high incidence of polyploidy[13]. In any case, a multiple parasite–predator model should be developed to check if the 'bad allele' concept holds in the face of tradeoffs between unrelated defences.

West *et al.*[14] recently argued that more than one mechanism is probably responsible for the prevalence of sex. They suggested that a pluralistic view, for example by combining Red Queen driven coevolution with mutation-based hypotheses, will offer advantages over different opposing hypotheses. Enlarging the concept of the Red Queen to all biotic interactions as it was originally intended[15], including parasites, predators and eventually also competitors, is in line with such modern, integrated approaches.

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Ecological stoichiometry: from sea to lake to land

Ecological stoichiometry (ES) studies the balance of energy and multiple chemical elements [e.g. carbon (C), nitrogen (N) and phosphorus (P)] in ecological interactions[1–3], to establish how the laws of thermodynamics affect food-web dynamics and nutrient cycling in ecosystems. Earlier this year, the historical Norwegian Academy of Sciences housed a conference* of diverse ecologists, who discussed how ES might improve our understanding of ecosystems, and might better integrate terrestrial and aquatic ecology. The organizers [limnologist Dag Hessen (University of Oslo, Norway) and soil ecologist Jan Bengtsson (Swedish University of Agricultural Sciences, Umeå, Sweden)] exemplified the spirit of the meeting to achieve a more cohesive ecology in which aquatic and terrestrial ecologists interact actively for the benefit of both endeavors. 20 scientists participated in the conference, representing a variety of disciplines, including limnology, oceanography, insect biology, forest ecology and soil biology. A mix of empirical and theoretical findings was highlighted.

*Stoichiometric Constraints on Carbon Sequestration in Ecosystems, Oslo, Norway, 28–29 May 2000.

Although ES began in the ocean as a result of Alfred Redfield's famous ratio, ES has been an active area in limnology over the past decade. This meeting was an attempt to infect terrestrial ecology with concepts of ES developed in lakes and to challenge ES researchers to establish if these ideas have generality outside the water. [A similar effort has been underway in the USA via a working group 'Ecological stoichiometry of autotroph–herbivore interactions in aquatic and terrestrial ecosystems' at the National Center for Ecological Analysis and Synthesis (NCEAS) (www.nceas.ucsb.edu)] Thus, what promise does ES hold for improving our understanding of energy and nutrient flows in food webs, and for facilitating information flow between aquatic and terrestrial ecology?

News from the aquatic realm

Aquatic systems dominated the first day of the meeting. Two speakers sought to clarify some theoretical issues. The first clarification was that the talks were presented by Tom Andersen (Norwegian Institute for Water Research, Oslo, Norway) and Tom Anderson (University of Southampton, UK), both active theoreticians working to incorporate stoichiometry into food-web models. Participants were glad to see the two 'T.A.'s' in the same place at the same time and thus to put a face to the similar names. Tom Andersen dissected the effects of mass conservation on predator–prey isoclines, building incrementally from the early Lotka–Volterra expression to the unusual (and potentially revolutionary) 'hump-shaped' isoclines of his stoichiometric 'Andersen model'. Tom Anderson took a more empirically motivated approach, seeking to extend simple models of mass balance of multiple elements to incorporate more biochemical detail. Hessen focused slightly lower in lake food webs, on unappreciated factors regulating elemental composition (and thus potential food quality) of phytoplankton. Most novel were data indicating that pCO_2 can increase the C:P ratio in freshwater green algae. Thus, a largely unappreciated effect of increasing atmospheric CO_2 on lakes might be in reducing the quality of autotrophic production for zooplankton (an effect widely documented for terrestrial herbivores).

Anne Lyche (Norwegian Institute for Water Research) moved the focus to the field, showing how P-fertilization of lake enclosures lowered the C:P and N:P ratios of seston biomass. The processing of C, N and P in marine systems was described by Marit Reigstad (University of Tromsø, Norway), who emphasized particle sedimentation. Maarten Boersma (Max Planck Institute for Limnology, Ploen, Germany) then returned to earlier threads begun by

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Andersen and Anderson, considering *Daphnia* food-quality limitation when consuming algae of high C:P ratio. However, most intriguing were data showing reduced *Daphnia* growth on algae with an unnaturally low C:P ratio. These animals either were ‘poisoned’ by excessive P intake or they had reduced their feeding levels, because they had so easily met their P requirements that they didn’t achieve sufficient energy (C) intake. The response suggests how the evolutionary history of a species (e.g. whether the metabolism and behavior of a species is adapted to high or low quality food) might influence the outcome of nutrition experiments, an issue addressed for insects by David Raubenheimer (University of Oxford, UK). The first of three talks to mention ribosomal RNA was given by Tobias Vrede (University of Uppsala, Sweden), who proposed that animal RNA:DNA ratios might reliably indicate zooplankton nutritional status.

Two limnologists returned matters to the theoretical side. Tangui Daufresne (École Normale Supérieur, Paris, France) addressed ecosystem conditions under which differential nutrient recycling of N and P can qualitatively alter autotroph nutrient limitation, and François Darchambeau (Laboratory of Freshwater Ecology, Namur Belgium) analysed how partitioning of nonassimilated food to excreta versus egesta might influence the stoichiometry of particle sedimentation. Jöhan Luvgren (University of Umeå, Sweden) then described how cascading trophic interactions might be affected by pelagic–littoral nutrient transfers. Finally, Karl Rothhaupt (University of Constance, Germany) brought attention to the crucial, but often neglected (as in this conference, unfortunately), microbial realm. This discussion showed how mineralization of P in the microbial food web depends on trophic interactions, in which bactivorous flagellates, rather than bacteria, are responsible for P release when P supplies are limited.

Meanwhile, back on land…

The second day of the meeting focused on terrestrial systems. Bas Koojiman (Vrije Universitet, Amsterdam, The Netherlands) began the day on a high level, summarizing his innovative ‘dynamic energy budget’ theory, and how it bears on a variety of major issues from the coupling of ribosomes to growth in microbes to understanding coral symbioses, plant root:shoot partitioning and producer–consumer dynamics. Picking up a theme introduced by Boersma, Raubenheimer presented his work with Steve Simpson on behavioral and physiological responses of locusts to unbalanced diets of carbohydrates and proteins. Using a geometrical approach, they measured the regulated intake point for the two nutrients and quantified the locust response to imbalanced foods that prevented achievement of the target intake. The data indicate an evolved effect of host range on this response, such that generalist feeders can tolerate an excess of surplus nutrients, whereas specialists will accept relatively large deficits of one nutrient to avoid excesses of the other.

Bill Fagan (Arizona State University, Tempe, USA – an organizer of the NCEAS working group) continued to expand the scope of the discussions, summarizing major patterns in the large NCEAS data set, including strong similarities and dissimilarities in the C:N:P stoichiometry of autotrophs and herbivores in aquatic and terrestrial ecosystems. Frank Berendse (Wageningen University, The Netherlands) considered the coupling of C and N during terrestrial succession, noting that plant life history traits (e.g. potential growth rate, and leaf and root life spans) were coupled to their associated habitat (e.g. high versus low fertility soils) and affected soil nutrient cycling. The coupling of C, N and P at a larger scale was discussed by Göran Ågren (Swedish University of Agricultural Sciences), who presented recent findings on foliar contents of N and P relative to plant optima. Ågren concluded that P limitation might be more prevalent in forests than is currently appreciated, an inference also supported by Fagan’s data. Peter De Ruiter (University of Utrecht, The Netherlands) summarized studies of C and material flows in agricultural soil food webs. Similar to Rothhaupt’s findings for aquatic microbes, net nutrient release in soil required a trophic interaction (e.g. bacteria being consumed by soil fauna) because the C:N ratio of soil organic matter was sufficiently high to require bacteria to take-up inorganic N. The day ended with a talk by Jim Elser (Arizona State University), who described diverse impacts of stoichiometric mechanisms in food webs, and proposed moving stoichiometric thinking beyond ecology and into the realms of evolutionary biology, cellular physiology and molecular genetics, by focusing on the central role of ribosomal RNA in coupling growth to C:N:P stoichiometry.

Prospects

What common themes arose from these diverse topics? What should be major goals for ES in coming years? Although most participants agreed that more time was needed for discussions along these lines, some tentative themes emerged. Given the qualitative effects of stoichiometric reality on food-web theory (as shown by Andersen) and various discussions about the nature of stoichiometric food-quality limitation of grazers, it seems clear that we need to better evaluate how grazer nutrient economy responds to food with a high C:nutrient ratio. Based on the presentations of Anderson, Raubenheimer and Boersma, incorporating the effects of both mineral and biochemical food quality in experimental and theoretical studies seems timely. Finally, the extremely diverse, but related, nature of the work discussed in Oslo indicates that stoichiometric thinking has much potential for integrating not only aquatic and terrestrial ecology but also for connecting ecology to other disciplines, such as evolutionary biology, physiology, behavior and cellular biology. This would help in producing a more coherent, vertically integrated science of biology. Perhaps, the threads assembled in Oslo can be the start of a richer and broader fabric, a ‘biological stoichiometry’, to be woven in coming years.

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