

Acknowledgements

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## Nutritional constraints in terrestrial and freshwater food webs

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Biological and environmental contrasts between aquatic and terrestrial systems have hindered analyses of community and ecosystem structure across Earth's diverse habitats. Ecological stoichiometry<sup>1,2</sup> provides an integrative approach for such analyses, as all organisms are composed of the same major elements (C, N, P) whose balance affects production, nutrient cycling, and food-web dynamics<sup>3,4</sup>. Here we show both similarities and differences in the C:N:P ratios of primary producers (autotrophs) and invertebrate primary consumers (herbivores) across habitats. Terrestrial food webs are built on an extremely nutrient-poor autotroph base with C:P and C:N ratios higher than in lake particulate matter, although the N:P ratios are nearly identical. Terrestrial herbivores (insects) and their freshwater counterparts (zooplankton) are nutrient-rich and indistinguishable in C:N:P stoichiometry. In both lakes and terrestrial systems, herbivores should have low growth efficiencies (10–30%) when consuming autotrophs with typical carbon-to-nutrient ratios. These stoichiometric constraints on herbivore growth appear to be qualitatively similar and widespread in both environments.

The concept of a food web has been a central organizing theme in ecology ever since its classical development<sup>5</sup>. Ecologists are now actively seeking ways to integrate interspecific interactions in food webs with the functional processes of energy flow and material cycling<sup>6–9</sup>. Here we use the perspective of ecological stoichiometry to analyse factors affecting energy and material flows at the autotroph–herbivore interface in terrestrial and freshwater ecosystems. Our analysis quantifies important divergences and convergences in the stoichiometric structure at the base of food webs in these diverse habitats.

The base of terrestrial and freshwater food webs differed dramatically in C:nutrient ratios (Fig. 1). Mean C:N and C:P ratios of the foliage of terrestrial autotrophs were more than threefold higher than for freshwater seston (lake particulate matter, generally dominated by phytoplankton) (*t*-tests, *P* < 0.0001), indicative of the influence of nutrient-poor, C-rich structural carbohydrates in vascular plant tissue. Thus, a generalist terrestrial herbivore consuming a plant with the average plant C:nutrient ratio would acquire less than a third as many nutrient atoms per C atom ingested as would a freshwater zooplankton feeding on average seston. Furthermore, C:N ratios varied more in the terrestrial data: the coefficient of variation (c.v.) of terrestrial autotroph biomass was 0.64 but only 0.29 for freshwater seston. Whereas autotroph C:nutrient ratios diverged widely between terrestrial and freshwater ecosystems, autotroph N:P ratios did not (Fig. 1; 28 for terrestrial foliage versus 30 for freshwater seston; *t*-test, *P* = 0.65). Furthermore, the biomass N:P ratio did not vary as greatly between terrestrial and freshwater habitats as did the C:N ratio (c.v. of N:P was 0.54 versus 0.53 for C:N). Thus, despite major differences in the size, complexity and taxonomic affiliation of autotrophic organisms in terrestrial and freshwater realms, patterns of biomass composition for N and P were very similar. Given the prevailing view that in general primary production is limited by P in freshwater ecosystems but by N in terrestrial systems<sup>10</sup>, the coincidence of autotroph biomass N:P in terrestrial and freshwater systems is intriguing (Fig. 1). This similarity may indicate that the prevalence of N-limitation in lakes is greater than previously thought<sup>11</sup> or that P-limitation in terrestrial systems is more widespread than generally acknowledged. Or, it is possible that biomass N:P values indicative of N versus P limitation differ for freshwater and terrestrial autotrophs, but this is not supported by recent investigations in wetland vegetation<sup>12</sup>.

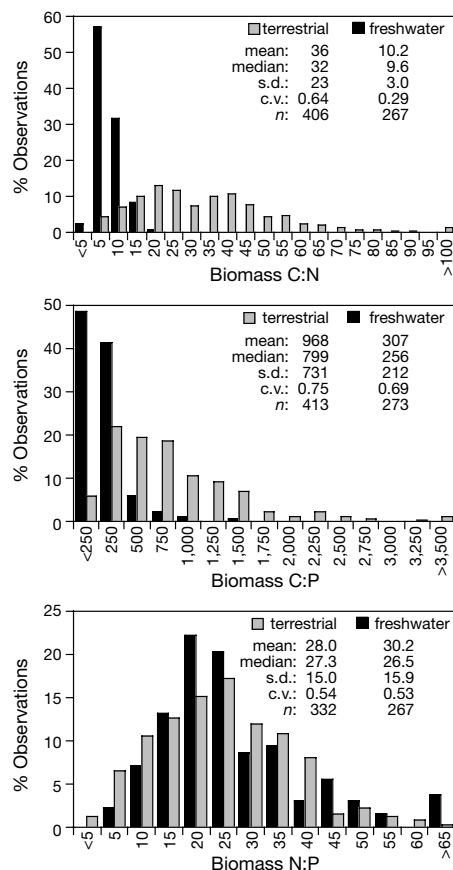


Figure 1 Frequency histograms summarizing C:N:P stoichiometry in autotrophs at the base of terrestrial and freshwater food webs. All stoichiometric ratios are atomic.

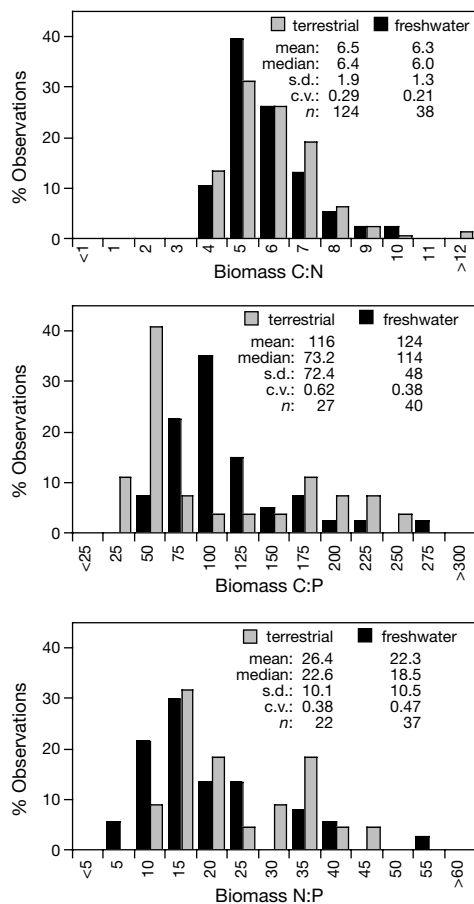
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Like autotrophs, metazoan herbivores in terrestrial and freshwater habitats differ considerably in size and taxonomic affiliation. Despite these contrasts, we found that herbivorous insects and zooplankton had similar mean C:N, C:P and N:P ratios in the two habitat types (Fig. 2; *t*-tests,  $P > 0.17$ ). In both groups C:P ratios varied more than C:N ratios among taxa, consistent with the relative constancy of N content but wide variation of P content in major biological molecules (that is, N-rich proteins versus N- and P-rich nucleic acids) and structures<sup>2</sup>. Associations of body C:N:P with body growth rate due to the necessity of increased allocation of resources to P-rich ribosomal RNA<sup>2</sup> have been documented in planktonic crustaceans<sup>2,13</sup>. We show that as much variation in body C:N:P ratios exists among insect herbivores as among zooplankton. However, connections between patterns of elemental and biochemical composition and growth rate in insects remain largely unexplored.

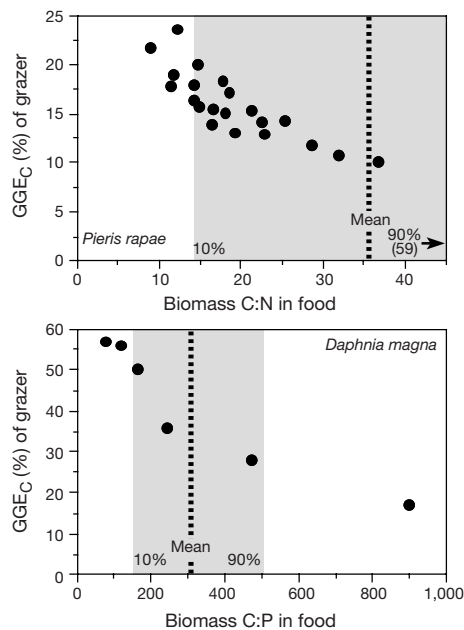
The C:N and C:P ratios of the herbivores were considerably lower than those of their potential foods, especially in terrestrial systems where C:nutrient ratios of foliage exceeded insect C:nutrient ratios by more than 5- to 10-fold on average. This indicates that stoichiometric food quality for herbivores is generally poor in lakes and especially in terrestrial habitats. The extreme imbalance in C:nutrient ratios between plant and insect biomass may contribute to the prevalence of feeding specialization among insect herbivores<sup>14,15</sup>, in which insects focus their consumption on those plant species, tissues, or time-frames for which food nutrient content is more suitable. In contrast, pelagic herbivores in lakes appear to face less daunting constraints and may thus succeed with relatively indiscriminate, filter-feeding modes of nutrition. Given elevated C:nutrient ratios, which element (N or P) is likely to be in shorter supply relative to herbivore needs? Mean body N:P of herbivore taxa (~24) was lower than that of average autotroph biomass (~30;

*t*-test,  $P = 0.02$ ), indicating that, on average, N is in excess relative to P for herbivores in these systems. Yet, because herbivore and autotroph N:P vary among species, the identity of the potentially limiting constituent will depend on the relative N:P of particular resource–herbivore combinations. However, the fact that plant N:P was significantly higher than insect N:P suggests that greater attention should be paid to the potential for inadequate P intake for herbivores in terrestrial ecosystems, where ecologists have focused primarily on N<sup>16</sup>.

Our data clearly show that the stoichiometry of the autotroph–herbivore interaction is greatly unbalanced in freshwater and especially terrestrial ecosystems. For example, in freshwater zooplankton, *Daphnia* are relatively P-rich with body C:P ratios of about 80:1<sup>4</sup>. According to stoichiometric food quality models and experimental investigations<sup>3,17,18</sup>, *Daphnia* face potential P-deficiency when food C:P exceeds ~250, a situation that appears commonplace in lakes (Fig. 1). Our data indicate that terrestrial herbivores with a P-rich lifestyle similar to *Daphnia*'s encounter even more daunting constraints: only 6% of the autotroph species sampled in our data set had plant C:P less than 250:1. Stoichiometric theory predicts that homeostatic herbivores consuming elementally imbalanced food will exhibit strongly diminished efficiency of conversion of ingested carbon into new biomass (for example, reduced "gross growth efficiency", GGE<sub>C</sub>). Indeed, examples of terrestrial and freshwater herbivores (caterpillars of *Pieris rapae*<sup>19</sup> and *Daphnia magna*<sup>20</sup>, respectively) show the reduction in GGE<sub>C</sub> with food C:nutrient ratio (Fig. 3) predicted by stoichiometric food quality models<sup>17,18</sup>. Comparison of these responses with the histograms in Fig. 1 indicates that such herbivores would exhibit low GGE<sub>C</sub> when consuming average autotroph biomass in their respective habitats (30% for *Daphnia*, <10% for *Pieris*). Given the possible connection between animal C:N:P ratios and growth rate<sup>2</sup>, such food quality limitations may fall disproportionately on fast-growing 'outbreak' herbivores that require nutrient-rich resources



**Figure 2** Frequency histograms summarizing C:N:P stoichiometry of invertebrate herbivores in terrestrial and freshwater habitats. All stoichiometric ratios are atomic.



**Figure 3** Decline in gross growth efficiency (GGE<sub>C</sub>) for typical terrestrial and freshwater grazers with increasing food carbon-to-nutrient ratio. The grazers were cabbage butterfly caterpillars, *Pieris rapae*<sup>19</sup> (terrestrial) and the zooplankter *Daphnia magna*<sup>20</sup> (freshwater). Data on GGE<sub>C</sub> (proportion of ingested carbon successfully converted to body growth) and food nutrient content were extracted from the cited studies. Percentage N in the caterpillar study was converted to C:N assuming a percentage C value of 46.4%. Responses are superimposed on observed values of C:N in foliage and C:P in seston; for each, the dashed line indicates the mean value and shading indicates the 10% and 90% limits from the frequency distribution (Fig. 1).

to rapidly build nutrient-rich bodies. In general, our analyses show large differences in C:nutrient balance across the autotroph–herbivore interface in freshwater and terrestrial ecosystem that may have important effects on the intensity of herbivory<sup>21,22</sup> and the fate of organic matter<sup>23</sup> in diverse ecosystems. However, terrestrial and aquatic food webs share great similarity in the N:P stoichiometry of autotroph–grazer interactions. □

## Methods

### Autotrophs

We supplemented the literature with unpublished data to develop databases documenting the C:N:P stoichiometry of terrestrial plants and suspended particulate matter ('seston') in lakes. We restricted our terrestrial autotroph database to elemental analyses of foliage collected under field conditions, excluding agricultural and greenhouse studies. Multiple data for a single species were averaged before analysis. Terrestrial data were most frequently reported in percentage dry weight terms (% N, % P); when % C values were not reported we converted % N and % P data to C:N and C:P ratios using the mean percentage C of reported values (46.4% C). To evaluate whether this procedure introduced any bias to observed patterns in foliage C:P and C:N, we calculated the mean and variability (coefficient of variation, c.v.) of the C:N and C:P ratios for that subset of species for which % C, % N, and % P were all reported ( $n = 44$ ). The mean and c.v. of C:N for this limited data set were 35.9 and 0.57, respectively, and 805 and 0.78 for C:P. These values are reasonably close to those for the remaining entries (for C:N, mean was 36.5, c.v. was 0.64; for C:P, mean was 990, c.v. was 0.75); thus, using a fixed percentage C value to estimate C:N and C:P probably did not influence the major patterns observed. A total of 501 plant species from 358 genera, 107 families, 62 orders, 20 subclasses, 8 classes and 5 divisions were included. We assessed C:N:P stoichiometry at the base of freshwater pelagic food webs by compiling a database of seston elemental composition in 226 lakes from published and unpublished reports. Only data for surface waters during the summer growing season were included; multiple observations during a year were averaged, and thus a 'lake-year' was the primary observation unit. Data were generally for lakes of small to moderate size but information for several of the world's great lakes was also included. Lakes were primarily located in North America but seston data for lakes in Europe, Africa and Asia were also obtained. Seston contains a mixture of living algae but also bacteria, protozoa and detritus and forms the food base for relatively indiscriminate planktonic filter-feeders. Although the contribution of these different components probably differs among lakes, various data indicate that, in general, seston particles in stratified lakes are dominated by phytoplankton biomass. For example, even in some lakes where seston C:P was high (and thus the contribution of low-nutrient detritus might be thought relatively important), algae contributed about 70% of total seston biomass (bacteria and protozoa contributed ~20% and <5%, respectively, implying little influence of detritus)<sup>24</sup>. Thus, the freshwater and terrestrial data sets for 'autotrophs' differ in that the terrestrial data involve observations for particular plant species while the lake data correspond to a mixture of particles, living and non-living. Finally, if different seston particles have substantially different C:N:P ratios, bulk seston C:N:P measurements may not accurately quantify actual stoichiometric food quality for particular herbivores that can discriminate among particles, such as some calanoid copepods<sup>5</sup>.

### Herbivores

Data for the C:N:P stoichiometry of terrestrial herbivorous insects and lake zooplankton were compiled from published and unpublished sources. Multiple data for a single species were averaged before analysis. As for terrestrial plants, when values of percentage C were not given, data reported as % N and % P were converted to C:N and C:P ratios using the mean percentage C value for the remainder of the herbivore database (48% C). We followed the same procedure used in analyses of the foliage data to evaluate possible bias introduced by assuming this fixed percentage C value. However, data for few species included all three parameters (% C, % N, % P); we thus confined our assessment of possible biases to data on herbivore C:N. The mean and c.v. values of C:N for the data subset with direct measurements of % C and % N ( $n = 67$ ) were 5.9 and 0.21 whereas values for entries for which the fixed percentage C value was used ( $n = 97$ ) were 6.7 and 0.28. Here again, using a fixed value of percentage C to estimate C:N and C:P from % N and % P probably did not unduly influence the observed patterns. A total of 130 species of insects from 93 genera, 40 families and 7 orders were included. By far, most insects included were leaf-eating, though a minority were phloem-feeding herbivores (such as aphids). Leaf-eaters and phloem-feeders did not differ in C:N:P ratios and therefore all taxa were analysed together. Predatory zooplankton were excluded from the compilation but several omnivorous taxa were retained. A total of 43 species of zooplankton from 23 genera, 12 families, 8 orders, 4 classes and 2 phyla were included. The majority of the taxa were crustaceans (mainly branchiopods ('cladocera'), malacostracans and copepods) but data for several rotifers were also compiled. All stoichiometric ratios were calculated on an atomic basis. A complete summary of the data sets, including original citations, can be obtained at <http://www.nceas.ucsb.edu/ecostochiometry>.

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1. Reiners, W. A. Complementary models for ecosystems. *Am. Nat.* **127**, 59–73 (1986).
2. Elser, J. J., Dobberfuhl, D., MacKay, N. A. & Schampel, J. H. Organism size, life history, and N:P stoichiometry: towards a unified view of cellular and ecosystem processes. *BioScience* **46**, 674–684 (1996).
3. Sterner, R. W. & Hessen, D. O. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.* **25**, 1–29 (1994).

4. Elser, J. J. & Urabe, J. The stoichiometry of consumer-driven nutrient cycling: theory, observations, and consequences. *Ecology* **80**, 735–751 (1999).
5. Elton, C. *Animal Ecology* (Sidgwick and Jackson, London, 1927).
6. Chapin, F. S. *et al.* Biotic control over the functioning of ecosystems. *Science* **277**, 500–504 (1997).
7. Leibold, M. A. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* **6**, 922–949 (1989).
8. Tilman, D. *et al.* The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302 (1997).
9. McCauley, E., Nisbet, R. M., Murdoch, W. W., DeRoos, A. M. & Gurney, W. S. C. Large amplitude cycles of *Daphnia* and its algal prey in enriched environments. *Nature* **402**, 653–656 (1999).
10. Schlesinger, W. H. *Biogeochemistry: An Analysis of Global Change* (Academic, San Diego, 1997).
11. Elser, J. J., Marzolf, E. R. & Goldman, C. R. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. *Can. J. Fish. Aquat. Sci.* **47**, 1468–1477 (1990).
12. Verhoeven, J. T. A., Koerselman, W. & Meuleman, A. F. M. Nitrogen- or phosphorus-limited growth in herbaceous wet vegetation: relations with atmospheric inputs and management regimes. *Trends Ecol. Evol.* **11**, 494–497 (1996).
13. Main, T., Dobberfuhl, D. R. & Elser, J. J. N:P stoichiometry and ontogeny in crustacean zooplankton: a test of the growth rate hypothesis. *Limnol. Oceanogr.* **42**, 1474–1478 (1997).
14. Futuyama, D. J. & Gould, F. Associations of plants and insects in a deciduous forest. *Ecol. Monogr.* **49**, 33–50 (1979).
15. Strong, D. R., Lawton, J. H. & Southwood, R. *Insects on Plants: Community Patterns and Mechanisms* (Blackwell Scientific, London, 1984).
16. White, T. C. R. *The Inadequate Environment: Nitrogen and the Abundance of Animals* (Springer, New York, 1993).
17. Andersen, T. *Pelagic Nutrient Cycles: Herbivores as Sources and Sinks* (Springer, Berlin, Heidelberg & New York, 1997).
18. Sterner, R. W. Modelling interactions between food quality and quantity in homeostatic consumers. *Freshwat. Biol.* **38**, 473–482 (1997).
19. Slansky, F. & Feeny, P. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated plants. *Ecol. Monogr.* **47**, 209–228 (1977).
20. DeMott, W. R., Gulati, R. D. & Siewertsen, K. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnol. Oceanogr.* **43**, 1147–1161 (1998).
21. Cyr, H. & Pace, M. L. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* **361**, 148–150 (1993).
22. Strong, D. R. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**, 747–754 (1992).
23. Cebrian, J. Patterns in the fate of production in plant communities. *Am. Nat.* **154**, 449–468 (1999).
24. Elser, J. J., Chrzanoski, T. H., Sterner, R. W., Schampel, J. H. & Foster, D. K. Elemental ratios and the uptake and release of nutrients by phytoplankton and bacteria in three lakes of the Canadian Shield. *Microb. Ecol.* **29**, 145–162 (1995).
25. Butler, N. M., Suttle, C. A. & Neill, W. E. Discrimination by freshwater zooplankton between single algal cells differing in nutritional status. *Oecologia* **78**, 368–372 (1989).

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## Bacterial dehalorespiration with chlorinated benzenes

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Chlorobenzenes are toxic, highly persistent and ubiquitously distributed environmental contaminants that accumulate in the food chain<sup>1</sup>. The only known microbial transformation of 1,2,3,5-tetrachlorobenzene (TeCB) and higher chlorinated benzenes is the reductive dechlorination to lower chlorinated benzenes under anaerobic conditions observed with mixed bacterial cultures<sup>2–4</sup>. The lower chlorinated benzenes can subsequently be mineralized by aerobic bacteria. Here we describe the isolation of the oxygen-sensitive strain CBDB1, a pure culture capable of reductive

