

unsolved thermomechanical problem. The answer may involve instabilities resulting from variations in spreading rates⁴. On the other hand, the system may be evolving towards a steady-state rift-transform configuration, in which the transfer zones will eventually develop into transform faults. □

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Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems

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HERBIVORES can consume a sufficiently large proportion of primary production to regulate plant biomass in some environments¹⁻³. Little is known, however, about how rates of herbivory vary among ecosystems and how herbivores influence the global distribution of vegetation. Patterns of herbivory in terrestrial ecosystems have been summarized recently^{4,5}, but comparisons with aquatic systems are uncertain because past generalizations about herbivory in aquatic systems are based on surprisingly few data⁶⁻⁸. Herbivory is thought to be higher in aquatic than in terrestrial ecosystems⁹⁻¹¹ and the impact of herbivores in aquatic systems is believed to decrease with increasing primary productivity¹²⁻¹⁵, a pattern opposite to that in terrestrial systems^{4,5}. Here we examine these hypotheses using data from 44 aquatic sites. Herbivore biomass and herbivory rates increase at similar rates with increasing primary productivity in aquatic and in terrestrial systems. For a given level of primary productivity, aquatic and terrestrial herbivores reach similar biomass, but aquatic herbivores remove on average 51% of annual primary production, three times more than terrestrial herbivores. Mass-specific rates of herbivory are greater in aquatic than in terrestrial systems.

To compare the impact of herbivores in different types of ecosystems, we compiled published measurements of herbivory rates, herbivore biomass and primary productivity for a wide range of aquatic systems¹⁶⁻³⁸ and used the data of McNaughton *et al.*^{4,5} for terrestrial systems. A modified version of this terrestrial data set³⁹, which condenses data from different years into long-term averages and excludes sites where the herbivores were managed, is slightly different, but does not alter the comparisons we make between aquatic and terrestrial systems. Herbivory is defined as ingestion of plant material, not its assimilation, and includes the effect of all major herbivores. Studies were discarded when herbivory and/or primary productivity were estimated indirectly, measured over a short time that could not be extrapo-

lated to annual values, or were not measured concurrently (for example, rates of herbivory and primary productivity measured in different years). Units were standardized, preferably with conversion factors measured by the original authors but if these were not available, we used standard values^{31,40-43}. Copies of the data set are available from the authors.

Herbivory rates vary among types of ecosystems (Fig. 1). Algae are grazed more intensively than aquatic vascular plants (Fig. 1a, b) and herbivores generally remove a larger proportion of net primary production in aquatic (median, 51%; $n = 44$) than in terrestrial systems (median, 18%). These results support the hypothesis that herbivory is generally greater in aquatic than in terrestrial ecosystems⁹⁻¹¹, even for aquatic macrophytes, which were traditionally thought to be largely immune to herbivory⁴⁴.

Herbivory rates increase with increasing annual net primary productivity. This relationship in aquatic systems is linear (slope of log-log relationship is not different from 1, t -test: $P = 0.7$; Fig. 2), suggesting that herbivores remove the same proportion of annual net primary production in poor as in rich aquatic systems. Similar relationships are found for algae and for aquatic vascular plants (comparison of slopes using an F -test: $P = 0.7$, after removal of the St Lawrence site (Fig. 2) to equalize the variance between the two groups of data), although algae are grazed 2.5 times more than vascular plants (ANCOVA,

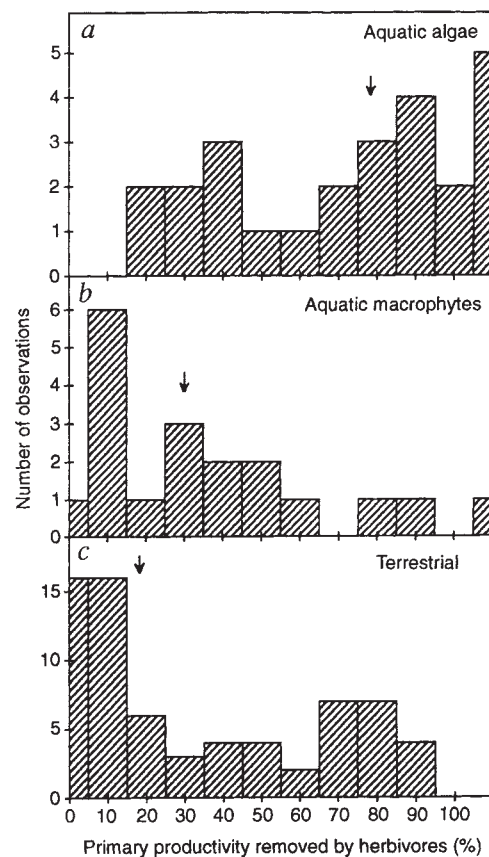


FIG. 1 Frequency distributions of the proportion of annual net primary productivity removed by herbivores in a, aquatic algae (phytoplankton¹⁶⁻²⁸, $n = 17$, and reef periphyton^{29,30}, $n = 8$); b, submerged³¹⁻³⁵ ($n = 5$) and emergent³⁶⁻³⁸ ($n = 14$) vascular plants; and c, terrestrial plants^{4,5} ($n = 67$). Primary productivity and herbivory data for aquatic and terrestrial rooted plants are limited to the aboveground portion of the plants. Comparison of herbivory on algae and rooted plants, therefore, assumes that the proportion of aboveground primary productivity grazed is representative of the whole plant, an assumption supported by the limited data available from terrestrial systems (aboveground^{4,5}: median, 18%, $n = 69$; belowground⁵⁰⁻⁵²: median, 13%, $n = 14$). Arrows indicate median values (aquatic algae, 79%; aquatic macrophytes, 30%; terrestrial plants, 18%).

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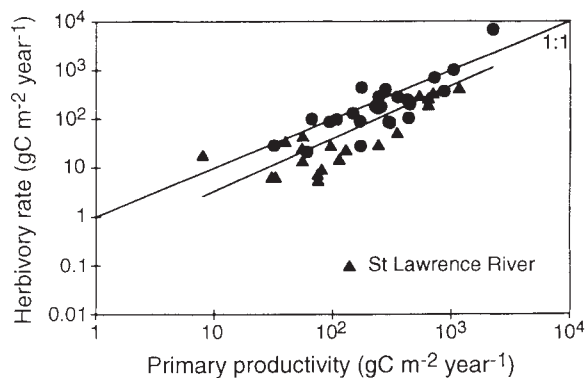


FIG. 2 Relationship between annual rates of herbivory (HR) and net primary productivity (PP) in aquatic systems ($\log_{10} HR = 1.07 \log_{10} PP - 0.55$; $r^2 = 0.45$, $n = 44$; removing low St Lawrence site: $\log_{10} HR = 1.03 \log_{10} PP - 0.39$; $r^2 = 0.63$). Circles represent planktonic and periphytic algae, triangles represent submerged and emergent vascular plants. The 1:1 line shows where 100% of primary production is grazed.

$P < 0.01$). These results do not support reports that herbivory declines along gradients of primary productivity in marine and freshwater plankton^{12-15,45}. Our analysis is more general than previous comparisons of aquatic systems^{12,15,45} because it is based on more data ($n = 44$, compared with $n = 3-9$), and covers the whole year rather than short sampling periods (one day to three months). The pattern we found in aquatic systems is not significantly different from the pattern in terrestrial systems (comparison of slopes using an F -test: $P > 0.6$; Fig. 3).

Higher rates of herbivory in aquatic systems (Fig. 3) suggest two non-exclusive corollaries: herbivores maintain a higher biomass and/or graze more per unit of biomass in aquatic compared with terrestrial systems. We compared annual average herbivore biomass among aquatic systems. Herbivore biomass was reported or could be calculated for 30 sites (Fig. 4). In two submerged macrophyte beds, herbivores reached much higher average biomass than in other aquatic systems of similar productivity (upper two triangles in Fig. 4; refs 32, 33). Excluding these two sites, average herbivore biomass in aquatic systems increases with net primary productivity (ANOVA: $P < 0.001$, $r^2 = 0.57$, $n = 28$; Fig. 4, filled symbols). The strength of this relationship may be surprising as some sites support mostly resident herbivores (planktonic invertebrates, coral reef fish and invertebrates; filled circles in Fig. 4), whereas others are mostly grazed by migratory herbivores (waterfowl, turtles; triangles in Fig. 4). The biomass of migratory herbivores might be expected to be poorly related to the productivity of a single feeding site, but the pattern in biomass of migratory herbivores agrees well with that of resident herbivores.

Annual average herbivore biomass also increases with increasing net primary productivity in terrestrial systems^{4,5} (Fig. 4, open symbols). McNaughton *et al.* report a slope of 1.52 ± 0.18 (s.e.),

but their relationship is strongly influenced by a tundra site with very low herbivore biomass (open circle with lowest herbivore biomass in Fig. 4). When this point is removed from the analysis, which also equalizes the variance of the aquatic and the terrestrial data, the relationship in terrestrial systems resembles that in aquatic systems (comparison of slopes using an F -test: $P = 0.3$; ANCOVA, $P = 0.15$; common slope: $b \pm \text{s.e.} = 1.17 \pm 0.11$, $r^2 = 0.60$, $n = 78$). For a given level of net primary productivity, herbivores reach similar average biomass in aquatic and terrestrial ecosystems.

Higher herbivory rates in aquatic systems (Fig. 3), despite similar herbivore biomass (Fig. 4), suggest that mass-specific herbivory rates are higher in aquatic than in terrestrial systems. Differences in mass-specific herbivory rates have been attributed to characteristics of the plants (such as nutrient content, chemical or physical defences⁴⁶⁻⁴⁸) and/or the herbivores (such as size, ectothermy versus endothermy, behaviour⁴⁶⁻⁴⁸), but the importance of these and other factors in determining herbivory at the scale of ecosystems remains to be tested.

Similarities and differences in herbivory have important implications for patterns of energy flow in ecosystems. Higher herbivory rates in aquatic than in terrestrial systems suggest that herbivores in aquatic systems recycle limiting nutrients more rapidly to primary producers and leave a smaller proportion of the plant material produced annually to decomposers. Higher herbivory rates in aquatic systems also suggest higher herbivore productivity because production efficiencies (ratio herbivore productivity: herbivory rate) do not differ systematically

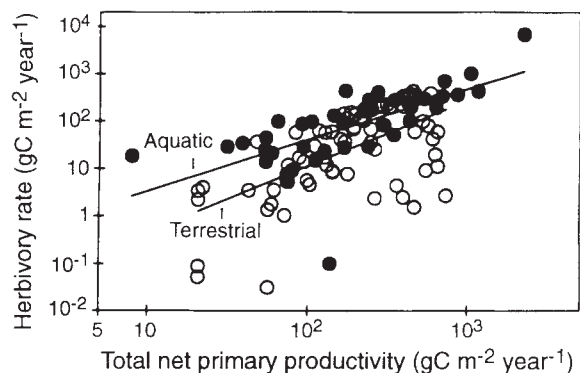


FIG. 3 Relationship between annual rates of herbivory and net primary productivity in aquatic (filled circles; slope $b \pm \text{s.e.} = 1.07 \pm 0.18$) and terrestrial (open circles; $b \pm \text{s.e.} = 1.38 \pm 0.22$) ecosystems. Rates of herbivory are on average three times higher in aquatic than in terrestrial systems (ANCOVA: $P < 0.001$).

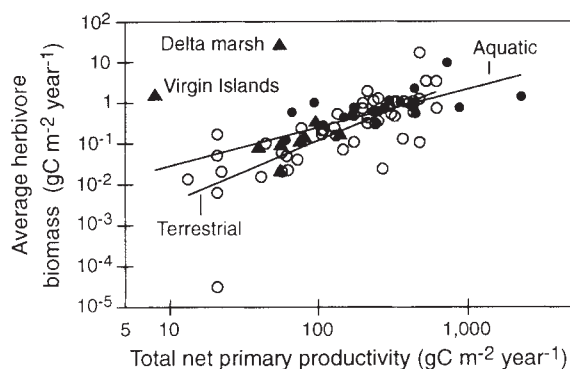


FIG. 4 Relationship between annual average herbivore biomass (HB) and net primary productivity (PP) in aquatic and terrestrial systems. Filled symbols represent aquatic sites (circles for algae¹⁶⁻³⁰; triangles for vascular plants³¹⁻³⁸); open symbols represent terrestrial sites^{4,5}. Waterfowl densities were transformed to biomass using species-specific average individual mass⁵³, assuming a 1:1 sex ratio. The relationship shown for aquatic systems excludes two submerged macrophyte beds (Delta marsh and Virgin Island excluded; $\log_{10} HB_{\text{aquatic}} = 0.94 \log_{10} PP - 2.48$; $r^2 = 0.57$, $n = 28$) and the relationship shown for terrestrial systems excludes one tundra site ($\log_{10} HB_{\text{terrestrial}} = 1.28 \log_{10} PP - 3.38$; $r^2 = 0.61$, $n = 50$).

between aquatic and terrestrial organisms⁴⁹. Assuming that herbivore productivity is higher in aquatic than in terrestrial systems, and that there is no systematic difference in herbivore biomass (Fig. 4), immigration, emigration and non-predatory mortality among types of ecosystems, we expect predation to be higher on aquatic than on terrestrial herbivores. □

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Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge

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PLANT growth in arctic tundra is strongly nitrogen-limited despite large pools of soil organic nitrogen^{1–4}. Here we report that field-collected roots of *Eriophorum vaginatum*, an arctic sedge, rapidly absorb free amino acids, accounting for at least 60% of the nitrogen absorbed by this species in the field. In solution culture, *Eriophorum* accumulates more nitrogen and biomass when supplied with amino acids than when grown on inorganic nitrogen, whereas *Hordeum vulgare* (a cereal adapted to mineral soils) grows least when nitrogen is supplied as amino acids. To our knowledge, this is the first documentation of preferential absorption and use of organic nitrogen by a non-mycorrhizal vascular plant. The direct absorption of amino acids by *Eriophorum* short-circuits the bottleneck in arctic nitrogen cycles imposed by temperature-limited mineralization.

In the moist tundra of arctic Alaska, mineralization of nitrogen from organic to inorganic form accounts for only about half of the annual nitrogen requirement^{1,2} of this nitrogen-limited^{2–4} vegetation. How do plants meet the rest of their nitrogen requirement? In well-drained heaths, ericoid mycorrhizal fungi (and perhaps ectomycorrhizal fungi of deciduous shrubs) hydrolyse proteins and transfer amino acids to their symbiotic host plants^{5–9}. But moist and wet tundras, which account for 40% of the area of the Low Arctic¹⁰, are dominated by sedges that are generally non-mycorrhizal or have an endomycorrhizal symbiont^{5–7,11} that cannot hydrolyse organic N¹¹. Moist and wet

tundra soils have higher concentrations of water-extractable free amino acids (2–8 µg N g⁻¹ dry soil) than of inorganic nitrogen (0.5–1.1 µg N g⁻¹) (ref. 2), perhaps because protease activity is an order of magnitude faster than net nitrogen mineralization¹². Here we demonstrate that *Eriophorum vaginatum* L., a non-mycorrhizal sedge¹² that dominates moist upland tundra throughout the circumpolar Arctic, can absorb amino acids and grow on them as its sole nitrogen source. By contrast, barley (*Hordeum vulgare* L., cv. Stepto), a north-temperate cereal that grows on mineral soils, does not efficiently utilize amino acids for growth.

In upland moist tundra at Toolik Lake in arctic Alaska (68° N, 149° W; 760 m elevation) we collected *Eriophorum* roots and measured kinetics of uptake of ¹⁴C-labelled methylamine (an ammonium analogue), glycine, glutamate and aspartate in four separate experiments. *Eriophorum* had a higher capacity (V_{max}) for ammonium than for amino-acid uptake, but higher affinity (lower apparent K_M) for most amino acids (Table 1). On the basis of these kinetics and the seasonal average concentration of free amino acids in the soil solution, we estimate that the field absorption rate of ammonium was lower than that of glycine but higher than that of aspartate or glutamate (Table 1). Assuming conservatively that other free amino acids that were present in the soil solution but omitted from our study² are not absorbed, amino acids would comprise 60% of the nitrogen absorbed by *Eriophorum*. Plants do absorb other amino acids^{13,14}, so amino acids probably comprise an even higher proportion of the nitrogen acquired by *Eriophorum* in the field. The rates of methylamine uptake in our experiments were similar to ammonium uptake rates reported for *Eriophorum* using ¹⁵N-ammonium, or to net uptake by intact plants measured with specific ion electrodes^{15–18}; this indicates that our uptake rates are not an artefact resulting from the use of methylamine as an ammonium analogue.

When grown in solution culture, *Eriophorum* accumulated most nitrogen and biomass when supplied with amino acids as its sole nitrogen source (Fig. 1). By contrast, *Hordeum*, a species that typically grows on mineral soils, grew most on nitrate and