

S. patens sites had lower sedimentation rates. Because of their higher elevations, the sites dominated by *S. patens* were subject to less frequent and shorter periods of flooding, and therefore had less opportunity to receive suspended material. Both the percentage of organic matter deposited and the sediment content of organic matter to a depth of 50 cm increased with elevation. Not only is sediment less available to these higher sites, but inorganic constituents are heavier and fall out of suspension before flooding reaches the elevation of the high marsh (8). The high marsh sites have a higher percentage of organic matter below the surface because they are accumulating peat (8), and the sediment deposited on the surface is mostly organic.

The sedimentation patterns we have observed give a brief picture of a two-month period. Factors not within the scope of our study, such as marsh microtopography, seasonal storm events, and mussel densities may also influence marsh sedimentation. Our estimates of sedimentation rates for this period indicate that elevation (or flooding frequency) is the most significant factor in determining the rate of sedimentation in salt marshes of the Rowley River. At first, these results seem to suggest that marshes will always be able to keep up with a rising sea level

because they will become lower in elevation and will thus be flooded more frequently. However, determining whether there will be a sufficient supply of sediment for salt marshes to rise at the same pace as the sea requires further investigation.

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Dependence of Herbivory on Autotrophic Nitrogen Content and on Net Primary Production Across Ecosystems

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To determine what factors control the abundance of herbivores in an ecosystem (1), and thus the effects these consumers have on autotrophic biomass (2), we must first understand why and how much herbivory differs among ecosystems. Previous reports suggest that ecosystems dominated by richer autotrophs (*i.e.*, those with a higher nutrient content) support higher rates of herbivory (2) and that the same is true for more productive ecosystems (1,3). If ecosystems composed of richer autotrophs are indeed subject to higher herbivory rates, the association between net primary production (NPP) and herbivory across ecosystems may point to a contradiction, because more productive ecosystems are not necessarily dominated by autotrophs with higher nutrient contents (4). For instance, although forests and phytoplanktonic communities may reach similar values of NPP, they are dominated by autotrophs with contrasting nutrient contents (5). Therefore, the interaction between NPP and autotrophic nutrient content in controlling herbivory in ecosystems needs to be further explored and clarified.

Here, we investigate, through a compilation of published data, the relationship between NPP, autotrophic nitrogen content, and herbivory across different types of ecosystems. We chose nitrogen because it is the nutrient most frequently reported in the literature. All the reports compiled met these requirements: first, they were representative of the ecosys-

tem considered—that is, they included the dominant autotrophs and herbivores (>75% of total abundance) in the ecosystem; second, they were annual or exceeded the growing period for seasonal producers; and finally, they referred only to natural conditions. Some reports of macrophyte-dominated ecosystems included only the above-ground compartment, but the patterns obtained overrode this variability. NPP and herbivory rates were expressed as grams of carbon per square meter per day, and autotrophic nitrogen concentration was expressed as percent dry weight. In some reports these units were derived by using standard conversion factors. The data set used is available from the first author. Relationships between variables were examined with least-square regression techniques. Variables were log-transformed to remove heteroscedasticity.

NPP is unrelated to autotrophic nitrogen content across ecosystems (Fig. 1a). This finding shows that, as suggested by previous reports (4), across ecosystems the magnitude of NPP is independent of its quality to herbivores (*i.e.*, nitrogen content). We further show that ecosystems composed of richer autotrophs lose a higher percentage of NPP to herbivores (Fig. 1b). This tendency indicates that herbivore feeding rates in ecosystems are limited by the nitrogen content of the dominant autotrophs. Hence, ecosystems composed of richer autotrophs have enhanced rates of herbivore feeding

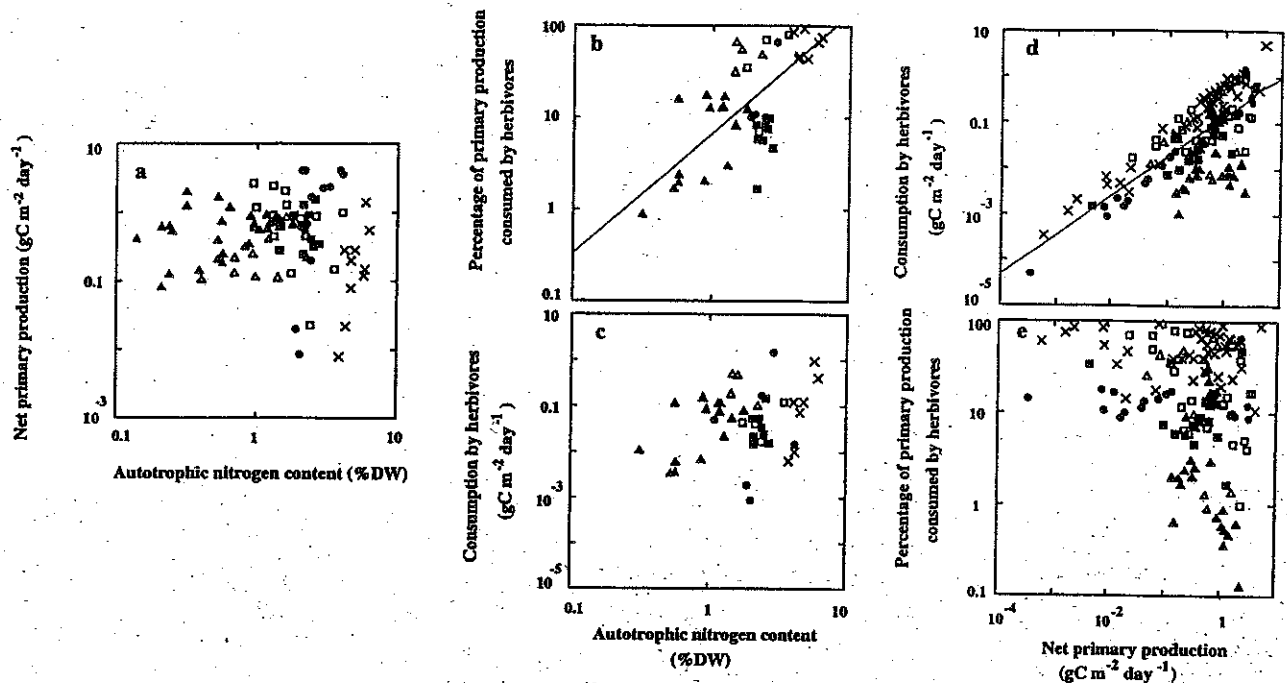


Figure 1. Relationships between pairs of variables across the range of ecosystems for which data were compiled. Symbols denote phytoplanktonic and microphytobenthic communities (\times), benthic macroalgal beds (\circ), seagrass meadows (\blacksquare), salt and freshwater marshes (\square), grasslands (Δ), and shrublands and forests (\blacktriangle). Lines correspond to the regressions adjusted. (a) Net primary production versus autotrophic nitrogen content ($r^2 = 0.02$, $n = 87$, F ratio = 0.03, $P = 0.86$) (b) Percentage of production consumed by herbivores versus autotrophic nitrogen content (log percentage consumed = $0.82 (\pm 0.09) + 1.3 (\pm 0.2) \log$ nitrogen content, $r^2 = 0.43$, $n = 41$, F ratio = 31.6, $P < 0.01$) (c) Absolute consumption by herbivores versus autotrophic nitrogen content ($r^2 = 0.07$, $n = 43$, F ratio = 4.3, $P = 0.046$) (d) Absolute consumption versus NPP (log absolute consumption = $-0.90 (\pm 0.06) + 0.84 (\pm 0.06) \log$ NPP, $r^2 = 0.54$, $n = 147$, F ratio = 169.9, $P < 0.01$) (e) Percentage of production consumed versus NPP ($r^2 = 0.04$, $n = 147$, F ratio = 6.4, $P = 0.01$).

and, as a consequence, lose larger percentages of NPP. This reveals that autotrophic nitrogen content is a major control of herbivory in ecosystems and overrides differences in herbivore characteristics (such as migratory vs. resident behavior or dissimilar metabolic constraints) among ecosystems (6).

Because ecosystems composed of richer autotrophs lose a higher percentage of NPP to herbivores (Fig. 1b) but reach relatively similar values of NPP (Fig. 1a), it would seem that they would also support a higher absolute consumption (in $\text{g C m}^{-2} \text{ day}^{-1}$) by herbivores. However, we found that absolute consumption is poorly ($r^2 = 0.07$), albeit significantly ($P = 0.046$), related to autotrophic nitrogen content across ecosystems (Fig. 1c). Instead, absolute consumption is associated with NPP, as indicated by previous results (1) and generalized here for a broader range of ecosystems (Fig. 1d). Absolute consumption is the product of NPP and the percentage of NPP consumed by herbivores. Among ecosystems, NPP varies by four orders of magnitude, whereas the fraction of NPP consumed varies by less than three (Fig. 1e). Consequently, the variability in absolute consumption among ecosystems is mostly dictated by the variability in NPP (Fig. 1d). This tendency combined with the finding that ecosystems with similar values of NPP differ remarkably in their autotrophic nitrogen contents (Fig. 1a) explain why absolute consumption and autotrophic nitrogen content are poorly related across ecosystems (Fig. 1c).

Our results clarify the role and interaction of NPP and autotrophic nitrogen content as controls of herbivory in ecosystems. If herbivory is regarded as percentage of NPP consumed, differences among ecosystems are related to differences in autotrophic nitrogen content, probably because higher nitrogen contents enhance herbivore feeding rates. On the other hand, when herbivory is regarded as absolute consumption, differences among ecosystems are associated with differences in NPP, because NPP variability among ecosystems overrides any enhancement of herbivore feeding rate that is caused by a higher autotrophic nitrogen content.

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