

SPECIAL FEATURE – EDITORIAL

WHETHER IN LIFE OR IN DEATH: FRESH PERSPECTIVES ON HOW PLANTS AFFECT BIOGEOCHEMICAL CYCLING

Whether in life or in death: fresh perspectives on how plants affect biogeochemical cyclingAmy T. Austin^{1*} and Amy E. Zanne²

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Summary

1. Plants have numerous impacts on biogeochemical cycling across both aquatic and terrestrial ecosystems. These effects extend well beyond the critical role of carbon (C) fixation through photosynthesis that provides the basis for ecosystem energy flow. While foliar and root traits of senescent plant material (litter) have been explored in detail in terrestrial ecosystems, there is a resurgence of interest in how plants modulate biogeochemical cycling in ways other than litter quality effects on C and nutrient mineralization.

2. This Special Feature represents a collection of ‘fresh’ perspectives on how plants alone, or in interaction with other organisms, have important and lasting impacts on biogeochemical cycles of C and nutrients in a range of terrestrial and aquatic environments.

3. We begin in the open ocean and then peer from the forest edge before moving into forest understoreys and grasslands to examine the control by live terrestrial plants on ecosystem C and nutrient cycling. Plants directly affect biogeochemical cycling while living through their diversity and composition, nutrient capture and strategies for assimilating C, and by altering the microclimate for decomposition. In addition, how they construct their tissues and alter the abiotic environment has large impacts on the turnover of C and nutrients once plants have senesced or died. From the direct impact of plants, we move onto the influence of plant–insect interactions, which effectively determine changes in plant stoichiometry in grasslands of varying diversity. Finally, looking directly in the soil, it is clear that plant–mycorrhizae interactions are important in modulating the response of litter decomposition to nutrient addition and the nature of C metabolism in the soil.

4. *Synthesis.* The papers here highlight careful matching between how plants live and their biotic and abiotic contexts. Taken together, it appears that the dynamic, rather than passive, nature of plant responses to variable environments is key in affecting ecosystem level processes of C and nutrient turnover. This Special Feature highlights a diversity of connections between plants and their environment and demonstrates that in both life and death, how plants respond to these changes differs among plant lineages and this diversity will play a central role in determining biogeochemical cycling in the future in aquatic and terrestrial ecosystems.

Key-words: afforestation, biogeochemistry, carbon cycle, decomposition, forests, global change, grasslands, nitrogen cycle, oceans, plant–soil (below-ground) interactions, Special Feature

Introduction

Plants are critical in many aspects of biogeochemical cycling (Falkowski, Barber & Smetacek 1998; Chapin, Matson &

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Mooney 2002), most notably as the controlling players of net primary production in all terrestrial and aquatic environments. At the ecosystem scale, however, plants are often treated solely as uniform green biomass that assimilates C and functions as sessile competitors for nutrients and other resources. Recent research has shown many diverse ways in which different plant lineages actively modulate biogeochemical cycling, going beyond the well-studied effects of changes in chemical composition of senescent plant material (litter).

Modern views on plant function in ecosystems have focused on their dynamic nature, demonstrating that plants actively modulate biogeochemical cycling through variation in functional attributes (Reich 2014), phylogenetic history (Cornwell *et al.* 2009), stoichiometric flexibility (Sistla & Schimel 2012), nutrient cycling feedbacks (Hobbie 2015) and positive and negative interactions with other organisms (Austin & Ballaré 2014). Moreover, the ways in which plants actively respond to changing biotic and abiotic environments can have important consequences during the lifetime of the plant, and even following them into the 'afterlife' once plant tissues senesce (Cornwell *et al.* 2008).

Perhaps most importantly, dynamic responses of plants to a variety of human impacts, including land-use change, elevated greenhouse gases and changing climates (Post & Kwon 2000; Bonan 2008) have opened a wide array of interesting research avenues, allowing us to evaluate the influence of plant identity on perturbations to biogeochemical cycling at the ecosystem scale. This Special Feature presents a collection of

research papers and reviews that offer fresh perspectives that broaden our understanding of how plants and the sum of their interactions can modulate biogeochemical cycling, on land and in the sea (Fig. 1).

We begin in the ocean with papers by Stepien (2015) and Litchman *et al.* (2015), focusing on how the special adaptations and diversity of aquatic plants facilitate the cycling of enormous quantities of key elements. We then move onto the land, much like the embryophytes, with papers by Templer *et al.* (2015) and Araujo & Austin (2015), which explore how terrestrial plants through community structure and biomass influence C and nitrogen (N) dynamics, especially through poorly explored abiotic interactions in the air with fog and sunlight. Finally, papers by Zanne *et al.* (2015), Borer *et al.* (2015), Moore *et al.* (2015) and Midgley, Brzostek & Phillips (2015) cover a range of topics including how plants and their biotic interactions affect C and nutrient accumulation in living plants and loss from plants once they are dead.

To start in the sea, unicellular phytoplankton are too small to see with the naked eye, but their abundance in the oceans makes their contribution to C and nutrient cycling massive, as phytoplankton are responsible for 50% of global net primary productivity (Field *et al.* 1998). They are a diverse paraphyletic group that includes both prokaryotes and eukaryotes. It was most likely among early bacterial relatives that photosynthesis first emerged several billion years ago (Blankenship 2010), irrevocably changing biogeochemical cycling on Earth. While phytoplankton are united as autotrophs, the review by

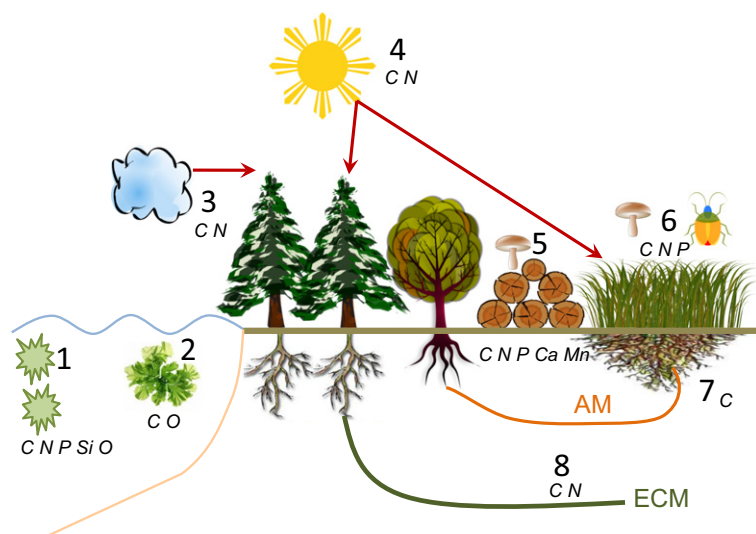


Fig. 1. The Special Feature spans the range of plants in all their glory – from the single-celled phytoplankton that rule the oceans to the towering redwoods of California, and onto temperate forests and grasslands, with pine afforestation and plant–mycorrhizal interactions. In this broad range of ecosystems, the connecting thread is an examination of how plants and their interactions with other organisms, especially insects and microbes, affect carbon (C) and nutrient cycling. The numbers in the diagram refer to the eight papers in this Special Feature: (1) Litchman *et al.* (2015), (2) Stepien (2015), (3) Templer *et al.* (2015), (4) Araujo & Austin (2015), (5) Zanne *et al.* (2015), (6) Borer *et al.* (2015), (7) Moore *et al.* (2015), and (8) Midgley, Brzostek & Phillips (2015). Papers 1 and 2 examine phytoplankton and macrophytes in the ocean (denoted by blue lines), and papers 3–7 examine conifers and angiosperms on land (denoted by the brown line). Italicized letters below the numbers refer to the elements being examined in each of the studies including C, nitrogen (N), phosphorus (P), silicon (Si), oxygen (O), calcium (Ca) and manganese (Mn). Arrows represent dominant abiotic inputs in papers 3 (fog) and 4 (solar radiation). Papers 5–8 investigate plants and their biotic partners with fungi and other microbes represented by mushroom fruiting bodies. Arbuscular mycorrhizal (AM) fungi are indicated with an orange line, while ectomycorrhizae (ECM) are shown with a green line.

Litchman *et al.* (2015) examines their phylogenetic and functional diversity by focusing on key traits and trade-offs that impact biogeochemical cycling. The authors suggest how these traits can be incorporated into biogeochemical models and how these critical organisms may respond to changing future climates. The information provided in this review gives us a synthetic functional understanding of these tiny organisms, allowing us to draw comparisons with their larger relatives, both in aquatic and terrestrial environments.

In contrast to the tiny phytoplankton, aquatic macrophytes are large enough to see, but we have spent little time examining their role in C cycling. The variable concentrations of carbon dioxide (CO₂) in aquatic environments are not usually appreciated; in place of a constant atmospheric source of CO₂, aquatic plants must cope with a suite of issues including the source of C (CO₂ or bicarbonate (HCO₃) ions) and variable pH in the water. Aquatic macrophytes have developed a series of carbon concentrating mechanisms (CCMs), which actively concentrate CO₂ in plant tissues to deal with this variability. These CCMs, in much the same way that C₄ photosynthesis creates a telltale ¹³C signature in its tissue (Farquhar, Ehleringer & Hubick 1989), should generate distinct ¹³C signatures in aquatic plant tissue (Maberly, Raven & Johnston 1992). Stepien (2015) explores these patterns in a global data set with a surprisingly new outlook on how aquatic plants manage their C – with increasing distance from the equator, plants rely more on CO₂ as their C source, but fall back on bicarbonate as their main source of C in highly variable environments. These patterns are truly novel insights into the ways in which macrophytes deal with a variable and unpredictable aquatic environment.

Moving onto terra firma, most plants obtain inorganic N from the soil through their roots in the form of nitrate and/or ammonium (Bloom 1988). This supply is dependent on available water in the soil to deliver N to the roots. In summer, though, plants may experience water and nutrient deficits as water availability decreases. Templer *et al.* (2015) examined the potential for an alternative supply of N via summer fog (Limm *et al.* 2009) in towering redwood crowns, by measuring natural abundances of $\delta^{15}\text{N}$ in plant and soil. They found that redwoods appear to have direct foliar uptake of N in the summer dry season and suggest that these trees are able to take advantage of N suspended as aerosols in marine air moving into terrestrial ecosystems as inland areas heat during the day. What the authors demonstrated was that this uptake was much greater along the forest margins as compared to the forest interior. Such creative N uptake has the potential to allow these long-lived trees to be more productive during times of year that otherwise would present considerable hardships.

Conifer canopies not only may uptake nutrients from the air, they may also differentially attenuate light to angiosperm canopies. While aridland ecosystems are known for their low biotic activity, litter decomposition is often much faster than would be predicted based on climatic parameters alone and has been attributed in part to the effects of solar radiation causing photodegradation and C loss of aboveground litter (Austin 2011). The question as to what controls litter

decomposition is important, as aridlands cover roughly 40% of the Earth's terrestrial land mass. Araujo & Austin (2015) show that land-use change through pine afforestation has a dramatic impact in reducing litter decomposition and C turnover in modified ecosystems. The authors attribute this change to an unforeseen 'shady' effect of the pines – by reducing the incident solar radiation at the soil surface due to canopy cover of the trees, photodegradation was essentially eliminated and C turnover halted. In addition, pine trees produced highly resistant litter for soil organisms to decompose. The combination of the two effects meant more than a 40% reduction in C turnover in pine plantations when compared to their natural aridland counterparts.

While photodegradation is especially important when vegetative cover is sparse, biotic decay agents, such as microbes and insects, can also be large contributors to plant decomposition in many ecosystems. Woody plants are an enormous terrestrial C pool (Denman 2007; Chave *et al.* 2009), with wood generally viewed as particularly slow cycling. Perturbations to this pool however can have important feedbacks to the climate system (Harmon, Brown & Gower 1993; Cornwell *et al.* 2009). The rate that plants decompose is reliant on how their tissues are constructed when they are alive, as well as where they are decaying on the landscape (Cornwell *et al.* 2009). Recent debate in the literature has focused on the relative importance of these two factors (Pietsch *et al.* 2014). To tease apart this question, Zanne *et al.* (2015) examined construction and decay rates for 21 woody species across leaves, fine branches and stems placed at different topographic positions. The identity of the species and how they are constructed was a much stronger predictor than where they were located, with predictor strength depending on tissue type. This variation may be driven by tissue-specific differences in rates of decay and thus rates of homogenization of plant tissues on their journey to rejoining the soil and air.

Decay rates and turnover of C and nutrients from plants have been clearly linked to various biotic agents; however, the role of biotic interactions in influencing the nutrient content of living plants has been poorly explored. Nutrient contents in leaves are known to change across gradients of soil nutrients or turnover in species composition, such as during succession (Kazakou *et al.* 2006; Asner *et al.* 2014). Borer *et al.* (2015) posed the intriguing suggestion that individual plants may change their nutrient status due to biotic interactions. For four focal grassland species (two grasses and two legumes), they manipulated insects and fungi on leaves and fungi in the soil. They found alterations in changes in leaf C and N stoichiometry associated with removal of foliar fungi and insects, although in opposing directions. The strength of the response was dependent on the plant species and their phylogenetic history (grasses versus legumes), suggesting the potential for consumers to affect plant- and community-level productivity through effects on plant stoichiometry.

Plant-microbe interactions can be key determinants of rates of flux of C into and out of the soil (Van Der Heijden & Horton 2009). Mycorrhizal fungi exchange plant fixed C for

nutrients and water via the plant roots and various soil fungi and bacteria break down C compounds, releasing the freed C back to the atmosphere (Brundrett 2002; Schimel & Schaeffer 2012). However, we know very little about below-ground interactions among the different players that influence C fluxes: roots, their associated mycorrhizal fungi and free-living soil microbes. Moore *et al.* (2015) took a double-pronged approach using manipulative mesocosms and modelling to examine the short- and long-term influences of such interactions on C dynamics and turnover. The authors demonstrate that antagonistic interactions among microbes may lead to unexpected depression of C metabolism. Additionally, the time-scale considered can alter whether one expects roots to speed up or slow down rates of C release from the soil.

Finally, similar to woody material, leaf litter decay rates are dependent on the construction of the leaves and environmental conditions (Cornwell *et al.* 2008). What is less well known in decay experiments is the strength by which local site factors may also control the rates that different litters decay (Bradford *et al.* 2014). The plant communities associated with ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi differ (Brundrett 2002) with some ECM-associated taxa (e.g. *Quercus*) having much lower litter quality than AM-associated taxa (e.g. *Acer*). Through a series of experiments along a gradient of ECM- to AM-associated taxa dominating, Midgley, Brzostek & Phillips (2015) examined the roles of N and background litter matrix quality influencing litter decay. The authors found that higher quality leaves (AM-associated litter) decay faster; however, these rates were especially enhanced for AM-associated litter when they decayed among other AM-associated leaves and with N addition. Such results reinforce what most of us already know from our daily lives – neighbourhood matters – but additionally highlight that how plants interact with other organisms can be a defining control of ecosystem processes.

Conclusions

Across the papers in this Special Feature, we show that both on land and in the sea an enormous breadth exists of how different plant lineages, individually or in association with biotic partners, influence biogeochemical cycles. Taken together, the message from this collection is that plants are active in modulating their biotic and abiotic environment. What this means is that through C capture strategies, allocation patterns, structural traits and plant–insect and plant–microbe interactions, plants actively alter their abiotic context, which has notable consequences at the ecosystem scale. Some consequences are direct, for example, where particular strategies for plant uptake alter pools and availability of nutrients. Some of these consequences are indirect, where increased plant cover or allocation strategies alter major controls on litter decomposition. Finally, specific interactions with other organisms generate dynamic plant responses which alter stoichiometry and C turnover. Rather than the classic view of sessile biomass passively adjusting to what comes their way, the evidence

demonstrated here shows a diversity of responses and mechanisms by which plants interact with their environment and directly and indirectly affect biogeochemical cycles.

With rising temperatures and shifting precipitation due to global change and altered land management practices, plants may find themselves existing in novel contexts (Parmesan 2006; Pompe *et al.* 2008). These novel settings will almost certainly have important effects on plant function and survival but additionally on plant interactions with other organisms. The dynamic nature of plant responses to a variable environment while alive and the consequences for biogeochemical cycling after death should not be ignored as we make future predictions of ecosystem function under changing climates. As we gain insight into plant responses to anthropogenic change, we will be better able to scale up our understanding of how plants may be impacted by and may impact biogeochemical cycling at ecosystem to global scales (Sitch *et al.* 2003).

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Data accessibility

This manuscript does not use data.

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