Patterns in the Fate of Production in Plant Communities

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ABSTRACT: I examine, through an extensive compilation of published reports, the nature and variability of carbon flow (i.e., primary production, herbivory, detrital production, decomposition, export, and biomass and detrital storage) in a range of aquatic and terrestrial plant communities. Communities composed of more nutritional plants (i.e., higher nutrient concentrations) lose higher percentages of production to herbivores, channel lower percentages as detritus, experience faster decomposition rates, and, as a result, store smaller carbon pools. These results suggest plant palatability as a main limiting factor of consumer metabolic and feeding rates across communities. Hence, across communities, plant nutritional quality may be regarded as a descriptor of the importance of herbivore control on plant biomass ("top-down" control), the rapidity of nutrient and energy recycling, and the magnitude of carbon storage. These results contribute to an understanding of how much and why the trophic routes of carbon flow, and their ecological implications, vary across plant communities. They also offer a basis to predict the effects of widespread enhancement of plant nutritional quality due to large-scale anthropogenic eutrophication on carbon balances in ecosystems.

Keywords: plant community, primary production, herbivory, decomposition, carbon storage.

The amount of CO₂ fixed by primary production in plant communities can follow diverse trophic routes (fig. 1). Herbivores remove a fraction of production, with the rest being accumulated as plant biomass and entering the degradable detrital compartment over the plant life span. This compartment may also receive plant detritus imported from other communities (Nixon 1980; Twilley et al. 1986). A fraction of plant detritus is exported off the community by means of physical agents, such as rivers in terrestrial communities or currents and waves in aquatic ones (Mann 1988; Pomeroy and Wiebe 1993). The rest of detritus undergoes decomposition within the community, with a small fraction of recalcitrant detritus escaping from further degradation and entering the refractory compartment (Schlesinger 1997).

Temporal changes in the biomass and degradable detrital mass of plant communities are related to the trophic routes of production by the following mass-balance equations:

\[ \Delta B(t) = NPP - C - DP, \]  

\[ \Delta DB(t) = DP + I - D - E - RA, \]

where \( \Delta B(t) \) and \( \Delta DB(t) \) correspond to the increments in plant biomass and degradable detrital mass per unit time (g C m\(^{-2}\) d\(^{-1}\)) respectively, and NPP, C, DP, I, D, E, and RA stand for net primary production, consumption by herbivores, detrital production, import, decomposition, export, and refractory accumulation, respectively (all variables in g C m\(^{-2}\) d\(^{-1}\)). Under steady state assumptions, \( B \) and \( DB \) remain constant with time, and, thus, the sum of primary production and import equals the sum of herbivory, decomposition, export, and refractory accumulation.

The assessment of the trophic routes of production in a plant community is important because these routes are indicative of the ecological role of the community. The extent of the fraction of production removed by herbivores reflects the importance of herbivores as controls of plant biomass (Petursdottir and Grodzinski 1975; Cebrian and Duarte 1994). On the other hand, the absolute flux of production consumed by herbivores (in g plant C m\(^{-2}\) d\(^{-1}\)) set limits to the abundance of herbivores supported by a plant community (McNaughton et al. 1989; Cyr and Pace 1993). The amount of detritus exported off a plant community points to the magnitude of allochthonous secondary production supported by the community because most exported detritus are consumed within the receiving communities (Mann 1988). In contrast, accumulation of refractory detritus within a community represents a net...
carbon sink since refractory carbon is preserved over long-term scales (Schlesinger 1997).

A few studies have analyzed the extent and controls of the variability in specific trophic routes of production across diverse plant communities. Comparisons among a broad range of aquatic and terrestrial communities show that more productive communities support higher levels of absolute consumption by herbivores, and consequently, they maintain larger herbivore abundances (McNaughton et al. 1989; Cyr and Pace 1993). Absolute consumption increases linearly with primary production across communities (McNaughton et al. 1989; Cyr and Pace 1993). This tendency implies that the percentage of production removed by herbivores, which is indicative of their potential role as controls of plant biomass, is independent of the magnitude of primary production when aquatic and terrestrial communities are compared (Cebrian and Duarte 1994). The fraction of production removed is associated with the biomass turnover rate (i.e., fraction of biomass renewed per day [d⁻¹]) of the plant community, probably because faster turning-over communities have a greater palatability for herbivores (Cebrian and Duarte 1994; Duarte and Cebrian 1996). Plant detritus from communities with faster biomass turnover rates also seem to undergo faster decomposition rates probably because of their expected greater palatability for decomposers (Enriquez et al. 1993; Cebrian and Duarte 1995). Plant communities having higher fractions of production removed by herbivores and faster decomposition rates store smaller biomass and detrital pools if differences in the intensity of heterotrophic consumption override differences in the magnitude of production (Cebrian et al. 1998). Marine plant communities typically exposed to substantial advection by waves and currents tend to export large amounts of detritus (Duarte and Cebrian 1996).

Nevertheless, no attempt to compare all the trophic routes of production combined into thorough carbon balances across a broad range of aquatic and terrestrial plant communities has been made. Our knowledge about how primary production, consumption by herbivores, detrital production, decomposition, refractory accumulation, export, and import dovetail carbon balances across a continuum of diverse aquatic and terrestrial plant communities is meager. Likewise, although controls of the variability in some particular routes across communities have been identified, we lack knowledge of mechanisms responsible for differences in the entire carbon balance among communities.

It has been suggested that plant communities with faster biomass turnover rates have higher fractions of production lost to herbivores and faster decomposition rates because they should have higher plant nutrient concentrations and,
thus, enhance the metabolism and feeding rates of heterotrophs (Cebrian and Duarte 1994, 1995; Duarte and Cebrian 1996). Nielsen et al. (1996) compare turnover rates and nutrient concentrations for a broad range of types of autotrophs (from microalgae to terrestrial macrophytes) under natural and experimental conditions and conclude a strong association between higher nutrient concentrations and faster turnover rates. Therefore, communities formed by plants with faster turnover rates should also have plants with higher nutrient concentrations. Yet, the association between plant nutrient concentrations and turnover rates across aquatic and terrestrial communities, and its effects on the levels of consumption by heterotrophs, remains to be tested. Moreover, greater levels of consumption by heterotrophs in communities with faster turnover rates could entail lower levels of accumulation of biomass and detrital mass within these communities, provided differences in consumption are greater than differences in production. Demonstrating these hypotheses would render the association between plant trophic quality and turnover rate as a main control of the carbon balance in plant communities: because plant communities with faster turnover rates are more palatable to heterotrophs, they would experience higher intensities of consumption (i.e., larger fractions of production removed and faster decomposition rates) and, as a result, they would accumulate less biomass and detrital mass. That would be so regardless of other numerous factors that could influence differences in consumption by herbivores (e.g., characteristics of the specific herbivore populations in the different plant communities compared) and in decomposition and carbon storage (e.g., temperature, humidity, sediment redox conditions) across the plant communities compared.

In this article, I examine, through an extensive compilation of published reports, differences in the trophic routes of carbon flow (eqq. [1] and [2]) across a wide range of aquatic and terrestrial types of plant communities and analyze how these differences affect their ecological role. Then I test whether communities composed of plants with higher nutrient concentrations also have faster biomass turnover rates. I further test whether, as a result of the association between higher plant palatability and faster turnover rates, communities with faster turnover rates are subject to higher levels of consumption by herbivores and faster decomposition rates and, as a consequence, accumulate less plant biomass and detrital mass. I end by discussing the contribution of the patterns found to an understanding of how much and why carbon balances differ across plant communities.

Methods

From over 200 published reports, I compiled an extensive data set of plant nutrient concentration, biomass, detrital mass, and magnitude and trophic fate (consumption by herbivores, detrital production, export, decomposition, and refractory accumulation) of production for the following types of plant communities: marine and freshwater phytoplanktonic communities, marine and freshwater benthic microalgal beds, marine macroalgal beds, freshwater macrophyte meadows, seagrass meadows, brackish and marine marshes, grasslands, mangroves, and shrublands and forests (see data set). The data set is available from the author upon request at http://www.mbl.edu/urs/just/.

Reports covering all the trophic routes of production for a given community were obviously uncommon, and, hence, the data set compiled combines reports covering different numbers of the variables considered. Moreover, the variables compiled only referred to the aboveground compartment in most of the reports for aquatic or terrestrial macrophyte communities, with only a few reports accounting for both the below- and aboveground compartments (see data set). Three initial criteria were applied when selecting papers: first, only studies of plant communities referring to natural conditions were considered (i.e., studies with manipulated conditions and artificial communities were discarded); second, studies focused on a single plant species were accepted only if that species accounted for most biomass and production within the community; and third, studies were considered if they covered at least 1 yr or the full growing season for seasonal producers (which usually spans from late winter to early fall).

Plant nutrient concentrations were reported as nitrogen (N) and phosphorus (P) concentrations expressed as the percentage of plant tissue dry weight (%DW). Nitrogen and phosphorus are the two nutrients most often reported in the literature. Plant biomass corresponds to the stock of alive plant material (g C m\(^{-2}\)). The values compiled of plant detrital mass (g C m\(^{-2}\)) correspond to particulate detritus above the upper sediment layers for aquatic and terrestrial macrophyte communities, and to dead cells for microalgal communities. Hence, the detrital pool of plant-dissolved carbon is disregarded because it was reported in very few articles. The values of detrital mass compiled for communities of macrophytes include both degradable and refractory detritus, although the total pools of degradable and refractory detritus were underestimated since only the upper sediment or soil layers were accounted for. When temporal changes in plant nutrient concentrations, biomass, and detrital mass through the study period were reported, yearly average values were calculated. Net primary production is defined as the net amount of atmos-
pheric CO₂ fixed by photosynthesis. It was expressed in g C m⁻² d⁻¹ by dividing the cumulative value for the study period by the number of days covered by the study. Plant turnover rate corresponds to the ratio of biomass renewed per day (d⁻¹), and it was estimated as the ratio of primary production to plant biomass when direct values were not provided in the report.

Plant consumption by herbivores is defined as the ingestion of plant biomass by herbivores (g C m⁻² d⁻¹). Detrital production (g C m⁻² d⁻¹) corresponds to the sum of plant mortality by senescence, metabolic exudation of organic carbon, and plant material removed but nonconsumed by herbivores. Metabolic carbon exudation was not measured in many of the reports compiled for aquatic and terrestrial macrophytes, but the magnitude of plant carbon exudation in these communities is normally small in comparison with that of mortality by senescence (Grier and Logan 1977; Wetzel 1984). Hence, detrital production in communities of macrophytes should not be underestimated importantly. Plant mortality by senescence is estimated as “litterfall,” that is, senescent material shed from the plant, for communities of macrophytes, and as cell sedimentation and lysis rates for communities of microalgal. Direct measurements of lysis rates were provided in few reports, with most rates thus being estimated as the difference between primary production and the sum of any biomass increment, consumption by herbivores, sedimentation, metabolic exudation, and horizontal advection. Values of plant consumption and detrital production were expressed on a daily basis by dividing the cumulative values over the study period by the number of days covered.

Plant decomposition (g C m⁻² d⁻¹) is the consumption of plant detritus by decomposers. Direct values of plant decomposition were not provided in most of the phytoplanktonic and benthic macroalgal communities compiled. I estimated it from respiration measurements of the total microplagotic or microbenthic communities enclosed in incubation bottles or benthic chambers, respectively, as explained by Duarte and Cebrian (1996): plant decomposition within the bottles or chambers was estimated by subtracting the sum of phytoplankton or microphytobenthos respiration and grazing by microherbivores (i.e., those contained in the bottle or chamber) from the total community respiration value. Phytoplankton and microphytobenthos respiration was estimated from values of gross primary production for the same communities by assuming that respiration represents 35.4% ± 6.9% and 26.4% ± 6.4% of gross phytoplankton and microphytobenthos production, respectively. Grazing by microherbivores was supposed to be 50% ± 30% of the total grazing value (micro- and macroherbivores) obtained for the same community. These conversion values (mean ± SD) were obtained by Duarte and Cebrian (1996) through a compilation of published reports. Finally, decomposition of sedimenting dead phytoplanktonic cells was assumed to be 17% of the net primary production measured in the community (Martin et al. 1987) and added to the decomposition values obtained from the bottles. The value of 17% corresponds to a mean for a vast oceanic area, and the percentage of phytoplanktonic production decomposed during sedimentation can vary considerably among regions (Müller and Suess 1979; Suess 1980). Nevertheless, the use of mean values of autotrophic respiration, grazing by microherbivores and decomposition of sedimenting phytoplanktonic detritus should not entail a consistent bias on the derivation of decomposition for phytoplanktonic and microphytobenthic communities. This is shown by the comparison of the estimated carbon budgets among the communities considered (see below). Moreover, the error in the estimates of phytoplanktonic and microphytobenthic decomposition involved by the mean values used is unimportant in relation to the broad range of decomposition encompassed by the aquatic and terrestrial communities compared (see results on decomposition).

When direct values of decomposition were not provided in communities of aquatic and terrestrial macrophytes, they were derived as

\[ D = (DP - E) \times (1 - e^{-\Delta t/k}), \]  

(3)

where \( D \), \( DP \), and \( E \) denote cumulative decomposition, detrital production, and detrital export over the duration of the study (i.e., g C m⁻² [study duration]⁻¹), \( \Delta t \) corresponds to the duration of the study (d), and \( k \) is the decomposition rate (d⁻¹). Decomposition was expressed into a daily basis (g C m⁻² d⁻¹) by dividing the cumulative values by the duration of the study. Equation (3) assumes that the pool of degradable detrital mass in the community (fig. 1) does not change over the study period, and, hence, it was only applied in climax communities with steady pools of degradable detrital mass. When decomposition rates (k, d⁻¹) were not derived directly, they were estimated as the ratio of detrital production (g C m⁻² d⁻¹) to degradable detrital mass (g C m⁻²) since the latter variable remained unchanged over the study period (Olson 1963). A few decomposition values in some types of communities of macrophytes were derived by using mean values of k for the specific types provided by Enríquez et al. (1993). The estimates of decomposition only cover the duration of the studies compiled (i.e., from one to a few years) and, hence, disregard long-term decomposition of refractory detritus.

Export corresponds to the transportation of plant detritus off the community through rivers in terrestrial communities and waves, tides, and currents in aquatic com-
munities. Export of phytoplankton communities in enclosed lakes and open ocean was assumed to be 0 since phytoplankton detrital carbon, albeit horizontally advected, never traversed the community boundaries. Hence, export values for phytoplanktonic communities refer only to coastal communities. None of the reports compiled accounted for export of dissolved detrital material, and, hence, these estimates correspond only to export of particulate detrital material. Export values were expressed on a daily basis (g C m\(^{-2}\) d\(^{-1}\)) by dividing the cumulative values over the study period by the number of days covered.

Refractory accumulation corresponds to the amount of nonexported detrital production that is not decomposed during the duration of the study (i.e., from one to some few years). It thus represents the amount of refractory detritus accumulated during the duration of the study but disregards long-term accumulation once diagenetic losses have occurred (i.e., burial). Whenever direct values were not reported, refractory accumulation was calculated as the difference between net primary production and the sum of consumption by herbivores, export, and decomposition over the study period (Schlesinger 1997). Refractory accumulation was then expressed on a daily basis (g C m\(^{-2}\) d\(^{-1}\)) by dividing the cumulative value by the number of days in the study. This procedure was valid only for climax communities with steady pools of plant biomass and degradable detrital mass.

All the different assumptions, methods, and mean values employed for the estimation of the trophic routes of production bring out the questions whether these estimates are representative of the real carbon balances in the communities considered and, thus, whether they are comparable among different communities. To address these questions, I calculated the mean percentage of production represented by consumption by herbivores, decomposition, export, and refractory accumulation for each type of community from all the values in the data set. Biomass and detrital mass were steady and import negligible during the study interval in practically all the communities compiled. Therefore, if the mean percentages of production consumed, decomposed, exported, or accumulated sum up to about 100% for each community type, the values in the data set should be in general representative of real carbon balances in the communities considered. The sums obtained were (mean ± SE): for phytoplankton, 112.2% ± 12.6%; for benthic microalgal beds, 102.4% ± 20.1%; for macroalgal beds, 98.5% ± 27.7%; for freshwater macrophyte meadows, 123.7% ± 23.8%; for seagrass meadows, 112.5% ± 22.6%; for marshes, 116.2% ± 18.7%; for grasslands, 126.7% ± 17.5%; for mangroves, 90.5% ± 22.2%; and for shrublands and forests, 95.6% ± 10.6%. None of these values is significantly different from 100% (t-test, P > .05). Hence, although the assumptions employed entail a certain bias in some of the estimates, the values in the data set generally represent valid carbon balances for the communities considered, and, therefore, the differences in the trophic fate of production found across these communities are reliable.

Values reported in g plant DW were multiplied by 0.4 for conversion into g C (Wiebe 1988; Schlesinger 1997). Values for phytoplankton reported on a volumetric basis (i.e., g C m\(^{-3}\) or g C m\(^{-3}\) d\(^{-1}\)) were integrated through the depth limits of phytoplankton distribution in the water column and transformed into an areal basis (i.e., g C m\(^{-2}\) or g C m\(^{-3}\) d\(^{-1}\)). ANOVA was performed on differences in plant nutrient concentration, plant carbon pools (biomass and detrital mass), and rates of carbon flow (herbivore consumption, detrital production, decomposition, export, and refractory accumulation) across communities. Differences between two specific types of communities were analyzed with a HSD Tukey multiple comparison test (Zar 1984). Relationship between variables were analyzed with correlation and least-square regression techniques. Differences among correlation coefficients were tested with the Fischer Z statistic (Fischer 1921). The variables were log-transformed when necessary to comply with the assumptions of the techniques used.

Results

The NPP varied significantly among the communities considered (fig. 2A; ANOVA, P < .05). Yet, when specific pairs of communities were compared, most pairs of communities showed similar ranges of NPP (Tukey HSD test, P > .05). Only benthic microalgal beds reached smaller values of production than most other community types (Tukey HSD test, P < .05). In contrast, both turnover rate and N and P concentrations declined from microalgal communities to communities of aquatic macrophytes to communities of terrestrial macrophytes (fig. 2B–2D; Tukey HSD test, P < .05). In fact, faster turnover rates were closely associated with higher N and P concentrations across communities (fig. 3A, 3B; table 1), whereas primary production was independent of N and P concentrations and turnover rate (fig. 4A–4C; table 1). The nutrient concentrations reported for phytoplanktonic communities refer only to marine phytoplankton. Freshwater phytoplankton normally have lower concentrations (mean N range: 3.9%–5.2%; mean P range: 0.35%–0.62%; Hecky et al. 1993). The inclusion of these values would have certainly increased the range for the phytoplankton communities, but the differences found across communities would still hold (fig. 2C, 2D). Moreover, because the nature of the dependence of phytoplankton turnover rates on internal nutrient concentrations seems similar in marine and fresh-
Figure 2: Box plots showing the distribution of (A) net primary production, (B) plant turnover rate, (C) plant nitrogen concentration, (D) plant phosphorus concentration, (E) percentage of primary production consumed by herbivores, and (F) absolute consumption by herbivores across the types of communities considered. Boxes encompass 25% and 75% quartiles, and the central line represents the median. Bars encompass the range of values between the 25% quartile minus 1.5 times the difference between the quartiles 75% and 25% and the 75% quartile plus 1.5 times the difference between the quartiles 75% and 25%. Circles and asterisks represent values outside these limits.
water communities (Kilham and Hecky 1988), freshwater phytoplankton with lower nutrient concentrations should show proportionally slower turnover rates. Therefore, the associations between turnover and nutrients found across communities (fig. 3A, 3B) should not have been affected significantly had freshwater phytoplankton been considered.

The percentage of production consumed by herbivores was higher in microalgal communities than in communities of macrophytes (fig. 2E; Tukey HSD test, $P < .05$). The distribution of percentage of production consumed across communities resembled the distributions of nutrient concentrations and turnover rate. Indeed, the percentage of production consumed increased with faster turnover rates across communities (fig. 5A; table 1). In contrast, absolute consumption did not show a significant increase from communities of macrophytes to microalgal communities (fig. 2F; Tukey HSD test, $P > .05$), although it varied among communities (ANOVA, $P < .05$). The distribution of absolute consumption across communities rather resembled that of primary production. In fact, absolute consumption was associated with primary production across communities, with more productive communities channeling larger fluxes of production toward herbivores (fig. 5B; table 1). Correspondingly, the percentage of production consumed and absolute consumption were very poorly related to primary production and turnover rate, respectively (fig. 5C, 5D).

The percentage of production entering the detrital compartment was lower in microalgal communities than in communities of macrophytes (fig. 6A; Tukey HSD test, $P < .05$). Absolute detrital production, however, was not smaller in microalgal communities (fig. 6B; Tukey HSD test, $P > .05$), but it displayed a distribution across communities similar to that of primary production. Accordingly, absolute detrital production and primary production were strongly related across communities, with more productive communities transferring proportionally larger fluxes of detrital production (fig. 7; table 1).

Decomposition rates were faster in microalgal communities than in communities of macrophytes (fig. 6C; Tukey HSD test, $P < .05$). Across communities, decomposition rates were associated with biomass turnover rates, with communities with faster turnover rates having also faster decomposition rates (fig. 8A; table 1). Conversely, absolute decomposition did not show an increase from macrophytic to microalgal communities (fig. 6D; Tukey HSD test, $P > .05$). Absolute decomposition was closely associated with primary production across communities, with more productive communities showing higher values of absolute decomposition (fig. 8B; table 1). Accordingly, decomposition rates and absolute decomposition were independent of primary production and turnover rates, respectively (fig. 8C, 8D; table 1).

Refractory accumulation, both in absolute terms and as percentage of primary production, was smaller in micro- and macroalgal communities than in the rest of communities (fig. 6E, 6F; Tukey HSD test, $P < .05$). Across
### Table 1: Relationships fitted across plant communities

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>Relationship</th>
<th>n</th>
<th>$R^2$</th>
<th>F-ratio</th>
<th>P</th>
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<td>0</td>
<td>A</td>
<td>.52</td>
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<td>PTR</td>
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<td>91</td>
<td>0</td>
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<td>.55</td>
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<td>PTR</td>
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</table>

Note: PTR, plant turnover rate; N, plant nitrogen concentration; P, plant phosphorus concentration; NPP, net primary production; PPC, percentage of primary production consumed by herbivores; C, absolute consumption by herbivores; DP, plant detrital production; k, decomposition rate; D, absolute decomposition; RA, accumulation of refractory plant detritus; B, plant biomass; DM, plant detrital mass. Asterisk signifies $\chi^2$ statistic.

Communities, absolute refractory accumulation was better related to turnover rate than to primary production (figs. 9A, 9B; table 1; Z-test, $H_2$; equality between correlation coefficients, $P < .05$). Export, expressed both in absolute terms and as percentage of primary production, varied widely among communities (fig. 10A, 10B) and tended to be largest in macroalgal beds (Tukey HSD test, $P < .05$). Plant biomass increased from microalgal communities to communities of aquatic macrophytes to communities of terrestrial macrophytes (fig. 10C; Tukey HSD test, $P < .05$). This distribution counters the distributions of turnover and percentage of production consumed across communities. Accordingly, communities with faster turnover rates and higher percentages of production consumed store smaller pools of biomass (fig. 11A, 11B; table 1). In contrast, biomass is only weakly related to primary pro-
duction across communities (table 1; Z-test, $H_0$: equality between correlation coefficients, $P < .05$).

Similarly, plant detrital mass seems to increase from microalgal communities to communities of aquatic macrophytes to communities of terrestrial macrophytes (fig. 10D; ANOVA, $P < .05$). Across communities, plant detrital mass is associated with turnover and decomposition rates, with a tendency for communities with faster turnover and decomposition rates to store smaller pools of detrital mass (fig. 12A, 12B; table 1). Conversely, detrital mass is very poorly related to primary production and detrital production (table 1). Estimates of detrital mass included only leaf detritus in some of the forests and shrublands compiled (see data set). Therefore, I used the values of production, turnover rate, decomposition rate, and detrital production for the foliar compartments in those communities when deriving the relationships between detrital mass and primary production, biomass turnover rates, decomposition rates, and detrital production for all communities.

**Discussion**

These results allow a synthetic view of the fate of production in plant communities. With the exception of
Figure 5: The relationships (A) between percentage of net primary production consumed by herbivores and plant turnover rate, (B) between absolute consumption by herbivores and net primary production, (C) between percentage of net primary production consumed by herbivores and net primary production, and (D) between absolute consumption by herbivores and plant turnover rate across the communities compiled. Lines represent the equations fitted. Symbols as in figure 3.

Microalgal communities, most production in all the communities considered is channeled as detrital production (fig. 6A). That generalizes the predominance of the detrital pathway in the trophic transfer of primary production to heterotrophs, in agreement with previous results in different communities (Schlesinger 1977; Thayer et al. 1984; Mann 1988; Cebrian and Duarte 1998). In general, most detrital production is decomposed within the community, with only modest fractions being exported even in communities typically exposed to substantial horizontal advection (fig. 10B). Macroalgal beds represent the only exception to this pattern, which, on the average, export about 50% of their production. This is because macroalgal beds often inhabit rocky shores exposed to intense wave scouring (Mann 1972; Marsden 1991). In general, only a small fraction of production is accumulated as refractory detritus within the community (fig. 6F), although this fraction may be sizable in grasslands, shrublands, and forests (Smith and Clymo 1984).

In spite of these generalities, my results reveal important qualitative and quantitative differences in the fate of production among plant communities. These differences are
Figure 6: Box plots showing the distribution of (A) percentage of primary production channelled as detritus, (B) plant detrital production, (C) decomposition rates, (D) absolute decomposition, (E) accumulation of refractory detritus, and (F) percentage of primary production accumulated as refractory detritus across the types of communities considered. Boxes encompass the 25% and 75% quartiles, and the central line represents the median. Bars encompass the range of values between the 25% quartile minus 1.5 times the difference between the quartiles 75% and 25% and the 75% quartile plus 1.5 times the difference between the quartiles 75% and 25%. Circles and asterisks represent values outside these limits.
of production to herbivores implies that these communities channel smaller percentages of production as detritus (fig. 6A). Across communities, the importance of herbivory as a trophic route of primary production increases with plant palatability, as it has been previously hypothesized (Sterner et al. 1997). Moreover, this tendency supports the notion that across the range of communities compared, herbivores do not increase their feeding rates over plants with lower nutrient concentrations as a means of compensating for lower nutritional qualities. This mechanism has been hypothesized as implausible in an evolutionary sense because higher feeding rates on less nutritional, slower turning-over plants would eventually lead to plant depletion (Sterner and Hessen 1994). Yet, enhanced feeding rates as a herbivore response to lower nutritional quality have been found during transient periods within some particular plant communities (Williams et al. 1994; Lindroth et al. 1995; Hughes and Bazzaz 1997).

The dependence of the intensity of herbivory (i.e., fraction of production consumed) on plant nutritional quality across communities overrides the effect of community-specific herbivore characteristics. For instance, some of the communities compared host mainly migratory herbivores, whereas others have only resident herbivores. This migratory-resident duality may introduce considerable variability in the intensity of herbivory among communities (Nienhuis and Groenendijk 1986; Portig et al. 1994). In addition, some communities shelter mainly invertebrate herbivores (e.g., most submerged communities), whereas others host vertebrate homeotherm herbivores. These two types of herbivores have different metabolic needs, and these differences may cause substantial variability in the intensity of herbivory across communities (Crawley 1983; Begon et al. 1990). Moreover, the intensity of predation on herbivores also varies among communities, which may entail different cascade effects on the intensity of herbivory in different communities (Hartley and Jones 1997). Finally, differences in herbivore stoichiometry among communities may also be responsible for differences in herbivory. Although communities of more nutritional plants should have herbivores with higher nutrient contents, the range of nutrient concentrations in herbivore tissues may vary notably within a given community (Sterner and Hessen 1994). Because herbivores with higher nutrient concentrations also have higher nutritional demands, variations in the range of herbivore stoichiometry among communities could also generate differences in the intensity of herbivory. All these factors could perhaps explain the >1 order-of-magnitude variability observed in herbivory intensity among communities with similar turnover rates (fig. 5A).

The tendency toward higher intensities of herbivory with higher plant palatability across communities suggests
that herbivores should exert a greater control of plant biomass in communities with more palatable plants. Accordingly, herbivores have been shown to limit plant biomass in communities with fast turnover rates (Lampert et al. 1986; McNaughton et al. 1988; Jing and Coley 1990), whereas they seem unimportant in communities with slow turnover rates (Bray 1964; Petrušewicz and Grodzinski 1975; Cebrian et al. 1996). My results suggest that, at least in part, communities with more palatable plants store smaller pools of biomass as a result of the higher intensities of herbivory supported; communities with faster turnover rates store smaller pools of biomass partially because they reach relatively similar values of production (fig. 4C) but lose higher percentages to herbivores (fig. 5A). This hypothesis is supported by the tendencies toward lower biomasses with faster turnover rates and larger intensities of herbivory across communities (fig. 11A, 11B).

Yet communities with faster turnover rates also have higher plant mortality rates (Odum 1971; Phillips and Gentry 1994), which can also contribute to the decline in plant biomass observed with faster turnover rates across communities. I used techniques of path analysis to differentiate the direct connection between faster turnover and decreasing biomass from the connection mediated
through increasing herbivory. These techniques allowed the categorization of variance in plant biomass across communities into the fraction directly explained by turnover, the fraction directly explained by herbivory, and the fraction explained by the interaction of both herbivory and turnover (Williams et al. 1990). The variance in plant biomass among communities explained by turnover is significantly reduced, albeit still significant \( (P < .01) \), when the interaction with herbivory is eliminated (from \( R^2 = .69 \) to \( R^2 = .44 \)). This suggests that the reduction in biomass with higher palatability (i.e., faster turnover) across communities is a partial effect of increasing herbivory. Furthermore, I used a randomization test (Pendleton et al. 1983) to test for spurious effects on the relationship between decreasing biomass and increasing turnover due to the presence of a biomass term in both variables (turnover rate was estimated as the quotient between production and biomass in many communities). The result demonstrates that the relationship obtained is different from that expected solely from the effect of a common term in both variables \( (H_3: \text{spurious slope} = \text{observed slope}, P < .001) \).

Detritus from communities composed of more nutritional plants undergo faster decomposition (fig. 8A). This indicates that plant communities that turn over their biomass compartment faster also turn over their degradable detrital compartment faster. This implies that communities with faster biomass turnover rates have higher nutrient recycling rates, as expected to meet their faster rates of nutrient uptake (i.e., higher nutrient demand; Chapin et al. 1986, 1987). This trend has been hypothesized recently (Sterner et al. 1997), and these results further support it. Accordingly, fast and efficient nutrient recycling generally plays a pivotal role in the maintenance of communities with fast biomass turnover rates and high nutrient demands (Crossland et al. 1991; Legendre and Rassoulzadegan 1995), whereas communities with slower biomass turnover rates normally exhibit slow recycling rates and low nutrient demands (Enriquez et al. 1993). The tendency toward faster decomposition rates with higher plant nutrient concentrations across communities is consistent with the idea that the metabolism and feeding rates of decomposers are limited by the nutrient concentrations in plant detritus (Enriquez et al. 1993). This limitation has been shown experimentally for a number of types of autotrophs (Swift et al. 1979; Goldman et al. 1987; Enriquez et al. 1993), and here it is suggested to exist across a broad range of plant communities. The tendency toward faster decomposition rates with higher plant nutrient concentrations overrides the effects on decomposition of different abiotic factors in the communities compared, such as temperature (Edwards 1975; Van Cleve et al. 1981), moisture (Wildung et al. 1977; Santos et al. 1984), and sediment redox conditions (Schlesinger 1977; Post et al. 1982). These factors could probably explain much of the residual variability in the tendency established.

Moreover, these results indicate that communities with more palatable detritus store smaller detrital pools as a consequence of the faster decomposition rates supported (fig. 12A): communities with faster biomass turnover rates
store smaller pools of detrital mass (fig. 12B) because they reach relatively similar values of production and detrital production (fig. 4C) but have faster decomposition rates (fig. 8A). Another corollary of these tendencies is that communities composed of more palatable plants show lower levels of refractory accumulation (fig. 9A). Refractory accumulation corresponds to the amount of primary production nonconsumed by herbivores that is neither exported nor decomposed over the study period. Because both the percentage of production consumed and decomposition rates increase nonlinearly with turnover rate across communities (figs. 5A and 8A, respectively) while being poorly related to primary production (figs. 5C and 8C), the decrease in refractory accumulation with faster turnover rates is exponential (fig. 9A). These results indicate that communities composed of more palatable plants are smaller carbon sinks because they experience higher intensities of consumption by heterotrophs, as it has been recently suggested (Cebrian et al. 1998).

So far I have discussed the dependence of intensity of herbivory and decomposition rates on plant palatability across communities. Absolute consumption by herbivores, however, is very poorly related to plant palatability across communities (fig. 5D). Instead, differences in absolute

Figure 10: Box plots showing the distribution of (A) export, (B) percentage of primary production exported, (C) plant biomass, and (D) detrital mass across the types of community considered. Boxes encompass the 25% and 75% quartiles, the central line represents the median, and bars encompass the range of values between the 25% quartile minus 1.5 times the difference between the quartiles 75% and 25% and the 75% quartile plus 1.5 times the difference between the quartiles 75% and 25%. Circles and asterisks represent values outside these limits.
consumption across communities are better related to differences in absolute production (fig. 5B), in agreement with results of other across-systems comparisons (McNaughton et al. 1989; Cyr and Pace 1993). The association between absolute consumption and production across communities is a mathematical consequence of the ranges of the variables compared: absolute consumption is the product between primary production and the percentage consumed by herbivores and, because primary production and the percentage consumed vary by four and three orders of magnitude across the communities compared, respectively (fig. 5C), differences in absolute consumption across communities are better correlated to primary production than to the percentage consumed. As a consequence, when a broad range of communities is compared, more productive communities tend to transfer greater fluxes of production to herbivores (fig. 5B). McNaughton et al. (1989) and Cyr and Pace (1993) also show that higher absolute consumptions in more productive communities are conducive to larger herbivore abundances. Therefore, differences in herbivore biomass across communities seem to be associated with differences in the magnitude of production rather than with the quality (i.e., nutrient concentration in plant tissues) of that production. These tendencies, if confirmed, would indicate that, across communities, increases in herbivore biomass due to larger absolute consumptions override any possible increases due to enhanced growth rates resulting from more palatable diets. Higher predation rates on herbivores feeding on more palatable plants could perhaps partially explain these hypothesized trends. Similarly, absolute decomposition is closely related to production across communities (fig. 8B), and it is independent of plant palatability (fig. 8D). Again, the reason depends on the relative range of the variables compared across communities. At the time scales covered by the studies compiled (i.e., from one to some few years), the variability in production across communities is greater than the variability in the percentage decomposed, and because decomposition is the product of production and percentage decomposed, its variability across communities is dictated by variability in production.

Differences in export, both as absolute magnitude and as percentage of production, across communities are independent of differences in plant palatability and are only weakly related to differences in production (least square regression of log export versus log production: $R^2 = .23$, $P < .05$). Differences in export across communities may be related to differences in the intensity of horizontal advection through the community. This is supported by the fact that communities with higher export rates are typically exposed to substantial horizontal advection through waves, currents or tides, such macroalgal beds, seagrass meadows, and land-ocean fringing communities such as marshes and mangroves (fig. 10A, 10B). Communities with high export rates have the potential to support large levels of secondary production in adjacent communities (Nixon 1980; Twilley et al. 1986; Duarte and Cebrian 1996). Moreover, high export rates must imply substantial nutrient losses for the exporting communities since virtually all of the exported detritus are consumed and recycled elsewhere (Hedges and
Parker 1976; Smith and MacKenzie 1987). Hence, communities with high export rates must have high rates of nutrient import from adjacent communities to offset nutrient losses and maintain primary production. This argument suggests important implications for the interplay between "new" (i.e., fueled by allochthonous nutrients) and recycled production in plant communities: communities with higher percentages of production exported should have greater fractions of their production fueled by imported nutrients (i.e., higher fractions of new production).

In summary, plant nutritional quality for consumers and primary production are independent predictors of the nature and magnitude of the trophic routes of carbon flow in plant communities. Communities composed of more palatable plants lose higher percentages of production to herbivores, channel lower percentages as detritus, and experience faster decomposition rates. I present evidence that communities with more palatable plants store smaller carbon pools as a result of the higher intensities of herbivory and faster decomposition rates supported, but more experimental work is needed to confirm this hypothesis. These results may have important implications for broad-scale carbon and nutrient balances because widespread anthropogenic eutrophication may enhance the nutritional quality of plant communities in large areas (Duarte 1995; Borum and Sand-Jensen 1996; Wedin and Tilman 1996). Absolute consumption and decomposition, however, are not associated with plant nutritional quality but with primary production across communities. The patterns in the nature and controls of the trophic fate of production reported here encompass contrasting communities ranging from unicellular autotrophs to structurally complex macrophytes. When the range of communities compared is reduced, factors other than plant nutritional quality and magnitude of production may be most important at explaining differences in the trophic fate of production. Hence, the dependence of the patterns reported on the range of communities encompassed needs investigation.

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