

The dependence of heterotrophic consumption and C accumulation on autotrophic nutrient content in ecosystems

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Abstract

Primary producers with high nutrient contents typically exhibit high herbivory rates and fast decomposition rates. These tendencies, however, have not been generalized across ecosystems with contrasting herbivore characteristics and abiotic properties. Here we demonstrate that ecosystem types dominated by richer autotrophs (i.e. higher nutrient contents) are subject to higher rates of herbivory and decomposition in spite of differences in herbivore characteristics and environmental conditions. We further show that, as a result of these tendencies, ecosystems with richer autotrophs accumulate less carbon. These results identify autotrophic nutrient content as a main control of heterotrophic consumption and carbon accumulation in ecosystems. They also provide a basis to evaluate changes in these ecosystem properties following anthropogenic eutrophication.

Keywords

Autotrophic nutrient content, C accumulation, decomposition, ecosystems, herbivore consumption, net primary production.

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INTRODUCTION

Previous research has shown that primary producers with high nutrient contents frequently support intense herbivory, whereas producers with low nutrient contents are often subject to small herbivory (Coley *et al.* 1985; Bryant *et al.* 1989; Duarte 1995). In some instances, this observation has been explained by herbivore selection of palatable (i.e. high nutrient and low defence contents) autotrophs (Fraser *et al.* 1984; Landsberg & Ohmart 1989; Bolser & Hay 1996). Additionally, rich autotrophs (i.e. with high nutrient contents) may enhance herbivore feeding rates if herbivore metabolism is limited by nutrients (Mattson 1980; Hartley & Jones 1997). Detritus from richer autotrophs also tend to undergo faster decomposition, even when subject to different environmental conditions (Melillo *et al.* 1982; Enríquez *et al.* 1993). This tendency results from the fact that decomposers have high requirements for nutrients (Goldman *et al.* 1987), with rich detritus thus enhancing decomposition.

It remains unclear, however, whether ecosystems composed of richer autotrophs tend to have higher herbivory rates, because differing herbivore characteristics among ecosystems may preclude this tendency. For

instance, differences in migratory *versus* resident behaviour (Nienhuis & Groenendijk 1986; Portig *et al.* 1994), or specific herbivore–plant coevolutions (Edwards 1989; Hochuli 1996), may entail substantial herbivory variability among ecosystems. Moreover, differences in temperature, humidity, and sediment or soil chemistry among ecosystems make it uncertain whether ecosystems dominated by richer autotrophs exhibit faster decomposition rates. Hence, demonstrating a tendency for ecosystems composed of richer autotrophs to have higher herbivory rates and faster decomposition rates would suggest autotrophic nutrient content as a main control of heterotrophic metabolism and feeding rates in ecosystems. Moreover, this tendency may have important implications for carbon (C) accumulation in ecosystems: if ecosystems with rich autotrophs support greater heterotrophic consumption, but do not reach higher net primary production (NPP), then ecosystems with poor autotrophs, then the former ecosystems should accumulate less C.

In this report we demonstrate, through a compilation of published data, that ecosystems dominated by richer autotrophs are subject to higher rates of herbivory and decomposition. We then show that, as a result of these tendencies, ecosystems with richer autotrophs accumulate less C.

METHODS

A large data set on NPP, consumption by herbivores, decomposition rates, C accumulation, and autotrophic nitrogen and phosphorus contents in different types of ecosystem was compiled from more than 200 reports. All the ecosystem types selected represented rather similar percentages of the total data set. The data set is available from the authors upon request. Reports were accepted only if they met the following criteria: (i) they were representative of the whole ecosystem dynamics (i.e. they included the dominant autotrophs in the ecosystem); (ii) they reported measurements covering at least 1 year or exceeding the growing period for seasonal producers; and (iii) they referred to natural conditions (i.e. experimental or manipulated studies were not accepted). Because the number of reports providing values for more than one variable was low, variables were averaged by ecosystem type prior to analyses.

NPP, herbivore consumption, and C accumulation were expressed in $\text{g C m}^{-2} \text{ day}^{-1}$. Autotrophic nitrogen and phosphorus contents were expressed in percentage DW as a proxy for autotrophic nutritional quality for heterotrophs. Whenever possible, values of nutrient content averaged green and woody above- and below-ground parts for macrophyte-dominated ecosystems. Standard conversion factors (Gasol *et al.* 1997; Schlesinger 1997) were used when these units were not directly provided in the reports. Decomposition rates corresponded to the fraction of detrital mass decomposed per day (units day^{-1}). Whenever direct values were not provided in the reports, they were estimated as the ratio of detrital production to detrital mass (Olson 1963), because detrital mass pools remained virtually steady during the time periods covered by the studies compiled (i.e. between one and a few years).

C accumulation corresponded to the amount of NPP not consumed by heterotrophs and thus incorporated as autotrophic biomass or detrital mass. Whenever direct values were not available in the reports, they were estimated as the difference between NPP and the sum of herbivore consumption and decomposition. These values overestimated net C accumulation in ecosystems because they only covered the study time interval and disregarded long-term decomposition. However, for most of the studies compiled most decomposition occurred within the study time period, and therefore the overestimation should not generally be large as supported by comparison of our values with other independent estimates (Smith & Clymo 1984; Romero *et al.* 1994; Schlesinger 1997). Some of the reports for macrophyte-dominated ecosystems included only the above-ground component, but this fact did not affect the patterns observed.

RESULTS

Comparison between the percentage of NPP removed by herbivores and autotrophic nitrogen content across the compiled ecosystem types showed that ecosystems composed of richer autotrophs tended to lose higher percentages of NPP to herbivores (Fig. 1a, *F*-test, $P < 0.01$). The percentage of NPP removed by herbivores also increased with autotrophic phosphorus content across the ecosystem types compared (Fig. 1b, *F*-test, $P < 0.05$). Macroalgal beds, however, supported low levels of herbivory relative to the ones expected from their nutrient contents (Fig. 1a, b).

Decomposition rates were strongly related to autotrophic nitrogen and phosphorus contents across the ecosystem types considered (Fig. 1c, d; *F*-test, $P < 0.001$ for both regressions), with ecosystems composed of richer autotrophs having faster decomposition rates. Indeed, differences in autotrophic nitrogen and phosphorus contents among the ecosystem types compiled accounted for up to about 90% of the variability in decomposition rates. Decomposition rates varied substantially within the ecosystem types considered, but this variability did not hinder the strong association between decomposition and autotrophic nutrient content across ecosystem types.

Contrastingly, NPP was independent of autotrophic nitrogen and phosphorus contents across the ecosystem types considered (Fig. 2a, b; *F*-test, $P > 0.05$). Ecosystems with similar autotrophic nitrogen and phosphorus contents, such as grasslands, mangroves, and forests, differed in NPP by three-fold (Fig. 2a, b). C accumulation was strongly related to autotrophic nitrogen and phosphorus content across the ecosystem types compiled (Fig. 3a, b, *F*-test, $P < 0.01$ for both regressions), in spite of substantial variability in C accumulation within some types. Ecosystem types composed by richer autotrophs accumulated less C, with this tendency accounting for 80% of the variability in C accumulation.

DISCUSSION

Differences in herbivore characteristics among the ecosystem types compiled, such as migratory *versus* residential behaviour (Nienhuis & Groenendijk 1986; Portig *et al.* 1994), specific plant-herbivore coevolutions (Edwards 1989; Hochuli 1996), physiological constraints of invertebrate and vertebrate herbivores (Crawley 1983; Begon *et al.* 1986), and different predator pressure (Heck & Valentine 1995; Hartley & Jones 1997), do not hamper a strong tendency towards greater herbivory rates with higher autotrophic nutrient contents across the ecosystems investigated (Fig. 1a, b). Macroalgal beds, however, lose lower percentages of NPP to herbivores than

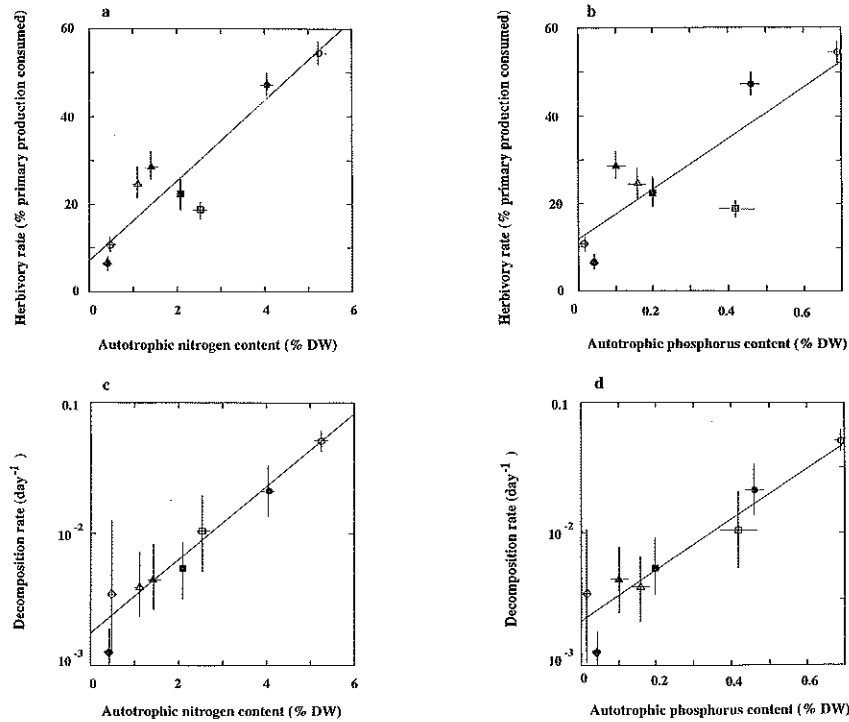
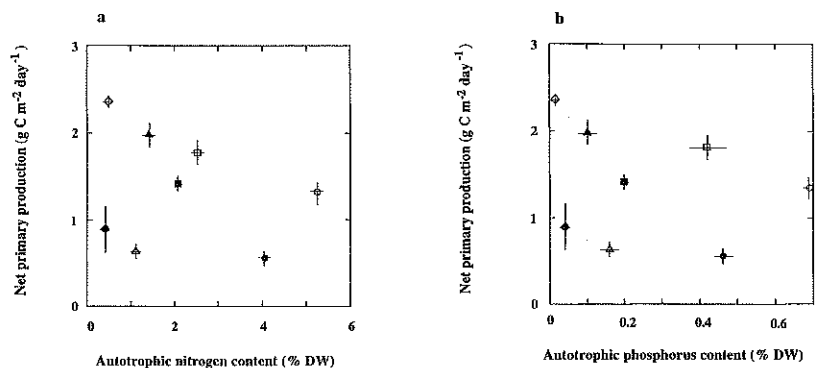


Figure 1 (a) The relationship between percentage of NPP consumed by herbivores and autotrophic nitrogen content across the ecosystem types compiled; percentage of NPP consumed = $7.4 (\pm 4.2) + 8.9 (\pm 1.5)$ nitrogen content ($P = 0.001$, $R^2 = 0.82$, $n = 8$). (b) The relationship between percentage of NPP consumed by herbivores and autotrophic phosphorus content across the ecosystem types compiled; percentage of NPP consumed = $11.4 (\pm 5.3) + 58.4 (\pm 15.5)$ phosphorus content ($P < 0.01$, $R^2 = 0.65$, $n = 8$). (c) The relationship between decomposition rate and autotrophic nitrogen content across the ecosystem types considered; log decomposition rate = $-2.8 (\pm 0.1) + 0.28 (\pm 0.03)$ nitrogen content ($P < 0.0001$, $R^2 = 0.93$, $n = 8$). (d) The relationship between decomposition rate and autotrophic phosphorus content across the ecosystem types considered; log decomposition rate = $-2.7 (\pm 0.1) + 2.0 (\pm 0.3)$ phosphorus content ($P = 0.0003$, $R^2 = 0.89$, $n = 8$). \circ , Phytoplankton; \bullet , benthic microalgae; \square , macroalgal beds; \blacksquare , seagrass meadows; \blacktriangle , marshes; \triangle , grasslands; \diamond , mangroves; and \blacklozenge , forests. Values and bars correspond to arithmetic means and their standard errors for variables expressed in linear units, and to geometrical means and their confidence intervals for variables expressed in logarithmic units. Lines depict the fitted equations.

Figure 2 (a) The relationship between NPP and autotrophic nitrogen content across the ecosystem types considered (H_0 : slope = 0, $P = 0.5$). (b) The relationship between NPP and autotrophic phosphorus content across the ecosystem types considered (H_0 : slope = 0, $P = 0.6$). \circ , Phytoplankton; \bullet , benthic microalgae; \square , macroalgal beds; \blacksquare , seagrass meadows; \blacktriangle , marshes; \triangle , grasslands; \diamond , mangroves; and \blacklozenge , forests. Values and bars correspond to arithmetic means and their standard errors.



expected from their autotrophic nutrient contents (Fig. 1a, b). Although modest levels of herbivory have long been reported in many different macroalgal beds (Dunton & Schell 1986; Man 1988; Duarte & Cebrian 1996), the reasons why macroalgal beds tend to support small

herbivory despite having relatively high nutrient contents are unclear and require more research. Moreover, environmental differences among the ecosystem types compiled, such as temperature, humidity, and sediment and soil redox conditions, do not impede a tendency

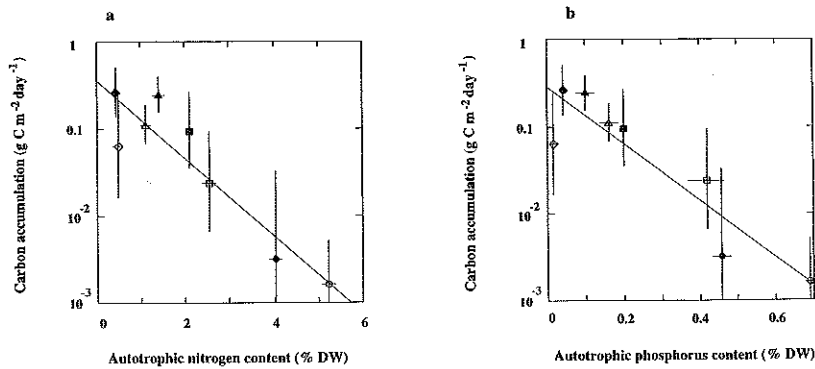


Figure 3 (a) The relationship between C accumulation and autotrophic nitrogen content across the ecosystem types considered; $\log C$ accumulation = $-0.4 (\pm 0.2) - 0.45 (\pm 0.08)$ nitrogen content ($P < 0.001$, $R^2 = 0.83$, $n = 8$). (b) The relationship between C accumulation and autotrophic phosphorus content across the ecosystem types considered; $\log C$ accumulation = $-0.6 (\pm 0.2) - 3.2 (\pm 0.6)$ phosphorus content ($P = 0.001$, $R^2 = 0.82$, $n = 8$). \circ , Phytoplankton; \bullet , benthic microalgae; \square , macroalgal beds; \blacksquare , seagrass meadows; \blacktriangle , marshes; \triangle , grasslands; \diamond , mangroves; and \blacklozenge , forests. Values and bars correspond to arithmetic means and their standard errors for variables expressed in linear units, and to geometrical means and their confidence intervals for variables expressed in logarithmic units. Lines depict the fitted equations.

towards faster decomposition rates with higher autotrophic nutrient contents across these ecosystems (Fig. 1c, d). This trend generalizes across ecosystems the association between plant decomposition rates and nutrient content described at the species level (Melillo *et al.* 1982; Enríquez *et al.* 1993).

These results are consistent with the idea that the metabolism and feeding rates of heterotrophs in ecosystems are mainly limited by the nutrient content of dominant autotrophs, as suggested by previous reviews (Enríquez *et al.* 1993; Hartley & Jones 1997; Sterner *et al.* 1997). Heterotrophic metabolism and feeding rates are enhanced by richer autotrophs, and, as a consequence, ecosystems dominated by richer autotrophs have larger percentages of NPP consumed by herbivores and faster decomposition rates. Although NPP may increase with higher nutrient contents of photosynthetic tissues within some ecosystem types (Williams *et al.* 1997; Waring *et al.* 1998), we find that NPP is unrelated to the nutrient content of total (photosynthetic and structural) autotrophic biomass across the ecosystem types compared (Fig. 2a, b), because these types, while reaching similar values of NPP, differ much in the ratio of structural, nutrient-poor to photosynthetic, nutrient-rich tissues. This indicates that the magnitude of NPP in ecosystems is unrelated to its quality for heterotrophs, which is in agreement with other across-ecosystems comparisons (Borum & Sand-Jensen 1996). Because C accumulation corresponds to the excess of NPP not consumed by heterotrophs, the increase in heterotrophic consumption with higher autotrophic nutrient contents (Fig. 1) and the independence between NPP and autotrophic nutrient contents across ecosystem types (Fig. 2), imply that

ecosystem types composed of richer autotrophs accumulate less C (Fig. 3a, b).

Moreover, our results imply that herbivory and decomposition rates are unrelated to NPP across the ecosystem types compiled (H_0 : Pearson correlation coefficient = 0, $P > 0.1$ for both correlations). This implication may seem to conflict with the dependence of herbivory rates on NPP established by McNaughton *et al.* (1989) and Cyr & Pace (1993) across ecosystems. In reality, these results are not contradictory and the explanation relies on the definition of herbivory rate used: whereas we define herbivory rate as the percentage of NPP consumed, these authors define it as absolute consumption (i.e. expressed in $\text{g C m}^{-2} \text{day}^{-1}$). Absolute consumption is the product between NPP and its fraction consumed by herbivores, and because NPP variability among ecosystems exceeds that in the fraction consumed (Cebrián & Duarte 1994; Griffin *et al.* 1998), it turns out that absolute consumption is associated with NPP across ecosystems. Accordingly, absolute consumption is not associated with autotrophic nutrient content across ecosystems (Griffin *et al.* 1998).

Recent research has shown a tendency towards faster biomass turnover rates (i.e. percentage of biomass renewed per day) with higher nutrient contents across different types of autotrophs (Nielsen *et al.* 1996). Hence, ecosystems composed of richer autotrophs show faster turnover rates of autotrophic biomass (Cebrián, unpublished). Consequently, differences in autotrophic turnover rate among ecosystems are associated with differences in the percentage NPP consumed by herbivores (Cebrián & Duarte 1994) and decomposition rates (Cebrián, unpublished), with ecosystems composed of faster turning-over

autotrophs supporting higher herbivory and decomposition rates. Moreover, as a result of these tendencies, ecosystems composed of faster-turning autotrophs accumulate less C (Cebrián & Duarte 1995; Cebrián, unpublished). Autotrophic nutrient content and turnover rate are therefore equivalent predictors of heterotrophic consumption and C accumulation in ecosystems.

Our results identify autotrophic nutrient content as a main control of heterotrophic consumption and C accumulation in ecosystems. Broad scale coastal eutrophication is replacing seagrass communities by nutrient-richer macroalgal and phytoplanktonic communities (Duarte 1995; Pedersen 1995; Borum & Sand-Jensen 1996; Valiela *et al.* 1997). Moreover, large forest areas are being replaced by grasslands and pastures (Subak *et al.* 1992; Vitousek *et al.* 1997), which also have higher plant nutrient contents. Our results suggest that these changes may be conducive to enhanced heterotrophic consumption and depressed C accumulation within these perturbed areas. However, deleterious effects of eutrophication on heterotrophic activity, such as anoxia and habitat change (Heip 1995; Valiela *et al.* 1997; Hauxwell *et al.* 1998), may prevent these expectations. Clearly, more research is needed to elucidate how global eutrophication and associated side-effects may alter the dependence of heterotrophic consumption and C accumulation on autotrophic nutrient content in ecosystems.

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BIOSKETCH

Just Cebrián's research interests include the nature and controls of the fate of autotrophic production in ecosystems. In particular, his research addresses the extent and causes of variability in primary production, herbivory, decomposition, export, and biomass and detrital mass storage among ecosystems. These questions are explored with diverse experimental techniques and with extensive compilations of published reports. Moreover, the scales at which this research has been conducted vary from comparisons among populations within a particular ecosystem to broad-scale comparisons among contrasting types of ecosystems. Finally, he is deeply interested in examining the extent, controls, and consequences of anthropogenic effects (e.g. global eutrophication, deforestation, climatic change) on heterotrophy, export, and carbon storage in ecosystems.

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