

## Editorial

# Introduction to a *Virtual Special Issue* on ecological stoichiometry and global change

Plants and other organisms have a diverse array of strategies with which they maximize growth and survival in a world of limited resources. These limiting resources include light and water, and also essential nutrients that are required for metabolism and growth but that are often in short enough supply to constrain those vital functions. Ecological stoichiometry focuses on the dynamics and interactions of multiple elements within organisms and the cycling between organisms and their environment.

The basis of this stoichiometric approach is straightforward (Sternner & Elser, 2002). Chemical reactions occur at characteristic ratios of reactants and yield characteristic ratios of products, all of which can be defined in terms of their elemental composition. Moreover, many biochemical reactions are catalysed by enzymes that themselves have defined elemental compositions, and take place within organisms that have more or less defined compositions. Chemical reactions and organisms both require all of their reactants and catalysts – and in the case of organisms, their structures – if they are to survive and grow. While the elemental composition of products, reactants, catalysts and structures is an incomplete description of reactions (or organisms), elements are the most conservative component of these reactions. Unlike energy, and unlike organic or inorganic compounds, elements are neither created nor consumed, and it is possible to calculate a mass balance for any element in any reaction (other than radioactive decay), and for any organism or ecosystem.

Stoichiometric approaches have long been embedded in ecology – for example, they underlie the use of critical C:N ratios in decomposition and nutrient release (Waksman & Tenny, 1928). Stoichiometry was applied explicitly on a very broad scale by Redfield (1958), who described relationships among C, N, P and S in marine algae and bacteria, and consequently among the cycles of C, N, P, S and O in the ocean. One legacy of his pioneering analysis is that C:N:P ratios in marine phytoplankton are termed the Redfield ratios. Reiners (1986) later described ‘the stoichiometry of life’ as one of the fundamental bases of ecosystem ecology. More recently, Sternner & Elser (2002) built upon their own and others’ research to broaden the scope of the stoichiometric approach substantially, developing and evaluating its implications on levels of organization from organelles to ecosystems. Among many contributions, they analysed the variability in element ratios both

within and among groups of organisms, demonstrating that the marine phytoplankton discussed by Redfield (1958) have the least variable ratios, while terrestrial plants are the most variable. Much of the variation within groups of organisms is caused by differences in the quantity and biochemistry of structural tissues, as Reiners (1986) suggested, and some is the result of storage or ‘luxury consumption’ (uptake in excess of immediate requirements) of elements when they are abundant. However, different groups of organisms may have fundamentally different ratios of N:P as well as C:N and C:P, in part because of an association between rapid growth rates and high P concentrations (Elser *et al.*, 1996).

This *Virtual Special Issue* (VSI) is a collection from *New Phytologist* publications focused on ecological stoichiometry, and combines the products of the 27th New Phytologist Symposium held in September of 2011, ‘Stoichiometric flexibility in terrestrial ecosystems under global change’, and recent papers published in *New Phytologist* that address the range of applications of ecological stoichiometry in terrestrial ecosystems (VSI: [www.newphytologist.com/virtualissues](http://www.newphytologist.com/virtualissues); Symposium: <http://www.newphytologist.org/stoichiometric/default.htm>). To begin, a modern look at ecological stoichiometry can be seen in the Tansley review by **Elser *et al.* (2010)**, which attempts to integrate metabolic scaling theory in a framework of variable nutrient ratios in plants and animals in a changing world. This overview serves as a valuable reference point from which more detailed exploration of species and community responses can be evaluated. A second perspective is presented in a review by **Sistla & Schimel (2012)**, which explicitly addresses the idea of stoichiometric flexibility – defined as the ability of organisms to adjust their elemental ratios while maintaining a constant function – across terrestrial ecosystems and at multiple scales from the individual to the large-scale biogeochemical processes. Their analysis suggests that stoichiometric flexibility tends to decrease with increasing scale, and the transition from the expression of stoichiometric plasticity within individuals to the community and ecosystem scales is a key mechanism regulating the extent to which environmental perturbations, including atmospheric and climatic change, may alter C and nutrient cycling dynamics.

The application of ecological stoichiometry includes multiple spatial, temporal and biological scales. For example, an underappreciated aspect of plant species’ control on nutrient balance stems from genotype–environment interactions, which were directly evaluated in willow species with a wide range of nutrient additions (**Ågren & Weih, 2012**). This manipulative experiment demonstrated that variability in environment, assessed through changes in nutrient availability, was more important in determining stoichiometric relationships than genotypic differences. At the species or functional group level, studies have demonstrated the plastic response of organisms to alter their nutrient ratios with changes in

Papers included in this *Virtual Special Issue* are indicated by their citations set in bold type ([www.newphytologist.com/virtualissues](http://www.newphytologist.com/virtualissues))

nutrient availability, including vascular epiphytes (Wanek & Zotz, 2011), which have the peculiarity of being isolated from soil nutrient sources, and symbiotic interactions of arbuscular mycorrhizas, which are intimately linked to the resource use and allocation of their host plants (Johnson, 2010). At the community and ecosystem scales, sources and controls on variation in element ratios have been evaluated for terrestrial ecosystems and demonstrate an enormous flexibility in terms of biomass N:P ratios, which can vary 50-fold as a result of differences in N and P supply in the environment (Güsewell, 2004). The variability in foliar N:P ratio, as opposed to extractable soil N and P, was associated with the community composition of alien and endangered plants in the Cerrado ecosystems of Brazil, where plots with low biomass and high N:P ratios contained a higher proportion of endangered plant species and few alien invaders (Lannes *et al.*, 2012). Finally, a modelling exercise with terrestrial plants (Ågren *et al.*, 2012) suggests that there is a smooth transition from N limitation to P limitation for plant growth rather than a single limiting resource, owing to the plants' ability to access more of a limiting resource given increased availability of the other. Taken together, these studies demonstrate that organisms actively respond to the resource heterogeneity in their environment, which is a major driver in explaining variability in stoichiometric relationships at the species and community levels.

But what happens when leaves senesce? The effects of nutrient availability and species identity on nutrient resorption can be seen to have large impacts on the stoichiometry of litter once at the soil surface, with consequences for decomposer and other soil organisms, as well as nutrient recycling. Reed *et al.* (2012) present a synthesis of data across biomes of patterns of N:P resorption patterns in plants, with a particular emphasis on understudied tropical ecosystems. This analysis focused specifically on N:P ratios, as opposed to a recent global analysis looking at single element resorption proficiencies (Vergutz *et al.*, 2012). The global synthesis showed that N:P resorption proficiencies were highly variable but predictable, increasing with latitude and decreasing with mean annual temperature and precipitation (Reed *et al.*, 2012). Adding another layer of complexity and following the litter after it begins to decompose, the efficiency of carbon use by decomposer microbes also appears to be a key factor that has an impact on rates of carbon release and nutrient mineralization, and that is, in part, determined by litter elemental ratios. Manzoni *et al.* (2012) synthesized published information on carbon-use efficiency (ratio of growth over C uptake) in both terrestrial and aquatic ecosystems, and found a general pattern of decreasing carbon-use efficiency with increased temperature and low nutrient availability.

It is important to note that stoichiometric relationships are not always the answer to understanding controls on litter decomposition. In a study conducted in sub-Arctic ecosystems, Aerts *et al.* (2012) showed that while nutrient ratios in litter were highly variable among species, litter traits that were much less flexible (including lignin content and leaf mass per unit area) were more important in determining litter decomposition in these high-latitude ecosystems. In warmer climes, nonlignin carbon compounds and soil fauna appear to be more important in determining

litter decomposition than nutrient ratios in green or senescent litter (Hättenschwiler *et al.*, 2011). It appears that the complexity of carbon chemistry may obscure straightforward effects of litter nutrient ratios controlling decomposition processes in some terrestrial ecosystems, and this issue clearly warrants further study in order to have a more complete picture of the relative impact of variation in litter stoichiometry on carbon and nutrient turnover.

Lastly, at the ecosystem scale, several studies have evaluated the direct impacts of global change on nutrient ratios and availability under conditions of elevated CO<sub>2</sub> and nutrient addition, with a clear demonstrated link between nitrogen (N) and phosphorus (P) cycling. A meta-analysis of the impacts of N addition on soil P cycling showed that across a wide range of ecosystems, addition of N stimulated activity of phosphatase, an enzyme exuded by both plants and microbes, suggesting a tight linkage in situations of colimitation by N and P (Marklein & Houlton, 2012). A different insight on N–P linkages came from an experiment with treatments of elevated CO<sub>2</sub> and temperature in a temperate grassland. These treatments differentially affected N and P availability, with variation in foliar N:P ratios associated with changes in soil moisture as opposed to direct effects of elevated CO<sub>2</sub> (Dijkstra *et al.*, 2012).

There is promise that ecological stoichiometry can serve as a tool for understanding how ecosystems will respond to human-induced global changes, including elevated CO<sub>2</sub>, nitrogen deposition and increased temperature. Particularly relevant may be the response of plants to increased atmospheric CO<sub>2</sub>, and the potential constraints on plant growth to increased carbon availability in the context of limited nutrient supply and a changing environment. There is evidence to suggest that carbon uptake in a high-CO<sub>2</sub> world could be restricted by a single element or a combination of several elements, and the extent to which plants can become more flexible in terms of the amount of carbon stored per unit of nutrient acquired will largely determine the magnitude of response to this clearly documented global change. Future research on the interactions among environmental variation, nutrient supply and biotic responses to these variations will be necessary to elucidate the importance of ecological stoichiometry in a changing world.

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