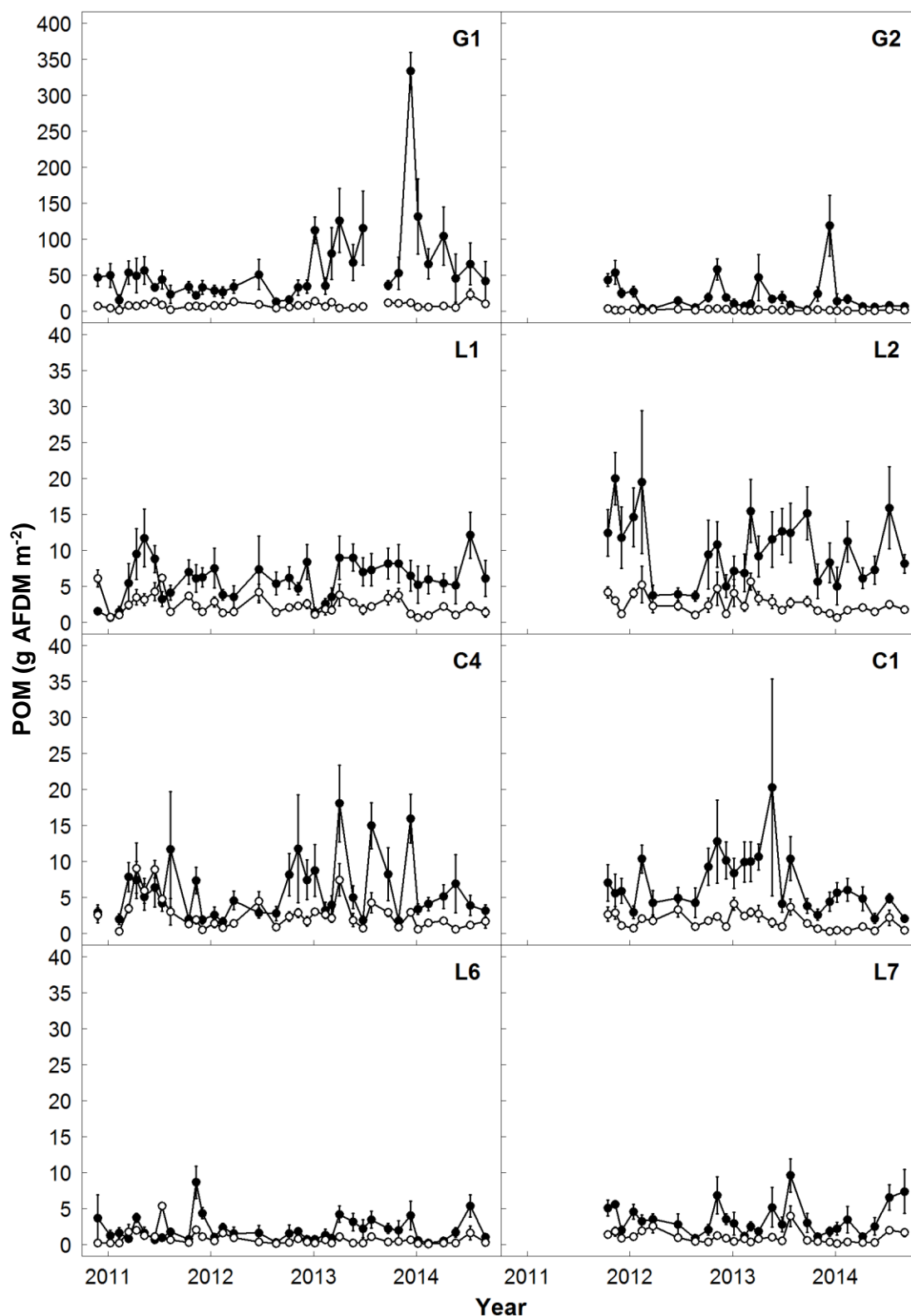


Figure 2.5. Temporal variation of benthic particulate organic matter (POM; expressed in grams ash-free dry mass $\text{m}^{-2} \pm 1$ S.E.) in the eight study sites during the study period (November 2010 to September 2014). Black circles = coarse benthic particulate organic matter (CPOM); open circles = fine benthic particulate organic matter (FPOM). Site codes and corresponding land cover types: G1 and G2 = broadleaved woodland; L1 and L2 = conifer plantation, C1 and C4 = acid moorland; L6 and L7 = circumneutral moorland. Note difference in axis-scale for broadleaf sites.

were weak. FPOM standing stocks were not significantly associated with the frequency of high flow events or with flow minima. FPOM standing stocks were not significantly associated with the magnitude of mean daily temperatures or mean daily temperature amplitudes. Mean daily temperature did not significantly reduce model fit ($\Delta AIC < 1$), and was used in subsequent analyses along with high flow magnitude to test for possible interactions with riparian land cover.

Table 2.2. Change in AIC values following addition of each candidate flow and temperature variable to the basic mixed effects model. Variables showing a significant relationship ($P < 0.05$) with POM standing stocks and resulting in a significant improvement of model fit ($\Delta AIC < -2$) are highlighted in bold.

Variable	CPOM					FPOM				
	<i>Slope</i>	<i>SE</i>	ΔAIC	<i>L</i>	<i>P</i>	<i>Slope</i>	<i>SE</i>	ΔAIC	<i>L</i>	<i>P</i>
M _A -0	-0.18	0.11	-0.3	2.35	0.1252	-0.36	0.14	-4.5	6.51	0.0107
M _A -3	-0.25	0.08	-6.0	8.02	0.0046	-0.28	0.11	-4.0	5.98	0.0145
M _A -7	-0.19	0.09	-2.2	4.22	0.0399	-0.30	0.11	-4.5	6.55	0.0105
M _A -14	-0.21	0.09	-2.5	4.49	0.0341	-0.34	0.11	-5.8	7.82	0.0052
M _A -30	-0.26	0.13	-2.1	4.08	0.0434	-0.47	0.15	-6.7	8.70	0.0032
M _H MAX	-0.25	0.07	-9.4	11.43	0.0007	-0.28	0.09	-6.2	8.22	0.0041
M _L MIN	0.10	0.10	1.0	0.96	0.3272	-0.01	0.12	2.0	0.02	0.8984
M _A Q50	-0.10	0.14	1.5	0.53	0.4662	-0.35	0.17	-2.2	4.21	0.0402
M _L Q95	-0.06	0.15	1.9	0.14	0.7126	-0.40	0.18	-2.5	4.52	0.0336
M _H Q5	-0.30	0.10	-6.8	8.79	0.0030	-0.41	0.12	-8.6	10.64	0.0011
F _H Q25	-0.13	0.12	0.8	1.18	0.2779	-0.16	0.16	1.0	1.01	0.3145
D _H Q25	-0.16	0.07	-2.7	4.66	0.0309	-0.23	0.09	-3.9	5.95	0.0147
D _H Q10	-0.20	0.07	-4.6	6.60	0.0102	-0.29	0.09	-7.0	9.02	0.0027
D _H Q5	-0.27	0.09	-6.2	8.21	0.0042	-0.39	0.11	-9.0	11.00	0.0009
M _A CV	-0.49	0.13	-10.4	12.38	0.0004	-0.38	0.18	-2.0	4.03	0.0447
T _{MEAN}	0.01	0.03	1.9	0.11	0.7395	0.04	0.03	0.5	1.52	0.2173
T _{RANGE}	0.04	0.14	1.9	0.07	0.7962	0.18	0.17	0.9	1.08	0.2982

2.3.3 Effects of riparian land cover on CPOM and FPOM standing stocks

The model selection procedure showed that variations in CPOM and FPOM standing stocks were mostly explained by differences in riparian land cover (Figures 2.6a and c, respectively) and flow regime (Figures 2.6b and d, respectively). Both CPOM and FPOM standing stocks were consistently greater in broadleaf sites, lower in circumneutral moorland sites, and intermediate in acid moorland and conifer sites. In concordance with

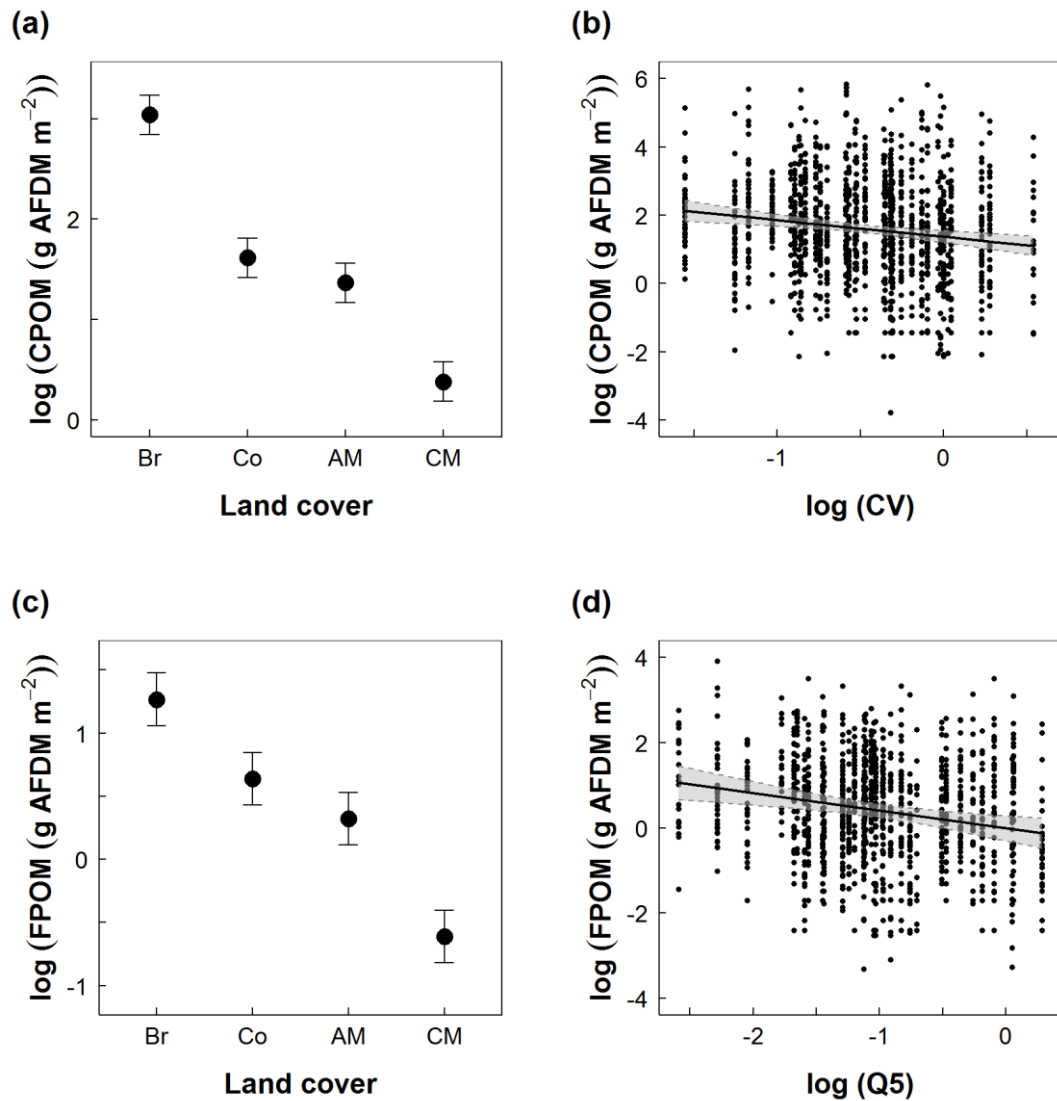


Figure 2.6. Estimated slopes and 95% confidence intervals for the optimal mixed effects models for log-transformed coarse (a, b) and fine (c, d) particulate organic matter (CPOM and FPOM, respectively) standing stock data versus riparian land cover and an explanatory flow variable (CV = monthly coefficient of variation of stream discharge at study site L1; Q5 = monthly stream discharge exceeded 5% of the time at study site L1).

the initial analyses (Table 2.2), CPOM and FPOM standing stocks were significantly reduced with increased flow variability and high flow magnitude, respectively. The effect of flow on CPOM and FPOM did not vary with riparian land cover type (CPOM: $L = 2.59$, $df = 3$, $p = 0.46$; FPOM: $L = 6.73$, $df = 3$, $p = 0.08$) or temperature (CPOM: $L = 0.55$, $df = 1$, $p = 0.46$; FPOM: $L = 2.73$, $df = 1$, $p = 0.10$). Temperature had no significant effect on CPOM ($L = 0.30$, $df = 1$, $p = 0.58$) or FPOM ($L = 0.28$, $df = 1$, $p = 0.60$), and this relationship did not vary with riparian land cover type (CPOM: $L = 7.92$, $df = 3$, $p = 0.05$; FPOM: $L = 0.98$, $df = 3$, $p = 0.80$).

2.4 Discussion

2.4.1 Summary

Over the four-year period of this study, stream flow and temperature were highly variable within and between years, reflecting long-term intra- and inter-annual variability. Both CPOM and FPOM standing stocks were negatively associated with a number of different aspects of the flow regime, mostly those describing the magnitude and duration of high flows, whereas the frequency of high flows had no significant effect on either CPOM or FPOM. FPOM, however, appeared to show stronger associations with most of the flow variables considered here by comparison with CPOM. Overall, CPOM was most strongly correlated with flow variability, whereas FPOM was most strongly correlated with high flow magnitude, with increases in these variables being associated with significant reductions in CPOM and FPOM standing stocks, respectively. Neither CPOM nor FPOM were significantly associated with stream temperature regimes. While the effects of flow and temperature on CPOM and FPOM were consistent across all riparian land cover types, streams with broadleaf riparian land cover supported consistently greater standing stocks of benthic POM than those with either moorland or coniferous riparian land cover.

2.4.2 Caveats

Before exploring the potential explanations for the results observed in this study, some caveats must be considered. The flow variables used to assess relationships with POM standing stocks were derived from stream discharge data from only one of the study sites, L1, which was used as a proxy for all sites since data were unavailable for the remaining sites. L1 land cover is dominantly composed of conifers (52%) of mixed aged stands and is the largest of the eight catchments used in this study. Differences in flow regime among

catchments mediated by land cover and catchment area and topography could exist, however, for example through differences in evapotranspiration and runoff rates. Existing long-term data from the nearby Plynlimon catchments (Robinson and Dupeyrat 2005; Marc and Robinson 2007) has shown that, while differences may exist in the flow regime between conifer forest and unforested moorland catchments, these differences are not consistent through time, and the contrasting effects that forestry practices of felling (increase) and re-growth (decrease) have on baseflow and peak flow make the overall effects of forestry on stream flow regimes difficult to predict (but see Chappell and Tych 2012). Nisbet (2005) suggested, however, that the current ‘patchwork management’ used on catchment conifer plantations means that differences may be minimal. Among wooded catchments, broadleaved catchments may be less variable than conifer catchments due to relatively higher evapotranspiration rates in broadleaves (Rust *et al.* 2014). This could partially explain why broadleaf catchments supported greater POM standing stocks than other land cover types, however it was not possible to test this directly.

2.4.3 Effects of stream flow and thermal regimes on CPOM and FPOM standing stocks

The data presented in this study show that stream discharge measured at the local scale reflected regional rainfall patterns over the four-year study period (Figure 2.3). To place the study in a historical climatic context, the four-year period reflected long-term intra- and inter-annual climatic variability and was characterised by two relatively warm and wet years, and two relatively cold and dry years (Figure 2.3). Notably, this study also captured the warmest autumn, the wettest summer and the wettest winter in the region in the last 100 years (Figure 2.4). Current climate change projections for the UK predict warmer, wetter winters, along with warmer, drier summers (Murphy *et al.* 2009). Specifically in Wales, by the 2080s, mean winter rainfall may change by -4% to +17%, while mean summer rainfall is estimated to change by -23% to +14% (Murphy *et al.* 2009). These projections are likely to translate into major changes in stream flow regimes, with increased winter discharges, reduced summer flows, increases in flood frequency and magnitude, and increases in overall variability (e.g. Arnell 2011; Prudhomme *et al.* 2012). During the course of this study, winter and summer rainfall exceeded even ‘worst-case’ projections in some cases. By encompassing a range of climatic conditions, it was possible to assess the implications of potential future climatic changes for POM availability in different types of headwater streams.

Numerous experimental field studies have shown that as stream discharge increases, POM transport increases (Webster *et al.* 1987; Thomas *et al.* 2001) and its retention on the stream bed decreases (Speaker *et al.* 1984; Webster *et al.* 1987; Pretty and Dobson 2004a; Koljonen *et al.* 2012) since particles are more likely to be kept in suspension at higher flow rates. The consequences for benthic stocks of POM over longer, annual timescales, however, have remained unclear. For example, Mollá *et al.* (2006) found a positive relationship between stream discharge and benthic POM standing stocks, likely because as discharge increases, so does the wetted perimeter and therefore the incorporation of leaf litter deposited on the stream banks or riparian zone increases. Meanwhile, some studies have found no strong relationship with stream flow at all (e.g. Wanner *et al.* 2002). This study found that both CPOM and FPOM standing stocks were significantly correlated with certain aspects of the antecedent (30-day) flow conditions. Specifically, CPOM and FPOM standing stocks were significantly reduced with increased magnitude and duration of high flows, with effects on FPOM being more pronounced by comparison with CPOM. Stronger effects on FPOM are likely due to smaller particles being more likely to be re-suspended and transported downstream than larger particles with increased flow rates (Speaker *et al.* 1984). Contrary to predictions, however, neither CPOM nor FPOM were significantly reduced with increased frequency of high flow events. In addition, increased temperature did not appear to reduce CPOM or FPOM stocks, as might be expected as a result of increased breakdown of POM at warmer temperatures (Graça *et al.* 2015) and subsequent increases in FPOM generation and transport. These results indicate that single, high intensity rainfall events, as well as persistent (multi-day) events, can deplete CPOM and, to an even greater extent, FPOM standing stocks in headwater streams. Meanwhile, the frequency of events alone does not appear to explain reductions in CPOM or FPOM standing stocks. Furthermore, the effects of higher flows appear to exceed any effects of temperature on POM dynamics in these streams (Acuña and Tockner 2010; Graça *et al.* 2015).

2.4.4 *Effects of riparian land cover*

The negative relationships that were observed between high flows and standing stocks of CPOM and FPOM were consistent across broadleaf, conifer, and both acid and circumneutral moorland streams. This result could be expected for fine particles of OM, since the physical size and structure of the particles are more similar across land cover types and would therefore be expected to have similar suspension/deposition dynamics in

response to changes in flow conditions. The consistent effects of flow on different types of CPOM, however, were unexpected for several reasons. Firstly, the overall quantity of leaf litter (i.e. CPOM) inputs is often higher in broadleaf streams by comparison with conifer or grassland streams (Isabelle Durance, *unpublished data*; Campbell *et al.* 1992; Delong and Brusven 1994). This suggests that more leaf litter would be available to replenish CPOM stocks following high flow events in broadleaved streams, and thus the effects of high flows on CPOM stocks in these streams would be comparably weaker. Secondly, previous studies have shown that the in-stream retention of these inputs depends on the structure of the leaf litter itself, with some types of leaf litter being more easily retained on the stream bed than others. For example, large, deciduous leaves are often more easily retained than smaller, less flexible types such as conifer needles (Pretty and Dobson 2004a; Quinn *et al.* 2007; Cordova *et al.* 2008; Hoover *et al.* 2010). Coniferous streams would therefore be expected to show greater reductions in CPOM standing stocks in response to high flows by comparison with broadleaved streams. Thirdly, although few studies have investigated the retention of grass litter in non-forested, open-canopy streams, moorland streams would be expected to retain less CPOM than broadleaved or coniferous streams during increased flows due to the absence of woody material, which provide efficient retention structures in streams (e.g. Bilby and Likens 1980; Cariss and Dobson 1997; Molinero and Pozo 2004; Eggert *et al.* 2012). Although the amount of wood in the benthic samples were not measured directly, field observations indicated a higher abundance of woody material stored in the broadleaf sites by comparison with other land use types. That CPOM standing stocks did not show land cover-specific responses to high flows in this study could therefore have resulted from the aforementioned differences in flow regimes that may have existed among the different land cover types, the effects of which, however, were overlooked in this study.

Although the results presented here suggest that – regardless of riparian land cover type – POM availability in headwater streams are sensitive to increased magnitude and duration of high flows, they showed that streams with broadleaved riparian land cover supported consistently greater standing stocks of both CPOM and FPOM than conifer and moorland streams. These differences are consistent with those observed previously (e.g. Cariss and Dobson 1997) and likely reflect the influence of different riparian vegetation types on the overall quantity of leaf litter supplies to these streams (Isabelle Durance, *unpublished data*). Broadleaved streams typically receive greater inputs of CPOM in the

form of leaf litter by comparison with conifer and moorland streams (Hart *et al.* 2013; Isabelle Durance, *unpublished data*). Furthermore, the higher abundance of CPOM could also support a greater abundance of leaf-shredding detritivores (Wallace *et al.* 1997), which in turn generate larger quantities of FPOM (Richardson 1991; Eggert *et al.* 2012). By contrast, inputs of conifer needles and grasses to these streams are comparably low (Isabelle Durance, *unpublished data*) and, coupled with acidic conditions (at least in the conifer and acid moorland sites), are likely broken down into FPOM at lower rates by comparison with leaf litter in broadleaved streams (Webster and Benfield 1986). This suggests that riparian land cover plays a significant role in regulating POM availability in streams despite significant intra- and inter-annual climatic variability.

1.4.1 Conclusions

Headwater streams are vulnerable to a range of environmental pressures, including climate change, through changes in temperature and precipitation patterns (Birsan *et al.* 2005; Orr *et al.* 2008; Hannaford and Buys 2012; Hannaford 2015) and land use and land cover change (Reed *et al.* 2009). This study indicates that benthic POM, an important basal food resource in headwater streams, could be sensitive to increases in the magnitude and duration of high flow events predicted under future climate change. Climate-induced reductions in the abundance and heterogeneity (via greater reductions in FPOM relative to CPOM) of benthic POM could have important indirect ecological effects, for example by disrupting energy fluxes to higher trophic levels and reducing ecosystem stability (Moore *et al.* 2004; Rooney *et al.* 2006). This study showed, however, that riparian broadleaves could play an important role in mitigating these effects by maintaining a greater abundance of detrital resources than both conifer plantation and open-canopy moorland streams, even when rainfall exceeds ‘worst-case’ projections.

CHAPTER 3: Tracing the effects of riparian land cover and climate on the quantity, quality and origin of suspended particulate organic matter in headwater streams

3.0 Summary

1. Headwater streams are arguably the most intimately connected with the landscape, and, as such, play a particularly important role in the processing and transport of organic matter within river systems. Forecasted increases in high and/or low flows in Northwest Europe, as wetter winters and drier summers are predicted to become more common, have the potential to alter the amount, composition and timing of suspended organic matter (seston) in streams.
2. This study aims to determine how riparian land cover and hydro-climatic variability could alter the amount, quality and origin of stream seston in headwater streams. Specifically, it tests whether i) concentrations and composition of seston differ among riparian land cover types, and ii) during higher flows, seston concentrations increase to reflect higher terrestrial inputs from the wetted perimeter.
3. To this end, monthly variations in fine and coarse fractions of suspended particulate organic matter (POM) were measured and isotopically analysed over four years in four headwater streams that differed in riparian land cover type (broadleaf woodland, conifer forest, acid moorland, circumneutral moorland) in Wales, UK.
4. This study showed that, contrary to expectations, concentrations of CPOM and FPOM in streams were remarkably similar across the different riparian land cover types, with only the coarse fractions of POM concentrations being marginally higher in the broadleaf site. It also revealed that increased discharge was linked to a decrease in FPOM, and to a lesser degree CPOM, consistent with an increased total export. While isotopic analyses were inconclusive, the elemental Carbon:Nitrogen (C:N) ratio of FPOM suggested a proportionately greater export of C from broadleaf catchments by comparison with those draining conifer or moorland.
5. This work suggests that higher sampling frequencies over larger temporal and spatial scales are needed for stronger inference of the effects of riparian land cover and stream discharge on POM concentrations.

3.1 Introduction

Freshwater ecosystems are highly connected with their surroundings through exchanges of energy and matter. Annually, freshwaters are estimated to receive 2.9 Pg of organic carbon from the terrestrial environment, of which ~50% is biologically processed and transformed into CO₂, ~20% is buried in sediments and ~30% is transported to the sea (Tranvik *et al.* 2009). Indeed, inputs of organic matter originating from terrestrial primary production can greatly exceed those that are produced within freshwaters themselves (Fisher and Likens 1973). Consequently, by storing, transforming, and transporting vast quantities of terrestrially-derived organic matter, freshwaters are often considered to play vital roles, not only as important linkages between land and sea, but also as major contributors to the global carbon cycle (Cole *et al.* 2007; Battin *et al.* 2008; Tranvik *et al.* 2009).

Within freshwater systems, headwater streams are arguably the most intimately connected with the landscape, forming dense networks and often making up the majority of total river length (Leopold *et al.* 1964). As such, headwaters play a particularly important role in the processing and transport of organic matter within river systems. While some of this organic matter is produced within the stream itself (e.g. aquatic plants, algae, microbes), the majority is generally considered to be of terrestrial origin (Vannote *et al.* 1980), primarily through inputs of leaf litter from riparian vegetation, as well as other forms such as woody debris, soil, and dissolved organic carbon (Cummins 1974). These sources of organic matter provide the energetic basis of stream food webs, and, when transported downstream, provide an important subsidy for food webs in lower reaches of the river network (Gomi *et al.* 2002; Wipfli *et al.* 2007).

Many studies have demonstrated the strong influence that variations in the quantity and quality of terrestrial organic matter inputs can have on the structure, function and productivity of stream communities (Polis *et al.* 1997; Richardson *et al.* 2010). For example, reduced inputs of leaf litter can lead to reductions in aquatic invertebrate production (Wallace *et al.* 1997; Wallace *et al.* 1999; England and Rosemond 2004), whilst a change in composition can alter the quality of leaf litter entering streams (Hart *et al.* 2013), and subsequently the rate at which these resources are broken down and assimilated into animal biomass (Hladyz *et al.* 2009; Cothran *et al.* 2014). These effects occur not only locally within streams, but can also propagate downstream via the export of organic material, which subsidises food webs in larger rivers (Wipfli *et al.* 2007), and

into the terrestrial environment in the form of emerging adult aquatic insects (Scharnweber *et al.* 2014; Stenroth *et al.* 2015). Changes in the supply of terrestrial organic matter to headwater streams could therefore have far-reaching consequences by altering fluxes of energy and matter from the organismal level through to the landscape level (Gomi *et al.* 2002; Richardson *et al.* 2010; Marcarelli *et al.* 2011).

Inputs of terrestrial organic matter to streams vary according to catchment vegetation cover and through time. For example, the extent and species composition of terrestrial vegetation cover directly influences the amount, quality and phenology of leaf litter inputs to streams (Abelho 2001). Simultaneously, terrestrial vegetation alters the availability of light and nutrients to streams, with consequences for aquatic primary production (Hill *et al.* 1995; Sweeney *et al.* 2004; Menninger and Palmer 2007), thereby enhancing the potential effects of land use on stream communities (England and Rosemond 2004; Kiffney *et al.* 2004). Increasingly, human modifications to the landscape through land management practices such as plantation forestry and agricultural food production are changing the vegetative cover of catchments worldwide (Millennium Ecosystem Assessment 2005). Among many other stressors linked with land use change, these changes are having marked effects on the amount and composition of organic matter resources that headwaters receive and export (e.g. Lu *et al.* 2014; Valiela *et al.* 2014; Imberger *et al.* 2014).

Temporal variations in terrestrial organic matter inputs to streams include seasonal variations in leaf litter inputs (e.g. autumnal leaf fall) and the influence of climatic variation over different timescales. For example, rainfall events increase lateral transport of terrestrial organic matter to streams via surface runoff and through the incorporation of bankside material as stream flow and wetted perimeter increases (Maridet *et al.* 1995; Naiman and Décamps 1997; Hart *et al.* 2013). Climate predictions suggest that high and/or low flows may become more frequent in Northwest Europe as wetter winters and drier summers are predicted to become more common, particularly in upland regions (Dixon *et al.* 2006; Hannaford and Marsh 2008; Biggs and Atkinson 2011; Hannaford and Buys 2012), with corresponding implications for organic matter dynamics in headwater streams (Tank *et al.* 2010; Kominoski and Rosemond 2012). Climatic variations, whether natural or anthropogenic, therefore have the potential to alter the amount, composition and timing of organic matter in streams.

Over recent decades, stable isotopes and elemental stoichiometry have been increasingly used in freshwater ecological studies as tools to trace energetic linkages across terrestrial-aquatic boundaries, and the factors that could modify them (Finlay 2001; Grey 2006; Layman *et al.* 2012). These include the effects of catchment land use modifications (Bunn *et al.* 1999; Valiela *et al.* 2014; Imberger *et al.* 2014) and hydrology (Atkinson *et al.* 2009; Frost *et al.* 2009; Hladysz *et al.* 2012). The stable carbon isotope ($\delta^{13}\text{C}$) signature of bulk organic matter in streams, which is often a mixture of amorphous material, can give an indication of the relative importance of terrestrial and aquatic sources of organic carbon contributing to streams, where source signatures are isotopically distinct (Doucett *et al.* 1996; Finlay and Kendall 2007). Data for stable nitrogen isotopes ($\delta^{15}\text{N}$) of organic matter resources, on the other hand, are lacking (Peipoch *et al.* 2012), but may provide a useful baseline for understanding the variability that is often observed in the $\delta^{15}\text{N}$ signatures of consumers, thereby improving the interpretation of $\delta^{15}\text{N}$ dynamics to determine energy pathways in food web studies (Peipoch *et al.* 2012). Meanwhile, the elemental composition (e.g. ratios of essential elements such as C:N) of resources, in addition to providing information on the nutritional quality of resources for consumers (Sterner and Elser 2002; Cross *et al.* 2005), can also provide a useful indicator of their origin, since terrestrial sources generally have higher C:N ratios relative to aquatic sources (Rostad *et al.* 1997; Kendall *et al.* 2001; Cross *et al.* 2005).

Investigating the factors that influence the quantity, quality and dynamics of key basal resources could help improve understanding of the energetic processes that underpin the responses of individual organisms, food webs and whole ecosystems to changes in catchment land use and climate (Richardson *et al.* 2010; Marcarelli *et al.* 2011; Kominoski and Rosemond 2012). Furthermore, such investigations could also increase understanding of the role that riparian restoration could play in supporting stream communities and functions, for example through efforts to enhance the availability and diversity of basal resources available to support stream communities (Thomas *et al.* 2016; Chapter 5). Few studies, however, have extended over timescales sufficient to characterise temporal variations in the origin, quality and fate of organic matter in streams across a range of land cover types. Such studies have the potential to allow not only stronger inference of the effects of riparian land cover on organic matter resources in streams, but could also allow an assessment of the potential impacts of hydro-climatic

change and associated shifts in flow regimes on the fate of organic matter in streams (see Frost *et al.* 2009; Atkinson *et al.* 2009; Hladyz *et al.* 2012).

Aims & Hypotheses

This study aims to determine how riparian land cover and hydro-climatic variability could alter the amount, quality and origin of stream seston in headwater streams. Monthly variations in fine and coarse fractions of suspended particulate organic matter (suspended FPOM and CPOM, respectively) were measured over four years in four headwater streams that differed in riparian land cover type (broadleaf woodland, conifer forest, acid moorland, and circumneutral moorland) in central Wales, UK. These land cover types were chosen to represent the broad contrasts in riparian characteristics that dominate many headwater streams in the UK uplands (UK National Ecosystem Assessment 2011). Stable C and N isotopic signatures and elemental composition of the seston were measured and an attempt made to identify the origin (terrestrial or aquatic). The following predictions were tested:

- (1) Concentrations of suspended CPOM and FPOM differ among riparian land cover types, being greatest in broadleaf streams by comparison with conifer and moorland streams.
- (2) The isotopic and elemental compositions of suspended CPOM and FPOM differ between riparian land cover types, reflecting differences in the composition and dominance of different sources of organic matter.
- (3) During higher flows, suspended CPOM and FPOM concentrations will increase, and isotopic and elemental compositions will more closely resemble terrestrial sources of organic matter.

3.2 Methods

3.2.1 Study sites

The study was conducted in four 2nd to 3rd order streams, selected from a wider pool of eight streams surveyed in another study (Chapter 2), located within the Llyn Brianne experimental catchments in central Wales, UK (Figure 2.1). Each of the four sites

represented a distinct riparian land cover type (defined here as the dominant vegetation within 10 m of the stream bank) typical of the UK uplands: Broadleaved woodland (Br; site code 'G1'), conifer plantation (Co; site code 'L1'), acid moorland (AM; site code 'C4') and circumneutral moorland (CM; site code 'L6'). All four streams were within ~ 10 km of each other ensuring that climatic conditions were similar throughout the study.

3.2.2 Stream flow and temperature measurements

Mean daily stream discharge and temperature values were calculated for each sampling date using 15-minute data derived from one of the study sites (site code L1; details provided in Chapter 2), and were used in subsequent data analyses to represent flow and temperature conditions (Sections 3.2.5 and 3.2.6, below). The stream flow and temperature data derived from L1 were assumed to reflect both local and regional climatic conditions, based on nearby long-term observations and comparisons with regional rainfall and temperature data (Chapter 2; Figure 2.3).

3.2.3 Seston sample collection and processing

Three replicate samples of suspended particulate matter were collected from each site every 4-8 weeks between November 2010 and September 2014 ($n=36$ sampling occasions). Fine and coarse suspended particulate matter were sampled by filtering known volumes (range=10-600 L, mean=142.6 L) of stream water through a stacked pair of 10 μ m (fine) and 1mm (coarse) mesh filters. Care was taken not to re-suspend benthic particles during sample collection. All samples were stored at ~4°C upon collection, returned to the laboratory, and frozen within 24 h of collection to minimise changes in composition due to microbial activity (Wallace *et al.* 2006). Ash-free dry mass (AFDM) of all suspended FPOM samples was estimated by combusting a subset ($n=92$) of all samples ($n=417$) at 550°C for 5h in a muffle furnace, and applying site-specific conversion factors to the freeze-dried mass. AFDM of suspended CPOM samples was estimated using conversion factors derived from combusted benthic CPOM samples (Chapter 2). Suspended FPOM and CPOM concentrations (mg L⁻¹) were then calculated by dividing the estimated total AFDM of each sample by the number of litres of stream water filtered. There was negligible variation between the three replicates at each time point, and so they were pooled, allowing simpler models to be fitted during the data analysis (Section 3.2.5, below).

3.2.4 Stable isotope and elemental analysis of seston and potential sources

Stable isotope and elemental analysis of C and N of suspended POM and potential sources was used to assess whether the origin (using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures) and quality (using C:N ratios) of suspended POM varied between different land cover types and through time. Suspended POM samples were freeze-dried at $-20\text{ }^{\circ}\text{C}$ for 48-72 h and weighed to the nearest 0.0001g on an analytical balance, before being ground, homogenised and sub-sampled ($3\text{ mg} \pm 0.3\text{ mg}$) for analysis of elemental (C, N) and stable isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) composition on a mass spectrometer (University of California Davis Stable Isotope Facility). To allow the origin of seston to be determined, stable isotopic data of potential sources of organic matter collected from each of the sites during 2007-2011 were used ($n = 8$ sampling occasions; Isabelle Durance, *unpublished data*). The sampling occasions spanned different seasons and years in order to encompass possible temporal isotopic variation inherent within sources (Finlay and Kendall 2007). The potential sources included leaf litter, epilithon and bryophytes. Leaf litter included pooled samples of abscised leaves from visually abundant riparian vegetation (including birch (*Betula*), oak (*Quercus*), bracken (*Pteridium*), conifer (*Sitka*), and moor grass (*Molinia*)), and was collected by hand from the riparian zone (within 10 m of the stream bank) of each site. Epilithon and bryophytes were sampled by scraping them from rocks within the stream reach. Upon collection, samples were returned to the laboratory, frozen, then processed and analysed for elemental and isotopic composition as for seston samples (Section 3.2.3, above).

3.2.5 Data analysis

To assess whether the isotopic and elemental composition of organic matter sources were distinct, differences in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N ratios between organic matter sources were tested using a general linear model (GLM), with source (bryophyte, epilithon, terrestrial leaf litter) and site as the main effects. Where significant effects were detected, differences among factor levels were assessed using Tukey's HSD *post-hoc* pairwise comparisons.

A generalized least-square (GLS) model was used to test the effects of site, stream temperature (as a proxy for season) and stream flow, and all 2- and 3-way interactions on suspended FPOM and CPOM concentrations, isotopic signatures and C:N ratios. GLS combines the simple interpretation of a conventional linear model with the ability to

handle non-independence in the data through the use of correlation models for the residuals, making it ideally suited to time series data (Pinheiro and Bates 2000). With only four streams, the data set was sub-optimal for mixed effects models (Gelman and Hill 2007). The optimal residual correlation structure for each response variable was found by fitting the global model (i.e. containing site, temperature, flow, and all two- and three-way interactions) with different auto-regressive moving average (ARMA) correlation structures, and selecting the one that minimised the Akaike Information Criterion (AIC) and did not have significant residual autocorrelation (Pinheiro and Bates 2000). The significance of the main effects were then assessed following a backwards selection procedure (see Zuur *et al.* (2009) for full details): starting with the global model, non-significant terms were removed sequentially using likelihood ratio tests with maximum likelihood estimation, selecting the models with the lowest AIC in each case, until only significant terms remained. The final optimal models were then refitted using restricted maximum likelihood (REML) estimation and were validated by visual inspection of the residuals (Zuur *et al.* 2009). Where necessary, response and explanatory variables were log-transformed prior to analysis to homogenise variances. GLS models were fitted using the *gls* function in the *nlme* package (Pinheiro *et al.* 2016) in R.

3.2.6 *MixSIAR* mixing models

A Bayesian mixing model was used to estimate the proportional contribution of the three potential organic matter sources to stream seston, and whether these contributions varied with stream discharge (Hypothesis 3). R's *MixSIAR* package (Stock and Semmens 2013) was used because it allows for the analysis of explanatory variables ('stream discharge' and 'site' in this instance; (Semmens *et al.* 2009), which can include a continuous variable (Francis *et al.* 2011), whilst accounting for uncertainty in source isotope signatures, uncertainty in discrimination factors, and concentration dependence (Stock and Semmens 2013). To account for N isotopic enrichment caused by microbial consumers associated with FPOM (Finlay and Kendall 2007), a discrimination factor of $1.76\text{‰} \pm 1.56\text{ SD}$ was estimated for $\delta^{15}\text{N}$ based on the raw data by calculating the mean difference between FPOM values and organic matter sources. For CPOM, a discrimination factor of $-0.42\text{‰} \pm 1.97\text{ SD}$ was similarly calculated. More precise estimates of $\delta^{15}\text{N}$ enrichment associated with the presence of microbes was not possible here due to the lack of published estimates. Direct measures of microbial fractionation of $\delta^{15}\text{N}$ and microbial biomass associated with seston were also beyond the scope of this study. There is little

fractionation of $\delta^{13}\text{C}$ expected between organic matter sources and microbes (Hullar *et al.* 1996), therefore there was no discrimination factor applied to $\delta^{13}\text{C}$ values.

Preliminary checks of the data prior to model fitting showed that the isotopic signatures of some CPOM samples (21 out of 353) fell outside the mixing polygons of organic matter sources, even after correcting for fractionation effects (Appendix A, Figure A.1). CPOM was therefore not analysed further since the data violated one of the major assumptions of the mixing model (Stock and Semmens 2013). Fewer FPOM values fell outside the mixing polygons (12 out of 391) following fractionation correction (Appendix A, Figure A.2), and to a lesser extent ($<0.5\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). MixSIAR mixing models were subsequently fitted to the FPOM data using a Markov Chain Monte Carlo (MCMC) procedure to simulate plausible values of the contribution of each source to the FPOM mixture based on a Dirichlet prior distribution. In order to test whether the contributions of different sources to FPOM varied with stream discharge, the mixing model was fitted with variables for discharge and site as a random effect, along with a residual error term to account for generic, normally distributed variability in FPOM isotope signatures beyond that explained by the mixing model (Parnell *et al.* 2010). The MCMC procedure was then run at incremental chain lengths (up to 1,000,000 iterations), run-ins (up to 100,000 of the first iterations discarded) and thins (up to 250 cycles) to determine whether mixing models had successfully converged (see Stock and Semmens (2013) for full details). Since model diagnostics indicated that mixing models did not successfully converge, it was not, however, possible to utilise and interpret the model estimates of source contributions to FPOM with confidence (Stock and Semmens 2013).

3.3 Results

3.3.1 Stream flow and temperature conditions during the study period

Over the four-year study period, stream discharge at L1 ranged between 0.001 and 4.080 $\text{m}^3 \text{s}^{-1}$ with an overall median of 0.120 $\text{m}^3 \text{s}^{-1}$ (Figure 2.2a), while stream temperature ranged between 0 and 18.08 $^{\circ}\text{C}$ with a median of 8.31 $^{\circ}\text{C}$ (Figure 2.2b). The first and third year of the study were relatively cold and dry, while Years 2 and 4 were relatively warm and wet (Figure 2.3). The two wet years notably included the warmest autumn (Year 2), the wettest summer (Year 2) and the wettest winter (Year 4) in Wales in the last 100 years (Figure 2.4).

3.3.2 Riparian land cover effects on seston concentration

Overall, CPOM concentrations were similar to those of FPOM (Figure 3.1), with CPOM values ranging between 0.00008 and 10.79 mg AFDM L⁻¹ (overall mean = 0.31 ± 0.07 mg AFDM L⁻¹), while FPOM ranged between 0.00074 and 17.18 mg AFDM L⁻¹ (overall mean = 0.46 ± 0.07 mg AFDM L⁻¹). Although CPOM concentrations appeared greater in

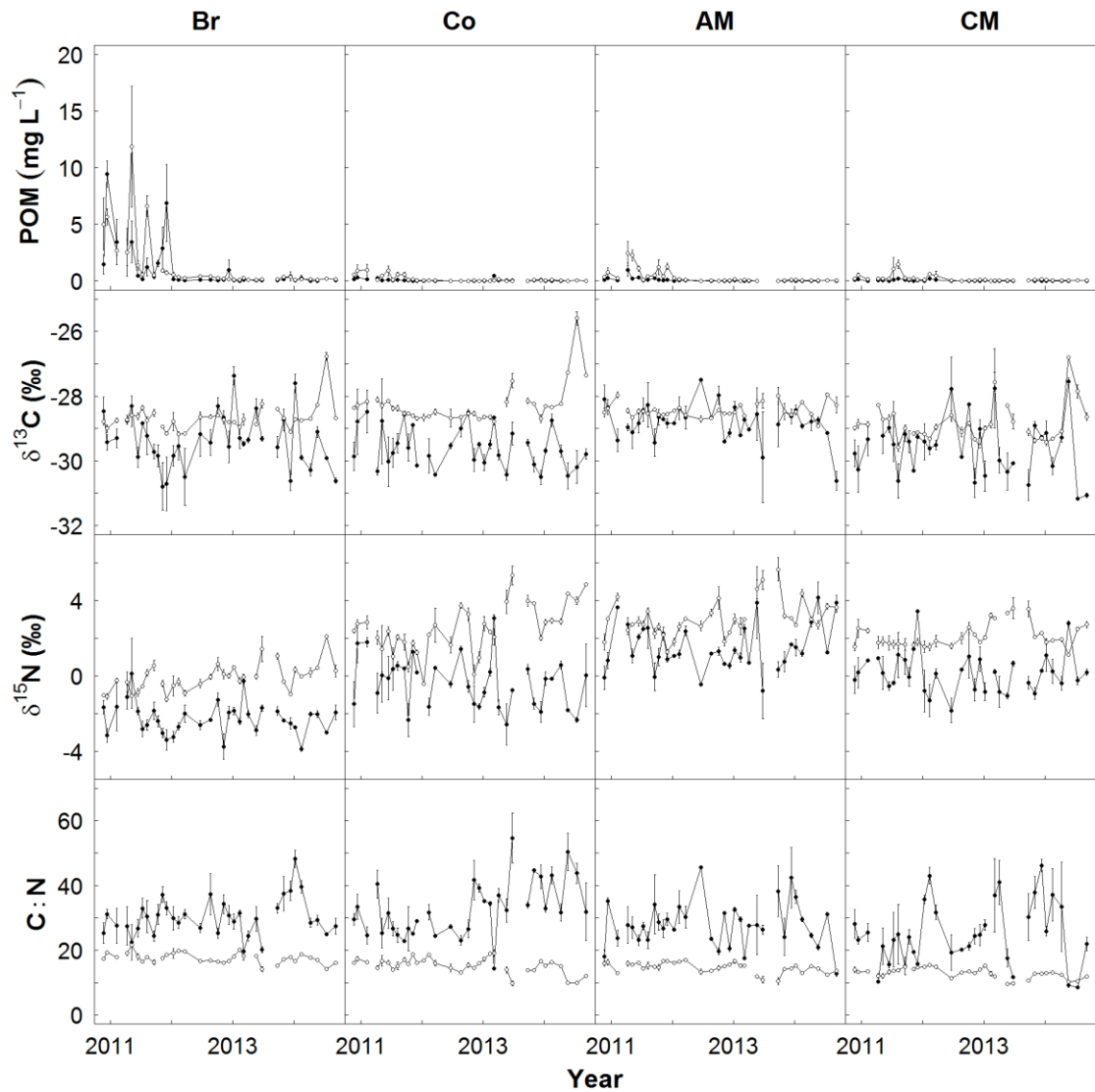


Figure 3.1. Temporal variation of suspended particulate organic matter concentrations, δ¹³C values, δ¹⁵N values and C:N ratios during the study period (± 1 S.E.). Black circles = suspended CPOM; white circles = suspended FPOM. Site abbreviations: Br = Broadleaf; Co = Conifer; AM = Acid Moorland; CM = Circumneutral Moorland.

the broadleaf site by comparison with all other sites (Figure 3.1), the overall site effect was weak (Table 3.1) and only approached significance between the broadleaf and circumneutral moorland site (Tukey's HSD, $p=0.062$; $p>0.1$ in all other cases). FPOM showed a similar pattern (Figure 3.1), though there was no significant difference in FPOM concentrations among sites (Table 3.1).

Table 3.1. Summaries of the best models for each response, showing change in AIC values and P -values following removal of terms from the model using likelihood-ratio tests. Where interactions were found to be significant, associated main effects were retained in the model but were not assessed for significance and are not displayed here.

Response		Parameters in final model	Δ AIC	df	P -value
CPOM	<i>Concentration</i>	Discharge x Temperature	-3.1	3	0.023
		Site	-2.2	3	0.043
	<i>C:N ratio</i>	Temperature x Site	-5.1	3	0.011
	$\delta^{13}C$	Site	-18.0	3	<0.001
FPOM	$\delta^{15}N$	Site	-110.1	3	<0.001
	<i>Concentration</i>	Discharge	-6.2	1	0.004
		Temperature	-5.6	1	0.006
	<i>C:N ratio</i>	Temperature	-20.5	1	<0.001
		Site	-13.1	3	<0.001
FPOM	$\delta^{13}C$	Site	-4.0	3	0.018
	$\delta^{15}N$	Temperature	-2.4	1	0.035
		Site	-21.3	3	<0.001

3.3.3 Riparian land cover effects on seston composition

C:N ratios of CPOM were higher than those of FPOM (Figures 3.1 and 3.2), with CPOM C:N ranging between 7.6 and 63.6 (overall mean = 29.3 ± 0.52), while FPOM C:N ranged between 8.7 and 21.6 (overall mean = 15.1 ± 0.13). CPOM also showed greater temporal variability in C:N values by comparison with FPOM (Figures 3.1 and 3.2), and while CPOM C:N ratios were lower on average in the circumneutral site, the site effect appeared to vary depending on temperature (Table 3.1; see Section 3.3.4, below). FPOM C:N ratios varied significantly between sites (Table 3.1), being higher in the broadleaf site by comparison with all other sites (Tukey's HSD, $p < 0.05$ in all cases), and intermediate in the acid moorland and conifer site (Tukey's HSD, $p = 0.891$). FPOM C:N was lower in the circumneutral site than the conifer site (Tukey's HSD, $p = 0.021$), but not significantly so than the acid moorland site (Tukey's HSD, $p = 0.124$).

CPOM was generally less enriched with ^{13}C than FPOM (Figures 3.1, 3.2 and 3.3), with CPOM values ranging between -32.7 and -25.33 ‰ (overall mean = -29.3 ± 0.05 ‰), while FPOM ranged between -29.7 and -25.2 ‰ (overall mean = -28.6 ± 0.03 ‰). $\delta^{13}\text{C}$ values showed little within-site variation, but showed some between-site variation, for both CPOM and FPOM (Table 3.1). CPOM $\delta^{13}\text{C}$ in the acid moorland site was significantly higher than the broadleaf, conifer and circumneutral moorland sites (Tukey's HSD, $p < 0.01$ in all cases), which did not differ significantly from each other (Tukey's HSD, $p > 0.05$ in all cases). FPOM $\delta^{13}\text{C}$ values did not show the same site differences as CPOM, with values being higher in the conifer site than the circumneutral moorland site (Tukey's HSD, $p = 0.022$), while no other site differences were significant (Tukey's HSD, $p > 0.05$ in all cases).

CPOM $\delta^{15}\text{N}$ values ranged between -4.7 and 7.3 ‰ (overall mean = -0.3 ± 0.10 ‰), while FPOM ranged between -1.6 and 6.8 ‰ (overall mean = 1.9 ± 0.08 ‰). Although CPOM and FPOM did not differ overall in terms of ^{15}N enrichment, CPOM was consistently less enriched with ^{15}N than FPOM within each site (Figures 3.1 & 3.3). CPOM $\delta^{15}\text{N}$ values varied significantly among sites (Table 3.1), being highest in the acid moorland site (Tukey's HSD, $p < 0.001$ in all cases), lowest in the broadleaf site (Tukey's HSD, $p < 0.001$ in all cases), and intermediate in the conifer and circumneutral moorland sites (conifer vs. moorland; Tukey's HSD, $p = 0.299$). FPOM $\delta^{15}\text{N}$ values were significantly lower in the broadleaf site by comparison with all other sites (Tukey's HSD, $p < 0.001$ in all cases), which did not differ significantly from each other (Tukey's HSD, $p > 0.05$ in all cases).

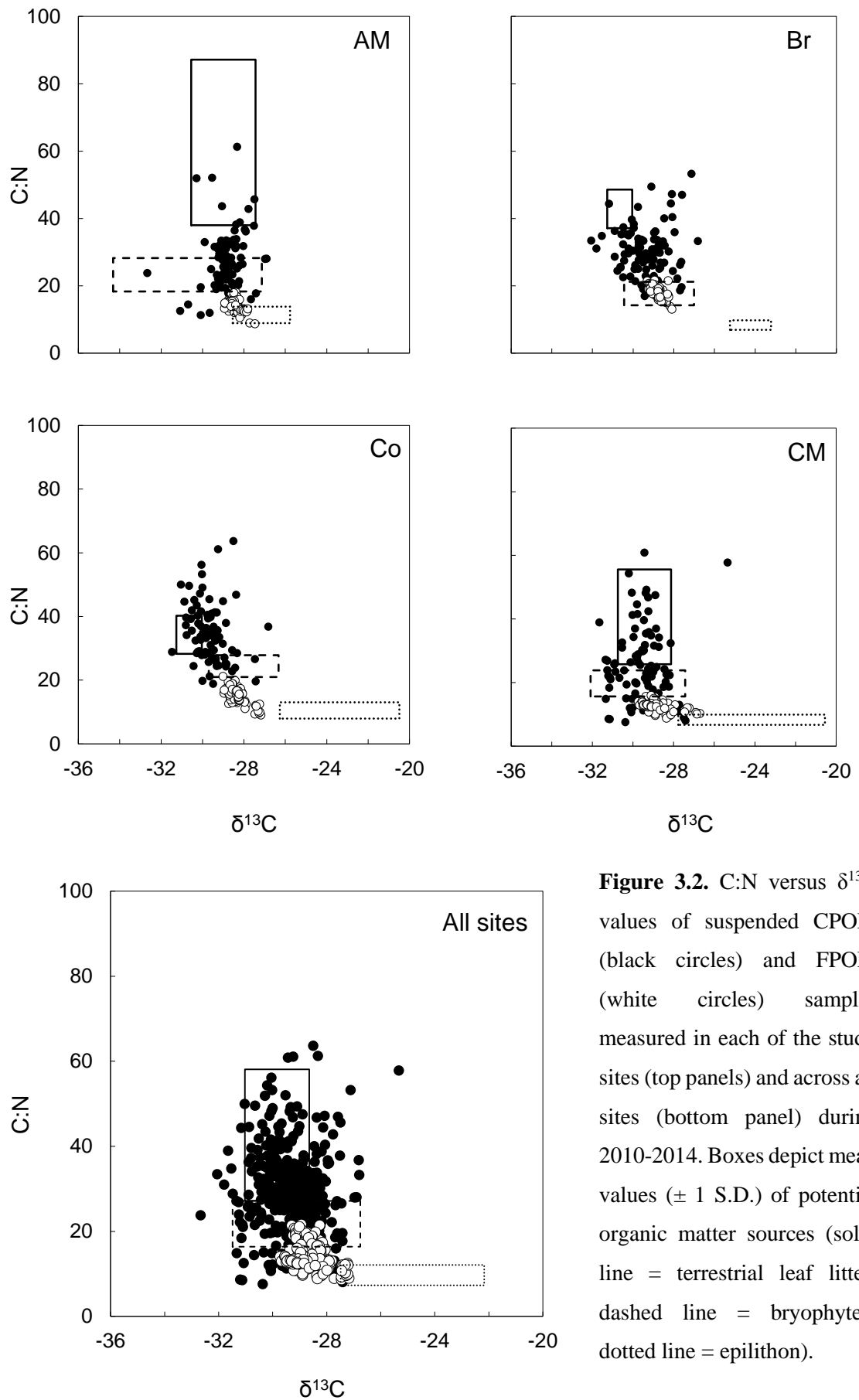


Figure 3.2. C:N versus $\delta^{13}\text{C}$ values of suspended CPOM (black circles) and FPOM (white circles) samples measured in each of the study sites (top panels) and across all sites (bottom panel) during 2010-2014. Boxes depict mean values (± 1 S.D.) of potential organic matter sources (solid line = terrestrial leaf litter; dashed line = bryophytes; dotted line = epilithon).

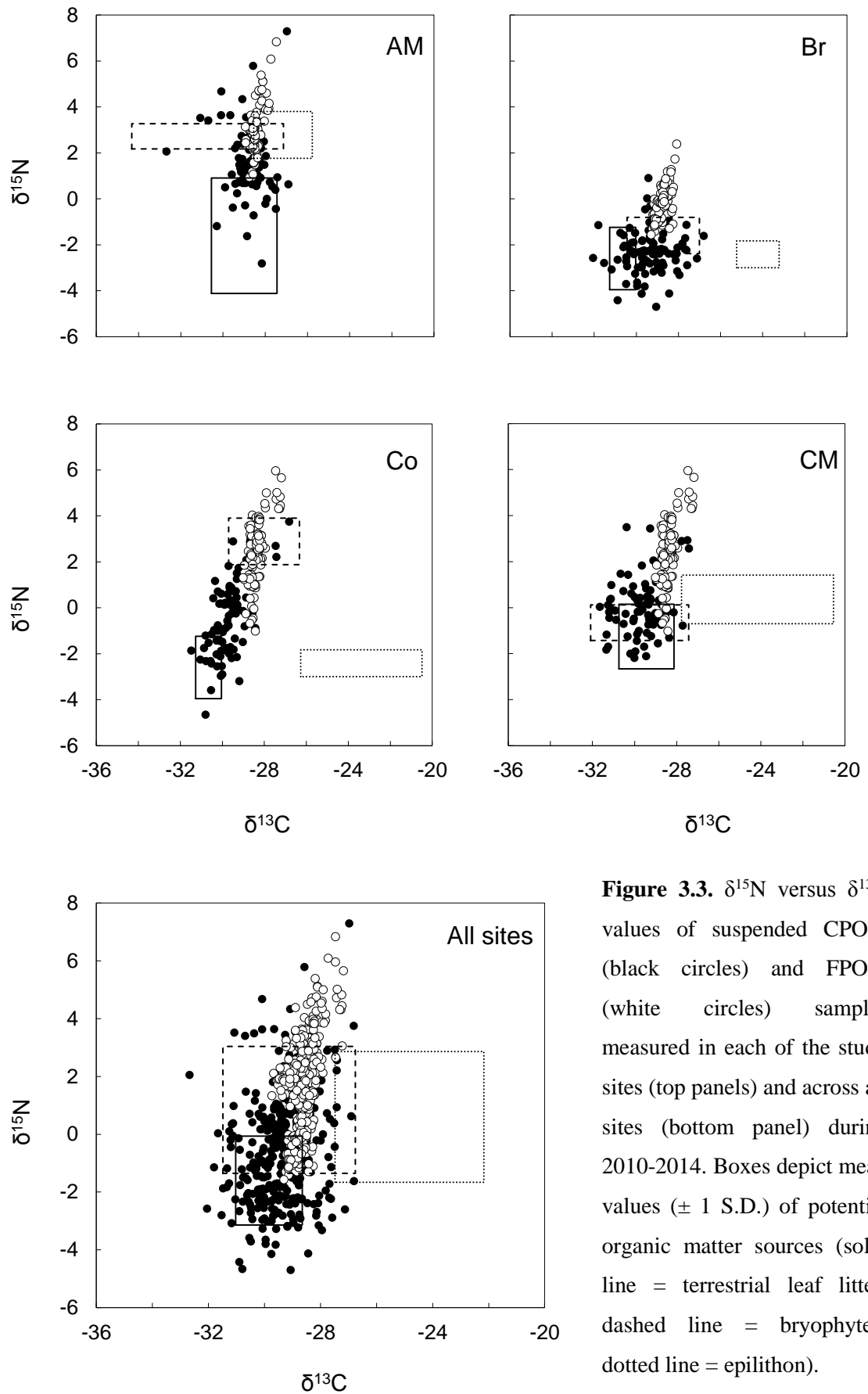


Figure 3.3. $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ values of suspended CPOM (black circles) and FPOM (white circles) samples measured in each of the study sites (top panels) and across all sites (bottom panel) during 2010-2014. Boxes depict mean values (± 1 S.D.) of potential organic matter sources (solid line = terrestrial leaf litter; dashed line = bryophytes; dotted line = epilithon).

3.3.4 Effects of stream discharge and temperature on seston concentration

CPOM concentrations decreased with increasing stream discharge across all sites, however this relationship was weaker during warmer periods by comparison with colder periods (Table 3.1). FPOM concentrations also decreased with increasing stream discharge in all sites (Figure 3.4a). The slope coefficient of the relationship between discharge plotted against concentration graph (0.24) is consistent with an increased total export (increased concentration more than compensating for increased discharge), rather than a simple dilution effect (i.e. same total export of POM). This relationship did not vary with temperature (Table 3.1). FPOM concentrations were significantly lower during warmer periods across all sites (Table 3.1; Figure 3.4b).

3.3.5 Effects of stream discharge and temperature on seston composition

There was no significant effect of stream discharge on the C:N ratios, $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of CPOM or FPOM (Table 3.1). C:N ratios of FPOM were significantly lower during warmer periods across all sites (Table 3.1; Figure 3.5b), but for CPOM this effect was only apparent in the circumneutral moorland site (Table 3.1; Figure 3.5a). Although

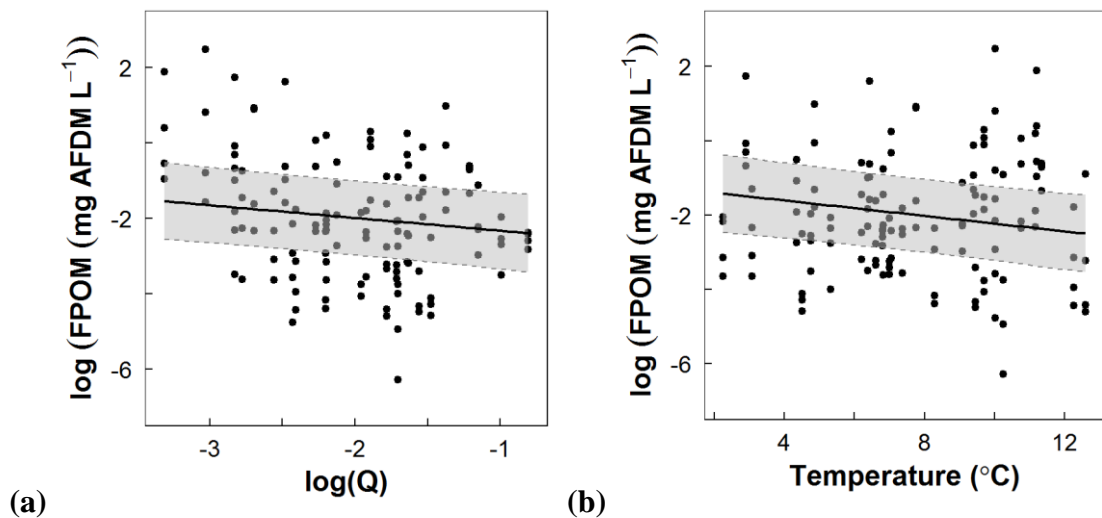


Figure 3.4. Estimated slopes and 95% confidence bands from the generalised least squares (GLS) models for log-transformed fine suspended particulate organic matter concentration at the four study sites within Llyn Brianne versus (a) stream discharge (Q) and (b) temperature data.

FPOM appeared to become more enriched with ^{13}C and ^{15}N during warmer periods (Figures 3.6a and b, respectively), these effects were weak (Table 3.1). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of CPOM did not vary with temperature (Table 3.1).

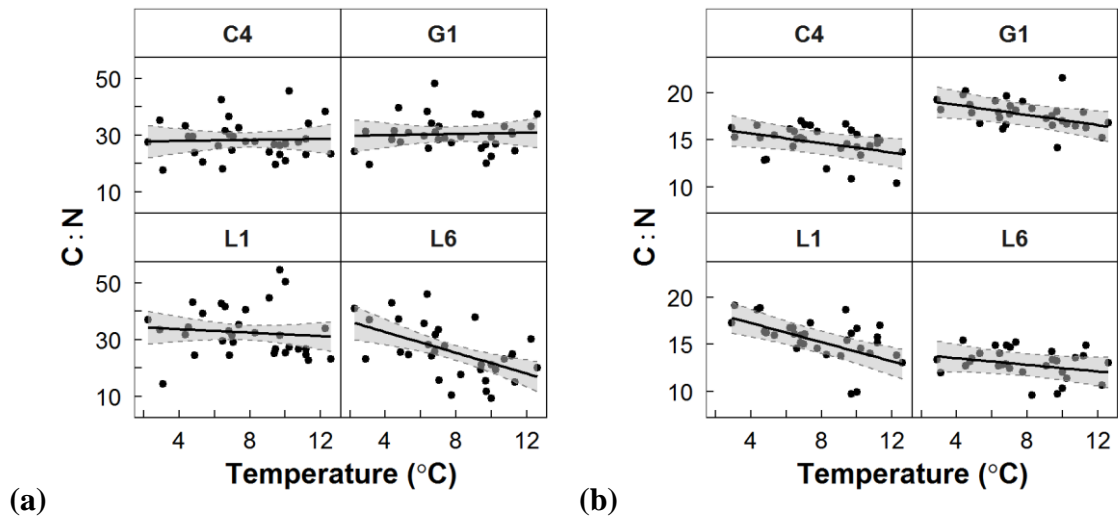


Figure 3.5. Estimated slopes and 95% confidence bands from the generalised least squares (GLS) models for C:N ratios of (a) coarse and (b) fine suspended particulate organic matter versus stream temperature data.

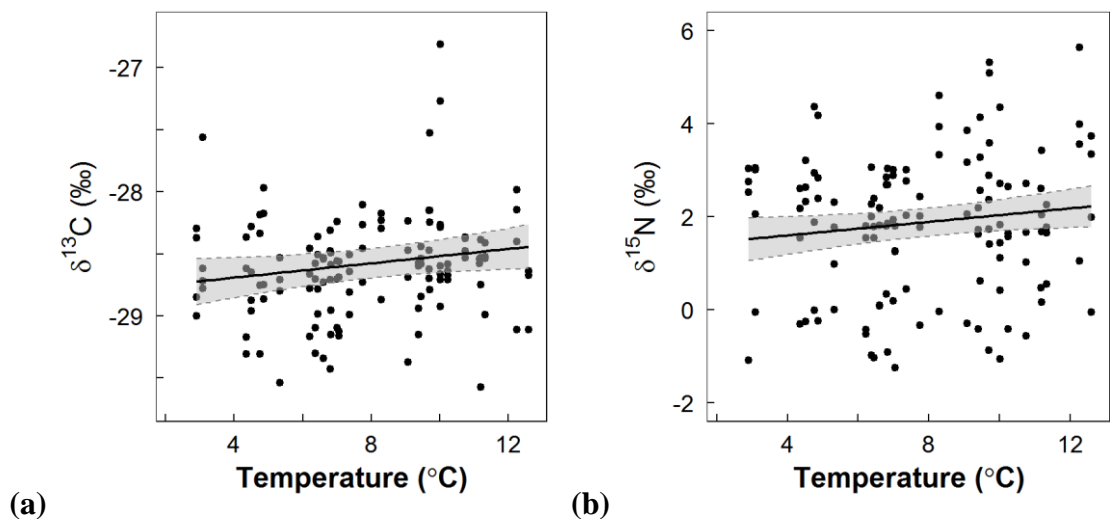


Figure 3.6. Estimated slopes and 95% confidence bands from the generalised least squares (GLS) models for $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) signatures of fine suspended particulate organic matter data versus stream temperature.

3.3.6 Isotopic and elemental composition of organic matter sources

Organic matter sources were significantly different in terms of their isotopic C ($\delta^{13}\text{C}$; $F_{2,90}=223.34$, $p<0.001$) and N ($\delta^{15}\text{N}$; $F_{2,90}=55.96$, $p<0.001$) signatures, as well as their elemental composition (C:N ratio; $F_{2,80}=223.34$, $p<0.001$) (Figures 3.2 and 3.3). Pairwise comparisons showed, however, that not all sources were compositionally distinct and that these differences were not always reflected by the origin (i.e. terrestrial or aquatic) of the organic matter sources. Epilithon was more enriched with ^{13}C than both bryophytes and terrestrial leaf litter (Tukey's HSD; $p<0.001$ in both cases), whereas bryophytes and leaf litter did not differ significantly from each other (Tukey's HSD; $p=0.375$). Leaf litter was less enriched with ^{15}N by comparison with both bryophytes and epilithon (Tukey's HSD; $p<0.001$ in both cases), which had similar $\delta^{15}\text{N}$ signatures (Tukey's HSD; $p=0.651$). C:N ratios were highest in leaf litter, lowest in epilithon and intermediate in bryophytes (Tukey's HSD; $p<0.001$ in all cases).

3.3.7 Proportional contributions of organic matter sources to FPOM

Model diagnostics indicated that the mixing model for FPOM did not successfully converge. Therefore, the model estimates of the proportional contributions of each source to FPOM were considered unreliable and, as such, are not presented.

3.4 Discussion

3.4.1 Summary

This study showed that, contrary to expectations, concentrations of CPOM and FPOM in streams were remarkably similar across the different riparian land cover types, with only the coarse fractions of POM concentrations being marginally higher in the broadleaf site. Meanwhile, there were clear differences in the isotopic and elemental compositions of CPOM and FPOM among different riparian land cover types. Discharge had a negative relationship with CPOM and FPOM concentrations, with the strength of this relationship being seasonally dependent for CPOM. In particular, the decrease in FPOM concentration with increased discharge was consistent with an increased total export. The compositions of CPOM and FPOM varied seasonally, but did not with discharge. In the absence of clear isotopic distinction between potential sources of organic matter, however, it was not

possible to ascertain with confidence what factors were driving the patterns observed in seston composition.

3.4.2 Riparian land cover effects on the amount of CPOM and FPOM

The similarities in POM concentrations among contrasting riparian land cover types observed in this study were unexpected: while other studies have reported markedly higher amounts of POM in broadleaf streams (e.g. Piccolo and Wipfli 2002), this study found CPOM to be only marginally higher, while FPOM concentrations were similar across all riparian land cover types. Higher retention of organic matter in broadleaf streams, for example due to the presence of woody debris (Cariss and Dobson 1997; Eggert *et al.* 2012), could explain why the amount of POM in transport was similar to the conifer and moorland streams, despite much greater inputs (Hart *et al.* 2013; Isabelle Durance, *unpublished data*) and benthic availability of POM (Chapter 2) in these streams. It remains possible, however, that the expected differences among riparian land cover types may have not been detectable within the range of flow conditions sampled (Figure 2.1), since the majority of POM transport occurs during storm events (Golladay *et al.* 1987; Wallace *et al.* 1995; Johnson *et al.* 2006), and sample collection was not practicable under such conditions. Meanwhile, under non-storm flow conditions, the feeding activity of benthic invertebrates may have played an important role in regulating the amount of POM in transport (D. C. Richardson *et al.* 2009). Indeed, others have demonstrated the influence that invertebrate filter feeding can have on FPOM concentrations by removing large portions of suspended particles from the water column (Voshell and Parker 1985; Monaghan *et al.* 2001). Further work involving a budget approach to link POM exports with direct measures of inputs, retention and breakdown of organic matter among different riparian land cover types could help elucidate the mechanisms underlying the observed similarities in POM concentrations observed here.

3.4.3 Riparian land cover effects on the quality of CPOM and FPOM

C:N ratios provide meaningful measures of the potential nutritional value (i.e. quality) of different food sources for consumers (Sterner and Elser 2002; Moore *et al.* 2004). In this study, there were clear differences in C:N ratios among the coarse and fine fractions of POM, with FPOM C:N ratios being consistently lower than CPOM C:N, irrespective of riparian land cover type. In addition, riparian land cover and seasonal variations in temperature appeared to affect the two size fractions differently. In combination, the

patterns observed among riparian land cover types and, more generally, among size fractions of POM, have important ecological implications.

Lower C:N ratios in smaller particles of POM have frequently been observed elsewhere (e.g. Krusche *et al.* 2002; Atkinson *et al.* 2009; Akamatsu *et al.* 2011), and are often attributed to the relatively higher surface to volume ratio of smaller particles that allows greater microbial colonisation, which actively incorporate N from the water column (Findlay *et al.* 2002; Cross *et al.* 2005). Though direct measurement of microbial biomass was beyond the scope of this study, the consistent ^{15}N enrichment of FPOM relative to CPOM could provide some indirect evidence for greater microbial influence associated with FPOM particles (see Section 3.4.6, below). In combination, these results suggest that fine particles of organic matter provide a relatively high quality, nutrient-rich resource for consumers such as filter-feeding invertebrates in headwater streams (Wallace and Merritt 1980).

CPOM quality was highly variable through time and showed no clear differences among riparian land cover types. Only during warmer periods did CPOM C:N ratios in circumneutral moorland streams become significantly lower than the other riparian land cover types. By contrast, FPOM quality showed consistent patterns in space and time, with C:N ratios being higher in the broadleaf stream by comparison with the conifer and moorland streams, and showing general trends towards lower C:N ratios during warmer periods across all riparian land cover types. Given the uncertainties with respect to the likely origins of POM in this study (see Section 3.4.6, below), explaining the causal mechanisms for spatial and temporal variations in the C:N ratios of POM are challenging. Nevertheless, given that FPOM exhibited higher C:N ratios in broadleaf streams than in streams draining conifer or moorland catchments, and that FPOM often represents the majority of the downstream flux of organic matter (Webster and Meyer 1997; Colón-Gaud *et al.* 2008; Eggert *et al.* 2012), these results indicate that broadleaf streams deliver proportionately larger quantities of organic C to downstream reaches than do conifer or moorland streams. Meanwhile, the reductions in the C:N ratios of FPOM during warmer periods suggests that FPOM may become increasingly important in supporting stream food web productivity during warmer periods of the annual cycle, by providing a nutrient-rich resource when organisms are most metabolically active (Gillooly *et al.* 2001; Sterner and Elser 2002).

3.4.4 *Hydro-climatic effects on the amount of CPOM and FPOM*

Many studies have investigated the relationship between stream discharge and suspended POM concentrations under both natural and experimental conditions, showing that numerous factors can influence the strength and direction of this relationship. These factors include the availability of POM on the stream bed, POM particle size, channel retentiveness, and the timing of sampling with respect to the hydrograph, season or antecedent flow conditions (e.g. (Wallace *et al.* 1982; Webster *et al.* 1987; Golladay *et al.* 1987; Thomas *et al.* 2001; Pretty and Dobson 2004a; Mollá *et al.* 2006; Cordova *et al.* 2008; D. C. Richardson *et al.* 2009)). In particular, the timing of sampling with respect to the stream hydrograph can have a strong influence on POM concentrations, since POM concentrations generally show a hysteretic relationship with stream discharge during storms (i.e. being higher on the rising limb than on the falling limb; Webster *et al.* 1987). In this study, the sampling regime meant that storm flow conditions were underrepresented, since sampling was often conducted at or near baseflow, or after peak flows had subsided (Figure 2.1). Therefore, the higher flow rates encountered in this study mostly reflected the falling limb of the hydrograph. As such, the lower FPOM concentrations observed at higher flow rates in this study could reflect a reduction in the amount of organic matter available for transport on the stream bed following high flow events (Chapter 2), since fine deposits of organic matter particles would be rapidly re-suspended and transported downstream on the rising limb (Webster *et al.* 1987). On this basis, the lower CPOM concentrations observed at high flows during cold, winter periods could also suggest a depletion of benthic CPOM following high flow events. Meanwhile, in warmer, summer periods, the effect of discharge on CPOM concentrations appeared to be weaker, suggesting that benthic CPOM was not depleted to the same extent following high flow events during these periods. It is possible that the high flows encountered during summer were less intense than those during winter, and did not exceed the threshold needed to re-suspend large particles of CPOM (Speaker *et al.* 1984).

3.4.5 *Hydro-climatic effects on the composition of CPOM and FPOM*

In this study, stream flow did not appear to explain any variation in the isotopic or elemental compositions of CPOM or FPOM. This contrasts with other studies conducted in larger rivers (Krusche *et al.* 2002; Atkinson *et al.* 2009; Frost *et al.* 2009), which suggested that during high flows, the C:N ratios and $\delta^{13}\text{C}$ of POM increased because the

hydrological connectivity between rivers and their floodplains was strengthened, resulting in increased incorporation of C-rich particles from terrestrial sources into the suspended organic matter pool. It is possible that the aforementioned inability to sample POM during storm flow conditions meant that any isotopic shifts that may have occurred during such events (i.e. resulting from increased incorporation of terrestrial organic matter in storm runoff) were not detected. Furthermore, detecting any shifts in POM compositions in relation to stream discharge may have been limited by the large temporal variability observed in the isotopic and elemental composition of organic matter sources potentially contributing to POM (see Section 3.4.6, below).

3.4.6 Tracing origins of CPOM and FPOM using $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N ratios

Although the amount of CPOM and FPOM was similar among riparian land cover types, there were clear differences in their isotopic and elemental composition. A robust assessment of whether these differences were driven by the effects of riparian land cover on the origin of CPOM and FPOM was limited, however, due to (i) the large variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures observed within and between individual sources of organic matter, (ii) the indications that additional, unmeasured sources were contributing to the seston mixtures, and (iii) the subsequent inability to reliably estimate the relative contributions of the different sources to CPOM and FPOM using Bayesian mixing models (Section 3.2.5). These uncertainties also rendered difficulties in assessing whether, and to what extent, the contributions of different sources to CPOM and FPOM vary through time. These challenges are discussed in the following text, and, with the limitations borne in mind, some ecologically significant conclusions as to the origins of CPOM and FPOM are then drawn based on a qualitative assessment of some of the observed patterns in the data.

3.4.6.1 Challenges in using stable C and N isotopes

In this study, the isotopic signatures of individual sources varied considerably over the three-year period within which they were sampled (Figures 3.2 and 3.3). In particular, the $\delta^{13}\text{C}$ signatures of aquatic sources showed high variability relative to terrestrial sources, and although epilithon was consistently more enriched with $\delta^{13}\text{C}$ than other sources, the wide ranging $\delta^{13}\text{C}$ signatures of bryophytes and their subsequent overlap with leaf litter signatures prevented an overall separation between ‘terrestrial’ and ‘aquatic’ sources. Similar patterns in aquatic sources have been observed elsewhere (Finlay and Kendall

2007; Peipoch *et al.* 2012; Imberger *et al.* 2014), and can be driven by temporal variability in stream water DIC signatures and CO₂ availability (Finlay and Kendall 2007; Ishikawa *et al.* 2012). Given the large variability in isotopic signatures within individual sources, it is difficult to determine what mechanisms might have underpinned the observed differences in the isotopic signatures of CPOM and FPOM among riparian land cover types.

An additional complicating factor is the possibility that other, unmeasured sources may have contributed to the CPOM and FPOM mixtures in unknown, varying proportions (Peipoch *et al.* 2012). While the dual isotope plots (Figure 3.3) suggest that a reasonable proportion of the data could be explained by a mixture of the three measured sources (bryophytes, epilithon and leaf litter), the large number of $\delta^{15}\text{N}$ values deviating from source signatures suggest the likelihood that additional sources were contributing to the POM mixtures. $\delta^{15}\text{N}$ values of both size fractions of POM were highly variable and often enriched relative to sources, particularly in FPOM. $\delta^{15}\text{N}$ enrichment of POM has frequently been attributed to the influence of microbial colonisers, for example due to their active incorporation of dissolved inorganic nitrogen (DIN) from stream water, which tends to have a higher $\delta^{15}\text{N}$ signature than that of terrestrial sources (Macko and Estep 1984; Caraco *et al.* 1998; Finlay and Kendall 2007; Peipoch *et al.* 2012). There appear to be wide ranging estimates of the proportions of microbial biomass associated with POM in aquatic systems reported in the literature, ranging from ~1% to >60% (e.g. Gessner 1997; Schumann *et al.* 2001; Findlay *et al.* 2002; Hamilton *et al.* 2004; Tremblay and Benner 2009), suggesting that the influence of microbes on the isotopic composition of POM may indeed be significant, and warrants further investigation (France 2011; Peipoch *et al.* 2012).

Recent advances in the statistical tools available for analysing isotopic data now allow investigators to account for uncertainties within the data (e.g. Parnell *et al.* 2010; Stock and Semmens 2013). In the present study, the uncertainties associated with the multiple sources of variation contributing to the isotopic composition of sources and POM mixtures (outlined above), however, highlight the challenges in attempting to assess how the origin and fate of organic matter in streams could vary through time. Further work incorporating measures of the temporal variation in source signatures and microbial biomass associated with basal resources, coupled with continuing developments in

statistical methods (e.g. Hossler and Bauer 2012) could provide a valuable basis for understanding drivers of variation in aquatic food webs.

3.4.6.2 Using C:N ratios to assess the effects of riparian land cover and hydro-climatic variability on the origins of CPOM and FPOM in headwater streams

Higher C:N ratios are often attributed to greater terrestrial contributions, while lower C:N ratios are assumed to indicate greater contribution from aquatic sources (e.g. Atkinson *et al.* 2009; Frost *et al.* 2009). Indeed, the C:N ratios of leaf litter were significantly higher than aquatic sources across all sites in this study: a pattern that has been consistently observed worldwide (Rostad *et al.* 1997; Finlay and Kendall 2007). These differences could explain some of the variation among riparian land cover types in the elemental composition of FPOM, with the broadleaf site possibly contributing greater proportions of high C:N terrestrial organic matter to FPOM due to greater leaf litter inputs by comparison with the conifer and moorland sites (Isabelle Durance, *unpublished data*). The differences in C:N ratios among sources could also explain the observed seasonal variations in CPOM and FPOM C:N ratios, with increased aquatic primary productivity in summer months possibly contributing more biomass to the organic matter pool, and thus giving rise to lower C:N ratios of suspended POM during warmer periods (Young and Huryn 1997). In the absence of supporting isotopic information, however, the likely origins of suspended POM cannot be inferred based on C:N ratios alone.

3.4.6.3 Likely origins of POM in headwater streams

Despite the challenges in determining the origins of suspended POM in this study, the data showed that CPOM and FPOM $\delta^{13}\text{C}$ values rarely fell within the range of epilithon, suggesting that epilithon was not a major contributor of organic matter to CPOM and FPOM in these streams, regardless of riparian land cover type. In the case of the broadleaf and conifer sites, this result is not surprising, given that the low light availability in these densely shaded streams would be expected to limit benthic algal production (Hill *et al.* 1995), and thus its contribution to the organic matter pool. In moorland streams, however, this result contrasts with the expectation that these open-canopy streams would have relatively greater contribution of organic matter from benthic algae (Hill *et al.* 1995). An alternative explanation is that epilithic production may be low in these high-gradient, turbulent systems, even where light is not limiting, and thus contributes little to the suspended organic matter pool.

The relative contributions of leaf litter and bryophytes to CPOM and FPOM in relation to riparian land cover type remains in question. Other studies have demonstrated that POM in forested streams has greater proportions of terrestrially-derived organic matter (such as leaf litter) than in open-canopy streams (e.g. Lu *et al.* 2014). In addition, Valiela *et al.* (2014) demonstrated that reductions in forest cover in tropical streams resulted in reduced terrestrial contributions of organic matter to stream POM. These examples suggest that forested streams, with greater inputs of leaf litter, contribute relatively more terrestrially-derived organic matter than aquatic sources to stream POM. In the absence of isotopic distinction between leaf litter and bryophytes, however, the potential importance of bryophytes in contributing to stream organic matter cannot be appraised. Indeed, previous work has shown that bryophytes are important contributors to aquatic primary production in many headwater streams (Ormerod *et al.* 1987), and while they may be considered a less nutritious food resource for stream invertebrates than other sources (Suren and Winterbourn 1991), it remains possible that bryophyte-derived organic matter – in addition to terrestrially-derived organic matter – could support stream food webs via detrital pathways, by forming part of the suspended POM load.

3.4.7 Conclusions

In this study, determining the likely origins of CPOM and FPOM were complicated by the temporal variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures inherent within organic matter sources, coupled with the potential for additional, unmeasured sources contributing to the POM mixtures in unknown quantities. This limited the ability to assess whether the patterns observed in POM compositions were driven by variations in the relative contributions of terrestrial and aquatic sources of organic matter to the POM pool. However, there was evidence for the likely influence of microbes on the composition and quality of POM, particularly in the smaller size fraction. Consequently, further work is needed in order to assess the importance of processes operating at different scales that may drive variations in the quality and fate of organic matter resources in streams. The pivotal role of microbes in mediating energy fluxes from basal resources to higher trophic levels has long been recognised in aquatic ecosystems (Cummins 1974). Quantifying the influence of microbes on organic matter resources in terms of biomass and isotopic fractionation could therefore provide an important link in the interpretation of stable isotopes in aquatic food webs studies (Peipoch *et al.* 2012).

Despite these limitations, the results presented here demonstrated remarkable similarities in the amount of CPOM and FPOM transported by streams that differed in riparian vegetation composition. Meanwhile, the elemental C:N ratio of FPOM was higher in the broadleaf stream, suggesting a proportionately greater export of C from broadleaf catchments by comparison with those draining conifer or moorland, at least under the range of flow conditions encountered. However, higher sampling frequencies over larger temporal and spatial scales are needed for stronger inference of the effects of riparian land cover and stream discharge on POM concentrations (Cuffney and Wallace 1988; Colón-Gaud *et al.* 2008; Wheatcroft *et al.* 2010). In turn, this would allow stronger predictions of the likely consequences of climate-driven shifts in stream flow regimes on organic matter dynamics (Acuña and Tockner 2010), and potential interactions with riparian land cover types.

CHAPTER 4: Effects of simulated high flow events on particulate organic matter transport and storage in stream mesocosms

4.0 Summary

1. Climate change in Northern Europe is expected to result in an increase in the frequency of winter storms, particularly in upland areas. In headwater streams, more frequent floods are likely to increase downstream transport and decrease retention of particulate organic matter (POM), thus potentially altering the structure and functioning of headwater streams by depleting key basal resources. The relationship is, however, likely to be complex, with climate interacting with channel structure and the riparian zone, and most work to date has been correlative, making it difficult to identify the underlying mechanisms.
2. This study investigates the effects of winter flood frequency on the transport and storage of POM by experimentally manipulating the flow regime of stream mesocosms in three headwater catchments within the Llyn Brianne Stream Observatory in mid-Wales, UK. Flood events were simulated by increasing the base flow rate for 48-hours at low frequency (~monthly) and high frequency (~weekly) intervals over 3 months during winter 2014-15. Daily Coarse POM export ($\mu\text{g AFDM s}^{-1}$) was measured during the experimental period, while standing stocks of Coarse and Fine POM were measured before, during and after the experimental period to assess the net effects of flood frequency on the benthic availability of particulate organic matter.
3. During the flood simulations, discharge levels were approximately doubled, resulting in a significant increase in the amount of CPOM exported from the experimental channels. Most CPOM export occurred during the early stages (0-24 h) of floods, and remained elevated above base flow levels during late flood (24-48 h), despite being lower than the initial peak. This reduction in CPOM export during late flood was only detectable in the high flood frequency treatment. Despite clear increases in CPOM export in response to the flood events, neither the amount of CPOM exported nor the amount of CPOM and FPOM stored on the

stream bed, showed evidence of depletion with successive flood events, regardless of the frequency of their occurrence.

4. These results suggest that POM stocks may not be depleted following successive flood events at the frequency and magnitude at which they were experimentally applied in this study. The magnitude and nature of flood events that occur in real ecosystems involve certain aspects that were unattainable in these mesocosms, such as greater magnitudes of flow and interactions with adjacent riparian zones. Consequently, further work is needed to characterise the effects of rainfall-runoff events on CPOM entrainment from the stream bed and the riparian zone, and to assess whether certain thresholds in flow rates exist above which depletion of organic matter resources in headwaters occur.

4.1 Introduction

Future climate projections predict an intensification of the global hydrological cycle (Huntington 2006), resulting in more frequent floods and droughts in many of the world's rivers and streams (Milly *et al.* 2005; Bates *et al.* 2008). These shifts are likely to have strong implications for the structure and functioning of aquatic ecosystems (Kominoski and Rosemond 2012; Death *et al.* 2015), since the flow regime affects habitat suitability, food availability, water quality, species composition and productivity (Poff *et al.* 1997). Given the multitude of goods and services that streams and rivers provide (Millennium Ecosystem Assessment 2005), there is an urgent need to understand the ecological effects of altered flow regimes in order to predict how these ecosystems will respond to future climate change.

Whilst the effects of an intensified global hydrological cycle on regional rainfall patterns and stream flow regimes are uncertain, there is already evidence that headwaters at higher latitudes and altitudes are showing 'early warning signs' of hydro-climatic change, with trends towards increased frequency, magnitude and persistence of winter high flows being observed over recent decades (e.g. Birsan *et al.* 2005; Dixon *et al.* 2006; Hannaford and Marsh 2006; Hannaford and Marsh 2008; Biggs and Atkinson 2011; Hannaford and Buys 2012; Marsh and Dixon 2012; Hannaford 2015). This reflects the dynamic nature of headwater streams, where rainfall patterns are rapidly manifest (Gomi *et al.* 2002). In turn, this highlights not only the sensitivity of headwaters to hydro-climatic variability,

but also their value as ‘sentinel systems’ and the subsequent need to investigate their responses to climate change (Perkins *et al.* 2010).

Headwater streams form a large proportion of river networks (Leopold *et al.* 1964) and play a key role in the storage, processing and downstream transport of particulate organic matter (POM), a key basal resource for aquatic food webs along the entire river continuum (Vannote *et al.* 1980; Gomi *et al.* 2002; Wipfli *et al.* 2007). A large proportion of POM enters streams as large particles such as leaf litter and woody debris from the neighbouring riparian zones, as well as aquatic plant fragments and dead organisms, often referred to collectively as coarse particulate organic matter (CPOM; Cummins 1974). The retention of CPOM on the stream bed is crucial for its colonisation and processing by aquatic microbes and invertebrates, which play a pivotal role in mediating energy transfer from CPOM to the rest of the aquatic food web (Cummins 1974). For example, the feeding activity of these organisms transforms CPOM into biomass, or into nutrient-rich fine particulate organic matter (FPOM), which is then amenable to downstream transport and consumption by filter-feeding invertebrates.

Numerous studies have demonstrated that POM retention decreases as stream discharge increases, reflecting a greater ability to entrain particles (e.g. Webster *et al.* 1987; Pretty and Dobson 2004a; Dewson *et al.* 2007; Hoover *et al.* 2010; Koljonen *et al.* 2012). Indeed, during high flow events, large amounts of POM are transported downstream, and a number of investigations have demonstrated that the majority of annual CPOM and FPOM exports occur during these events (e.g. Webster *et al.* 1987; Wallace *et al.* 1991; Wallace *et al.* 1995; Johnson *et al.* 2006; Richardson *et al.* 2009; Eggert *et al.* 2012). Despite the inherent challenges in sampling extreme events, investigating how altered flow regimes could influence the dynamics and availability of these resources in headwater streams could therefore provide important insights into the ‘bottom-up’ processes that may underpin ecological responses to climatic change (Kominoski and Rosemond 2012).

It has been suggested that more frequent flood events may deplete POM resources in headwaters due to frequent scouring of the channel bed and adjacent riparian zones (Kominoski and Rosemond 2012; Riedl *et al.* 2013; Graça *et al.* 2015). Indeed, long-term observations have indicated that headwater streams export less POM following multiple storm events (Wallace *et al.* 1995; Eggert *et al.* 2012; Heartsill-Scalley *et al.* 2012). However, many factors interact to influence how much POM is transported downstream

and how much remains for biological uptake following flood events in streams. These include the seasonal timing of flood events, antecedent flow conditions, particle size, channel substrate, as well as the influence of riparian vegetation on POM availability (e.g. via inputs of leaf litter) and channel hydromorphology (e.g. Wallace *et al.* 1991; Gurnell *et al.* 2002; Molinero and Pozo 2004; Pretty and Dobson 2004a; Ylla *et al.* 2010; Eggert *et al.* 2012; Koljonen *et al.* 2012; see also Chapter 2). Given the multitude of factors that affect organic matter storage and transport, our ability to predict the likely effects of changes in stream flow regimes on the availability of POM resources to benthic organisms is still limited (Hoover *et al.* 2006; J. S. Richardson *et al.* 2009; Acuña and Tockner 2010; Tank *et al.* 2010).

Identifying causal mechanisms for the effects of climate change on ecosystem structure and functioning are often challenging based on long-term observations alone (Dunne *et al.* 2004; Cahill *et al.* 2012; see Chapters 2 and 3). Experimental mesocosms, on the other hand, offer a strong compromise for addressing such questions by allowing investigators to manipulate and isolate factors of interest, whilst constraining confounds that may be inherent in long-term field observations (Ledger *et al.* 2009; Stewart *et al.* 2013). To date, few mesocosm studies have explicitly addressed whether a greater frequency of flood events could deplete organic matter resources in the longer term (but see Webster *et al.* 1987). Moreover, most experiments investigating the effects of altered flow regimes on organic matter dynamics have focussed on average changes (e.g. Dewson *et al.* 2007). As climatic conditions are expected to become increasingly variable, there is, however, also a need to assess the role of environmental variability in addition to the effects of general trends, since extreme events and disturbances could have stronger or longer-lasting impacts on ecosystems than average changes (Dunne *et al.* 2004).

Aims & Hypotheses

Using an experimental approach, this study aims to assess the effects of increased flood frequency on the transport and storage of particulate organic matter (POM) in headwater streams. To this end, flow regimes were manipulated in outdoor stream mesocosms throughout the winter season in order to test the following predictions:

1. Downstream export of coarse POM increases during flood events

2. The amount of coarse POM exported during flood events decreases with successive flood events
3. Standing stocks of coarse and fine POM become depleted when floods are more frequent

4.2 Methods

4.2.1 Study sites

The experiment was conducted in three sets of outdoor experimental stream mesocosms, each located at each of three sites within the Llyn Brienne Stream Observatory in central Wales, UK ($52^{\circ}08'N$ $3^{\circ}45'W$; Figure 4.1). One site (L3) is situated in conifer forest of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) with Lodgepole pine (*Pinus contorta* Dougl.) and is episodically acidic (minimum pH 4.9–5.6). The other two sites (L6 and L7) are circumneutral and are situated in open sheep grazed moorland with occasional bracken, mountain ash, willow and hawthorn in the riparian zones (pH > 6.9).

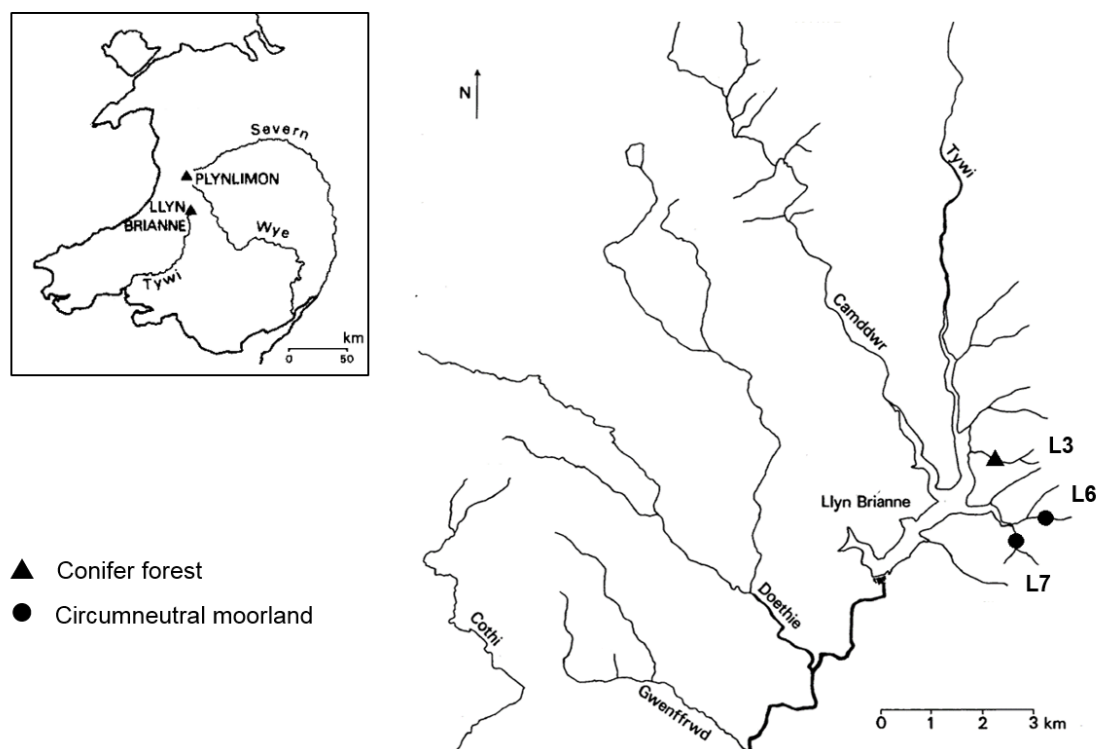


Figure 4.1. Map showing the locations of the three sites where the experimental mesocosms are situated, within the Llyn Brienne Stream Observatory in central Wales, UK. Major river systems are labelled. Images adapted from Edwards *et al.* (1990) and Broadmeadow and Nisbet (2002).

At each site, three identical flow-through mesocosm channels were situated directly adjacent to the stream (Appendix B, Figures B.1-3). Each mesocosm channel consisted of a cascading series of 20, 1 m long stainless steel troughs, each one 0.2 m wide by 0.2 m deep (4 m² total area). Troughs were filled with a 10-15cm layer of loose cobble stone substrate similar to the adjacent stream, and extracted from the Afon Tywi catchment. Each mesocosm channel was connected to a header tank that was fed directly with water and suspended particles from the adjacent stream via an inlet pipe, which was fitted with a coarse filter (3 cm² aperture) at the opening to minimise blockages caused by large debris. Stream water from the headwater tank flowed into each channel via individual inlet pipes fitted with adjustable control gates. These control gates allowed the aperture of the pipes, and hence the amount of water flowing into the channels, to be regulated manually. Water flowed through the channels by gravity, mimicking step-pool-riffle sequences, and drained into individual tanks at the bottom before draining back into the stream via an outflow pipe.

4.2.2 *Experimental design*

All mesocosms were established in April 2014 and, directly following other experiments in early September 2014, were manually disturbed and flushed at maximum flows ($\sim 10 \text{ L s}^{-1}$) for 24-h to ensure homogeneity between channels, then left flowing at baseflow levels of $\sim 2.5 \text{ L s}^{-1}$ until the experiment began. Monthly sampling of benthic CPOM and FPOM occurred on two occasions *before* (late-September, November), three occasions *during* (December, early-January, late-January) and two occasions *after* (March, April) the experimental manipulation period. From 16th November 2014 to 31st January 2015, the frequency of flood events in the mesocosms was manipulated. Each set of three mesocosms (i.e. each site) consisted of the same series of treatments: one 'reference' treatment (no flood events), one 'low flood frequency' treatment (one flood event per 24-day interval = 3 events in total) and one high flood frequency treatment (one flood event per 6-day interval = 12 events in total). Each flood event was simulated by increasing the opening of the control gates to the channel and allowing discharge to increase from baseflow levels to on average twice the baseflow level for ~ 48 hours, then returning them to baseflow levels, equal with pre-flood and reference levels.

4.2.3 *Flow and temperature measurements*

Water depth and temperature in the mesocosms was measured every 10 minutes throughout the experiment using HOBO U20L-04 water level data loggers that were pre-

calibrated before deployment (Onset Computer Corporation, Bourne, Massachusetts, USA). Water depths were converted into discharge (L s^{-1}) using a depth-discharge curve that was estimated based on volumetric measurements averaged across all channels (Marian Pye & Ifan Jâms, *unpublished data*).

4.2.4 *Benthic standing stocks of CPOM and FPOM*

Three replicate samples of benthic particulate organic matter (POM) were collected using a randomly-positioned medium Hess sampler (area 0.0165 m^2 ; $500 \mu\text{m}$ mesh aperture; sampling depth 10 cm) from each mesocosm channel on all seven sampling occasions, ensuring that no 1 m segment of each cascade was sampled more than once over the duration of the experiment (to minimise disturbance/destructive sampling). Samples were immediately preserved in 70% industrial methylated spirit (IMS; Fisher Scientific, UK) on-site. In the laboratory, samples were rinsed in tap water over a $500 \mu\text{m}$ sieve, and all macroinvertebrates were separated from the debris. The remaining POM was then separated into fine ($>500 \mu\text{m} <1 \text{ mm}$; benthic FPOM) and coarse ($>1 \text{ mm}$; benthic CPOM) size fractions using graduated sieves (Endecotts Ltd., UK). Both size fractions of POM were air-dried at room temperature and weighed to the nearest 0.01 g. Ash-free dry mass (AFDM) of all samples was estimated by combustion at 550°C for 5 h in a muffle furnace.

4.2.5 *Suspended particulate organic matter*

Daily export of suspended coarse particulate organic matter (suspended CPOM, $>1\text{mm}$) was measured by fitting 1 mm mesh filters at the outlet of each channel. Approximately every 24 h, the contents of each filter was emptied into plastic bags and frozen until subsequent processing. On several occasions, water flow into the mesocosms was unintentionally cut off due to rainfall events occurring within the study catchments and subsequent debris flows within the streams blocking the inlet pipes. All channels were inspected on a daily basis, and any debris on the inlet pipe filters removed. Daily CPOM samples were omitted when blockages occurred.

In the laboratory, frozen samples were thawed, air-dried and weighed to the nearest 0.01 g. Ash-free dry mass (AFDM) of all samples was estimated by combusting a subset ($n=247$) of all ($n=631$) samples at 550°C for 5 h in a muffle furnace and applying conversion factors to the air-dried mass. CPOM export ($\mu\text{g AFDM s}^{-1}$) was calculated by dividing the AFDM of each daily CPOM sample by the time elapsed in seconds (s).

4.2.6 Data analysis

4.2.6.1 Effects of simulated floods on CPOM export

To assess the overall effect of simulated floods on CPOM transport, daily CPOM export ($\mu\text{g AFDM s}^{-1}$) was modelled using the *lme* function within the *nlme* package in R (Pinheiro *et al.* 2016), with ‘Flow’, ‘Treatment’, ‘Flow x Treatment’ interaction, and ‘Site’ as fixed effects. ‘Flow’ was a three-level factor accounting for different stages of the flow regime: Base flow (non-flood levels), Early flood (0-24 h of simulated flood) and Late flood (24-48 h of simulated flood). ‘Treatment’ represented the different flood frequency treatments: Low flood frequency (~monthly), High flood frequency (~weekly) and Reference (no manipulation) channels. ‘Channel identity’ was included as a random term to account for non-independence of samples from the same channel and an autoregressive moving average (ARMA) residual correlation structure included to account for the remaining auto-correlation among samples up to a few days apart. CPOM data was log-transformed prior to analysis to homogenise variances. Where significant effects were detected, differences among factor levels were assessed using Tukey’s HSD *post-hoc* pairwise comparisons.

4.2.6.2 Effects of repeated flooding on CPOM export

To test whether repeated flooding decreased the magnitude of suspended CPOM export during floods, suspended CPOM data were selected from the day prior to each flood, and during Early and Late flood for each flood event (Low frequency and High frequency channels only). Two responses were calculated, representing (i) the change in CPOM export during Early flood relative to pre-flood levels (Δ_{E-B}) and (ii) the change in CPOM export during Early flood relative to Late flood (Δ_{E-L}), using the formulae:

$$(i) \quad \Delta_{E-B} = Y_E - Y_B$$

$$(ii) \quad \Delta_{E-L} = Y_E - Y_L$$

where: Y = CPOM export ($\mu\text{g AFDM s}^{-1}$); B = CPOM export on the day preceding each flood event; E = CPOM export during Early flood; L = CPOM export during Late flood.

The changes in Δ_{E-B} and Δ_{E-L} over the duration of the experiment were modelled in relation to: ‘Time’ since the start of the experiment (in days), ‘Treatment’ (Low frequency, High frequency), ‘Time x Treatment’ interaction, and ‘Site’ on Δ_{E-B} and Δ_{E-L} . A general linear model was used, with the residuals checked to ensure no residual autocorrelation.

4.2.6.3 *Effects of flood frequency on standing stocks of CPOM and FPOM*

To test the net effect of simulated floods on the availability of benthic CPOM and FPOM within the channel, standing stocks (g AFDM m⁻²) of CPOM and FPOM were modelled using a mixed-effects model containing ‘Time period’ (Before, During, After), ‘Treatment’, ‘Time period x Treatment’ interaction, and ‘Site’ as fixed effects. ‘Flow’ accounted for different stages of the flow regime: Base flow (non-flood levels), Early flood (0-24 h of simulated flood) and Late flood (24-48 h of simulated flood). Less autocorrelation was evident in the monthly benthic data compared to the daily suspended CPOM data, and so a random effect for channel was not required. ‘Sampling occasion’ was included as a random term to account for longer-term temporal variation in the data that was observed across all the channels (e.g. seasonal variation). The residuals from the model were checked to ensure no remaining spatial or temporal autocorrelation. Benthic CPOM and FPOM data were log-transformed prior to analysis to homogenise variances. Where significant effects were detected, differences among factor levels were assessed using Tukey’s HSD *post-hoc* pairwise comparisons.

4.3 *Results*

4.3.1 *Experimental conditions and flood simulations*

During flood simulations, estimated water discharge was approximately doubled in all the treatment channels, increasing on average from 2.6 L s⁻¹ at baseflow (\pm 0.8 S.D.) to 5.7 L s⁻¹ (\pm 1.7 S.D.; Figure 4.2). Meanwhile, water discharge in the reference channels remained at a mean of 2.8 L s⁻¹ (\pm 0.7 S.D.) throughout the experiment.

4.3.2 *Effects of simulated floods on CPOM export*

Each flood event exported on average 22.1 g AFDM (\pm 3.2 S.E.) of CPOM relative to baseflow exports, equating to a loss of almost 6 g AFDM m⁻² from each channel per event. The increase in CPOM export during simulated flood events was significant in both the low and high frequency treatments (Figures 4.2 and 4.3; flow:treatment interaction: $F=96.03$, $df=4$, $p<0.001$), showing a significant peak during early floods (i.e. 0-24 h of the simulated flood event) by comparison with base flows (Tukey’s HSD; low frequency: $p<0.001$; high frequency: $p<0.001$), and when compared with concurrent flows in reference channels (Tukey’s HSD; low frequency $p=0.011$; high frequency: $p=0.006$).

(a)

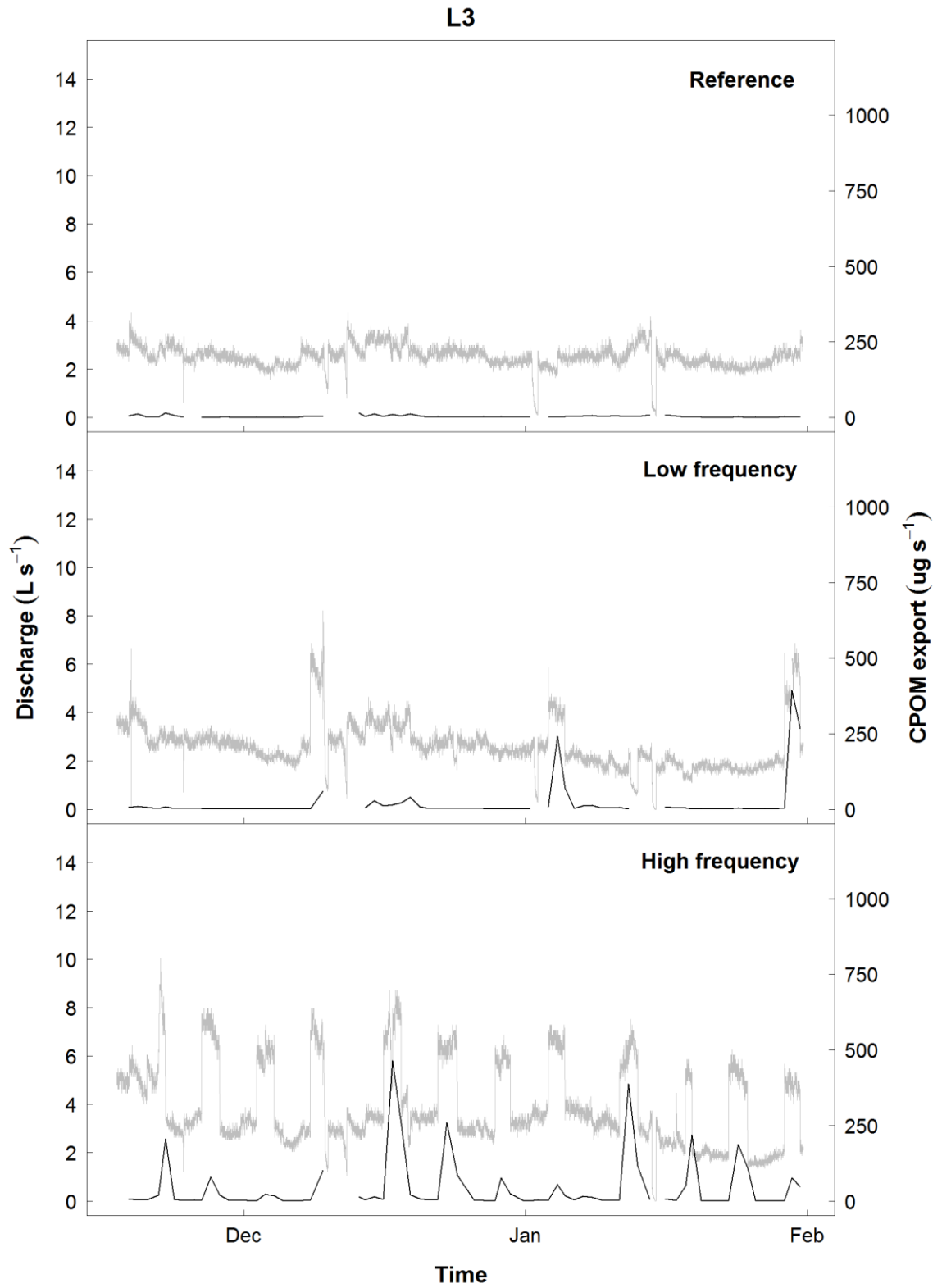


Figure 4.2. 10-minute discharge (L s⁻¹; grey line) and daily CPOM export (µg ash-free dry mass s⁻¹; black line) recorded in each experimental channel at sites L3 (a), L6 (b) and L7 (c) during the experimental flow manipulations (17-Nov-2014 – 31-Jan-2015).

(b)

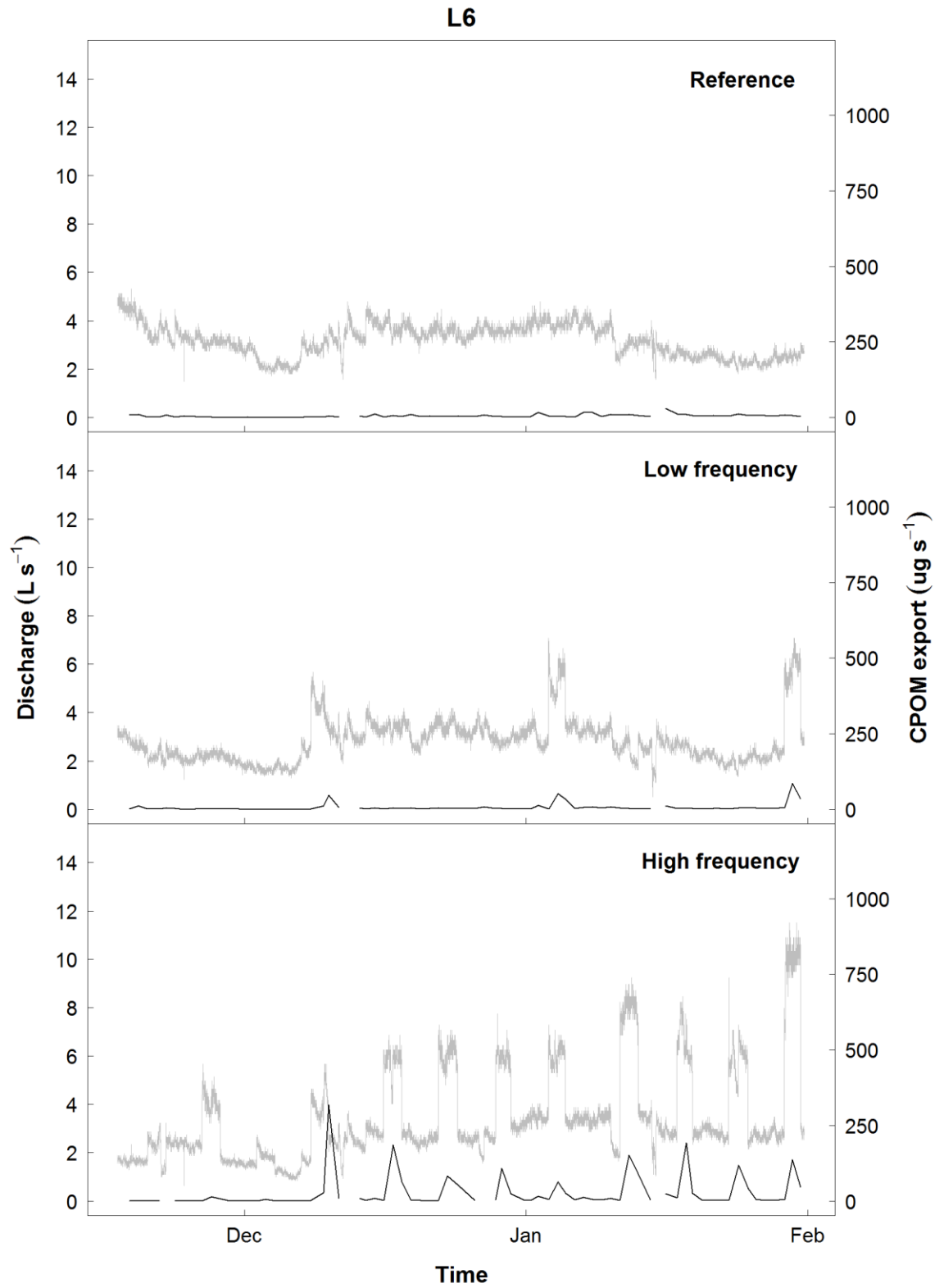


Figure 4.2. (continued)

(c)

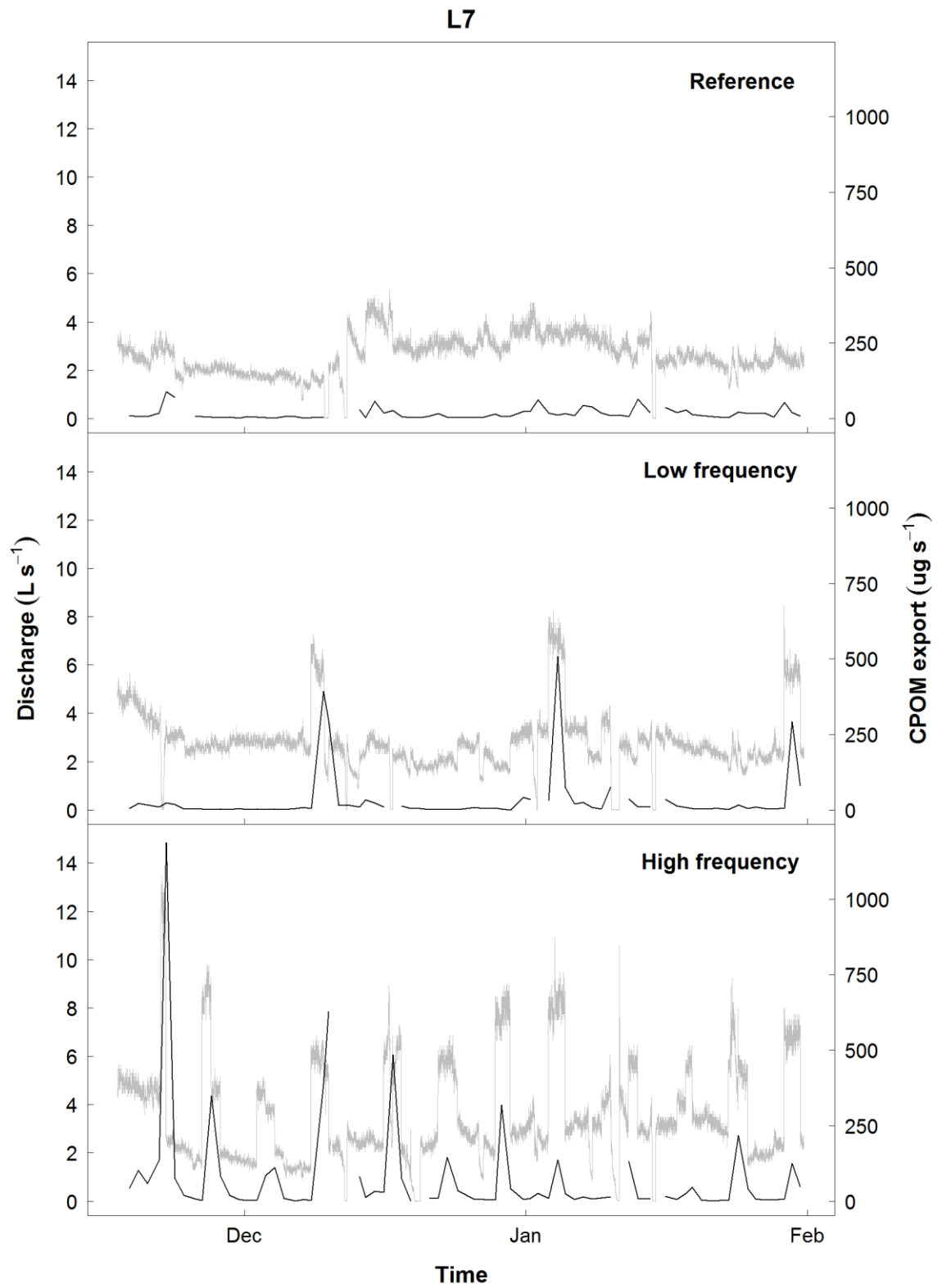


Figure 4.2. (continued)

During late flood (i.e. 24-48h), CPOM export was significantly lower than the initial peak within high frequency channels (Tukey's HSD; $p=0.003$), whereas in low frequency channels, there was no detectable difference between early and late flood (Tukey's HSD; $p=0.510$). CPOM export remained higher during late flood than during base flow (Tukey's HSD; low frequency: $p<0.001$; high frequency: $p<0.001$) and reference levels (Tukey's HSD; low frequency: $p=0.028$; high frequency: $p=0.015$) in both low and high frequency channels.

CPOM export during base flow was relatively constant throughout the experiment (Figures 4.2 and 4.3), and did not differ between the low frequency, high frequency or reference channels (Tukey's HSD; $p>0.99$ in all cases). CPOM export within reference channels also remained constant throughout the experiment (Tukey's HSD; $p>0.99$ in all cases; Figures 4.2 and 4.3).

Overall, CPOM export showed some differences between sites ($F=9.83_{2,4}$, $p=0.029$), being significantly higher in L7 (circumneutral moorland) than in L6 (circumneutral moorland; Tukey's HSD, $p=0.034$), but not L3 (conifer forest; Tukey's HSD, $p=0.051$). Meanwhile, CPOM exports in L3 and L6 were similar (Tukey's HSD, $p=0.880$).

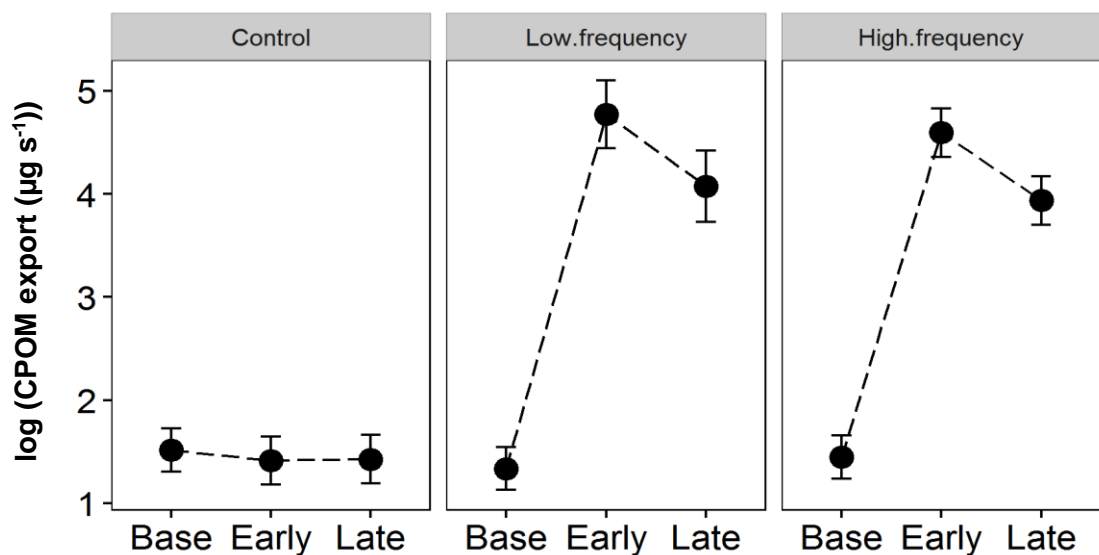


Figure 4.3. Predicted mean values (with 95% confidence intervals) of log-transformed CPOM export data ($\mu\text{g s}^{-1}$) in control, low frequency and high frequency treatment channels, during base flow (Base), early floods (Early; 0-24 h) and late floods (Late; 24-48 h).

4.3.3 Effects of flood frequency on CPOM export

There was no evidence of CPOM depletion over time, regardless of the frequency of events (Figure 4.4; Table 4.1). In fact, the peak in CPOM export during early flood relative to base flow (Δ_{E-B}) increased significantly over time across both treatments (Figure 4.4a). The initial peak in CPOM export relative to late flood (Δ_{E-L}) showed no significant trend over time, however, in neither treatment (Figure 4.4b). Δ_{E-B} differed significantly between sites, being greater in L7 by comparison with L6 (Tukey's HSD, $p=0.002$), and L3 being intermediate between L7 ($p=0.315$) and L6 ($p=0.085$). Δ_{E-L} did not differ significantly between sites ($p>0.05$ in all cases).

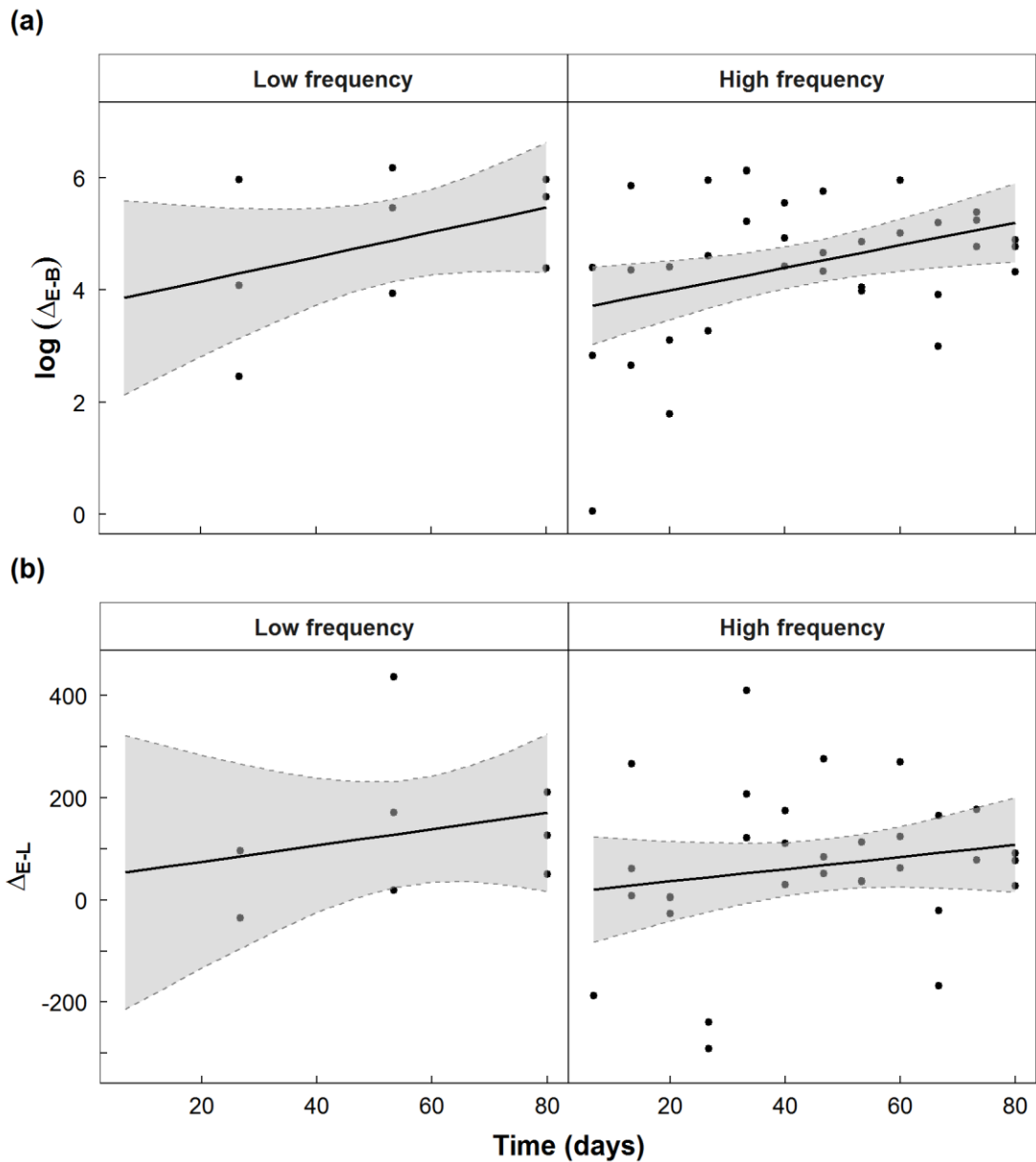


Figure 4.4. Estimated slopes and 95% confidence bands from the general linear models, showing trends over time (in days) in the relative changes in CPOM export between Early flood and (a) pre-flood levels (Δ_{E-B}) and (b) Late flood (Δ_{E-L}) for the low- and high-frequency flood treatments.

Table 4.1. Summary table of general linear model results for the effects of ‘Time’ (event number 1-12), ‘Treatment’ (low flood frequency, high flood frequency and reference treatments), ‘Time x Treatment’ interaction, and ‘Site’ (L3 – conifer forest, L6 and L7 – circumneutral moorland) on the relative changes in CPOM export between Early flood and (i) pre-flood Base flow levels (Δ_{E-B}) and (ii) Late flood (Δ_{E-L}). P-values <0.05 are highlighted in bold, along with significant pairwise differences (Tukey’s post-hoc comparisons, $p < 0.05$).

	Time		Treatment		Time x Treatment		Site		Pairwise differences
	$F_{1,38}$	P	$F_{1,38}$	P	$F_{1,38}$	P	$F_{2,38}$	P	
Δ_{E-B}	7.84	0.008	1.22	0.276	0.01	0.923	6.69	0.003	Site: L7 > L6
Δ_{E-L}	1.51	0.228	1.45	0.237	0.02	0.881	2.30	0.116	-

4.3.4 Effects of flood frequency on standing stocks of CPOM and FPOM

Despite significant increases in CPOM export in response to simulated flood events, standing stocks of CPOM and FPOM did not decrease in response to either the low or high frequency flood treatments (Table 4.2; Figure 4.5). Although the effect of time was not significant, CPOM and FPOM standing stocks appeared to increase from before to after the treatment period in all channels (Figure 4.5). There were no overall differences between control, low frequency or high frequency flood treatments, however, and the time:treatment interaction was not significant (Table 4.3). CPOM standing stocks differed significantly between sites, being greater in L3 than in L6 (Tukey’s HSD, $p < 0.001$), while L7 was intermediate between L3 ($p = 0.372$) and L6 ($p = 0.064$). FPOM was greater in LI3 than in both LI6 and LI7 ($p < 0.001$ in both cases), which did not differ from each other ($p = 0.932$).

Table 4.2. Summary of the mixed effects models for benthic CPOM and FPOM, showing F and P-values as estimated by the Kenward-Roger approach for the effects of ‘Time’ (before, during, and after the flow manipulation period), ‘Treatment’ (low flood frequency, high flood frequency and reference treatments), ‘Time x Treatment’ interaction, and Site (L3 – conifer forest, L6 and L7 – circumneutral moorland). P-values <0.05 are highlighted in bold, along with significant pairwise differences (Tukey’s post-hoc comparisons, $p < 0.05$).

	Time		Treatment		Time x Treatment		Site		Pairwise differences
	$F_{2,4}$	P	$F_{2,171}$	P	$F_{4,171}$	P	$F_{2,171}$	P	
Benthic CPOM	2.74	0.178	0.85	0.428	0.58	0.674	6.60	0.002	Site: L3 > L6, L7
Benthic FPOM	3.35	0.140	0.45	0.637	0.68	0.607	33.91	<0.001	Site: L3 > L6

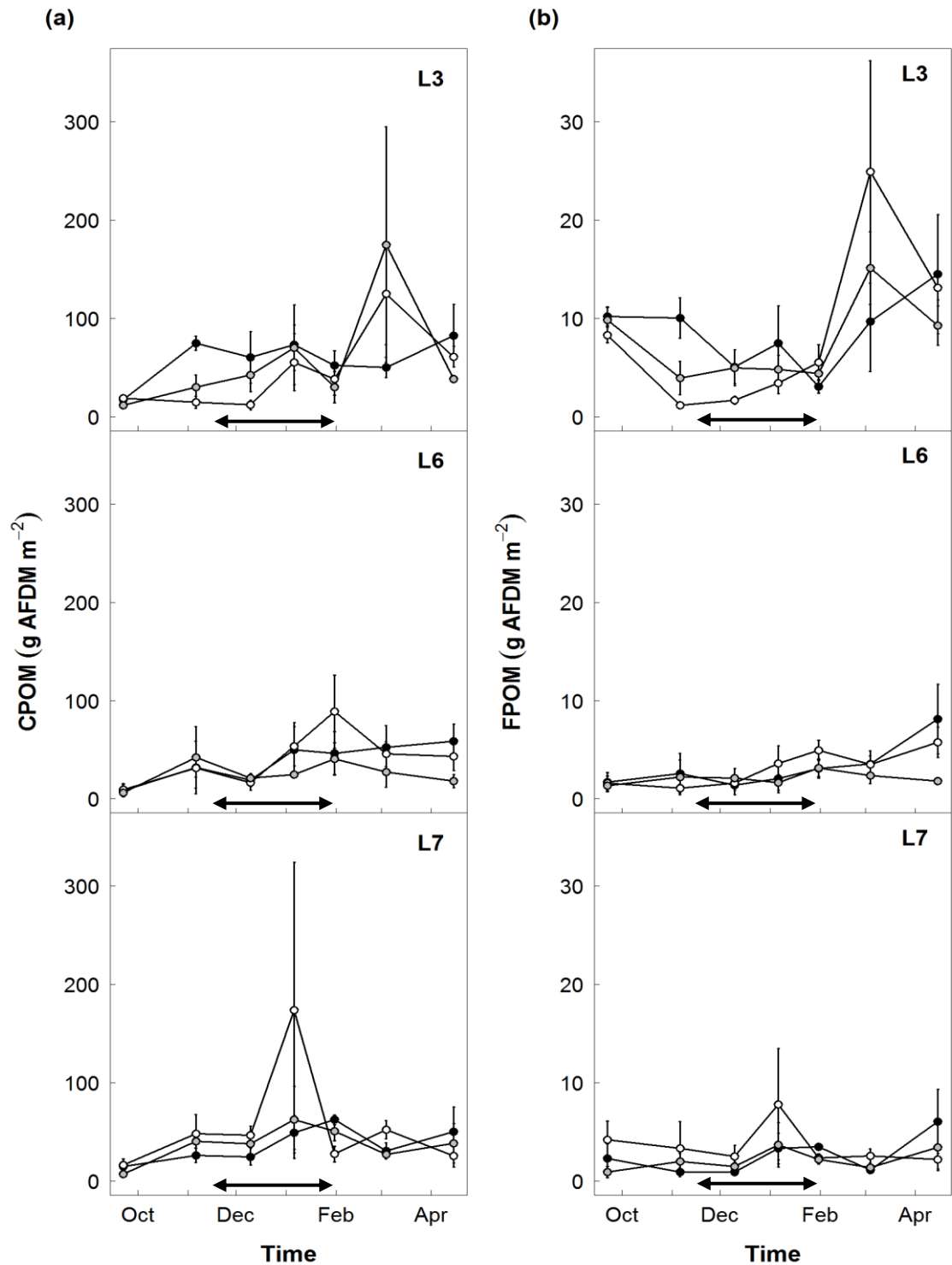


Figure 4.5. Temporal variation of (a) coarse and (b) fine benthic particulate organic matter (expressed in grams ash free dry mass $\text{m}^{-2} \pm 1$ S.E.) recorded in all flumes during the study period. Arrows denote the period during which experimental manipulations of flow regimes took place. White circles = Reference treatment; grey circles = Low flood frequency treatment; black circles = High flood frequency treatment. Note difference in axis-scale between coarse and fine fractions.

4.4 Discussion

4.4.1 Summary

The experimental flow manipulations conducted in this study resulted in an approximate doubling of discharge levels within the stream mesocosms during the simulated 48-hour floods. This caused an increase of >2000% in the amount of CPOM exported from the channels relative to baseflow levels, particularly during the early stages (0-24 h) of floods. By late flood (24-48h), CPOM export remained higher than baseflow levels, but were lower than the initial peak. This reduction in CPOM export during late flood was, however, only significant under the high flood frequency treatment. Despite significant increases in CPOM export during flood events, there was no evidence of CPOM depletion over the course of the experiment, regardless of flood frequency. This was supported by the lack of a decreasing trend in the magnitude of CPOM flood peaks over time. Furthermore, benthic standing stocks of POM did not show any evidence of depletion over time, or of any long-lasting (i.e. post-experiment) effects.

4.4.2 Caveats

This experiment was the first to be conducted over the winter season within these mesocosms, and involved some challenges in executing consistent experimental conditions during the study period. Despite daily monitoring efforts to minimise the influence of natural flood events on the experimental conditions within the mesocosms (i.e. through the use of mesh filters on the inlet pipes and daily inspections), the large amounts of debris transported by the adjacent streams during such events blocked the filters in the inlet pipes, resulting in the loss of water supply to the channels on several occasions (Figure 4.2). This meant that some samples of suspended CPOM had to be omitted from the analysis, thereby reducing statistical power. In addition, import of organic matter during natural flood events and subsequent deposition within the channels may have dampened any effects of the flow manipulations themselves on total standing stocks of CPOM and FPOM within the channels. These limitations must therefore be borne in mind when interpreting the results.

While experiments in outdoor mesocosms have the benefits of isolating certain factors of interest, they may still be lacking the realism of real ecosystems (Ledger *et al.* 2009). Indeed, flood events in headwater catchments involve aspects that were unattainable in these mesocosms. For example, flood events can involve 30-fold increases in flow rates

from baseflow levels (Figure S4.4), which contrasts with the levels achieved in the mesocosms in this study (Figure 4.2). Furthermore, as stream discharge increases, so too does the wetted channel width and thus the likelihood of incorporating POM deposits from the stream bank or riparian zone into the suspended load (Mollá *et al.* 2006; Riedl *et al.* 2013). Consequently, the flow rates achieved in this study may not have induced the same magnitude of effects as those that occur in real streams in terms of water velocities, turbulence, connectivity with riparian zones and, therefore, the amount of organic matter in transport. This study is therefore likely to underestimate the effects of real flood events and, as such, caution must be taken in extrapolating these results to real ecosystems. Nevertheless, some clear patterns emerged in response to the manipulations that have important ecological implications.

4.4.3 Overall effects of flood events on CPOM transport

The effects of the flow manipulations on CPOM export in this study support previous observations that high flow events greatly increase downstream transport of CPOM (e.g. Webster *et al.* 1987; Johnson *et al.* 2006; D. C. Richardson *et al.* 2009; Eggert *et al.* 2012). The fact that the majority of export occurred during the early stages of the flood, coupled with lower export during late flood, could reflect the hysteretic relationship often observed between discharge and particle concentrations during flood events, with concentrations being higher on the rising limb than at corresponding flows on the falling limb (e.g. Bilby and Likens 1979; Golladay *et al.* 1987; Webster *et al.* 1987; Riedl *et al.* 2013). This pattern occurs because much of the transportable material that is trapped or settled on the stream bed under baseflow conditions is rapidly re-suspended as flow rates increase (Bilby and Likens 1979). That CPOM export remained higher than base flow levels during late flood, despite dropping below the initial pulse, also shows that more CPOM transport occurs at higher flows, when higher velocities increase the ability of stream water to keep particles in transport, thereby reducing retention (e.g. Jones, and Smock 1991; Webster *et al.* 1999; Dewson *et al.* 2007).

4.4.4 Effects of flood frequency on CPOM transport and storage

Despite clear effects of the simulated floods on CPOM transport, the prediction that the magnitude of CPOM exports would decrease over successive flood events, particularly where floods were more frequent, was not supported. Many studies have, however, suggested that the amount of POM transported during high flow events is strongly influenced by the availability of benthic POM on the stream bed (Webster *et al.* 1987). In

this study, there was no apparent reduction in the amount of benthic CPOM in the ‘high’ or ‘low’ flood frequency treatments by comparison with concurrent stocks in the ‘reference’ channels during the manipulation period, or compared with stocks before the manipulation period began. Unsurprisingly, therefore, there were also no changes in benthic CPOM after the manipulation period, which would have otherwise indicated possible legacy effects, or recovery of stocks, if a reduction in benthic CPOM had occurred during the flooding treatments. The same results were also observed for benthic FPOM, which showed no evidence of reductions following the simulated flood events. In the case of FPOM, this result was surprising, since smaller particles are often more easily entrained than larger particles due to their lower deposition velocities, and are therefore more likely to be kept in transport during high flows (Speaker *et al.* 1984; Thomas *et al.* 2001). Proportionally very low export levels as well as spatial variability within each channel are probably the most likely explanations. Indeed, the total amounts of CPOM or FPOM that were entrained and exported from the channels following successive flood events may not have been sufficient to cause an overall mean reduction in the amount of benthic POM that remained on the channel beds. For example, on average, CPOM exports during individual 48-h flood events equated to a loss of approximately 14% of the benthic CPOM pool, though variability within channels, as well as through time, was high (Figure 4.4). This could have been exacerbated when flood events within the adjacent streams naturally replenished POM in reference and experimental channels alike. This suggests that even the total amount of CPOM exported from the channels following multiple flood events may have had undetectable effects on benthic CPOM above the background variability in standing stocks within the mesocosms. These weak effect sizes are further supported by long-term observations of benthic POM at several locations within this study region (see Chapter 2), which found no significant relationship between benthic CPOM or FPOM standing stocks and the frequency of antecedent (30-day) flood events. Meanwhile, benthic CPOM and FPOM were significantly reduced as the magnitude and duration of antecedent flood events increased. In combination with the present study, these findings suggest that there may be thresholds in flow rates above which depletion of benthic POM, and consequently, POM exports, occur, requiring further investigation.

4.4.5 Conclusions

Overall, this study demonstrates that CPOM export is elevated at higher flow rates, but shows no evidence of depletion of POM stocks following successive flood events, at least at the frequency and magnitude at which they occurred in this experiment. Existing evidence suggests that organic matter stocks in headwaters become depleted in response to more frequent, high-intensity or persistent flood events (Sabater *et al.* 2008; Eggert *et al.* 2012; Chapter 2). Clearly, further experimental work is needed to determine whether certain thresholds in flow rates exist above which depletion of organic matter resources in headwaters occur. Indeed, recent attempts to model CPOM dynamics and exports in headwater streams have highlighted the paucity of information with respect to the rate of CPOM re-entrainment in relation to increasing discharge (Hoover *et al.* 2006; J. S. Richardson *et al.* 2009; Acuña and Tockner 2010; Stenroth *et al.* 2014). Consequently, experimental work to characterise this relationship for different flow regimes and CPOM types, including entrainment from adjacent riparian zones, would allow better predictions of the effects of altered flow regimes on the fate of organic matter in river networks, as well as a better quantification of carbon exports from headwaters (Bunte *et al.* 2016).

CHAPTER 5. Effects of simulated riparian restoration on the abundance and composition of detrital resources in headwater streams

5.0 Summary

1. Riparian restoration through the planting of riparian broadleaved trees is often advocated as an adaptive management strategy to buffer against changes in climate and catchment land use on the structure and functioning of stream ecosystems. Few studies, however, have attempted to assess the potential for riparian tree planting to restore terrestrial-aquatic linkages in headwater streams by enhancing the abundance and diversity of basal resources available to stream organisms through leaf litter subsidies.
2. Using a Before-After-Control-Impact (BACI) field experiment with spatial replication, this study aimed to assess the effects of simulated riparian restoration on the amount and composition of detrital resources in headwater streams. Riparian land cover change to broadleaf woodland was simulated by subsidising eight headwater streams with leaf litter resources at volumes typical of broadleaf woodland streams. Standing stocks of benthic particulate organic matter (BOM) were measured, along with the concentration and isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and elemental (C:N ratio) composition of suspended particulate organic matter (SOM) in control and impact reaches before and after the litter addition.
3. Despite maintaining leaf litter in the impact reaches at levels that exceeded those in a reference broadleaf stream over a period of six months, there was no increase in the amount of BOM or SOM detected at the reach scale. In addition, there were no shifts in the isotopic or elemental composition of suspended particulate organic matter that would indicate an increased contribution of organic matter from terrestrially-derived leaf litter in response to the litter addition. Instead, observed differences in organic matter among reaches and experimental time periods seemed to reflect background spatial and temporal variability as opposed to any effects attributable to the litter addition *per se*.
4. The overall non-response to the manipulation could mean that the extent of the manipulation was insufficient to bring about a detectable response, particularly given the high levels of background noise within these highly dynamics system, within the time frame of this experiment. Longer-term assessments are needed, coupled with more extensive manipulation, in order to determine the viability of

riparian restoration as an adaptive strategy for mediating the impacts of climate change and wider catchment land use change and restoring ecosystem functions in headwater streams.

5.1 Introduction

Global changes in land use and climate have fundamentally altered the structure and functioning of many ecosystems worldwide (Millennium Ecosystem Assessment 2005). As climate change is expected to become increasingly apparent (Bates *et al.* 2008), along with the need to increase global food production to sustain a growing human population (Godfray *et al.* 2010), there is increasing pressure on ecosystems to continue to deliver goods and services. Consequently, there is an urgent need for the sustainable management and adaptive restoration of ecosystems in order to ensure resilience to multiple stressors linked to climate change and human activity.

Freshwater ecosystems are among the world's most vulnerable to changes in climate and land use, but are also among the most valued for the goods and services that they provide (Dudgeon *et al.* 2006; Ormerod 2009; Vörösmarty *et al.* 2010). Headwater streams are particularly vulnerable due to their high connectivity with their surrounding environment. For example, due to their small size, the hydrological and thermal regimes of headwater streams closely track variations in rainfall and air temperature (Gomi *et al.* 2002; Caissie 2006), meaning that changes in climate are rapidly manifest both physically and biologically (Durance and Ormerod 2007; Perkins *et al.* 2010). In addition, headwaters rely heavily upon the neighbouring riparian zones for inputs of organic matter (e.g. leaf litter from terrestrial vegetation) as a supply of energy to support the food web (Wallace *et al.* 1999). This means that changes in catchment land use, such as reductions in forest cover or conversions to plantation forestry and pasture, can disrupt the flow of energy and matter to headwater ecosystems. This simultaneously creates challenges for managing headwaters, but also presents opportunities for management interventions in the riparian zone.

Riparian restoration, through the planting of broadleaf trees alongside river margins, is often advocated as an adaptive management strategy to mitigate the effects of land use and climate change on stream ecosystems (e.g. Abell *et al.* 2007; Ormerod 2009; Palmer *et al.* 2009; Seavy *et al.* 2009). Such efforts may also help to restore some of the natural

functions of river ecosystems, particularly in regions where wooded landscapes are thought to have dominated prior to extensive deforestation of native trees for agriculture (Svenning 2002; Lake *et al.* 2007; Kaplan *et al.* 2009). Indeed, there is increasing evidence as to the likely benefits of riparian restoration. For example, studies have shown that riparian trees have the potential to buffer against hydrological (Bradshaw *et al.* 2007) and thermal (Broadmeadow *et al.* 2011; Garner *et al.* 2015) extremes, reduce sediment and nutrient inputs (Broadmeadow and Nisbet 2004; Sweeney *et al.* 2004), increase aquatic and terrestrial biodiversity (Naiman *et al.* 1993; Suurkuikka *et al.* 2014), and increase in-stream habitat diversity through inputs of woody debris (Naiman and Décamps 1997; Gurnell *et al.* 2002).

Less well understood is the potential for riparian tree planting to restore terrestrial-aquatic energetic linkages via inputs of leaf litter. Numerous studies have highlighted the important role that riparian trees play in supplying sources of energy and matter to stream ecosystems in the form of leaf litter. For example, Wallace *et al.* (1999) demonstrated how benthic standing stocks of organic matter were drastically reduced following experimental exclusion of litter inputs in a temperate forested stream. The role of riparian trees in enhancing benthic organic matter stocks has also been supported by comparative studies (e.g. Jones, 1997; Thomas *et al.* 2015; Chapter 2). In addition, stable C and N isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), and elemental ratios (e.g. C:N) have been used increasingly to trace the potential importance of riparian litter in subsidising in-stream organic matter stocks and secondary production (e.g. Leberfinger *et al.* 2011; Dekar *et al.* 2012; Imberger *et al.* 2014; Junker and Cross 2014; Chapter 3). These detrital subsidies increase the diversity of basal resources available to consumer organisms, and are considered important in increasing food web stability (Moore *et al.* 2004; Rooney *et al.* 2006). Furthermore, leaf litter subsidies can increase productivity at multiple trophic levels both locally and downstream (Wallace *et al.* 1997; Wipfli *et al.* 2007), and contribute to neighbouring terrestrial food webs via aquatic insect emergence (Scharnweber *et al.* 2014; Stenroth *et al.* 2015). Clearly, the effects of enhancing the abundance and diversity of basal resource in streams via riparian tree planting have the potential to be far-reaching.

It has been suggested that planting trees in riparian buffer strips may reinstate these subsidies, bringing ecological benefits such as greater productivity (Thomas *et al.* 2016), restoring ecological processes (Kominoski and Rosemond 2012), and increasing the availability and diversity of basal resources (Koljonen *et al.* 2012; Kupilas *et al.* 2016),

but few attempts have been made to test this prediction (but see Dobson *et al.* 1995; Thomas *et al.* 2016). Appraising the effects of riparian restoration, in particular planting riparian trees, is challenging because the trees could take several years to mature, requiring monitoring beyond the temporal and financial scale of most projects. Furthermore, river ecosystems are highly complex, dynamic, and closely connected to their surroundings, and persistent changes in catchment land use and climate are altering the context in which they must respond to restoration efforts. In combination, these factors present significant challenges in predicting their likely responses to restoration with confidence. Yet, policy decisions require a high level of certainty before management interventions are implemented. Recent correlative studies have provided valuable insight into the potential response of stream ecosystems to riparian restoration in headwater streams (Thomas *et al.* 2015; 2016). Complementary approaches are, however, needed to enhance our understanding and enable informed management decisions (Fukami and Wardle 2005; Stevenson and Sabater 2010).

Experimental manipulations of natural systems have the benefits of constraining potential confounds and allowing stronger inferences about cause and effect, whilst allowing relatively short-term assessments to be made (Dobson *et al.* 1995; McGarigal and Cushman 2002). Experimental approaches have been used previously to test whether restoring channel complexity – for example via the addition of wood or boulders – could enhance channel retentiveness, and subsequently the overall quantity of basal resources that are made available to stream organisms (e.g. Muotka and Laasonen 2002; Lepori *et al.* 2005; Flores *et al.* 2011; Eggert *et al.* 2012). Attempts to restore both the abundance and composition of basal resources via direct inputs of leaf litter have, however, only been made once before (Dobson *et al.* 1995).

Aims & Hypotheses

This study aimed to assess the effects of riparian restoration on the amount and composition of detrital resources in headwater streams. Using a Before-After-Control-Impact (BACI) field experiment with spatial replication, riparian land cover change to broadleaf woodland was simulated by subsidising eight headwater streams with leaf litter resources at volumes typical of broadleaf woodland streams. Specifically, the following predictions were tested:

- (1) Simulated riparian restoration would increase stocks of benthic and suspended particulate organic matter in streams.
- (2) Simulated riparian restoration would alter the isotopic signature (i.e. increase $\delta^{13}\text{C}$ and decrease $\delta^{15}\text{N}$ values) and elemental composition (i.e. increase C:N ratio) of suspended particulate organic matter, consistent with greater contributions of organic matter from terrestrial sources.

5.2 Methods

5.2.1 Experimental design & study sites

A six-month Before-After-Control-Impact (BACI) experiment was used to assess the short-term response of eight upland streams to simulated riparian restoration. We looked for changes in stocks of benthic and suspended organic matter before and after simulation, which aimed to enhance the input and retention of broadleaved litter within the streams. Two study reaches, ~ 50 m long, were established on each stream, comprising a control reach (no experimental manipulation) ~ 20-50 m upstream of an impact reach (where riparian restoration would be simulated).

The eight study sites comprised 2nd to 3rd order streams in the Cambrian Mountains in central Wales, UK (Figure 5.1). These streams are situated in the headwaters of the Rivers Tywi, Severn and the Wye, and have been monitored routinely as part of ongoing long-term research at the Llyn Brianne Stream Observatory (52°08'N 3°45'W; www.llynbrianne-liter.org) and the Plynlimon research catchments (52°28'N 3°45'W; www.ceh.ac.uk). The study sites were selected to encompass the typical variation in land management and acid-base status observed across upland catchments. In these regions, land is managed primarily for commercial forestry and sheep-grazing, and acid-base status ranges from naturally circumneutral to episodically or chronically acidic waters. Stream discharge ($\text{m}^3 \text{s}^{-1}$) was recorded at 15-minute intervals at a study site located within the Llyn Brianne Stream Observatory (site code: L1), over the duration of the study (data supplied by Natural Resource Wales; Station number 060S0589W) and was assumed to reflect flow conditions for all the study sites and wider hydro-climatic conditions (see Chapter 2, Section 2.2.2).

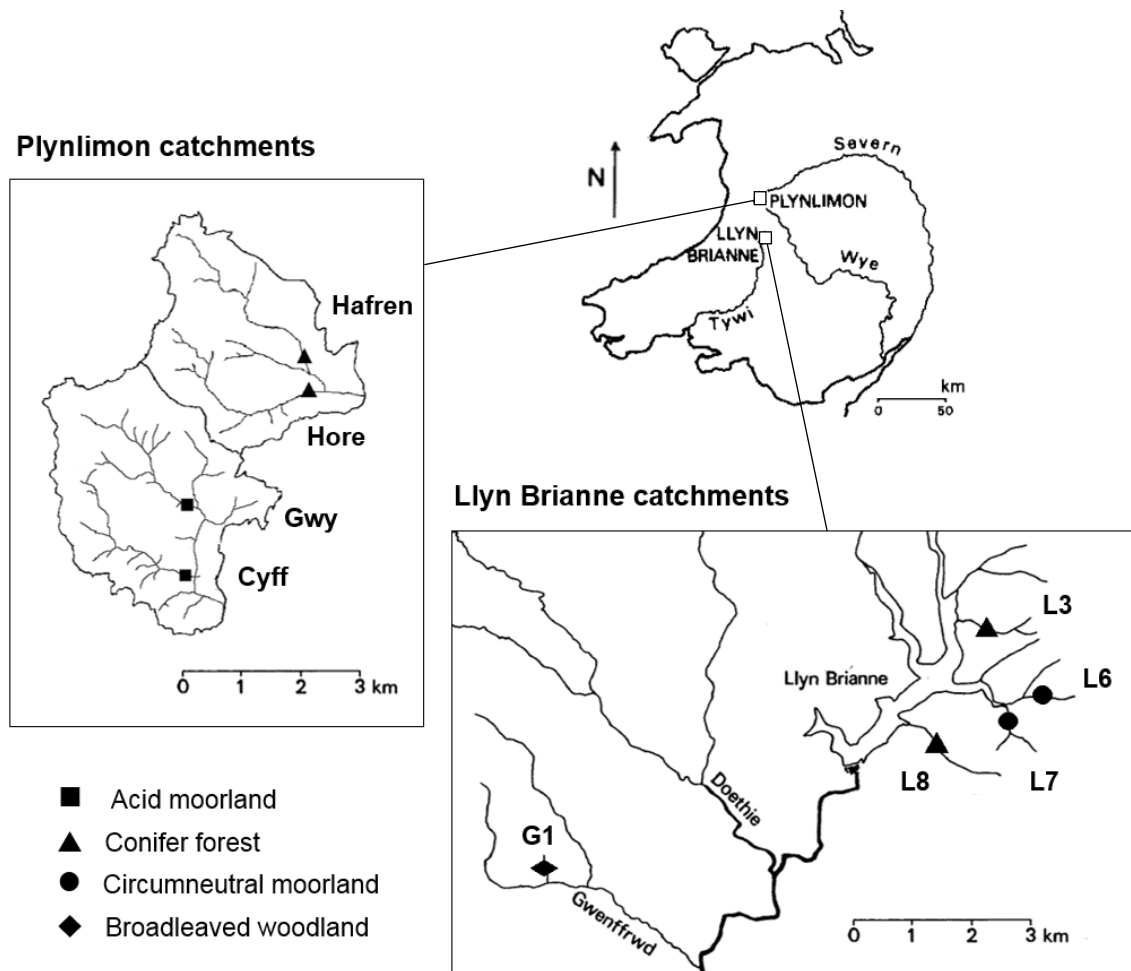


Figure 5.1. Map showing the locations of the eight experimental sites used in this study within the Plynlimon research catchments and the Llyn Brianne Stream Observatory in central Wales, UK. Images adapted from Edwards *et al.* (1990), Broadmeadow and Nisbet (2002) and Marc and Robinson (2007).

5.2.2 Simulating riparian restoration

During late Autumn 2012, abscised leaves were collected from broadleaved woodlands at Llyn Brianne and stored outdoors in large refuse sacks until required. Ten ~1 kg subsamples of the litter mixtures were inspected for identification of species composition, and comprised primarily oak (*Quercus* sp.; $91.1\% \pm 6.4\%$ SD of the total mass), along with small amounts of birch (*Betula pubescens* Ehrh.; $7.8\% \pm 6.3\%$ SD) and alder (*Alnus glutinosa* L.; $1.1\% \pm 1.2\%$ SD).

Simulated riparian restoration began in early January 2013. This aimed to mimic the typical volumes and patchiness of organic matter stocks that occur in woodland streams

(Smock 1990; Wallace *et al.* 1995; Ferreira *et al.* 2013) through inputs of loose leaf litter and localised retention of leaf packs on boulders, wood jams and in pools. We added ‘leaf packs’ to the river bed at volumes of 0.35 kg dry mass of litter per m² of stream bed, in the form of filled mesh bags (50 x 30 cm; 1 cm aperture; ~ 0.8 kg dry mass litter per bag) secured in place with steel poles and boulders. The volume for the leaf packs was established based on autumn standing stocks collected in a broadleaf stream of similar hydro-morphological characteristics within the study region during three consecutive years (Isabelle Durance, *unpublished data*). We also created ‘wood jams’ by securing ten retention nets (40 x 40 cm; 5 cm aperture) aligned perpendicular to the river flow throughout each of the ‘Impact’ reaches (Dobson and Hildrew 1992; Dobson *et al.* 1995). We then added large quantities of loose leaf litter to the upper end of each reach at volumes of 3 kg dry mass of litter per m length of stream bank. The volumes of leaf litter added here were established based on a combination of published estimates of total annual litter inputs to temperate streams draining wooded catchments and estimates made from data collected in a broadleaf stream within the study region (Isabelle Durance, *unpublished data*).

Following litter addition, we estimated leaf litter standing stocks (in g dry mass m⁻²) in the impact reaches on each sampling occasion by counting all ‘leaf packs’ and dividing the estimated total mass (~ 4 kg dry mass per pack) by the reach area. On two occasions after the litter addition (1 and 4 weeks into the experiment), we added ‘leaf packs’ to each stream to replace those that were lost following large storm-flow events. Typical leaf litter standing stocks for reference broadleaf streams were also estimated using litter data collected on corresponding months during 2011-2014 from a representative broadleaf stream within the study region (Isabelle Durance, *unpublished data*). These measurements were made by hand collecting loose litter from 5 x 1 m² transects along a 10 m reach and converting to mean g dry mass m⁻².

5.2.3 Benthic and suspended POM sampling and laboratory processing

We measured stocks of benthic and suspended organic matter (BOM and SOM, respectively) in December 2012 (SOM only) and January 2013 (BOM and SOM) before litter addition, and approximately monthly for four months after litter addition (February, March, April and May 2013). Coarse and fine BOM (Coarse = >1 mm; Fine = > 350 µm and ≤1 mm) was sampled on each occasion using a randomly positioned Surber sampler

($n = 6$ replicates per reach; area 0.1 m^2 ; mesh aperture $330 \text{ }\mu\text{m}$; sampling depth 10-15 cm) and was preserved on-site in 70% industrial methylated spirit (IMS; Fisher Scientific, UK). In the laboratory, all macroinvertebrates were separated from debris and preserved in 70% IMS. The remaining material was then thoroughly rinsed under tap water to remove sediment and separated into coarse ($>1 \text{ mm}$) and fine ($> 350 \text{ }\mu\text{m}$ and $\leq 1 \text{ mm}$) size fractions using graduated sieves (Endecotts Ltd., UK), then air-dried and weighed to the nearest 0.0001 g . Coarse and fine SOM (Coarse = suspended particles $>1 \text{ mm}$; Fine = suspended particles $>10 \text{ }\mu\text{m}$ and $<1 \text{ mm}$) were sampled at the lower end of each reach on each occasion ($n = 3$ replicates per reach). Fine SOM was sampled by filtering 100 L of stream water through a stacked pair of $10 \text{ }\mu\text{m}$ and 1 mm mesh filters. Coarse particulate matter concentrations were estimated separately (due to lower concentrations of coarse particles in suspension) by diverting larger volumes of stream water (range = 240-10,000 L; mean = 1805.7 L) through a PVC pipe fitted with a 1 mm mesh filter and a flow meter (Wallace *et al.* 2006). Upon collection, all SOM samples were refrigerated at $\sim 4 \text{ }^\circ\text{C}$, returned to the laboratory and frozen within 24 h. Freeze-dried SOM samples were ground, homogenised and subsampled ($3 \text{ mg} \pm 0.3 \text{ mg}$) for analysis of elemental (C, N) and stable isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) composition on a mass spectrometer (University of California Davis Stable Isotope Facility). Frozen SOM samples were freeze-dried at $-20 \text{ }^\circ\text{C}$ for 48-72 h and then weighed to the nearest 0.0001 g . All BOM and SOM samples were corrected for inorganic content by combusting a subset ($\sim 1/3$) of samples from each site at $550 \text{ }^\circ\text{C}$ for 5 h, and applying an ash-free conversion factor.

5.2.4 Data analysis

To assess the impact of the simulated riparian restoration on BOM and SOM stocks, each response variable was modelled using a linear mixed-effects model using the *lmer* function within the *lme4* package in R (Bates *et al.* 2015), with ‘Time’ (Before, After), ‘Reach’ (Control, Impact) and their interaction (‘Time x Reach’) as fixed terms. ‘Month’ and ‘Site’ were included as random terms, which accounted for unexplained temporal variation likely to affect all locations (e.g. seasonal variation or antecedent flow condition) and the non-independence of samples collected from the same site. All models were fitted using restricted maximum likelihood (REML) validated by visual inspection of the distribution of the standardised residuals versus the fitted values and of the distribution of the random effects (Zuur *et al.* 2009). The p -values of the fixed effects were estimated using conditional F -tests based on Kenward–Roger approximation for

degrees of freedom (Kenward and Roger 1997), using the R package *pbkrtest* (Halekoh and Højsgaard 2014). The predictive power of the model parameters (i.e. marginal R^2 ; the proportion of variance explained by the fixed factors alone, and conditional R^2 ; the proportion of variance explained by both the fixed and random factors) were estimated using the *r.squared.GLMM* function in the R package *MuMin* (Nakagawa and Schielzeth 2013; Bartón 2015).

5.3 Results

5.3.1 Stream flow conditions during the study

During the study period, representative stream discharge records showed that stream flow conditions were highly variable during the study period, ranging between 0.069 and 3.230 $\text{m}^3 \text{s}^{-1}$ with an overall median of 0.142 $\text{m}^3 \text{s}^{-1}$ (Figure 5.2). Two storm flow events at approximately 1 and 4 weeks into the experiment following litter addition caused numerous leaf packs to be dislodged and transported from the impact reaches, which were subsequently re-stocked with freshly filled leaf packs. On the first occasion, between 7 and 60% of all leaf packs were lost from all but one of the impact reaches. On the second, only one site was affected, losing 40% of all leaf packs.

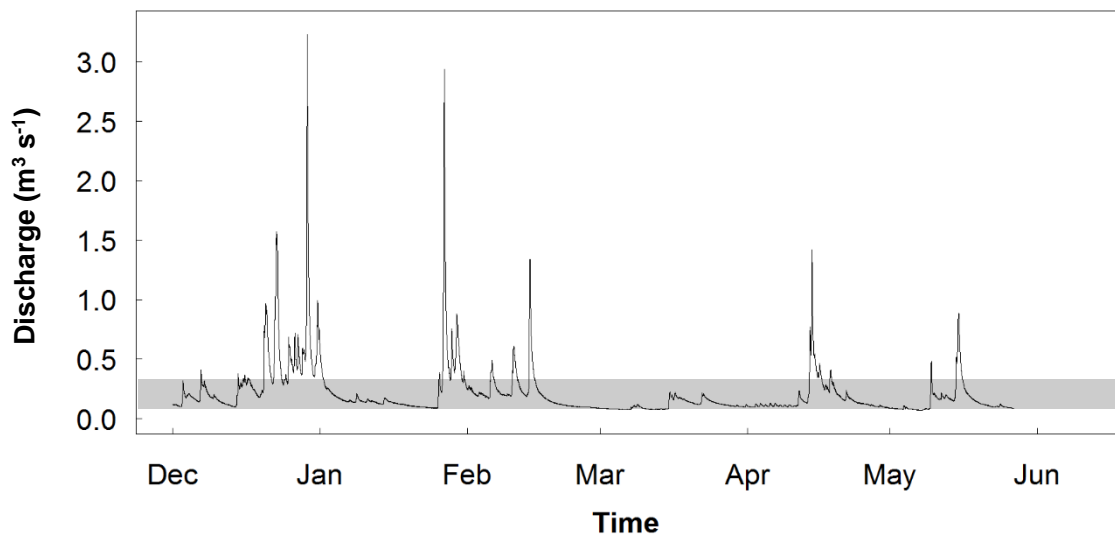


Figure 5.2. Example 15-minute stream discharge ($\text{m}^3 \text{s}^{-1}$) recorded at the Llyn Brianne Stream Observatory (study site L1) during the study period (December 2012 – June 2013). Shaded band depicts the range of stream flows under which organic matter sampling took place. Contains Natural Resources Wales information © Natural Resources Wales and database right.

5.3.2 Benthic particulate organic matter

Aside from losses owing to high flow events, the presence of leaf packs and retention nets ensured that standing stocks of broadleaved litter was much more abundant in the impact reaches than in a nearby reference broadleaf site from January to May (Figure 5.3). However, the leaf addition had no significant effect upon coarse or fine BOM at the reach scale, as demonstrated by the non-significant time x reach interactions (Table 5.1; Figure 5.4; Appendix C; Figures C.1-2). Overall, there were no significant differences observed in coarse or fine BOM between impact and control reaches, or between time periods.

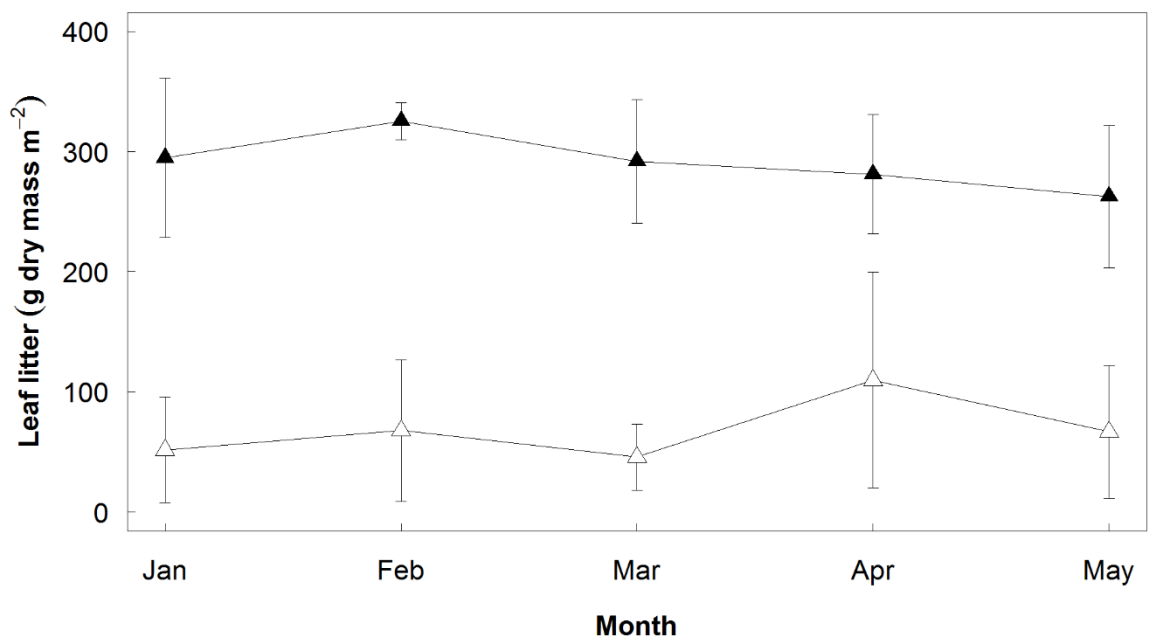


Figure 5.3. Mean (± 1 S.E.) standing stocks of leaf litter across all impact reaches (black triangles) after riparian restoration simulation (January-May 2013) relative to those observed in a nearby reference broadleaf site (open triangles) during corresponding months in 2011-2014.

5.3.3 Suspended particulate organic matter

The concentration and composition of coarse and fine SOM were unaffected by the litter addition, as shown by the non-significant time x reach interactions across all suspended POM responses (Table 5.1; Figure 5.5, Appendix C; Figures C.3-10). Instead, observed differences among reaches and time periods appeared to reflect background spatial and temporal variability as opposed to any effect attributable to the litter addition *per se*.

Suspended CPOM concentrations did not differ between reaches, or between time periods (Figure 5.5a), but $\delta^{13}\text{C}$ signatures were higher in the impact reaches than the control reaches throughout the experiment (both before and after litter addition; Figure 5.5e). The C:N ratios (Figure 5.5c) and $\delta^{15}\text{N}$ signatures (Figure 5.5g) of suspended CPOM, however, showed no differences between reaches or time periods. Suspended FPOM concentrations were significantly higher in the impact reaches than the control reaches throughout the study, and were marginally lower after litter addition in both reaches (Figure 5.5b). Meanwhile, suspended FPOM compositions (C:N ratios, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$; Figures 5.5d, f, and h, respectively) showed no differences between reaches or time periods.

Table 5.1. Summary of mixed effects models for benthic and suspended particulate organic matter, showing F (degrees of freedom in subscript) and *P*-values, as estimated by the Kenward-Roger approach for the effects of ‘Time’ (before and after litter addition), ‘Reach’ (control and experimental) and ‘Time x Reach’ interaction. R^2_{M} = Marginal R^2 (proportion of variance explained by fixed effects only); R^2_{C} = Conditional R^2 (proportion of variance explained by fixed + random effects). *P*-values <0.05 are highlighted in bold.

Response	Model parameters						Variance explained	
	Time		Reach		Time x Reach		R ² _M	R ² _C
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>		
<i>Benthic organic matter</i>								
<i>Coarse BOM</i>	0.37 _{1,3}	0.586	0.69 _{1,440}	0.406	0.14 _{1,440}	0.71	0.01	0.42
<i>Fine BOM</i>	0.08 _{1,3}	0.79	2.39 _{1,345}	0.123	1.32 _{1,345}	0.252	0.01	0.54
<i>Suspended organic matter (Coarse)</i>								
<i>Concentration</i>	3.53 _{1,4}	0.132	0.04 _{1,239}	0.839	1.27 _{1,239}	0.261	0.02	0.31
<i>C:N ratio</i>	0.31 _{1,4}	0.607	1.25 _{1,227}	0.265	2.39 _{1,226}	0.124	0.02	0.39
<i>δ¹³C</i>	4.86 _{1,4}	0.090	4.32 _{1,228}	0.039	0.40 _{1,227}	0.526	0.06	0.34
<i>δ¹⁵N</i>	0.34 _{1,4}	0.589	0.00 _{1,220}	0.978	0.05 _{1,220}	0.821	0.00	0.26
<i>Suspended organic matter (Fine)</i>								
<i>Concentration</i>	7.21 _{1,4}	0.055	6.15 _{1,232}	0.014	0.01 _{1,231}	0.929	0.11	0.61
<i>C:N ratio</i>	1.09 _{1,4}	0.353	0.02 _{1,227}	0.900	1.19 _{1,227}	0.277	0.06	0.83
<i>δ¹³C</i>	0.82 _{1,4}	0.415	0.01 _{1,223}	0.916	0.09 _{1,223}	0.765	0.03	0.85
<i>δ¹⁵N</i>	0.33 _{1,4}	0.597	0.12 _{1,215}	0.726	0.38 _{1,215}	0.536	0.01	0.67

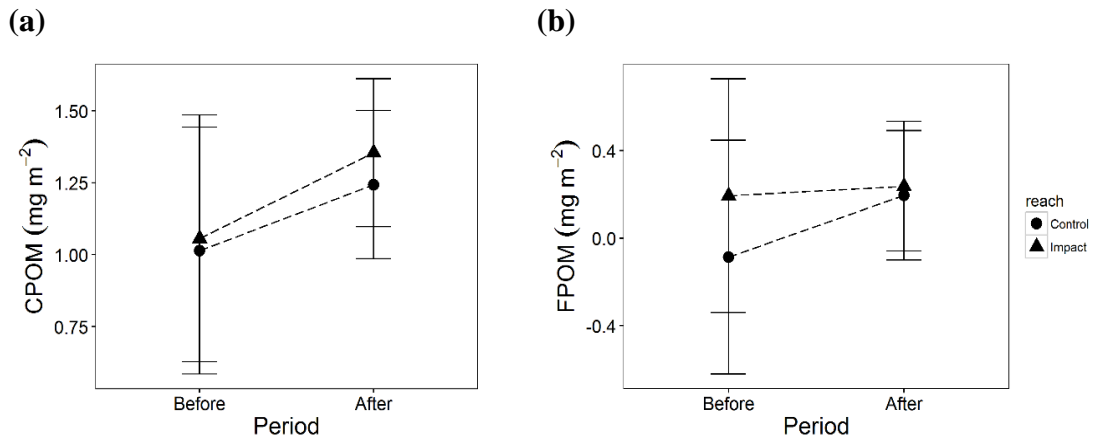


Figure 5.4. Predicted mean values (with 95% confidence intervals) of log-transformed (a) coarse and (b) fine benthic standing stocks of particulate organic matter (CPOM and FPOM, respectively) in impact and control stream reaches, before and after simulated riparian restoration.

5.4 Discussion

5.4.1 Summary

Despite maintaining leaf litter stocks in experimental reaches over a period of six months at levels that exceeded those observed in a nearby reference broadleaf site, there were no detectable increases in the amount of benthic or suspended particulate organic matter in response to the manipulation. Furthermore, there were no shifts in the elemental or isotopic composition of suspended particulate organic matter that would indicate an increased contribution of organic matter from terrestrially-derived leaf litter following the litter addition. Overall, observed differences among reaches and time periods seemed to reflect background spatial and temporal variability as opposed to any effects attributable to the litter addition *per se*, as indicated by the relatively large proportion of the variation accounted for by the random effects.

5.4.2 Effects of simulated riparian restoration on benthic and suspended organic matter

This study aimed to simulate riparian restoration by enhancing the input and retention of leaf litter to reaches of historically deforested streams. In doing so, average leaf litter standing stocks were elevated to levels that exceeded those observed in a nearby reference broadleaf stream (Figure 5.3), and were within the range of those observed in woodland streams elsewhere in the world (1 to 1300 g AFDM m⁻²; Jones, 1997; Abelho 2001).

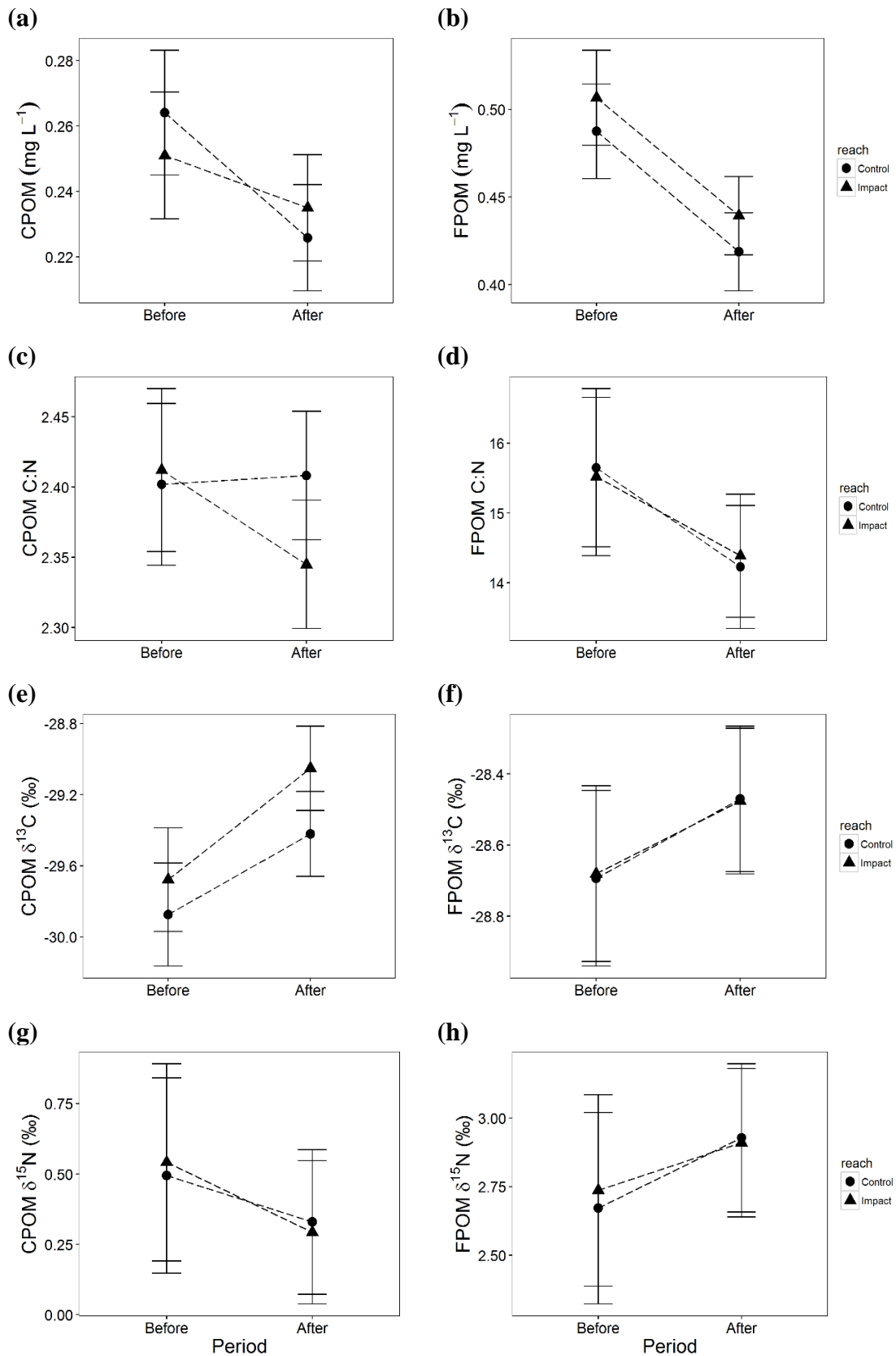


Figure 5.5. Predicted mean values (with 95% confidence intervals) of (a-b) concentrations, (c-d) C:N ratios, (e-f) $\delta^{13}\text{C}$ values, and (g-h) $\delta^{15}\text{N}$ values of suspended coarse and fine particulate organic matter (CPOM and FPOM, respectively) in impact and control stream reaches, before and after simulated riparian restoration.

Despite this clear manipulation, a concomitant increase in benthic standing stocks of CBOM was not detected at the reach scale. This discrepancy, coupled with visual observations of leaf litter cover within the impact reaches during the study period, suggests that the added leaf litter may have remained in highly localised patches of naturally formed and/or artificial leaf packs throughout the study period. Furthermore, any loose litter that was distributed among the impact reaches following litter addition may have been transported downstream during high flows (Hoover *et al.* 2010; see Chapter 4). In a study on short-term leaf retention in small streams, Hoover *et al.* (2010) demonstrated that leaves tend to be trapped in exposed locations within the stream reach, making them susceptible to transport as discharge increases and are therefore less stable in space and time than smaller particles. The resultant patchiness of leaf litter within the impact reaches in the present study could therefore mean that any overall, reach-scale increase in CBOM was unlikely to be detected based on small-scale estimates (i.e. using replicate Surber samples), despite the presence of ‘foreign’ leaf litter in some benthic samples (personal observation).

Given that there was no apparent increase in CBOM following litter addition, the concurrent lack of increase in FBOM was to be expected. This could be because the generation of fine fragments from the added leaf litter may have been curtailed in the first half of the experiment due to limited biological activity in colder winter temperatures (Cuffney *et al.* 1990; Gillooly *et al.* 2001), coupled with the recalcitrant nature of the added leaf litter, resulting in relatively slow litter breakdown rates (Webster and Benfield 1986). While an immediate increase in fine particles of BOM may not have been expected following litter addition, a delayed increase was predicted by the end of the experimental period. By this time, artificial leaf packs had been retained within the channels for approximately five months, which, in theory, would have allowed microbial colonisation of leaf litter to occur, allowing increased palatability and fragmentation by invertebrates (Kaushik and Hynes 1971; Benke *et al.* 1988), and a subsequent increase in the generation of fine organic matter particles (Cuffney *et al.* 1990). There was, however, no apparent increase in FBOM by the end of the experiment (Appendix C; Figure C.2). This suggests that any fine organic matter particles that may have been generated either occurred in quantities too low to be detected, and/or were more readily transported downstream than they were to be retained on the stream bed (Speaker *et al.* 1984; Thomas *et al.* 2001).

If CBOM and any associated FBOM were indeed transported downstream rather than being retained within the impact reaches, then an increase in SOM concentrations following litter addition could have provided some support for this scenario. A concomitant shift in isotopic and elemental compositions of SOM towards more terrestrial signals could also have supported this scenario. In the absence of such responses, however, and since the SOM sampling frequency provided only ‘snapshots’ within the full range of flow conditions (Figure 5.2), it was not possible to directly determine whether the downstream transport of CBOM and FBOM could explain the lack of increase in BOM in the impact reaches following litter addition. The loss of numerous artificial leaf packs following two high flow events does, however, suggest that under high flow conditions the streams would be capable of re-suspending BOM from their beds and exporting it downstream. Furthermore, other studies have demonstrated that the vast majority of organic matter export occurs during high flow events (e.g. Eggert *et al.* 2012; Chapter 4). It is also possible that any changes in SOM concentrations, at least in the fine fraction, could have been too small to be detected above the high levels of background temporal and spatial variability among sampling occasions and stream reaches independent of the leaf additions (Appendix C; Figure C.4).

In general, inputs of organic matter from terrestrial sources are expected to increase the C:N ratios and $\delta^{13}\text{C}$ values of SOM (Finlay and Kendall 2007). Recent data collected from headwater streams near to the current study suggest that any shifts in SOM composition may be subtle and difficult to detect (Chapter 3). For example, the isotopic and elemental compositions of leaf litter from broadleaved woodland streams were not markedly different from other sources of organic matter in conifer or moorland sites (Chapter 3, Figures 3.2 and 3.3; Appendix C, Figure C.11). Unsurprisingly, therefore, CSOM in a broadleaved woodland stream was intermediate between the conifer and moorland streams in terms of C:N ratios and $\delta^{13}\text{C}$ signatures (Chapter 3, Figure 3.2). This, coupled with the high temporal variability observed in CSOM $\delta^{15}\text{N}$ signatures (Appendix C, Figure C.7), suggests that an increased ‘broadleaf signal’ may not have been detectable in CSOM following litter addition in this experiment. Although the previous study showed that FSOM had higher mean C:N ratio in the broadleaf stream (17.6 ± 0.2 S.E.) by comparison with the conifer and moorland streams (14.3 ± 0.1 ; Figure 3.2), these values were within the range of those observed within the control reaches of the study sites in the present study (9.5 – 19.5; Appendix C, Figure C.11). Furthermore, the likely

slow breakdown rates of leaf litter mentioned previously suggests that overall a ‘broadleaf signal’ within FSOM would have been too small to detect following litter addition within the time frame of this experiment.

5.4.3 Challenges in simulating and experimentally manipulating natural systems

Some significant challenges are inherent in attempting to simulate experimentally real conditions in natural systems. In the case of simulating riparian restoration of headwater streams, this includes the difficulty in mimicking the high level of connectivity that exists between streams and their terrestrial surroundings in terms of organic matter input, and in working in systems that have a high level of ‘background noise’.

Under non-experimental reference conditions, it is likely that additional processes would result in higher standing stocks of BOM, which may only be observed under well-established conditions. For example, any downstream losses of BOM would have been replenished by the continual supply of organic matter from the adjacent riparian zone via lateral transport. Indeed, lateral inputs form a substantial proportion of total annual litter supplies to streams, and extend well beyond periods of peak leaf fall (Benfield 1997; Kochi *et al.* 2010; Hart *et al.* 2013). In addition, inputs from upstream or from the re-surfacing of buried OM (Cornut *et al.* 2012; see also Chapters 2 and 4) are also likely to replenish downstream losses of organic matter within a given reach under natural conditions. Furthermore, despite attempts to mimic ‘wood jams’ (see Section 5.2.2, above), it is unlikely that they achieved the same channel complexity and subsequent OM retentiveness that is often observed in the presence of in-stream wood (e.g. Gurnell *et al.* 2002; Pretty and Dobson 2004a; Flores *et al.* 2011; Eggert *et al.* 2012; Koljonen *et al.* 2012). While higher standing stocks of organic matter have been observed in broadleaf streams by comparison with conifer and moorland streams (Chapter 2), others have demonstrated that the effects of increased broadleaved tree cover on organic matter stocks may only become apparent once catchment cover is extensive (Thomas *et al.* 2016). Nevertheless, these examples demonstrate the strong influence of riparian and wider catchment land cover on in-stream organic matter stocks. As such, the scale of this simulation experiment may have been insufficient for any differences in organic matter stocks to parallel those that are generally observed between treeless and established woodland streams.

The high level of ‘background noise’ that is inherent within these complex systems may have meant that any marginal responses to the BACI treatment were undetectable. Indeed, any significant differences that were observed in this experiment reflected background spatial and temporal variability, as opposed to any effects of the litter addition *per se*. In modelling the effects of the BACI treatment, for example, random factors in the model that accounted for spatial (i.e. ‘site’) and temporal (i.e. ‘month’) variability explained a large amount of the variation in the data (Table 4.1). Even after accounting for this variability, some responses differed between reaches before the litter addition had occurred, or showed general increasing or decreasing trends from before to after the litter addition. Indeed, BOM and SOM show high levels of intra- and inter-annual variability in headwater streams, both in terms of quantity and composition (see Chapters 2 and 3). While the BACI design would have accounted for this ‘background noise’ (Underwood 1994), this highlights the heterogeneous nature of these systems, and the subsequent need for a strong signal if a response is to be detected. In the terms of predicting the likely response of stream ecosystems to restoration efforts, or indeed increasing the likelihood of restoration success, the overall extent of restoration could be an important factor dictating the outcomes and must be considered (Palmer *et al.* 2010). For example, the length of restored reach may need to extend over several kilometres and monitoring may need to span longer timescales for ecological responses to restoration to become apparent (Hering *et al.* 2015; Kail *et al.* 2015).

5.4.4 Conclusions

This study highlights the challenges in making short-term, experimental assessments of the potential response of headwater streams – highly dynamic natural systems – to riparian restoration. Overall, there was no signal of litter addition detected, despite one of the largest scale leaf addition experiments ever carried out. This non-response to the manipulation, however, does not necessarily mean that riparian restoration would not affect organic matter stocks in headwater streams under non-experimental conditions. Indeed, several studies have demonstrated the potential for riparian broadleaved trees to enhance organic matter stocks in headwater streams. It remains possible that any responses were too small to detect above the high levels of background noise, that such responses may require longer time scales to become apparent, or that the extent of the manipulation was insufficient to bring about a detectable response within the time frame of this experiment. Further work is needed in order to determine the viability of riparian

restoration as an adaptive strategy for mediating the impacts of climate change and wider catchment land use change on headwater stream ecosystems and restoring ecosystem functions. This could include increasing the extent of restoration through larger-scale experiments, spanning longer timescales (i.e. incorporating seasonal and annual variability) and reach lengths, and mimicking more closely the annual supply of litter inputs (*sensu* Dobson *et al.* 1995; Bañuelos *et al.* 2004). This may allow greater stocks of organic matter to be distributed, retained and biologically processed within experimental reaches, and may therefore allow for stronger inference.

CHAPTER 6: General Discussion

6.1 Context and purpose of the project

Climate change is having widespread impacts on ecosystem service sustainability, while human activity continues to degrade the very ecosystems that support these services (Millennium Ecosystem Assessment 2005; UK National Ecosystem Assessment 2011; Runting *et al.* 2017). With a growing human population, pressure on ecosystems to deliver goods and services to sustain societal needs is likely to intensify (Godfray *et al.* 2010), so that decision makers now urgently require the evidence-based, high-certainty solutions to respond to these global challenges. While there is a significant body of ecosystem science and ecology to answer some of these needs, predictable, quantifiable and large-scale evidence is still scarce or uncertain. Uncertainties stem not least from gaps in knowledge, for example on the quantitative links between biodiversity and ecosystem services, but also from methodological challenges that are inherent in addressing global change questions (Durance *et al.* 2016). As a consequence, robust management solutions for securing ecosystem resilience and service sustainability are often difficult to identify (Runting *et al.* 2017).

This is the context from which this study arises, building around a model – freshwater ecosystems – that has proven to be particularly suited to understand the processes that underpin ecosystem function and ultimately the level of services that ecosystems can provide. To start with, the study has been able to build on a long standing body of freshwater research (Chapter 1) that has been at the forefront of large-scale ecosystem science, with famous experiments at Hubbard Brook (e.g. Fisher and Likens 1973) only one of the many examples where links between catchment management, biodiversity and ecosystem function were quantitatively evidenced. Perhaps just as importantly, the central position of these diverse ecosystems at the interface between land and sea, confers them with a key role in the transfer of energy that fuels everything from microbes to fish and birds across the globe. This study, which explores how organic carbon sources captured from bankside vegetation, are stored, processed and released, contributes to this body of research on energy transfers, and its findings detailed below offers some key evidence for decision makers.

6.2 Synthesis and lessons learnt

6.2.1 On the response of freshwater ecosystems to climate change

A warmer world is likely to intensify the global hydrological cycle (Huntington 2006), resulting in more frequent floods and droughts (Milly *et al.* 2005; Bates *et al.* 2008), with small, headwater streams being particularly responsive because of their geo-morphology. Already, marked changes in stream flow regimes are being observed at higher latitudes and altitudes, including increases in the magnitude, frequency and duration of high flow events (e.g. Birsan *et al.* 2005; Biggs and Atkinson 2011; Hannaford and Buys 2012), highlighting the need to gather evidence for understanding and predicting the ecological responses of these ‘early-warning systems’ to climate change (Perkins *et al.* 2010).

The results presented in Chapters 2, 3 and 4 suggest that expected increases in the magnitude and duration of flood events under future climate change will re-distribute organic matter resources downstream within river networks, thereby reducing the quantity of detrital resources retained within headwater streams, but also potentially the quality of downstream carbon sources. Whether an increase in the *frequency* of flood events will deplete benthic standing stocks or exports of organic matter remains in question. Experimental evidence using outdoor mesocosms (Chapter 4) gave some mechanistic insight into CPOM dynamics during flood events, confirming that more CPOM is transported at higher flow rates, and that the majority of transport occurs during early stages of flood events. Similar, if not stronger, effects are expected for FPOM (Chapter 2), with this resource being smaller in size and therefore more susceptible to transport in high flows. Despite these observations, an increased frequency of flood events – whether simulated (Chapter 4) or natural (Chapter 2) – did not result in an overall reduction in benthic standing stocks of CPOM or FPOM, or a declining trend in the amount of CPOM exported downstream. In combination, these results suggest that thresholds in flood intensity exist above which the balance between transport and retention is compromised; imports from upstream and adjacent riparian zones are instead rapidly exported downstream, and depletion of organic matter stocks occurs. It is likely that such thresholds were, however, unattainable under experimental conditions, and infrequently encountered under natural conditions. Nevertheless, this study provides empirical support for previous suggestions that climate-induced shifts in precipitation

patterns will decrease organic matter retention in headwater streams (Kominoski and Rosemond 2012).

A reduction in the amount of basal resources retained within headwater streams, particularly structurally complex resources that particulate organic matter represents, could have far-reaching ecological and societal implications. Fewer resources at the base of the stream food web will ultimately reduce the amount of energy and matter available to be biologically processed and transferred to higher trophic levels (Wallace *et al.* 1997), and therefore limit overall food web productivity in the upper reaches of river networks. These effects will not simply be local to headwater reaches, but could extend beyond their aquatic boundaries and downstream: Streams, like many ecosystems, are open and permeable, and reciprocate subsidies to the adjacent terrestrial ecosystem in the form of emerging adult aquatic insects, which, in turn, provide important prey items for river birds (Polis *et al.* 2004; Marczak *et al.* 2007). Furthermore, while studies that investigate quantitatively the energetic contribution of headstreams to downstream rivers, estuaries and coasts are scarce, it is generally surmised that upstream contributions of organic matter are critical to the functioning of downstream ecosystems, including fish production (Wipfli *et al.* 2007). Consequently, findings from this work relating to the change in quantity and quality of upstream subsidies to lower reaches following climatic changes, are likely to have profound consequences on food webs downstream, potentially altering the sustainability of important services such as fisheries or shellfish provision. In fact, this work could even suggest that management choices for the uplands could be central to coastal economies and marine conservation.

6.2.2 On the management of river ecosystems to ensure resilience and continued service delivery in the face of global change

Given the potential scale at which altered processes in headwaters could impact on important societal issues, this study highlights the importance of adopting large-scale perspectives in management actions and conservation policies. One of the most widely advocated management strategies for mitigating the effects of human activity and climate change on freshwaters is riparian tree planting (e.g. Abell *et al.* 2007; Ormerod 2009; Palmer *et al.* 2009; Seavy *et al.* 2009), with increasing benefit evidence: Riparian trees can buffer against thermal and hydrological extremes, and regulate excess nutrients and sedimentation, and increase habitat complexity and regional biodiversity (e.g. Naiman *et*

al. 1993; Gurnell *et al.* 2002; Sweeney *et al.* 2004; Bradshaw *et al.* 2007; Garner *et al.* 2015).

As important, but scarcely explicitly investigated, is the potential role of riparian vegetation in restoring and protecting fundamental ecosystem functions – namely organic matter processes – that underpin the resilience and productivity of food webs (Naiman *et al.* 2012; Eloise and Pozo 2016). Chapters 2 and 3 demonstrated, however, that not all riparian vegetation is equal in this respect: Riparian broadleaves clearly most benefit streams both locally and downstream in terms of energetic resilience, by storing consistently higher levels of food resources in the form of benthic particulate organic matter, and transporting more carbon downstream in the form of suspended particulate organic matter than streams bordered by conifer plantations or moorland vegetation, even when climatic conditions exceed worst-case projections. Chapter 5 used a complementary approach to assess whether a similar riparian broadleaf effect could be triggered: Using reach-scale experimental manipulation, this experiment was one of the largest-scale attempts made to simulate riparian broadleaved tree planting in conifer and moorland catchments (*cf.* Dobson *et al.* 1995), and yet did not illicit the same response in terms of organic matter stocks. Though the mechanisms for these differences were not explicitly tested, a wealth of experimental evidence exists in the literature to suggest that streams bordered by mature broadleaved tree species not only supply more leaf litter to streams (Abelho 2001), but also have a greater retention capacity than their coniferous or moorland counterparts. This is due to the characteristics of the litter itself (e.g. Pretty and Dobson 2004a; Quinn *et al.* 2007; Cordova *et al.* 2008; Hoover *et al.* 2010) and the presence of large woody retention structures in the form of fallen branches and mature trees (e.g. Muotka and Laasonen 2002; Lepori *et al.* 2005; Flores *et al.* 2011; Eggert *et al.* 2012). Together these properties promote retention, longer-term storage, and thus a constant, heterogeneous supply of food resources to sustain a diverse array of stream organisms (Petersen and Cummins 1974; Webster and Benfield 1986; Moore *et al.* 2004; Rooney *et al.* 2006).

The disparity between these two approaches could serve to highlight the scale of experimentation, and indeed restoration efforts, needed to successfully re-establish complex stream-riparian linkages in deforested catchments. Indeed, the establishment of retentive headwater systems – capable of storing abundant organic matter along the entire river continuum – would involve large-scale efforts, resources and decades of tree growth

(Eggert *et al.* 2012). Moreover, planting trees in the riparian zone alone may not be sufficient: recent studies suggest that catchments with more extensive tree cover are capable of not only storing more organic matter (Thomas *et al.* 2016), but also moderating flood severity (Bradshaw *et al.* 2007; Marc and Robinson 2007; Chappell and Tych 2012; Rust *et al.* 2014). To effectively mitigate climatic effects on river ecosystem functions and services, therefore, widespread action must be implemented in policy and practice to protect and restore tree cover in headwater catchments. Firstly, headwater streams can no longer be neglected in major water policies, such as the European Water Framework Directive (Lassaletta *et al.* 2010; Biggs *et al.* 2016). Second, adaptive management actions should explicitly consider the fundamental importance of organic matter processes in supporting ecosystem function and resilience, and their sensitivity to future climate. These actions could include: (1) increasing organic matter supplies to river networks by enhancing broadleaved tree cover in headwater catchments via catchment-wide tree planting; (2) increasing the retentiveness of headwaters by introducing organic matter retention structures, such as log jams and boulders, to stream reaches; (3) allowing the development of mature woodlands along river margins to establish complex and sustainable stream-riparian linkages, and; (4) protecting existing natural woodlands in headwater catchments from deforestation to maintain complex ecological properties.

6.3 Future directions

To answer the most urgent stakeholder questions entails developing our capacity to understand and predict the likely ecological consequences of management interventions and climate change, in real life, large-scale settings. To aid in the development of this understanding, this study applied two complementary scientific approaches used in ecological global change research: observations and experimental manipulation in the field. In doing so, this study illustrated some of the major challenges that freshwater ecologists face in conducting experiments at sufficient scale to be able to predict ecological responses to real complex changes with more certainty, above the high levels of variability that exist in these natural systems.

The use of natural abundance stable isotopes in Chapters 3 and 5 to detect land use signals highlighted just how variable these natural systems can be. In these studies, isotopic signatures of both suspended POM and its potential sources exhibited large temporal

variability, with strong indications that additional unmeasured sources – namely microbes – were contributing to suspended POM in unknown proportions. Indeed, multiple sources of variability operate at different scales to affect the isotopic signatures of basal resources in freshwaters in ways that are still poorly characterised (Peipoch *et al.* 2012). This unexplained variability highlights the current limitations of these tools for quantifying the role of headwaters in subsidising downstream systems under future land use and climate scenarios. Nevertheless, by providing much-needed empirical data on isotopic variability in basal resources, this study makes an important step towards better determination of energy pathways in food web studies (Peipoch *et al.* 2012). At the same time, this work highlighted avenues for future research, such as estimating microbial biomass associated with different organic matter pools, and the degree to which they cause isotopic enrichment.

Observational, correlative field studies such as those reported in Chapters 2 and 3 are important to grasp the extent of natural variability, thereby allowing realistic predictions to be made. For example, these studies captured substantial interannual climatic variability, which provided a natural climate change gradient against which responses could be tested (Dunne *et al.* 2004). Such studies are resource intensive, however, with sampling often being restricted to snapshots in time and/or space (e.g. Cariss and Dobson 1997; Molinero and Pozo 2004; Mollá *et al.* 2006; Wallace *et al.* 2015). To avoid context-dependence and subsequent difficulties in generalising results, therefore, future observational studies of organic matter dynamics should incorporate high-frequency automated sampling techniques in the field. Such tools would improve mechanistic understanding of organic matter-discharge dynamics under realistic settings, for example during real flood events. In addition, by allowing greater temporal and spatial replication of field data, stronger predictions could be made of organic matter dynamics throughout entire river networks under future climate (Acuña and Tockner 2010), and catchment management scenarios.

By comparison with observational studies, conducting experimental manipulations in the field, such as the riparian land use (Chapter 5) and climate (Chapter 4) manipulations, have the benefits of constraining potential confounds and allowing stronger inferences about cause and effect (McGarigal and Cushman 2002). They also allow questions to be answered in a relatively short period of time (Dobson *et al.* 1995). On the other hand, creating realistic treatments in the field at sufficient scale is logistically and practically

challenging. Experimental treatments are therefore often implemented in a short space of time, constraining them to representing short-term responses (McGarigal and Cushman 2002; Dunne *et al.* 2004). Indeed, the overall non-response to the large-scale litter addition (Chapter 5) suggests that this experiment may have been limited in its scope, possibly in terms of duration or realism, for assessing the viability of riparian restoration as an adaptive management strategy. Future experimental approaches for determining the potential longer-term role of riparian broadleaved planting for supporting river ecosystem services could therefore be improved by incorporating multiple stages and scales of restoration in the form of differing litter supplies and retention structures. Realism could also be improved by spanning longer timescales and reach lengths, and mimicking more closely the temporal dynamics of leaf litter inputs (*sensu* Dobson *et al.* 1995; Bañuelos *et al.* 2004).

Mesocosm studies offer a strong compromise to overcome field-based challenges, and are being increasingly used in global change ecological research (Stewart *et al.* 2013). By potentially allowing more replication and control than observational studies and field experiments, as well as more realism than microcosm studies (Ledger *et al.* 2009), mesocosm experiments have the advantage of allowing researchers to gain a more detailed, mechanistic understanding of complex abiotic-biotic interactions in semi-natural settings. By manipulating flow regimes in outdoor mesocosms (Chapter 4), for example, it was possible to characterise CPOM dynamics during flood events within a three-month period. Future mesocosm experiments could explore inputs, exports, transport and retention of a range of other resource types, such as different leaf litter species, dissolved organic carbon (DOC) and benthic biofilm, under different flow regimes. Biotic responses to manipulated resources could also be measured to better understand the ecological implications of altered basal resources under different scenarios. In turn, such information could be used to develop comprehensive organic matter budgets, and advance understanding of upstream-downstream linkages within riverine landscapes (Webster 2007; Tank *et al.* 2010). Such studies would also allow better parameterisation of mechanistic models, which are often limited by gaps in process-based understanding (e.g. Acuña and Tockner 2010; Stenroth *et al.* 2014), but are useful tools for predicting future responses and informing management decisions. It is important to note, however, that mesocosms still lack the true extent of complexity and variability that exists in natural systems, such as riparian linkages and flood intensities (Chapter 4). In fulfilling the needs

of stakeholders, experimental manipulation in both natural and semi-natural systems can, however, strongly complement other approaches, such as large-scale comparative assessments, long-term monitoring of restoration projects, and modelling future scenarios. When combined, these approaches are central to advancing knowledge and finding real solutions to global change problems, and should be fully integrated into the freshwater ecologist's toolbox.

6.4 Conclusions

The findings of this study suggest that climate-driven changes in flow regimes will reduce organic matter retention in headwater streams, but that riparian broadleaves could be effective in mitigating these effects. Consequently, this study reinforces the notion that a broad ecosystem approach to climate change adaptation must be adopted and implemented. Specifically, headwaters must be explicitly considered in water policies, and actions must be taken to protect existing natural woodlands and support large-scale restoration in headwater catchments. This study also highlights the value of combining large-scale observational and experimental field studies to answering global change questions. Gaps in knowledge remain, however, and continued long-term monitoring is needed, along with large-scale field experimentation and mesocosm studies. These approaches will greatly improve our capacity to predict landscape-scale responses to future climate change and inform management actions.

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APPENDIX A

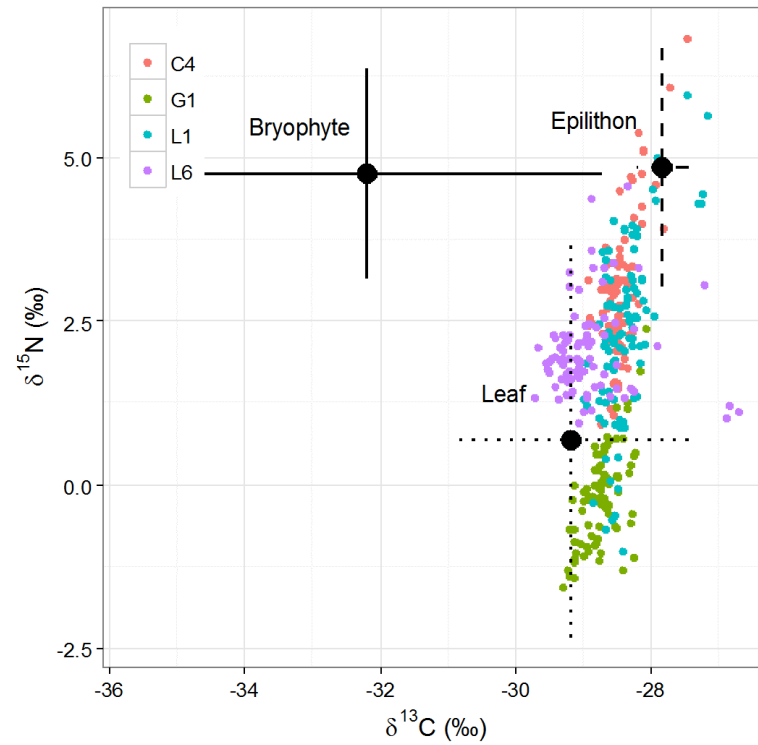
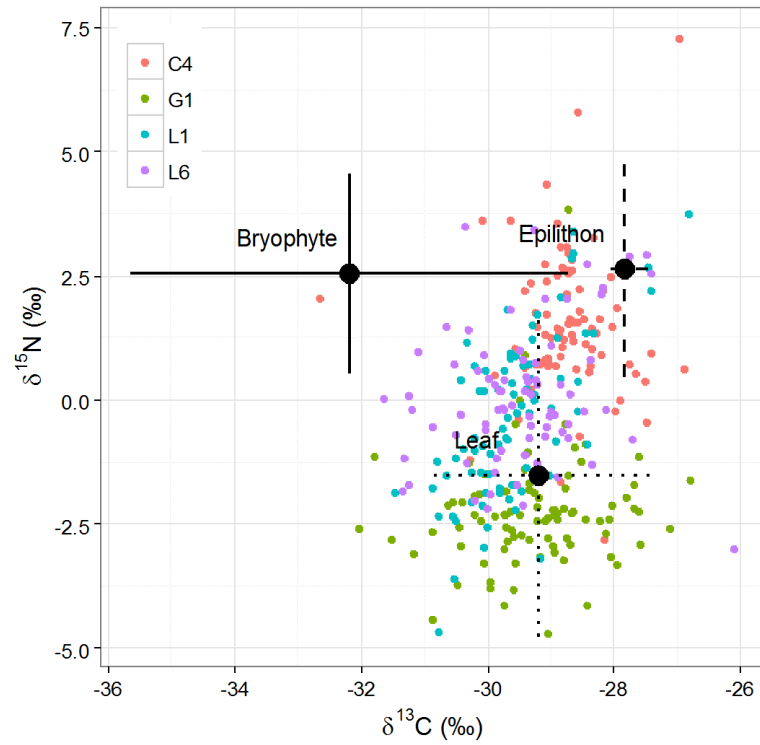


Figure A.1. MixSIAR isospace plot, showing $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ values of suspended (a) coarse and (b) fine particulate organic matter samples measured at the four study sites (C4 = acid moorland; G1 = broadleaved woodland; L1 = conifer forest; L6 = circumneutral moorland), and potential sources (bryophyte, epilithon and terrestrial leaf litter) adjusted for N enrichment (Section 3.2.6). Error bars indicate ± 1 S.D., which is the combined source and discrimination S.D.

APPENDIX B



Figure B.1. Site L3, looking upstream, with mesocosms situated on right-hand bank. Photo: Stephanie Ridge.



Figure B.2. Site L6, looking downstream, with mesocosms situated on right-hand bank. Photo: Marian Pye.



Figure B.3. Site L7, looking upstream, with mesocosms situated on left-hand bank. Photo: Marian Pye.

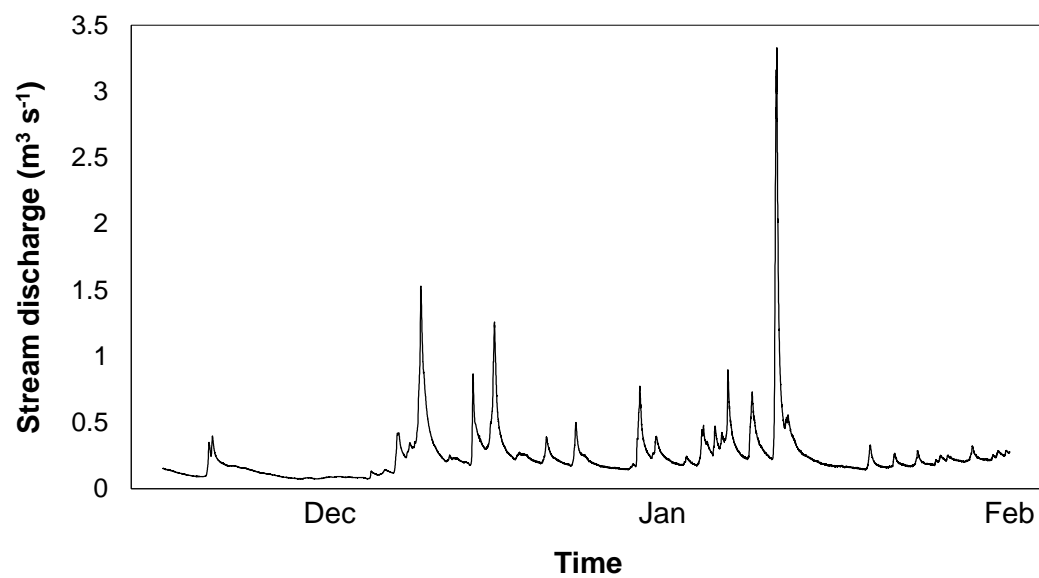


Figure B.4. Example stream discharge ($\text{m}^3 \text{s}^{-1}$) at a study site within the Llyn Brianne Stream Observatory over the period when experimental manipulations took place (Nov 2014 – Jan 2015).

APPENDIX C

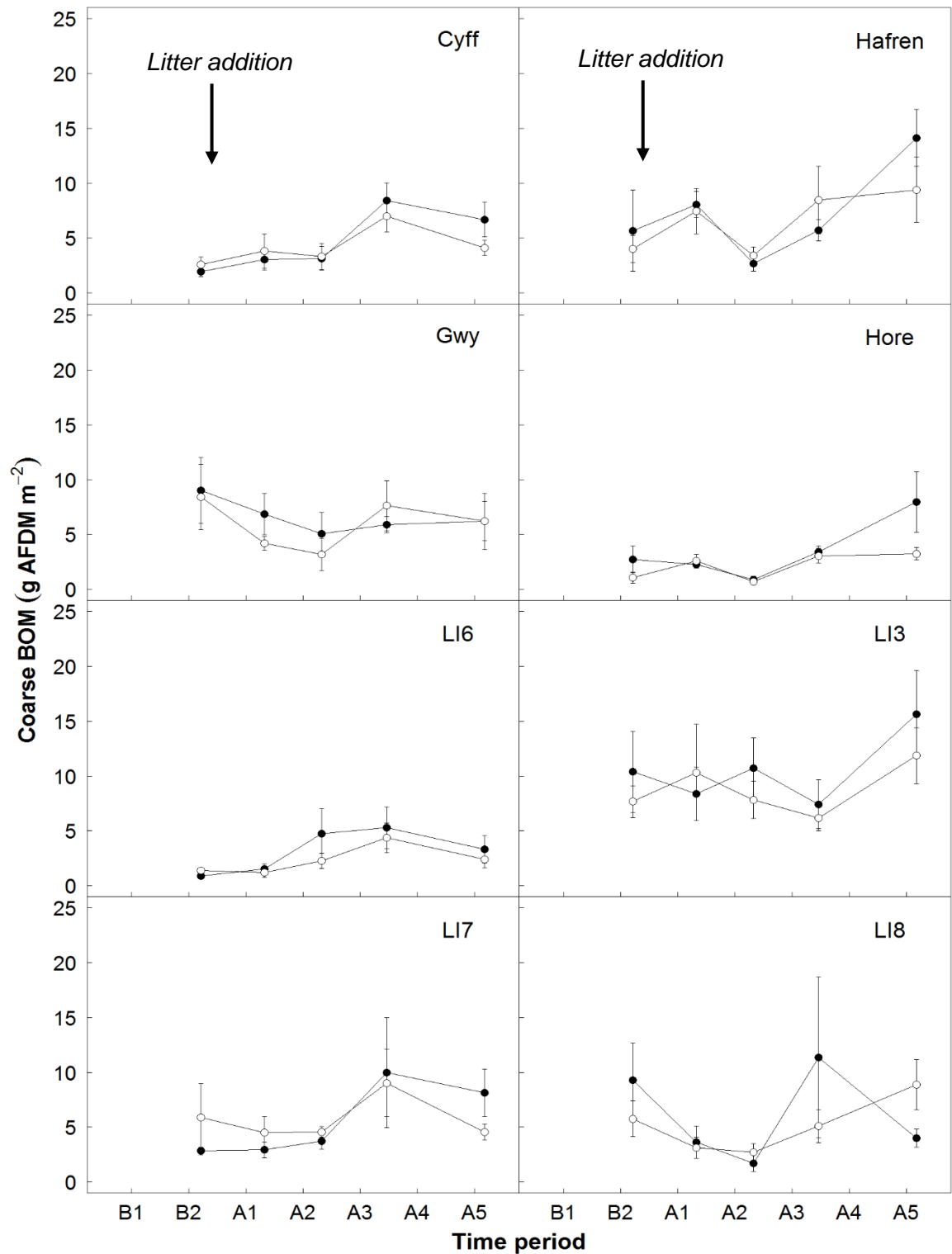


Figure C.1. Mean (± 1 S.E.) standing stocks of coarse benthic organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

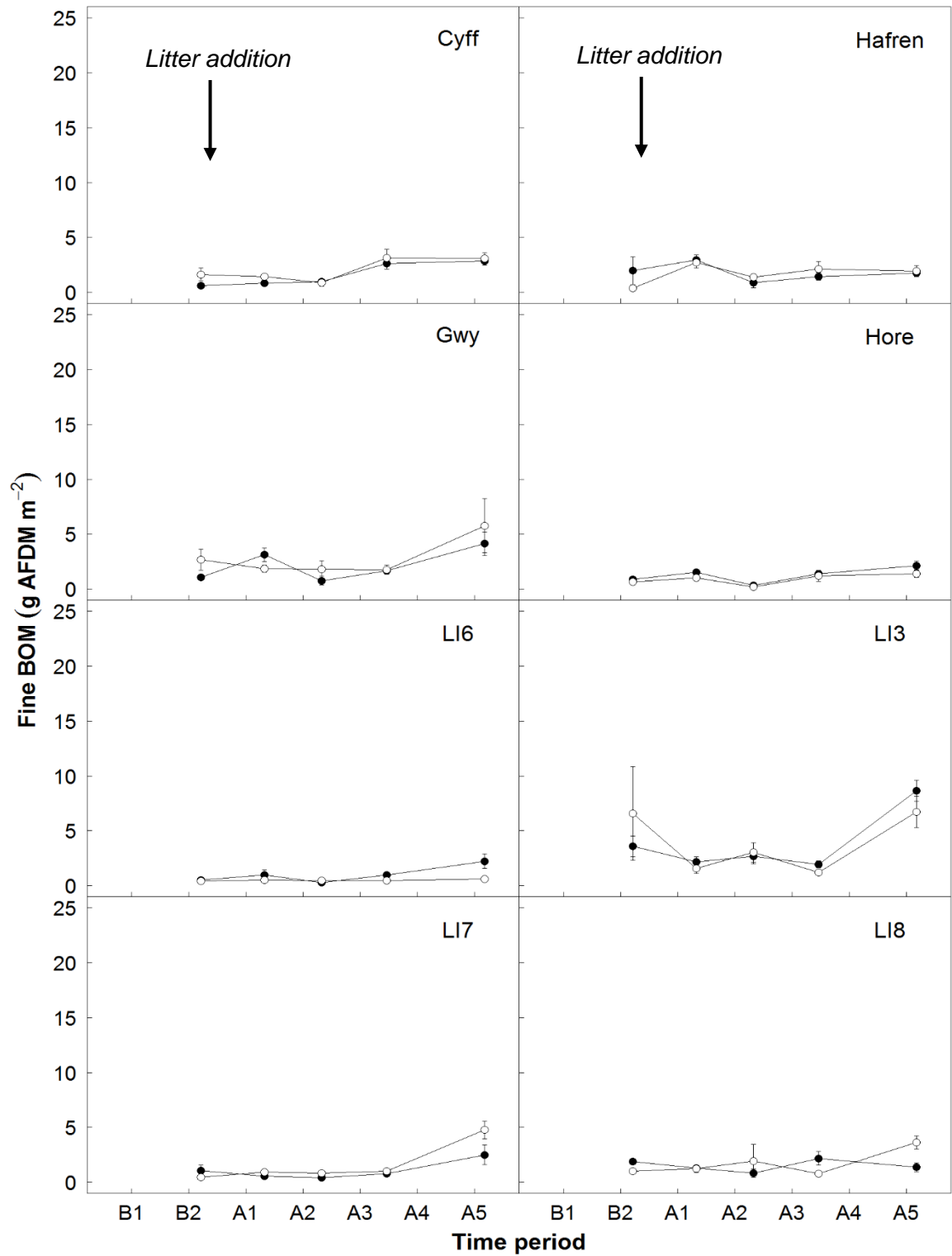


Figure C.2. Mean (± 1 S.E.) standing stocks of fine benthic organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

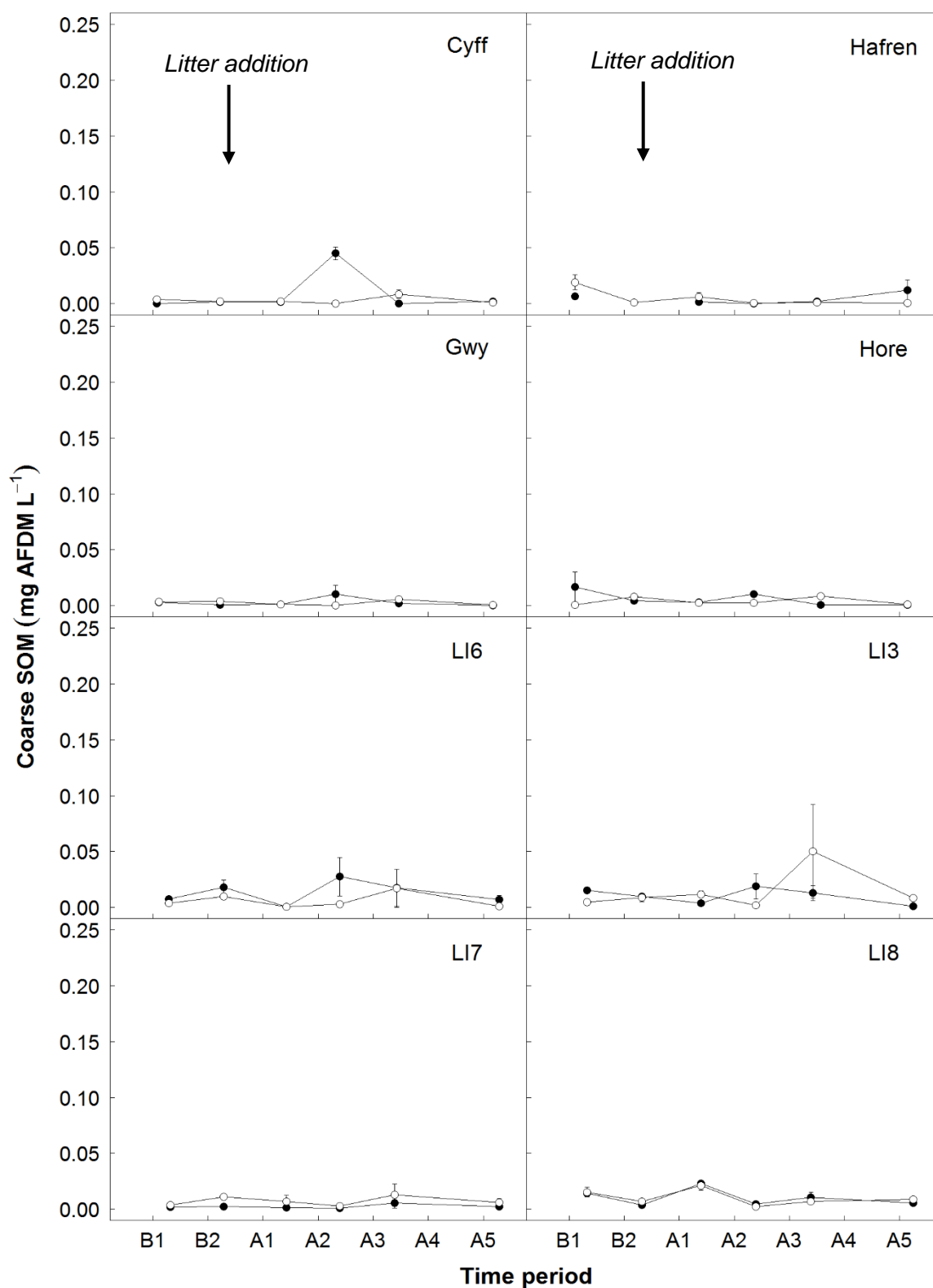


Figure C.3. Mean (± 1 S.E.) concentrations of coarse suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

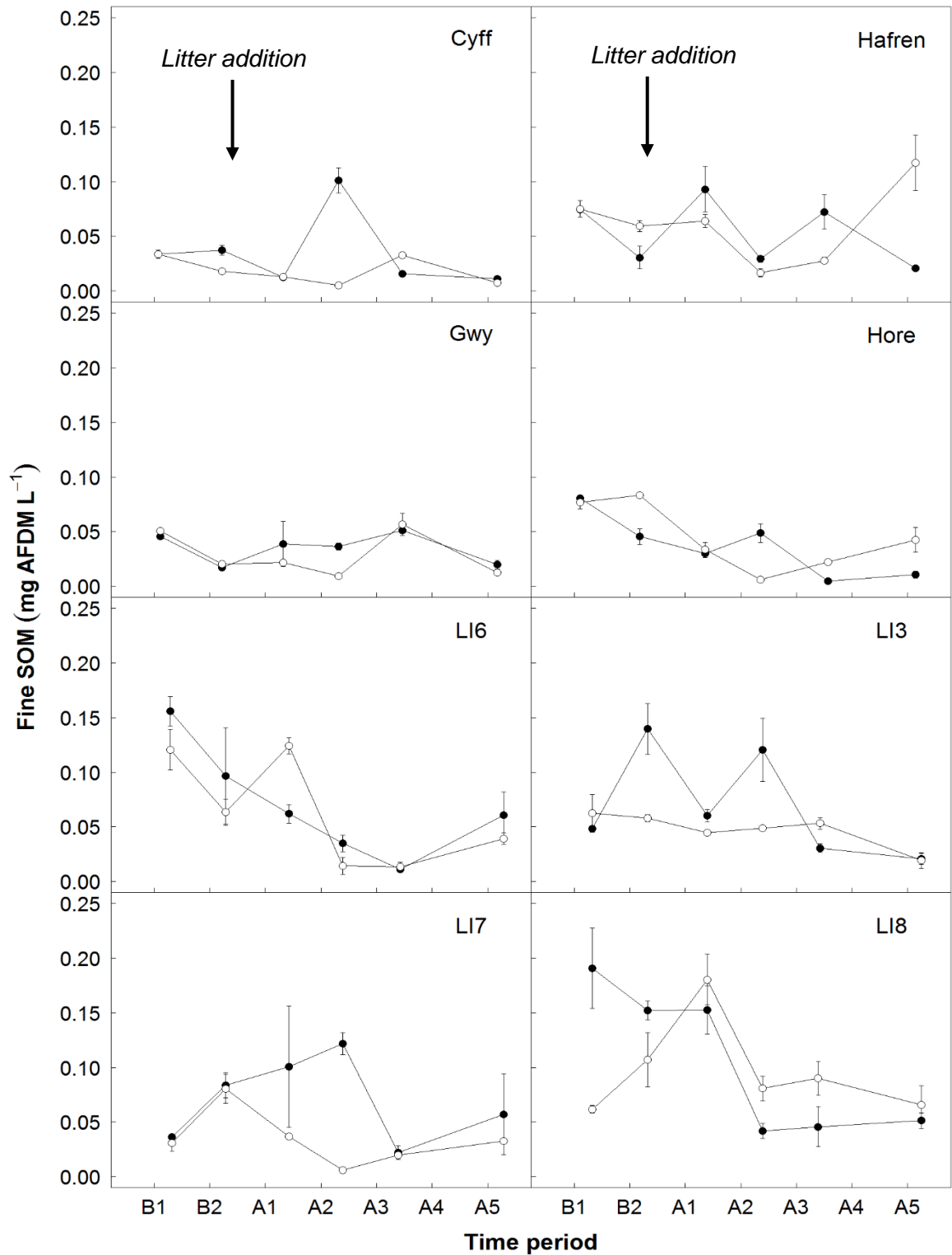


Figure C.4. Mean (± 1 S.E.) concentrations of fine suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

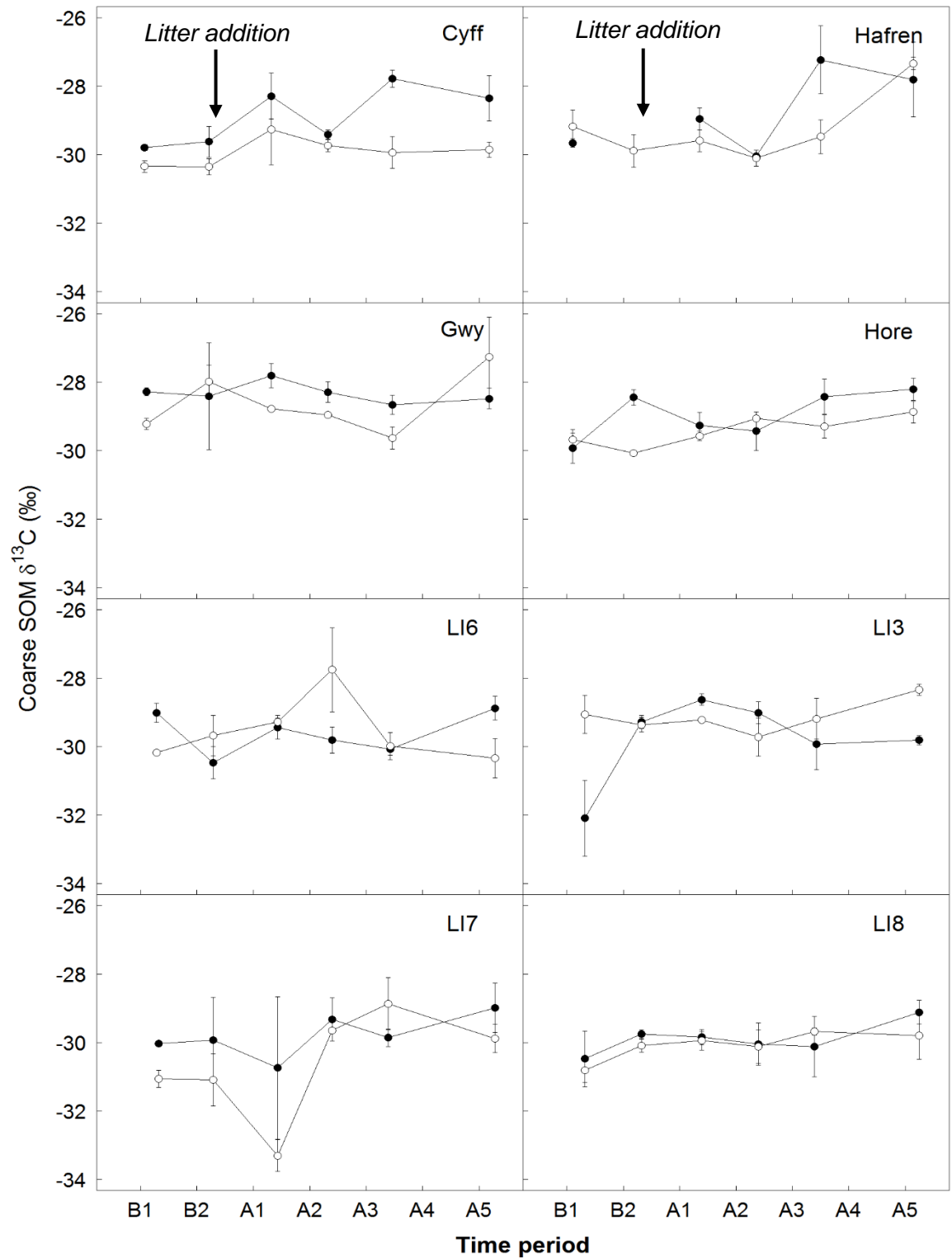


Figure C.5. Mean (± 1 S.E.) $\delta^{13}\text{C}$ of coarse suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

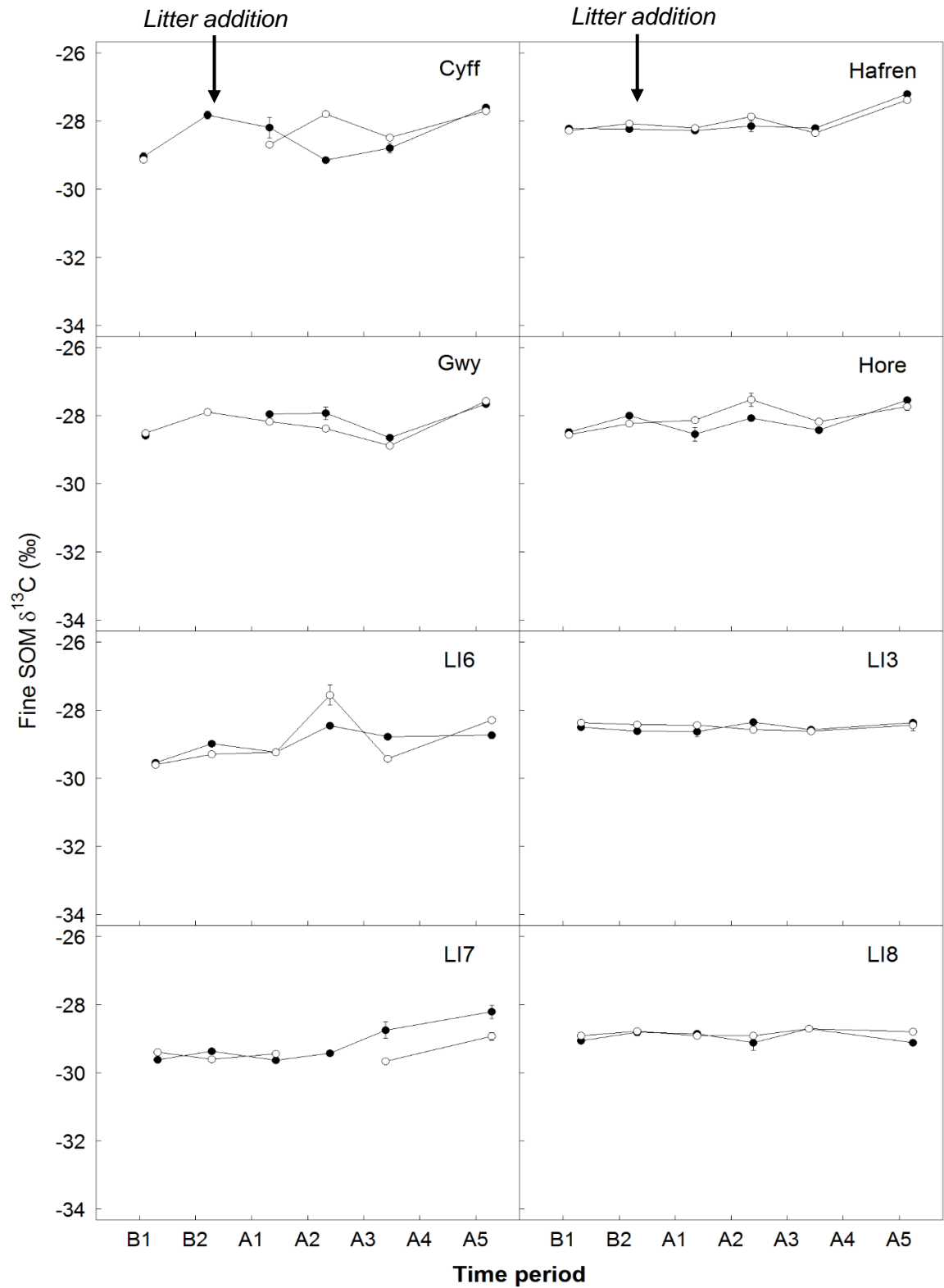


Figure C.6. Mean (± 1 S.E.) $\delta^{13}\text{C}$ of fine suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

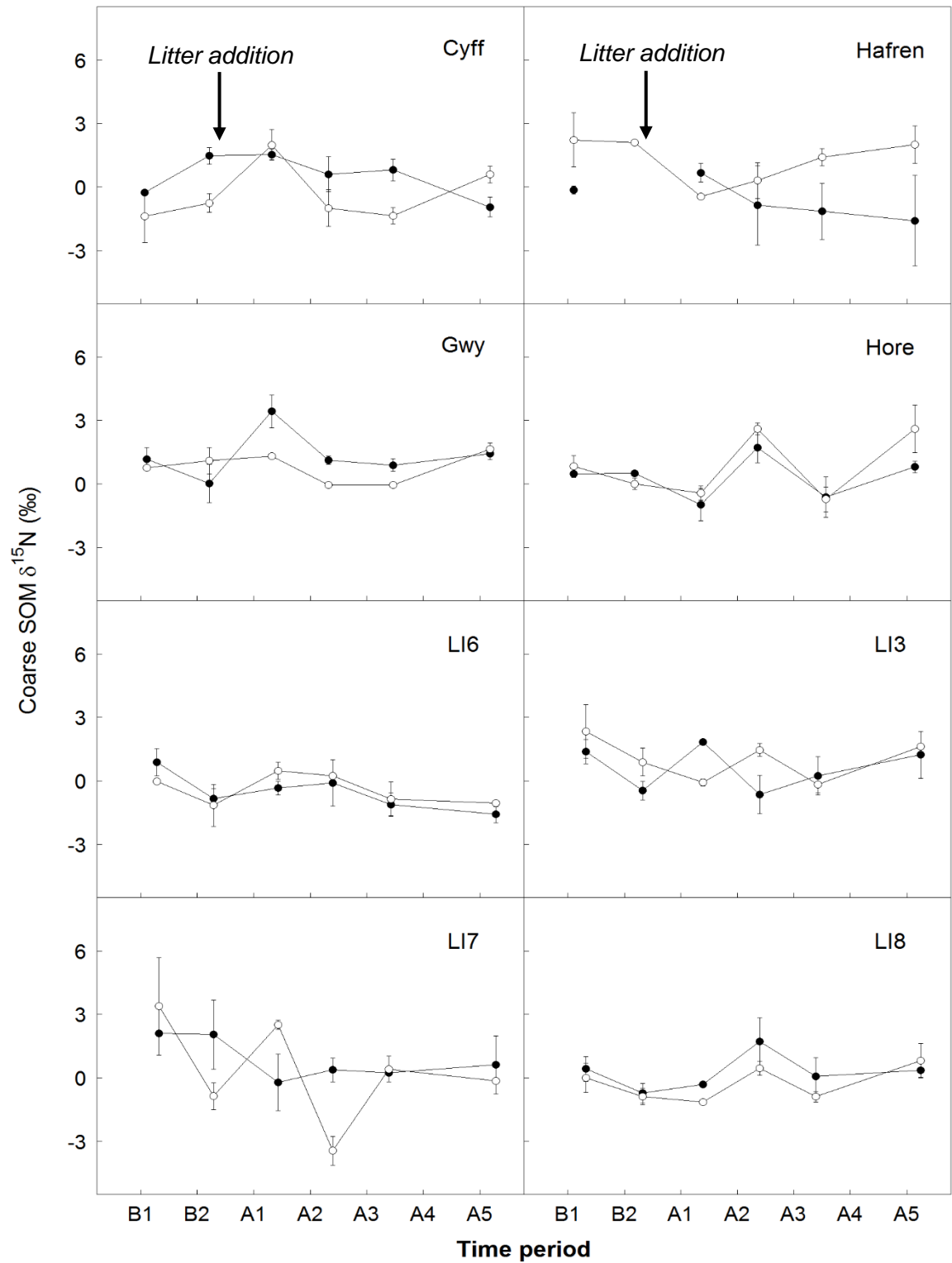


Figure C.7. Mean (± 1 S.E.) $\delta^{15}\text{N}$ of coarse suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

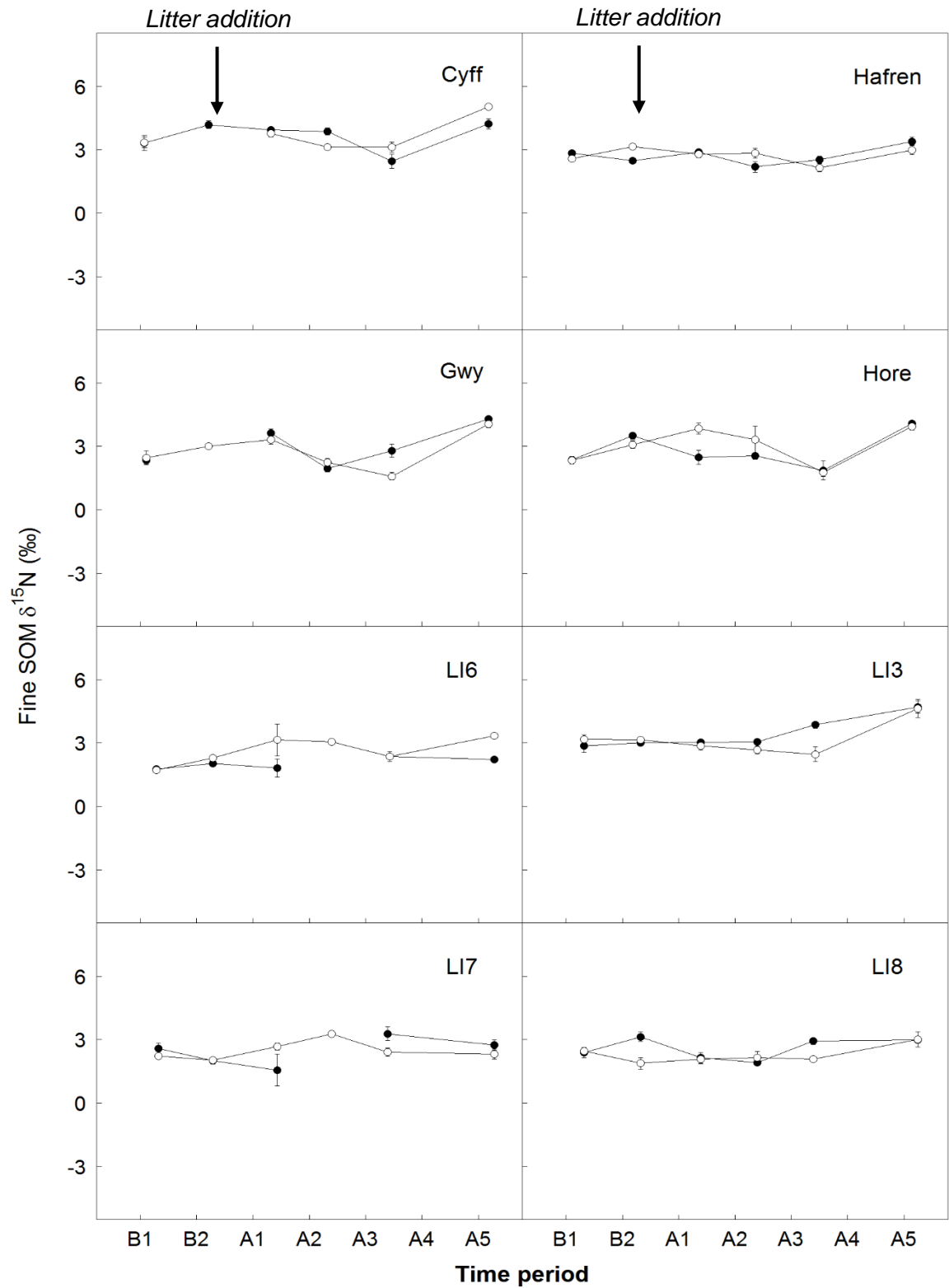


Figure C.8. Mean (± 1 S.E.) $\delta^{15}\text{N}$ of fine suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

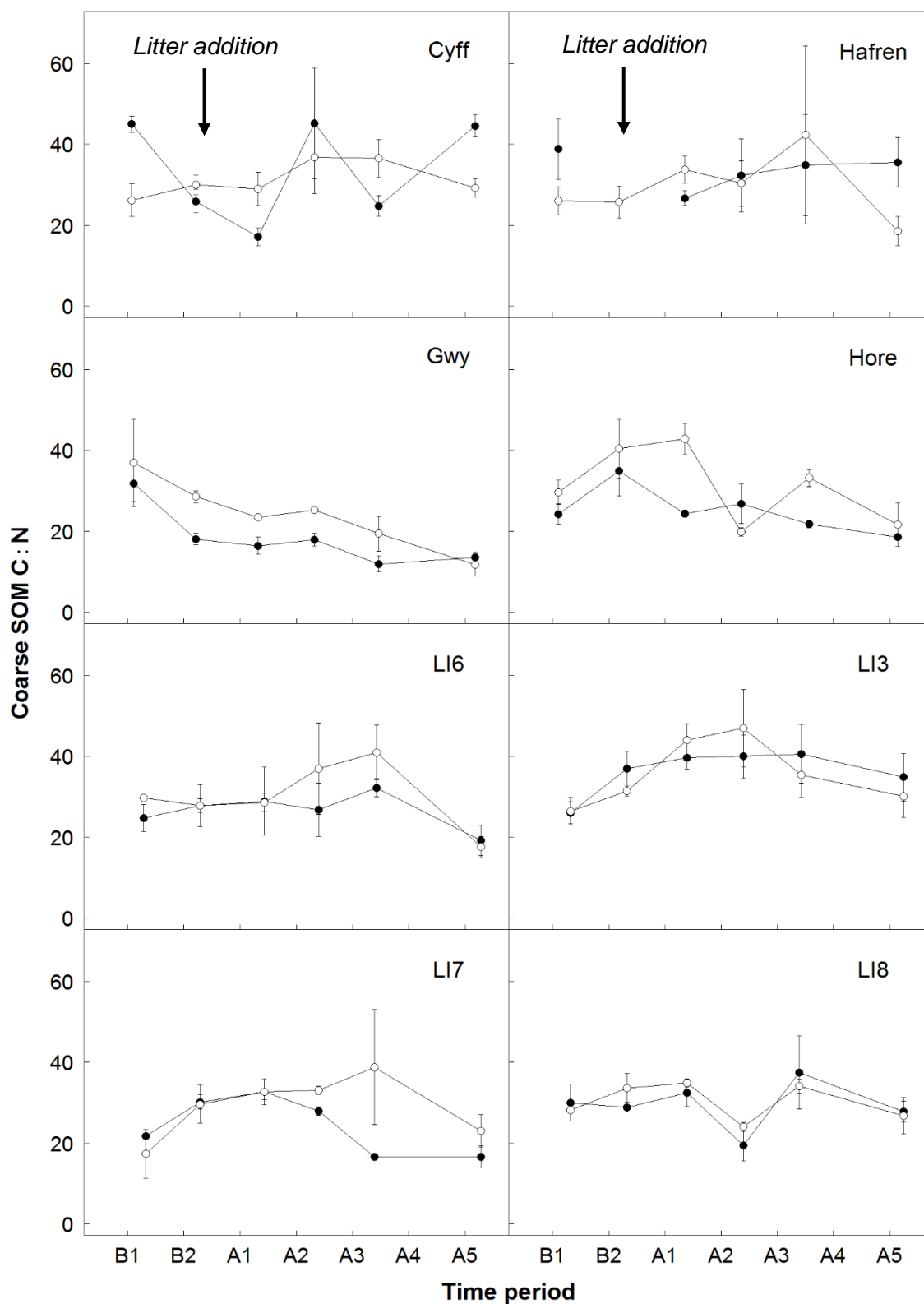


Figure C.9. Mean (± 1 S.E.) C:N ratio of coarse suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

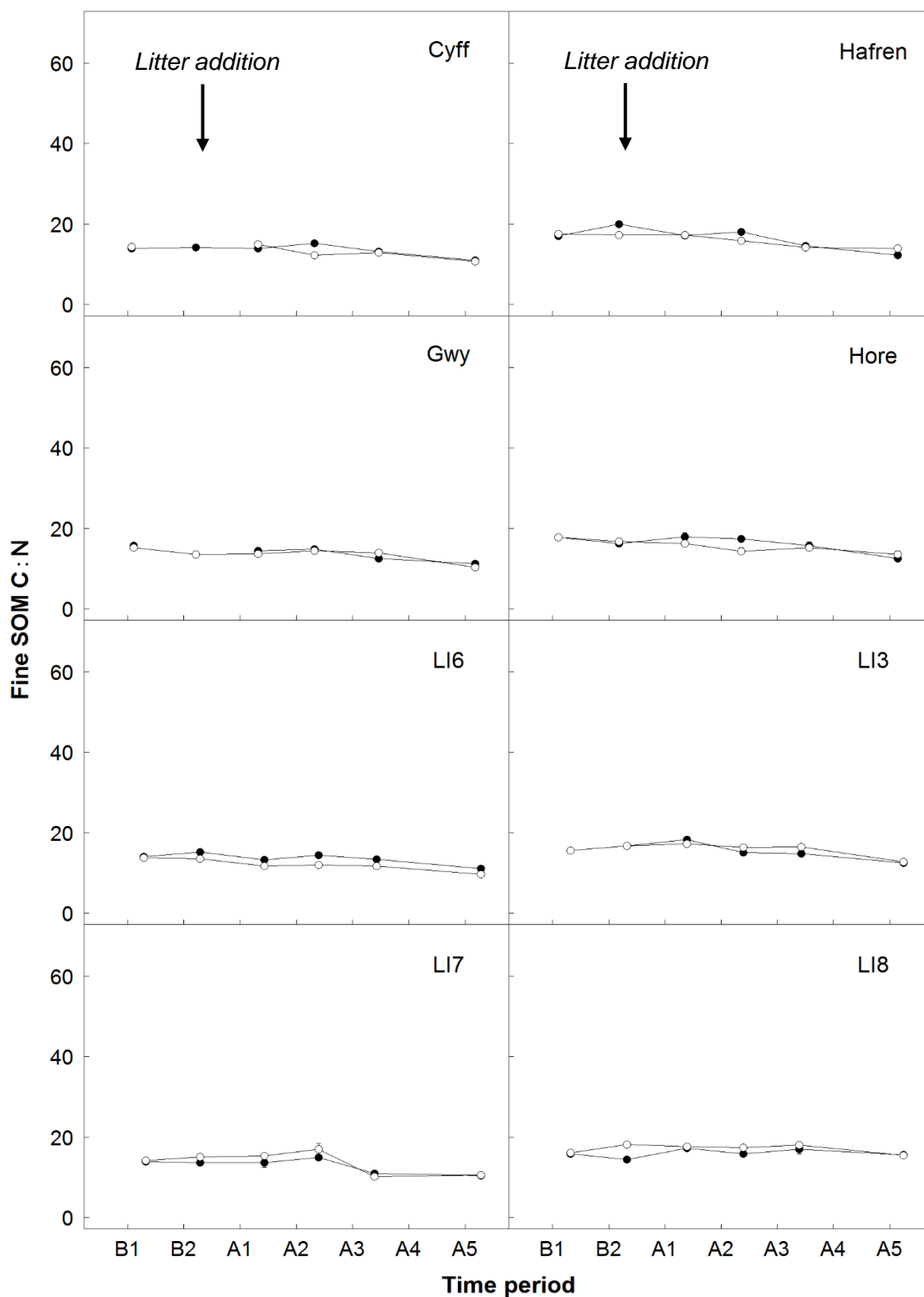


Figure C.10. Mean (± 1 S.E.) C:N ratio of fine suspended organic matter in the control reaches (white circles) and impact reaches (black circles) of each study site for 8 weeks before (B1–B2: Dec–Jan 2012–13) and 20 weeks after (A1–A5: Feb–May 2013) simulated riparian restoration. Arrows indicate the timing of litter addition.

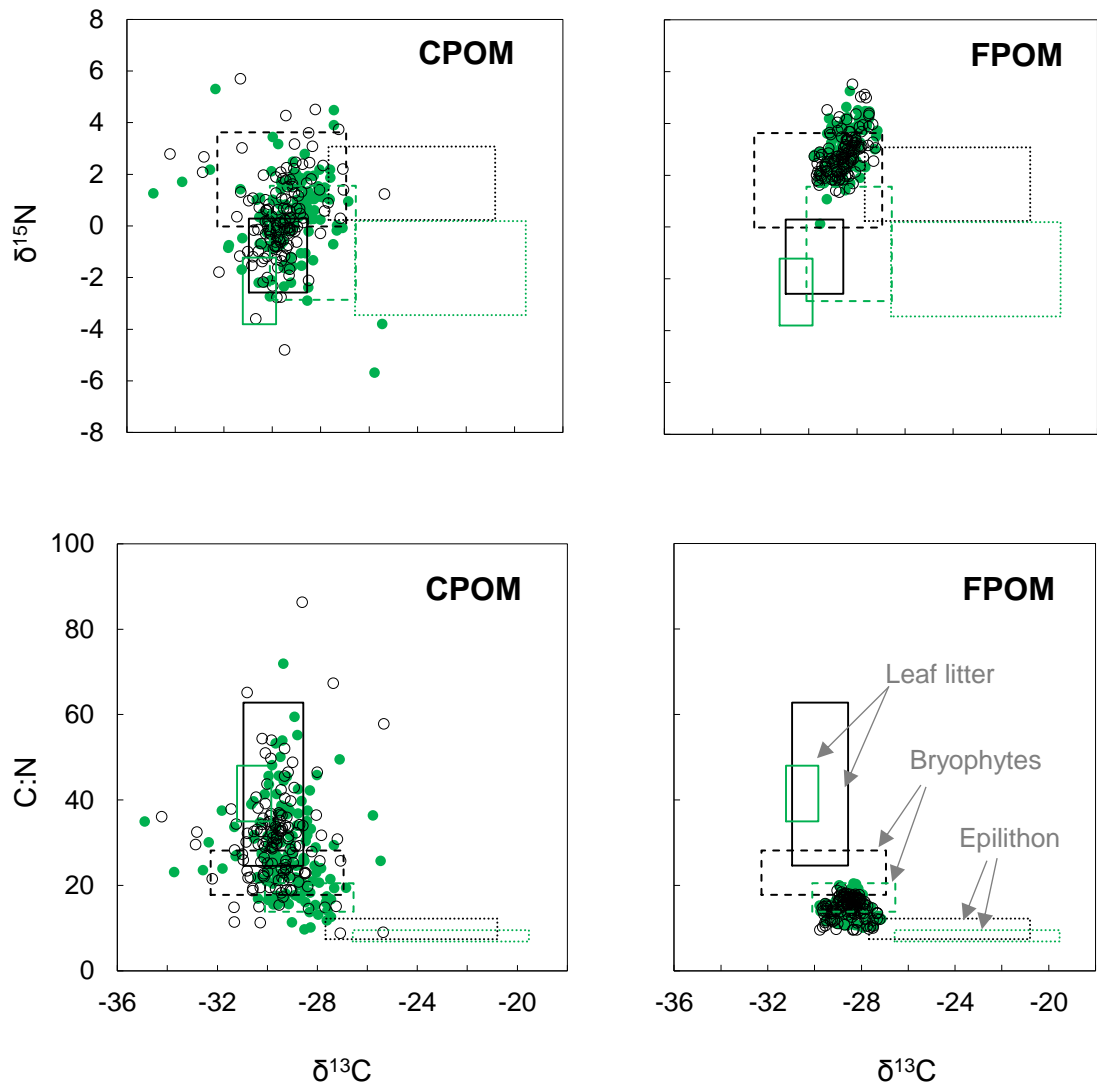


Figure C.11. Bi-plots of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ (upper panels) and C:N versus $\delta^{13}\text{C}$ (lower panels) values of coarse and fine suspended particulate organic matter (CSOM and FSOM, respectively) in all control reaches (black circles) and impact reaches (green circles) throughout the study period. Boxes depict mean values ± 1 S.D. of organic matter sources (solid line = leaf litter; dashed line = bryophytes; dotted line = epilithon) sampled from broadleaved streams (green boxes) and conifer/moorland streams (black boxes) within the Llyn Brianne Stream Observatory during 2007-2011.