Abstract. Describing the relative magnitude and controls of herbivory and decomposition is important in understanding the trophic transference, recycling, and storage of carbon and nutrients in diverse ecosystems. We examine the variability in herbivory and decomposition between and within a wide range of aquatic and terrestrial ecosystems. We also analyze how that variability is associated with differences in net primary production and producer nutritional quality. Net primary production and producer nutritional quality are uncorrelated between the two types of system or within either type. Producer nutritional quality is correlated to the percentage of primary production consumed by herbivores or percentage of detrital production decomposed annually, regardless of whether the comparison is made between the two types of systems or within either type of system. Thus, producer nutritional quality stands out as a consistent indicator of the importance of consumers as top-down controls of producer biomass and detritus accumulation and nutrient recycling. However, absolute consumption by herbivores and absolute decomposition (both in g C·m$^{-2}$·yr$^{-1}$) are often associated with absolute primary production and independent of producer nutritional quality, because the variability in net primary production across systems largely exceeds that in the percentage consumed or decomposed. Thus, primary production often stands out as an indicator of the absolute flux of producer carbon transferred to consumers and of the potential levels of secondary production maintained in the system. These patterns contribute to our understanding of the variability and control of herbivory and decomposition, and implications on carbon and nutrient cycling, in aquatic and terrestrial ecosystems. Furthermore, in view of their robustness, they may offer a template for global change models seeking to predict anthropogenic effects on carbon and nutrient fluxes.

Key words: decomposition; detritus; herbivory; net primary production; producer nutritional concentration.

INTRODUCTION

Transfer of fixed carbon to herbivores and decomposers/detritivores are major pathways of material flow in both aquatic and terrestrial ecosystems. The absolute and proportional size of these transfers has consequences for carbon storage, nutrient recycling, and consumer populations. When regarded as an absolute flux, herbivory reflects the levels of herbivore biomass and production maintained in the ecosystem. Herbivore production is a fraction of the amount of producer biomass ingested and the proportion is less variable than absolute consumption among diverse ecosystems (Krebs 1994, Begon et al. 1996). Consequently, systems supporting higher consumption tend to support larger herbivore standing stocks and production (McNaughton 1983, McNaughton and Duarte 1994, Paine 2002). Similarly, consumer-driven recycling also increases with the percentage of primary production consumed (Sterner et al. 1997, Sterner and Elser 2002). It is important to notice that absolute consumption and percentage of primary production consumed are not necessarily related: absolute consumption can be relatively high but only represent a small percentage of primary production in communities with high levels of primary production (Cebrian and Duarte 1994, Cebrian 1999). In such cases, herbivores usually exert little control on elemental cycling or storage as plant biomass.

Considering herbivory as the percentage of primary production removed has consequences for the role of herbivores in carbon and nutrient storage (as plant biomass) and recycling in the ecosystem. When herbivores remove a large percentage of primary production, they leave only a small percentage of carbon and nutrients fixed by producers available for accumulation as producer biomass, and thus have the potential to act as significant controls of carbon and nutrient storage by producers (top-down regulation; Carpenter et al. 1985, McNaughton 1983, Cebrian and Duarte 1994, Paine 2002). Similarly, consumer-driven recycling also increases with the percentage of primary production consumed (Sterner et al. 1997, Sterner and Elser 2002). It is important to notice that absolute consumption and percentage of primary production consumed are not necessarily related: absolute consumption can be relatively high but only represent a small percentage of primary production in communities with high levels of primary production (Cebrian and Duarte 1994, Cebrian 1999). In such cases, herbivores usually exert little control on elemental cycling or storage as plant biomass.

The percentage of primary production consumed by herbivores tends to be higher in aquatic than in terrestrial systems (Whittaker 1970, Petrushewicz and Grodzinski 1975, Cyr and Pace 1993, Cebrian and Duarte 1994, Griffin et al. 1998), but this percentage may be highly variable within either type of system (see re-
views by Cebrian et al. 1998 and Cebrian 1999). Several reports have suggested that the variability in the percentage of primary production consumed by herbivores found among diverse systems is associated with differences in the internal concentrations of the dominant producers (Sterner et al. 1997, Cebrian et al. 1998, Griffin et al. 1998, Cebrian 1999). The underlying rationale is that herbivore metabolism and growth are often limited by the nutrient concentrations of their plant diets (Mattson 1980, Sterner and Hessen 1994, Elser et al. 1996, Hartley and Jones 1997). On these grounds, producers with a higher nutritional quality would promote herbivore metabolism and growth (Sterner et al. 1998, Elser et al. 2000b, Stelzer and Lamberti 2002, Urabe et al. 2002) and thereby support higher consumption rates and have a larger percentage of production removed by herbivores. The association between producer nutritional quality and herbivore growth seems to apply to both aquatic and terrestrial systems (Elser et al. 2000a, Sterner and Elser 2002) but the role of producer nutrient concentrations as a control of the variability in the percentage of primary production consumed needs further examination. Other factors, such as herbivore size (Crawley 1983), ectothermy vs. endothermy (Begon et al. 1996), behavior (Portig et al. 1994), and predation intensity (Heck and Valentine 1995), may be of greater importance and override the expected effects of producer nutritional quality.

A number of reports have shown that aquatic systems, along with larger percentages of primary production removed by herbivores, also tend to support higher levels of absolute consumption than do terrestrial systems (Cyr and Pace 1993, Cebrian and Duarte 1994, Cebrian 1999). Absolute consumption, however, may vary over several orders of magnitude within either type of system. Within aquatic and terrestrial systems, the variability in absolute consumption is associated with the variability in primary production, with more productive systems supporting higher levels of consumption (McNaughton et al. 1989, Cyr and Pace 1993, Cebrian 1999). However, whether larger absolute consumption is also associated with higher producer nutritional quality within aquatic and terrestrial systems is still unclear. Existing comparisons suggest that association should not exist because primary production and producer nutritional quality seem unrelated within either type of system (Cebrian et al. 1998, Griffin et al. 1998, Cebrian 1999).

As for herbivory, decomposition may also be viewed as an absolute flux or as the proportion of detrital production decomposed per unit time. When viewed as an absolute flux, decomposition corresponds to the amount of detritus consumed by microbial decomposers and detritívorous organisms. This process leads to the gradual breaking of particulate and dissolved detritus into simpler constituents and eventually, to nutrient mineralization (Tenore et al. 1982, Mann 1988, Schlesinger 1997, Cebrian 1999). Because the efficiency of microbial and detritívorous production (ratio of productivity to carbon ingestion) does not seem to vary among diverse ecosystems as much as absolute decomposition (Begon et al. 1996), higher values of absolute decomposition should lead to larger standing stocks and production of microbial decomposers, invertebrate and vertebrate detritívores, and microbial predators (Bird and Kalff 1984, Sanders et al. 1992, Zak et al. 1994). On the other hand, the proportion of detrital production decomposed per unit time reflects how fast carbon and nutrients flow through the detrital pool (Enríquez et al. 1993, Schlesinger 1997, Sterner et al. 1997). Ecosystems where the proportion of detrital production decomposed per unit time is high also tend to store smaller detrital carbon pools in spite of large differences in detrital production (Cebrian and Duarte 1995, Cebrian 1999). Higher values of absolute decomposition are not necessarily associated with higher proportions of detrital production decomposed per unit time. For instance, some ecosystems have a high proportion of detrital production decomposed per unit time, but low absolute decomposition because they produce little detritus (oligotrophic planktonic systems; Welschmeyer and Lorenzen 1985, Legendre and Rasoulzadegan 1995). Other ecosystems (e.g., boreal shrublands and forests) have a small proportion of detrital production decomposed per unit time, yet high levels of absolute decomposition and production of decomposers and detritivores because detrital production is high (Harris et al. 1975, Zak et al. 1994).

The proportion of detrital production decomposed per unit time is generally higher in aquatic than in terrestrial systems (Enríquez et al. 1993, Cebrian and Duarte 1995, Schlesinger 1997, Cebrian et al. 1998), although that proportion is highly variable within either type of system. This variability has been attributed to the concentration of nutrients in the detritus, with systems composed of detritus with a higher nutrient content having higher proportions decomposed (Melillo et al. 1982, Enríquez et al. 1993, Schlesinger 1997). One of the reasons for this association seems to be that the growth and metabolism of microbial decomposers and detritívorous organisms, similarly to herbivores, is often limited by the nutrient concentrations in their detrital diets (Goldman et al. 1987, Vadstein and Olsen 1989, Elser et al. 1996, 2000b). On that basis, decomposers and detritívores in systems composed of detritus with higher nutrient concentrations would have higher metabolic and growth rates and, as a consequence, consume a larger proportion of detrital production per unit time. However, whether greater levels of absolute decomposition are also associated with detritus of higher nutritional quality remains to be determined. Past reports suggest that the variability in absolute decomposition within aquatic and terrestrial systems should instead be associated with variation in detrital production because the magnitude of detrital production varies.
to a larger extent than does the proportion decomposed (Cebrian 1999, 2002).

In this paper, we use published values to first seek patterns of variability in herbivory and decomposition between and within aquatic and terrestrial ecosystems, and then determine whether that variability is associated with net primary (or detrital) production and/or producer (or detritus) nutritional quality. Specifically we examine whether (1) the magnitude of primary production is independent of producer nutritional quality; (2) herbivory and decomposition, when expressed as a percentage of primary or detrital production, increase with higher producer or detritus nutritional quality; (3) herbivory and decomposition, when expressed as absolute fluxes, increase with higher primary or detrital production and are independent of producer or detritus nutritional quality. We end by discussing how our results contribute to a better understanding of the extent, controls, and effects of herbivory and decomposition in aquatic and terrestrial ecosystems.

METHODS

Variables compiled: definition and derivation of indirect estimates

We compiled an extensive data set with values of net primary production, nitrogen and phosphorus concentrations in producer biomass and detritus, herbivory, detrital production, decomposition rates (proportion of detritus decomposed per unit time), and absolute decomposition in a wide range of aquatic and terrestrial ecosystems. Reports were considered only if they met three criteria. First, they corresponded to natural conditions (i.e., not deliberately impacted by human activities). Second, they represented the community studied (i.e., included the most abundant species of producers and consumers). Finally, they spanned at least one year or the growing season for annual producers. See the Supplement for the data set and references.

In total, we gathered >350 reports with data for >800 systems. When collecting the reports, we made an effort to search a wide range of scientific journals and other sources of information (e.g., "gray literature" and web pages). Such a procedure and extensive collection should warrant that each community type is represented in accordance with its availability in the literature. Indeed, the number of entries obtained per community type ranged from <10 for little studied communities such as freshwater benthic microalgal beds to >100 for much more studied communities such as marine phytoplankton, seagrass meadows, and temperate and tropical forests and shrublands (see data set for the exact representation by each community type). A close look at the patterns presented here also reveals that, even for those patterns based on the fewest observations (e.g., Figs. 8 and 10), the number of community types contained is in accordance with their relative occurrence in the data set. Aquatic ecosystems included communities of marine pelagic or coastal phytoplankton, freshwater phytoplankton, marine and freshwater benthic microalgae, marine macroalgae, submerged freshwater macrophytes, and seagrasses. Terrestrial ecosystems included communities of freshwater and marine marshes (i.e., emergent macrophytes), mangals (i.e., mangroves), temperate and tropical shrubs and trees, temperate and tropical grasses, and tundra shrubs and grasses.

Net primary production (in g C m⁻² yr⁻¹) corresponds to the excess of carbon assimilated through photosynthesis that is not respired by the producer. In communities dominated by microalgae, net primary production was usually measured with methods based on the ¹⁴C technique. Alternatively, it was calculated from measurements of community metabolism as the difference between gross community production and producer respiration, both in g oxygen-m⁻²yr⁻¹, and subsequently transformed to carbon units using conversion factors provided by the authors or elsewhere (Qasim and Bhattathiri 1971, Strickland and Parsons 1972). In a few reports of benthic microalgae, net primary production was derived as biomass accrual after correcting for losses due to herbivory and dislodgment due to water scouring. If gross primary production was directly provided, but not producer respiration, we estimated producer respiration from the mean values (±1 se) of the percentage of gross primary production respired by phytoplankton (35.4 ± 2.3%) and benthic microalgae (26.4 ± 2.9%) compiled by Duarte and Cebrian (1996) and calculated net primary production as the difference between gross primary production and our estimate of producer respiration. This was done for ~40% of the values compiled for both phytoplanktonic and benthic microalgal communities.

Net primary production in macroalgal and seagrass communities was measured with ¹⁴C techniques or metabolism measurements as explained in the previous paragraph for microalgae, using the punching method (for kelp species or broad-leaved seagrass species; Zieeman and Wetzel 1980), or as biomass accrual after correcting for losses due to herbivory and dislodgment by water scouring. Net primary production in communities of freshwater macrophytes was most often measured using the latter approach. In terrestrial systems, net primary production was frequently measured as biomass accrual after correcting for losses due to herbivory and senescence, or else as the product of mean annual biomass and mass-specific growth rate (g C produced g C⁻¹ yr⁻¹) derived in the absence of herbivory and senescence losses. For a number of communities of macroalgae and seagrasses, only values of gross primary production, but not net primary production, were provided. Most of those macroalgal communities were composed of coral reef algae. In those cases, we estimated primary production following the same procedure explained in the previous paragraph.
for phytoplanktonic and benthic microalgal communities (mean percentage gross primary production (±1 SE) respired by macroalgae, 14.1 ± 3.4%; and by seagrasses, 57.1 ± 5.7%; Duarte and Cebrian 1996). These indirect estimates represented ~25% and 50% of all the values of net primary production compiled for macroalgae and seagrasses. Finally, for a few (<10%) communities of aquatic macrophytes (macroalgae, seagrass or freshwater macrophytes) and terrestrial communities where only producer biomass was provided, we estimated net primary production as the product of mean biomass and the mean mass-specific growth rate for that kind of producer as reported by Cebrian (1999).

We also compiled values of nitrogen and phosphorus concentrations in producer biomass and detritus (percentage of dry mass). Values were weighted for the dominant producers in the system and, if based on one species, they were only accepted if that species was dominant in the system considered. Most values (>90%) were directly provided in the reports or obtained from other reports of the same system. Otherwise, we compiled them from other systems that were dominated by the same type of producer or, alternatively, they corresponded to type-specific mean values provided by Duarte (1992), Enríquez et al. (1993), and Cebrian (1999). Because the variability in nitrogen and phosphorus concentrations among producer types largely exceeds that within types (Duarte 1992, Enríquez et al. 1993, Cebrian 1999), the error introduced by using those mean values is small. Values reported as atomic ratios of carbon to nutrients were converted to a percent dry mass basis using the producer carbon concentration (percent dry mass), which was provided in the report or obtained from the literature (Gasol et al. 1997, Wiebe 1988, Elser et al. 2000a). Carbon concentrations vary little within a given producer type (Duarte 1992, Elser et al. 1996, Elser et al. 2000a) and, hence, the error committed when using producer-specific mean values obtained from the literature is also unimportant for the patterns presented here.

Depending on the measurement technique used, herbivory (in g C·m⁻²·yr⁻¹) corresponded to the amount of producer biomass ingested by herbivores or to the total amount removed (i.e., also including discarded biomass). Very few reports quantified the two fractions and, thus, we did not make any attempt to do so in our data set. Usually, much of the producer biomass removed by herbivores is subsequently ingested, although in some systems the amount of discarded biomass may be sizeable ("wasteful herbivory"; Ziemann et al. 1979, Thayer et al. 1984). Nevertheless, the variability introduced by comparing total removal with ingestion is small in comparison with the several orders of magnitude encompassed by all of the herbivory values compared here. Most of the herbivory values compiled (>95%) corresponded to quantitative estimates directly provided in the reports or in other reports of the same system. The rest of values corresponded to qualitative approximations given by the authors. We then assumed that low herbivory corresponded to 10% of the net primary production in the system, moderate to 25%, intermediate to 50%, and high to 75%. Because this was done for a small percentage of the total number of herbivory values compiled, and because all the values compared here range over five orders of magnitude, the error introduced by these qualitative estimates should bear no noticeable consequences on the resultant patterns.

For phytoplanktonic communities, herbivory was most often estimated following methods based on gut evacuation rates, if the main herbivores were macrozooplankton (Kiorbe and Tiselius 1987), or based on the dilution technique if the main grazers were ciliates and flagellates (Landry and Hassett 1982, Dolan et al. 2000). For communities of benthic microalgae, field exclosures/enclosures were frequently used for estimating herbivory by macrograzers (e.g., snails, crabs; Worm et al. 2000, Hillebrand and Kahler 2001) and, for herbivory by meiofauna, measurements of individual-based consumption rates were done in the laboratory and subsequently extrapolated to the field using natural grazer densities (Admiraal et al. 1983). Models of grazer metabolism (Ziemann et al. 1993) were used to derive herbivory for a few communities of phytoplankton and benthic microalgae. For communities of aquatic macrophytes (macroalgae, seagrasses, and freshwater macrophytes), field exclosures/enclosures were most often used (Valentine and Heck 1991, Heck et al. 2000). Alternatively, herbivory was derived as the product of herbivore densities in the field and individual-based consumption rates measured in the lab or in the field (Jacobs et al. 1981). In a few reports, herbivory was derived from models of herbivore metabolism (Nienhuis and Groenendijk 1986). In addition, the number and size of bite marks imprinted on leaves was used as a means to estimate herbivory in a number of seagrass communities (Greenway 1976, Cebrian et al. 1996). Field exclosures/enclosures, combining field herbivore densities and individual consumption rates (measured in the field or in the laboratory), and models of herbivore metabolism were also the techniques most often used to derive herbivory in terrestrial communities.

Detrital production (in g C·m⁻²·yr⁻¹) corresponds to the amount of net primary production that is not consumed by herbivores and enters the detrital compartment after senescence. We derived 50% of detrital production values for aquatic communities, and 40% for terrestrial communities, as the difference between net primary production and herbivory over the study period (≥1 yr). This approach assumes steady state of producer biomass (i.e., no significant net change) over the study period, which was apparent in most of the reports considered.
Most authors estimated decomposition rate (proportion of detrital mass decomposed per day, in d−1) by fitting the following single exponential equation to the pattern of detritus decay observed in experimental incubations:

\[ DM_t = DM_{t_0} e^{-kt} \]  

(1)

where \( k \) is the decomposition rate (proportion of detritus decomposed per day), \( DM \) is the detrital mass remaining in the experimental incubation at time \( t \), \( DM_{t_0} \) is the initial detrital mass, and \( (t - t_0) \) is the incubation time. In most cases, other models of detritus decay (linear and double-exponential equations; O’Connell 1987, Romero et al. 1992) did not yield a better adjustment. Alternatively, some authors estimated decomposition rate as the ratio of detrital production to standing detrital mass, since the latter variable remained unchanged over the duration of the study (i.e., the degradable detrital pool remained in steady state; Olson 1963, Schlesinger 1997). We also used this latter approach in a number of aquatic (10% of all the decomposition rates compiled) and terrestrial (50% of all the rates compiled) systems where the pool of degradable detritus was seemingly in steady state.

Absolute decomposition (in g C m−2 yr−1) corresponds to the amount of detritus consumed by microbial decomposers (e.g., bacteria, fungi; “Dec”) and invertebrate and vertebrate detritivores (“Det”). Invertebrate detritivores range from detritivorous micro-, macro-, and gelatinous zooplankton in pelagic systems, to micro- (<100 μm), meio- (100–500 μm), and macrofauna (>500 μm) in benthic and terrestrial systems. Bacteria and fungi metabolize detritus, and invertebrate and vertebrate detritivores usually feed on detritus and attached bacteria and fungi. During decomposition, dissolved and particulate detritus are broken down into simpler constituents and, eventually, into remineralized nutrients (Begon et al. 1996, Schlesinger 1997, Findlay et al. 2002). Direct values of absolute decomposition in pelagic and benthic meioalgal communities were rare (~15%). When directly provided, they were mostly estimated using the equation

\[ D = DM (1 - e^{-kt}) \]  

(2)

where \( D \) is absolute decomposition, \( DM \) is the in situ detrital mass, \( k \) is the decomposition rate (proportion of detrital mass decomposed per day) derived using Eq. 1, and \( t \) is duration of the study period. Other reports derived absolute decomposition from the rate of oxygen consumption in detritus incubations in the lab or in the field (i.e., respiration by Dec + Det), which was subsequently converted to carbon units. In some reports for oceanic phytoplankton, absolute decomposition was estimated as the decay in the mass of particulate detritus with increasing water-column depth (Muller and Suess 1979, Suess 1980).

When not directly provided in the reports, we estimated absolute decomposition in communities of pelagic and benthic microalgae from measurements of community respiration (\( R_c \)) obtained with in situ incubations in dark containers. \( R_c \) corresponds to \( R_p + R_{Det} + R_{Det} \) (Valiela 1995), where \( R_p \), \( R_{Dec} \), and \( R_{Det} \) are the respiration by producers, (Dec + Det), and by the grazers enclosed in the incubation container (flagellates and ciliates in pelagic communities and micro- and meiofauna in benthic communities). \( R_{Dec} + R_{Det} \) can be interpreted as a proxy for absolute decomposition (Valiela 1995, Begon et al. 1996) and, thus, we estimated absolute decomposition as \( R_c - R_p - R_{Det} \). When reports did not provide direct estimates of \( R_p \), we estimated it from community-specific mean values of the percentage of gross primary production respired by the producers as described in the third paragraph of this subsection. Few reports provided direct estimates of \( R_p \). As a result, we used the conversion factor that, on average, \( R_p \) corresponds to 50% (±30%) of the respiration by the entire grazer community (Duarte and Cebrian 1996). A few reports provided values of total grazer respiration. For reports with measurements of total herbivory, but not total grazer respiration, we estimated total grazer respiration by applying models of grazer metabolism (i.e., the ratio of respiration to ingestion; Valiela 1995, Begon et al. 1996) to the herbivory measurements. Otherwise, and most often, we first estimated total herbivory by multiplying net primary production and the community-specific mean percentage of production consumed by herbivores reported by Cebrian et al. (1998) and Cebrian (1999), and then estimated total grazer respiration by applying the models of grazer metabolism to the total herbivory estimates. Finally, the absolute decomposition of sedimenting phytoplankton detritus beyond the mixing layer was assumed to be 17% of the net primary production of the phytoplanktonic community (Martin et al. 1987) and that value was added to the estimates of absolute decomposition obtained from measurements of community respiration. Values were transformed to carbon units using conversion factors provided by the authors or elsewhere (Qasim and Bhattathiri 1971, Strickland and Parsons 1972).

When absolute decomposition was directly reported for communities of aquatic macrophytes and terrestrial communities, it was most often estimated using Eq. 2, or alternatively, from models of community metabolism (Odum 1971, Woodwell et al. 1979). Direct values, however, were not common (~35% of all values compiled for those communities). When not directly reported, we estimated absolute decomposition (\( D \)) from the equation

\[ D = (DP - E) \times (1 - e^{-kt}) \]  

(3)

where \( DP \) and \( E \) are the cumulative detrital production and detritus exported from the community over the study duration (g C m−2 [study period]−1), \( k \) is the de-
composition rate (proportion of detrital production decomposed per day), and \( t \) is the duration of the study (in days), which is at least one year. This approach is valid in communities with a steady pool of degradable detritus, which was seemingly the case in most of the systems examined, and where all detrital production is exported, decomposed in situ, or incorporated into the pool of refractory detritus. If DP was not given directly by the authors, we then estimated it as the difference between net primary production and herbivory. In \( \sim 25\% \) of these cases, we also estimated herbivory as the product of net primary production and the community-specific mean percentage of net primary production consumed by herbivores reported by Cebrian et al. (1998) and Cebrian (1999). Very few reports provided direct measurements of \( E \). As a result, we mostly estimated it as the product of net primary production and published community-specific mean values of the percentage of primary production that is exported from the community (Cebrian 1999, Cebrian 2002). For \( \sim 25\% \) of the absolute decomposition values estimated with Eq. 3, we used community-specific mean values of \( k \) provided by Enriquez et al. (1993).

Finally, we estimated \( \sim 75\% \) of the absolute decomposition values compiled for both macroalgal and seagrass communities from measurements of community respiration following a similar procedure as described in this subsection for communities of phytoplankton and benthic microalgae. In this case, though, and since most grazers are excluded from the incubation chambers, we estimated decomposition as \( R_c - R_p \) where \( R_c \) is community respiration and \( R_p \) is the respiration by the macroalgal or seagrass producers. Most of the macroalgal communities where this approach was used were dominated by coral reef algae. If \( R_p \) was not directly provided in the report, we calculated it from the mean percentage of gross primary production respired by the producer type, as described earlier in this subsection (Duarte and Cebrian 1996).

Our indirect estimates of absolute decomposition for communities of pelagic and benthic microalgae are based on measurements of respiration by \( R_c \), and, thus, they should be indicative of the extent of detritus consumption by these organisms. This is also the case for a fraction of the direct values gathered for communities of pelagic and benthic microalgae (see earlier in this subsection). The rest of direct values for those communities, except when absolute decomposition was measured from the decay in the mass of sedimenting particulate detritus with increasing water-column depth, were obtained following the mass decay rate of algal detritus enclosed in experimental containers. Since the only possible reason for detritus loss in those containers is consumption by \( R_c \), those measurements are also indicative of the extent of detritus consumption by these organisms. On the contrary, many direct values and indirect estimates of absolute decomposition for communities of aquatic macrophytes and terrestrial communities rely on measuring the mass loss of detritus enclosed in litter bags. Besides consumption by \( R_c \), that loss also includes the flushing of fragmented detrital particles and dissolved detritus out of the bags (Harrison 1989, Romero et al. 1992). Nevertheless, since a substantial fraction of the fragmented and dissolved detritus flushed out of experimental litter bags is metabolized by \( R_c \) within the same year as the detritus is produced (Mateo and Romero 1996, 1997), the error introduced when comparing values based on \( R_c \) with values based on detritus loss in litter bags should be small in relation to the four orders of magnitude covered by all the absolute decomposition values compiled in the data set.

Statistical methods

Due to the markedly non-normal nature of the variables examined, we used the nonparametric Mann-Whitney statistic to test for differences between aquatic and terrestrial systems. Nonparametric tests are more conservative than parametric approaches but, in view of the large sample size of all our comparisons, our statistical power is high (Zar 1998). Associations between variables were examined with techniques of Model I least-square linear regression and data were log-transformed to comply with the assumptions of this technique. Both the dependent and independent variables used in our regression analyses are subject to measurement error, but two reasons allow for the legitimate use of Model I regression here. First, Model I regression yields acceptable results when the measurement error committed with the dependent variable largely exceeds that committed with the independent variable (Sokal and Rohlf 1995). This is the case here since, as it can be easily inferred from the detailed description of methods provided in the Methods: Variables compiled; definition and derivation of indirect estimates, the techniques used to measure our independent variables (i.e., producer and detritus nutrient concentrations and net primary production) normally bear much less measurement error and are based on fewer assumptions than the techniques used to measure our dependent variables. Second, our intention is to examine the strength of associations between variables (i.e, predictive aspect of regression analyses), and not functional differences (i.e., comparison of slopes and intercepts) among regression equations. In such cases, Model I regression yields robust results (Sokal and Rohlf 1995).

Effects of within-study variability on the results obtained

Attempts to draw conclusions from the comparison of published values in different studies should consider the within-study variability of the data compiled. Failure to do so may involve serious problems for the conclusions achieved, such as low statistical power (i.e.,
high possibility of accepting a false null hypothesis) and considerable uncertainty around the significance level of the test applied (i.e., α value). Meta-analysis comprises a series of statistical techniques that allow for the inclusion of within-study variability in comparisons among studies by weighting each study contribution by the inverse of its sampling variance (Hedges and Olkin 1985, Gurevitch and Hedges 1999, Rosenberg et al. 1999). These techniques provide adequate tools to derive robust conclusions on diverse ecological issues when comparing studies with different sample sizes and reliability (Downing et al. 1999, Osenberg et al. 1999). Unfortunately, the use of meta-analysis techniques requires knowledge of within-study variability (i.e., sample size or variance in each study), which, due to poor reporting on data acquisition and characteristics in the studies compared, is often not possible (Gurevitch and Hedges 1999, 2001). Only a small percentage of the many studies examined here provide variance estimates for the values compiled. Therefore, our results inevitably rest on an unweighted (i.e., not corrected for within-study variability) comparison of the values compiled. We provide a series of arguments as to why this limitation should not significantly affect our conclusions.

First, our analysis corresponds to a community-level comparison, which implies that the values compiled integrate the main producers and consumers in the community rather than averaging much of the within-study spatial variability. Most of the values compiled also integrate several observations spanning at least one year, or the growing season for highly seasonal systems, which should also substantially reduce the within-study temporal variability in the variables compiled. Therefore, these two characteristics of the data set should reduce the possible impact of neglecting within-study variability on the patterns reported.

The second argument emerges from examining our significant regression equations (H_0: regression slope = 0, P > 0.05; Table 1). In this case, one is concerned about how neglecting within-study variability may affect the significance level (α) of the test and, thus, the possibility of rejecting a true null hypothesis (Hedges and Olkin 1985, Gurevitch and Hedges 1999). To examine how neglecting within-study variability could affect the less significant regressions (0.05 > P > 0.000001), we ran a randomization test on two of the regression equations: the percentage of production consumed by herbivores vs. producer nitrogen concentration in terrestrial systems (P = 0.000002) and absolute herbivory vs. producer phosphorus concentration in aquatic systems (P = 0.01), see Table 1. The test consisted of randomly generating new pairs of independent and dependent values without repetition, calculating the significance (F ratio) of the regression model fitted to each random generation, and contrasting the distribution of random significance levels with the significance of the pattern observed. This is one of the paths of action for examining the validity of regression models based on unweighted data (Gurevitch and Hedges 1999), and it assesses the probability of the pattern results from random processes. We ran 30 random adjustments for each of the two regressions, and in all cases we found our observed pattern much more significant (much higher F ratio) than any of the random adjustments.

The third argument refers to our nonsignificant regressions (H_0: regression slope = 0, P > 0.05; Table 1). This may seem a serious limitation since it is well known that failure to weight individual observations in meta-analyses may result in drastically reduced statistical power and, thus, a much greater chance to accept a false null hypothesis (Hedges and Olkin 1985, Gurevitch and Hedges 1999). To shed some light on the importance of this caveat, we calculated the power of our nonsignificant regressions as 1 - β(1), where β(1) is the one-tailed probability of the normal deviate (Cohen 1977):

\[ Z_{\text{null}} = (z - z_a) (n - 3)^{0.5} \]  

where \( z \) and \( z_a \) are the values of the Fisher z transformation for the sample and critical values of the correlation coefficient (i.e., the correlation coefficient between the two variables compared is the square root of the coefficient of determination of the regression equation), and \( n \) is the number of observations in the regression model. In view of their large number of observations (see Table 1), most of our nonsignificant regressions have low β(1) and, thus, high power (1 - β(1) > 0.75). Weighting the observations by dividing by the inverse of their within-study variance would certainly increase the power of our analysis, but the power of the unweighted regressions is generally too high that their validity does not seem compromised.

Finally, there is a fourth argument that our conclusions should be robust in spite of our ignorance of within-study variability. Working on a logarithmic scale and covering several orders of magnitude, our conclusions are mostly based on comparing the coefficient of determination of the regressions fitted (i.e., the strength of the associations) and not as much on comparing their significance values (F ratio of the regression). From the arguments elaborated in the previous two paragraphs, it seems that weighting the observations compiled here might, at the most, render some barely significant regressions (0.01 < P < 0.05) nonsignificant (P > 0.05) and/or some nonsignificant regressions (P > 0.05) based on relatively few data significant (P < 0.05). However, the coefficients of determination for those corrected regression equations would continue to be low and, therefore, the conclusions of the paper would remain unchanged.

Effects of the calculation error involved with our indirect estimates on the results obtained

In the Methods: Variables compiled: definition and derivation of indirect estimates, we have explained how
TABLE 1. Least-squares regression equations and statistics for the relationships presented.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>System type</th>
<th>Equation</th>
<th>n</th>
<th>R²</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPP</td>
<td>N_{biomass}</td>
<td>Aquatic</td>
<td>log(NPP) = 0.33(±0.15) + 1.71(±0.28) log(N_{biomass})</td>
<td>62</td>
<td>0.37</td>
<td>36.65</td>
<td>0.0000001</td>
</tr>
<tr>
<td></td>
<td>PC</td>
<td>Terrestrial</td>
<td>log(PC) = 0.83(±0.09) + 1.19(±0.21) log(N_{biomass})</td>
<td>45</td>
<td>0.40</td>
<td>20.81</td>
<td>0.0000005</td>
</tr>
<tr>
<td></td>
<td>PC</td>
<td>Terrestrial</td>
<td>log(PC) = 1.84(±0.13) + 1.47(±0.22) log(P_{biomass})</td>
<td>57</td>
<td>0.44</td>
<td>44.32</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>PC</td>
<td>Terrestrial</td>
<td>log(PC) = -1.96(±0.23) + 1.34(±0.18) log(P_{biomass})</td>
<td>30</td>
<td>0.65</td>
<td>54.94</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>Terrestrial</td>
<td>log(H) = 1.31(±0.09) + 1.06(±0.20) log(N_{biomass})</td>
<td>45</td>
<td>0.38</td>
<td>27.51</td>
<td>0.0000003</td>
</tr>
<tr>
<td></td>
<td>P_{biomass}</td>
<td>Aquatic</td>
<td>log(P_{biomass}) = 0.10(±0.01) + 0.85(±0.05) log(NPP)</td>
<td>160</td>
<td>0.66</td>
<td>313.59</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>PC</td>
<td>Terrestrial</td>
<td>log(PC) = -1.04(±0.36) + 0.88(±0.15) log(NPP)</td>
<td>106</td>
<td>0.25</td>
<td>36.49</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>PC</td>
<td>Aquatic</td>
<td>log(PC) = 6.70(±0.40) + 0.72(±0.25) log(NPP)</td>
<td>20</td>
<td>0.72</td>
<td>15.00</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>P_{biomass}</td>
<td>Terrestrial</td>
<td>log(P_{biomass}) = 0.80(±0.07) + 0.08(±0.13) log(NPP)</td>
<td>124</td>
<td>0.94</td>
<td>2016.67</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>P_{biomass}</td>
<td>Aquatic</td>
<td>log(P_{biomass}) = 0.72(±0.08) + 0.06(±0.01) log(NPP)</td>
<td>172</td>
<td>0.92</td>
<td>1762.61</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>k</td>
<td>Terrestrial</td>
<td>log(k) = -2.16(±0.10) + 1.01(±0.21) log(NPP)</td>
<td>88</td>
<td>0.21</td>
<td>23.62</td>
<td>0.0000005</td>
</tr>
<tr>
<td></td>
<td>k</td>
<td>Aquatic</td>
<td>log(k) = -2.48(±0.04) + 1.01(±0.12) log(NPP)</td>
<td>83</td>
<td>0.46</td>
<td>70.45</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>k</td>
<td>Aquatic</td>
<td>log(k) = -1.24(±0.09) + 0.89(±0.17) log(P_{biomass})</td>
<td>51</td>
<td>0.48</td>
<td>26.64</td>
<td>0.0000004</td>
</tr>
<tr>
<td></td>
<td>k</td>
<td>Aquatic</td>
<td>log(k) = -1.68(±0.14) + 0.79(±0.10) log(P_{biomass})</td>
<td>47</td>
<td>0.54</td>
<td>56.06</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>Aquatic</td>
<td>log(D) = 0.80(±0.10) + 1.16(±0.04) log(NPP)</td>
<td>170</td>
<td>0.84</td>
<td>913.41</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>Aquatic</td>
<td>log(D) = -0.55(±0.10) + 1.08(±0.06) log(NPP)</td>
<td>90</td>
<td>0.76</td>
<td>276.87</td>
<td>&lt;0.0000001</td>
</tr>
<tr>
<td></td>
<td>k</td>
<td>Aquatic</td>
<td>log(k) = 0.01(±0.01) + 1.14(±0.30) log(DP)</td>
<td>23</td>
<td>0.01</td>
<td>1.14</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>k</td>
<td>Terrestrial</td>
<td>log(k) = 2.72(±0.05) + 2.34(±0.14) log(DP)</td>
<td>27</td>
<td>0.05</td>
<td>1.14</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>Aquatic</td>
<td>log(D) = 0.08(±0.01) + 0.08(±0.01) log(DP)</td>
<td>24</td>
<td>0.08</td>
<td>913.41</td>
<td>&lt;0.0000001</td>
</tr>
</tbody>
</table>

**Notes:** Non-significant or poor (R² ≤ 0.11) equations are not included. Abbreviations: NPP, net primary production (g C m⁻² yr⁻¹); N_{biomass}, nitrogen concentration in producer biomass (percentage dry mass); P_{biomass}, phosphorus concentration in producer biomass (percentage dry mass); PC, percentage of NPP consumed by herbivores; H, absolute consumption by herbivores (g C m⁻² yr⁻¹); DP, detrital production (g C m⁻² yr⁻¹); PDP, percentage of NPP channeled as detritus; N_{biomass}, nitrogen concentration in producer detritus (percentage dry mass); P_{biomass}, phosphorus concentration in producer detritus (percentage dry mass); k, decomposition rate (proportion of detrital mass decomposed per day, d⁻¹); D, absolute decomposition (g C m⁻² yr⁻¹).

we estimated some of the values contained in the data set from a number of assumptions and conversion factors. For some variables, it is straightforward that the calculation error committed with those indirect estimates should bear no significant effect on the patterns described because (1) those estimates are only a small proportion of all the values compiled (<10%) and (2), based on the procedure followed to derive those estimates, it is easy to see that the error committed is small in comparison with the many orders of magnitude encompassed by all the values compiled. Examples of this scenario are our indirect estimates of producer and detritus nutrient concentration and the quantitative conversion of qualitative estimates of herbivory (see Methods: Variables compiled: definition and derivation of indirect estimates). For some other variables, the potential effect of our indirect estimates on the validity of our results is not so straightforward. We now address those cases and justify why the error committed should still have no noticeable effects on our conclusions. The variability of our estimates of net primary production may be readily quantified with techniques of error propagation (Tsokos 1972) following the equations

\[ s(A + B) = [s(A)^2 + s(B)^2]^{0.5} \]  
\[ s(A \times B) = [s(A)^2 \times s(B)^2 + |B \times s(A)|^2 + |A \times s(B)|^2]^{0.5} \]

where A and B are the mean values used and s denotes their standard errors. Because the standard errors of the mean conversion factors used to derive our estimates of net primary production are small (see Methods: Variables compiled: definition and derivation of indirect estimates for details), those estimates should bear little calculation error, especially in comparison with the sev-
In some other cases, however, it is more difficult to set limits to the calculation error committed in deriving the indirect estimates. Detrital production is one example, as the uncertainty of our calculation error will greatly depend on the validity of the assumption that producer biomass remains in steady state over the study duration. As that assumption seemed to hold in most cases, the error committed with our indirect estimates of detrital production should also be inconsequential for the many orders of magnitude covered by all the values compiled and, thus, for the results obtained. To further support this expectation, we compared, for aquatic and terrestrial ecosystems separately, the regression equation fitted between values of detrital production directly provided by the authors and net primary production to the equation fitted between our detrital production estimates and net primary production. The four regression equations were highly significant ($P < 0.00001$ and $R^2 > 0.85$ for all regressions) and, for both ecosystem types, the slope and intercept of the regression fitted with direct values of detrital production did not differ from the slope and intercept of the regression fitted with our estimates (slope, $t$ test, $P > 0.05$; intercept, ANCOVA, $P > 0.05$).

Our absolute decomposition estimates are another example where the calculation error committed is difficult to ascertain because the standard errors of some of the mean conversion factors used (see Methods: Variables compiled: definition and derivation of indirect estimates) are not known with rigor. It seems that the uncertainty of our absolute decomposition estimates may be substantial because they are based on a relatively high number of conversion factors and the standard errors of some of those conversion factors seem high. For instance, the assumption that the absolute decomposition of sedimenting phytoplankton is 17% of the net primary production in the community is a rough oversimplification since that percentage can vary tremendously among different oceanic areas (Muller and Suss 1979, Suss 1980). In addition, our indirect estimates account for most (>75%) of the absolute decomposition values contained in the data set.

We ran two sensitivity analyses to investigate how the calculation error committed with our many estimates of absolute decomposition affected the strong associations found between absolute decomposition and net primary production in aquatic and terrestrial systems (Table 1, see also Fig. 11A). Our rationale is that if the error committed with our absolute decomposition estimates is important, it should then affect significantly those associations. To run the sensitivity analyses, we first estimated, using Eqs. 5 and 6 and some first-order approximations, that the maximum calculation error of our indirect estimates of absolute decomposition (i.e., the standard error of the estimate) oscillated around ±50% of the estimate, but was frequently less. For the first analysis, we assigned to each of the initial absolute decomposition values an error term randomly distributed between −50% and +50% of the value, and recalculated each initial value as

$$\text{new value} = \text{initial value} + [\text{initial value} \times (\text{error assigned}/100)]$$

(7)

Following this procedure, we generated five new series of absolute decomposition values for both aquatic and terrestrial systems. Then, for aquatic and terrestrial systems separately, we regressed each of those absolute decomposition series against the initial values of primary production and compared each of those new regressions with the initial regressions (see Table 1). The new regressions were also highly significant ($P < 0.00001$ and $R^2 > 0.70$ for all ten regressions) and with similar slopes and intercepts to the initial regressions (all $t$ tests and ANCOVA, $P > 0.05$).

In the second analysis, we examined the effects under the assumption that the calculation error is not randomly distributed among the absolute decomposition values but associated with the magnitude of the value. Namely, we assumed that the calculation error changed monotonically (either positively or negatively, see next paragraph) for observations progressively farther from the median using the equation

$$\text{calculation error} = 50\% \text{(number of values between median and given value)} + \text{total number of values between median and minimum or maximum value)}$$

(8)

Using Eq. 7, we then generated, separately for aquatic and terrestrial systems, a first series of new absolute decomposition values by subtracting the absolute calculation error (i.e., value $\times$ [error derived using Eq. 8]/100) from the values above the median and adding the absolute error to the values below the median. This "worst case" biasing acts to rotate the regression clockwise towards a zero slope. We also calculated a second series by adding the absolute error to the values above the median and subtracting it from the values below the median. This biasing represents another "worst-case" scenario that rotates the regression slope counterclockwise towards infinity. We regressed the new absolute decomposition values against the initial values of primary production. The four new equations (i.e., clockwise and counterclockwise rotations for both aquatic and terrestrial systems) were highly significant
which further supports the robustness of the initial associations observed between absolute decomposition and primary production. If the calculation error committed with our absolute decomposition estimates does not seem to impact the strong associations between absolute decomposition and net primary production, it should not impact either the strong independence between absolute decomposition and detritus nutrient concentrations that our results reveal (Table 1, see also Fig. 10). In all, these analyses support that the error committed with our indirect estimates of absolute decomposition does not affect the conclusions obtained.

Effects of comparing different producer compartments on the results obtained

Most direct values and indirect estimates compiled for communities of aquatic rooted macrophytes and terrestrial communities refer only to the aboveground compartment (see Appendix). A few others also include the belowground compartment, while the rest only referred to the leaf compartment. It seems that the variability introduced by comparing different producer compartments is small in relation to the wide range encompassed in our data set (DeAngelis et al. 1981) and, thus, that variability should bear little effect on the patterns presented here. To examine this expectation, we analyzed how comparing different producer compartments affected two of the associations found in this paper, i.e., the association between absolute herbivory and net primary production and the association between absolute decomposition and net primary production (see Results). Namely, we fitted one regression equation between absolute herbivory and net primary production to the entries for aquatic rooted macrophytes and terrestrial producers that included both the below- and aboveground compartments and a second regression equation to the rest of entries for aquatic-rooted macrophytes and terrestrial producers. We then compared the slopes ($t$ test, $H_0$: equality of slopes) and intercepts (ANCOVA, $H_0$: equality of intercepts) of the two regression equations. We did the same thing for the regression between absolute decomposition and net primary production.

For the association between absolute herbivory and net primary production, we found a similar slope ($t$ test, $P > 0.05$) but a different intercept (ANCOVA, $P < 0.05$) between the two sets of data. Differences in intercept for the association between absolute herbivory and net primary production are expected since generally herbivores consume only aboveground organs and, hence, a given level of absolute herbivory should correspond to a larger level of primary production if both the below- and aboveground compartments are included. However, ANCOVA also revealed that the variability in absolute herbivory explained by the producer compartments included is minute (eight times lower) in comparison with the variability explained by primary production, which implies that comparing different producer compartments has little effect on the association between absolute herbivory and primary production. For the association between absolute decomposition and net primary production, we found no differences in slope and intercept ($P > 0.05$ for both tests). In all, this analysis supports that, in view of wide range covered by the values compiled here, the inclusion of different producer compartments in our analysis is of little importance, if any, for the patterns found.

Results

Net primary production ranged over five orders of magnitude within aquatic ecosystems and over three orders of magnitude within terrestrial ecosystems (Fig. 1A). Overall, however, net primary production did not differ greatly between aquatic and terrestrial ecosystems, with only a marginal tendency for the former ecosystems to show higher values (Mann-Whitney, $P = 0.03$). Nitrogen and phosphorus concentrations varied greatly within aquatic and terrestrial producers (Figs. 1B and 1C), with aquatic producers tending to have higher concentrations (Mann-Whitney, $P < 0.01$ for both nutrients). The percentage of net primary production consumed by herbivores was also highly variable, ranging from <1% to 100% within aquatic systems and from <0.1% to 75% within terrestrial systems. Overall, however, aquatic systems tended to have higher percentages consumed (Fig. 1D; Mann-Whitney, $P < 0.01$). A similar result was found with absolute consumption, which also varied greatly within either type of ecosystem but tended to be greater in aquatic ecosystems (Fig 1E; Mann-Whitney, $P < 0.01$).

Net primary production was independent of producer nutrient concentration in aquatic and terrestrial ecosystems (Fig. 2, Table 1). Indeed, for a given concentration, net primary production could vary over two orders of magnitude within aquatic systems and over one order of magnitude within terrestrial systems. The percentage of net primary production consumed by herbivores was positively associated with producer nutrient concentration within aquatic and terrestrial ecosystems (Fig. 3, Table 1). Yet for a given nutrient concentration, the percentage consumed varied considerably. Accordingly, the strength of the association was generally moderate, as indicated by the coefficient of determination for the regression equations ($0.37 \leq R^2 \leq 0.65$; Table 1).

Within terrestrial ecosystems, increasing absolute consumption was also associated with higher producer nutrient concentrations with varying degrees of strength ($0.38 \geq R^2 \geq 0.64$), but, in contrast, absolute consumption and producer nutrient concentration were very poorly related within aquatic ecosystems ($0.11 \geq R^2$; Fig. 4, Table 1). Instead, absolute consumption was strongly associated with net primary production within aquatic ecosystems ($R^2 = 0.66$; Fig. 5A, Table 1). Within these ecosystems, the percentage of net primary pro-
duction consumed by herbivores only varies about one order of magnitude throughout most of the production range (0.1–100 g C m⁻² yr⁻¹), and it varies a little more than two orders of magnitude for production values which ranged between 100 and 3000 g C m⁻² yr⁻¹ (Fig. 5B). Absolute consumption corresponds to the product of net primary production and the percentage consumed and hence, in view of the interaction between production and percentage consumed, the variability in absolute consumption within aquatic systems remains closely associated with that in production. In view of the independence between net primary production and producer nutrient concentration (Fig. 2), it is also clear why absolute consumption and producer nutrient concentration are very poorly associated within aquatic systems (Fig. 4).

Conversely, the association between absolute consumption and net primary production within terrestrial ecosystems was weak ($R^2 = 0.25$; Fig. 5A, Table 1). Again, the reason lies in the interaction between net...
primary production and the percentage consumed within terrestrial ecosystems. The percentage consumed varies by three orders of magnitude throughout the entire range of terrestrial production values, which only encompasses about two orders of magnitude (Fig. 5B). Hence, within terrestrial ecosystems the variability in absolute consumption is poorly related to that in primary production, but better related to the percentage consumed and, as a consequence, to producer nutrient concentration (Fig. 4).

The percentage of net primary production channeled as detritus varied from ~0% to 100% within aquatic ecosystems, and from ~25% to 100% within terrestrial ecosystems (Fig. 6A). The percentage was >50% in most aquatic and terrestrial systems, demonstrating the general predominance of the detrital pathway. Overall,
however, terrestrial ecosystems tended to channel a higher percentage of production as detritus (Mann-Whitney; $P < 0.01$), as expected from the lower percentage of production lost to herbivores (Fig. 1D). Detrital production varied widely within aquatic systems, and to a lesser extent within terrestrial systems, and it also tended to be larger in terrestrial systems (Fig. 6B; Mann-Whitney, $P < 0.01$). Aquatic detritus had higher nitrogen and phosphorus concentrations than did terrestrial detritus (Figs. 6C and 6D; Mann-Whitney, $P < 0.01$ for both nutrients), although nutrient concentrations could vary substantially within either type of detritus. A similar result was found with decomposition rates (proportion of detrital mass decomposed per day), with substantial variability within either type of system but higher values overall for aquatic systems (Fig. 6E; Mann-Whitney, $P < 0.01$). Absolute decomposition also varied widely within either type of system but did not differ significantly between the two types of system (Fig. 6F; Mann-Whitney, $P = 0.20$).

Larger detrital production was strongly associated with higher net primary production within either type of system. Changes in primary production accounted for 88% of the variability in detrital production within aquatic systems, and for 94% within terrestrial systems (Fig. 7A, Table 1). The strong association between detrital production and primary production results from the fact that, in general, most primary production enters the detrital compartment in both types of systems (Fig. 6A). Indeed, the percentage of primary production...
channeled as detritus varies little in comparison with the extent of variability in primary production both within aquatic and within terrestrial systems (Fig. 7B). In contrast, detrital production is independent of, or only weakly \((0 \leq R^2 \leq 0.20)\) related to, detritus nutrient concentration (Fig. 8, Table 1).

Aquatic and terrestrial detritus with higher nutrient concentrations tended to have a larger proportion of its mass decomposed per day (Fig. 9, Table 1). This proportion, however, varied substantially for any given nutrient concentration and the tendency varied from weak (proportion decomposed vs. nitrogen concentration in aquatic systems, \(R^2 = 0.21\)) to moderate (proportion decomposed vs. phosphorus concentration in terrestrial systems, \(R^2 = 0.54\)). In contrast, absolute decomposition was totally unrelated to detritus nutrient concentration within either type of system (Fig. 10, Table 1), but instead strongly \((0.76 \leq R^2 \leq 0.84)\) associated with net primary production (Fig. 11A, Table 1). The reason for the strong dependence of absolute decomposition on primary production lies in the fact that the percentage of detrital production that is decomposed within a year varies little in relation to the extent of variability in annual detrital production both
within aquatic and terrestrial ecosystems (Fig. 11B). Hence, within either type of ecosystem the variability in absolute decomposition remains closely associated with that in detrital production and, in turn, with that in primary production. The independence between detrital production and detritus nutrient concentration (Fig. 8) further explains why absolute decomposition and detritus nutrient concentration are also independent (Fig. 10).

DISCUSSION

Overall differences between aquatic and terrestrial ecosystems

Our results present an integrated view of how much aquatic and terrestrial ecosystems differ in net primary production, nutritional quality of producer biomass and detritus, consumption by herbivores, in absolute decomposition, and in the proportion of detritus decomposed per unit time. Overall, net primary production differs little between aquatic and terrestrial systems, but the former systems support much greater losses to herbivores, both as an absolute carbon flux and as a percentage of primary production. Greater absolute fluxes of producer carbon transferred to herbivores in aquatic systems suggest that these systems support higher levels of herbivore production than do terrestrial systems because production efficiency (ratio of herbivore growth to producer carbon ingested) does not seem to vary significantly between the two types of system (Schroeder 1981, Elser et al. 2000a). Past re-
ports also suggest that aquatic systems should have higher levels of herbivore production than terrestrial systems (Cyr and Pace 1993), but empirical demonstration of this hypothesis is lacking. On the other hand, higher percentages of primary production removed by herbivores in aquatic systems suggest that herbivores play a greater role in carbon and nutrient recycling and accumulation of producer biomass in aquatic systems than they do in terrestrial systems. Indeed, most reports of top-down control of producer biomass refer to aquatic systems (Valiela 1995, Valentine and Heck 1999, Paine 2002), although herbivores may also occasionally regulate plant biomass in terrestrial ecosystems (McNaughton 1985, McNaughton and Georgiadis 1986). There is also abundant evidence that herbivores may be important agents of nutrient recycling in aquatic systems (Zieman et al. 1984, Urabe et al. 1995, Elser et al. 2001, Sterner and Elser 2002), whereas such evidence is scant for terrestrial systems (Day and Detling 1990, McNaughton et al. 1997).

Aquatic producers tend to have much higher nutrient concentrations than do terrestrial producers and many reports have shown that the growth rates of aquatic and terrestrial herbivores are limited by the nutrient content

Fig. 9. The relationship between the proportion of detrital mass decomposed per day and detritus nutrient concentration in aquatic and terrestrial ecosystems: (A) proportion of detrital mass decomposed (d⁻¹) vs. detritus nitrogen concentration and (B) proportion of detrital mass decomposed (d⁻¹) vs. detritus phosphorus concentration. Dashed (aquatic ecosystems) and continuous (terrestrial ecosystems) lines depict the regression equations (see Table 1). Thin dashed lines and percentage numbers indicate the percentage of detrital production decomposed within a year at the given k value. This percentage was calculated as \( (1 - e^{-k}) \times 100 \) (Olson 1963). Symbols are as in Fig. 2.

Fig. 10. The relationship between absolute decomposition and detritus nutrient concentration in aquatic and terrestrial ecosystems: (A) absolute decomposition vs. detritus nitrogen concentration and (B) absolute decomposition vs. detritus phosphorus concentration. Symbols are as in Fig. 2.
of their diets (Mattson 1980, Batzli 1986, Sterner and Hessen 1994, Valiela 1995, Elser et al. 1996, 2000b, Hartley and Jones 1997, Ritchie 2000, Stelzer and Lambert 2002, Sterner and Elser 2002, Urabe et al. 2002). Therefore, higher per capita demand and/or greater herbivore standing stocks could ultimately lead to greater herbivory in aquatic systems, although current evidence does not show overall aquatic ecosystems maintaining greater levels of herbivore biomass (Cyr and Pace 1993). Some terrestrial herbivores may compensate for low plant nutritional quality by increasing their feeding rates and removing a larger quantity of producer biomass (Raubenheimer 1992, Williams et al. 1994, Lindroth et al. 1995, Hughes and Bazzaz 1997), but overall aquatic herbivores remove more producer biomass. Other contrasts between aquatic and terrestrial producers, such as the high levels of structural carbon compounds (e.g., lignin) often found in terrestrial plants (Herm and Mattson 1992, Hartley and Jones 1997), could also contribute to the higher levels of herbivory found in aquatic systems. Furthermore, other producer compounds, such as fatty acids and digestible carbohydrates, may be important in determining herbivore preference and growth rates (Brett and Muller-Navarra 1997, Choat and Clements 1998) but their role in explaining the differences in herbivory observed between aquatic and terrestrial systems needs investigation.

The higher levels of herbivory found in aquatic systems, along with the fact that net primary production differs little between aquatic and terrestrial systems, explains why aquatic systems transfer a smaller flux of producer carbon, both in absolute terms and as percentage of primary production, to the detrital compartment than do terrestrial systems. Yet in both aquatic and terrestrial systems, most primary production is not used by herbivores and enters the detrital compartment. These results generalize the predominance of detritic trophic pathways over herbivory that has been observed in many aquatic and terrestrial communities (e.g., Tenore et al. 1982, Mann 1988, Schlesinger 1997, Cebrian and Duarte 1998, Cebrian 1999, Chapin et al. 2002).

In comparison with terrestrial detritus, aquatic detritus has higher nutrient concentrations and a higher proportion of its mass decomposes per unit time, possibly because the metabolism and growth rates of micro- and macro-consumers are often limited by the nutrient concentrations in their diets (Elser et al. 1996, Elser et al. 2000b, Sterner and Elser 2002), and Dec + Det (microbial decomposers and invertebrate and vertebrate detritivores) seem no exception (Iversen 1974, Goldman et al. 1987, Vadstein and Olsen 1989, Tezuka 1990). Therefore, aquatic Dec + Det should generally have higher metabolic and growth rates than their terrestrial counterparts because they normally feed on types of detritus that are more nutritional. On these grounds, higher consumption rates per capita and/or larger Dec + Det standing stocks would lead to higher consumption rates per unit of detrital mass in aquatic systems and, thus, to a higher proportion of detrital mass decomposing per unit time. Accordingly, past comparisons have shown that frequently a larger proportion of the mass of aquatic detritus, vs. terrestrial detritus, decomposes per unit time in spite of substantial environmental variability (Enriquez et al. 1993, Schlesinger 1997, Cebrian et al. 1998, Cebrian 1999). Despite the larger proportions of detrital mass decomposed per unit time found in aquatic systems, we also show that the absolute quantity of detritus decomposed annually does not differ between aquatic and terrestrial systems. This is a consequence of the differences in
Aquatic and terrestrial ecosystems composed of producers that have higher nutrient concentrations tend to have a larger percentage of production removed by herbivores. The tendencies range from moderate to strong, with coefficients of determination varying between 37% and 65%, but they are still relevant considering the diversity of herbivore populations (invertebrate vs. vertebrate), metabolic patterns (ectothermy vs. endothermy), behavior (migratory vs. resident), and feeding specificity (specialized vs. generalists) encompassed by the data set. Hence, producer nutrient concentration stands out as a significant correlate of the percentage of primary production consumed by herbivores within both aquatic and terrestrial systems. Based on substantial evidence that the growth rates of aquatic and terrestrial herbivores are often limited by the nutrient content of their diets (Mattson 1980, Batzli 1986, Sterner and Hessen 1994, Valiela 1995, Elser et al. 1996, Hartley and Jones 1997, Ritchie 2000, Stelzer and Lambert 2002, Sterner and Elser 2002, Urabe et al. 2002), faster consumption rates per capita and/or larger herbivore standing stocks could be responsible for the larger percentage of primary production consumed in high nutrient-content aquatic and terrestrial systems. The patterns presented imply that herbivores, by removing a greater percentage of primary production, should play a greater role as controls of producer biomass accumulation and carbon and nutrient recycling in systems composed of producers with higher nutrient concentrations, regardless of whether we compare aquatic or terrestrial systems. This is in accordance with numerous experimental observations in the two types of system (e.g., Cebrian and Duarte 1994, McNaughton et al. 1997, Sterner et al. 1997, Cebrian 1999, Sterner and Elser 2002).

In contrast to the positive association between the percentage of primary production consumed by herbivores and producer nutrient concentration, absolute consumption by herbivores is only poorly associated with producer nutrient concentration within aquatic systems but strongly associated with the absolute magnitude of primary production. The reason for these patterns lies in the interaction between the variability in primary production and that in the percentage consumed within aquatic systems. Aquatic systems composed of producers with higher nutrient concentrations lose a higher percentage to herbivores, but that percentage varies little in relation to the differences in primary production. Hence, absolute consumption, which corresponds to the product of primary production and percentage consumed, remains closely associated with primary production and only poorly related to the percentage consumed and producer nutritional quality. In other words, aquatic systems that are more productive, and not those composed of producers that are more nutritional, transfer more producer carbon to herbivores. In turn, because the efficiency of herbivore production does not seem to vary consistently across

detrital production and proportion decomposed annually between the two types of system; aquatic systems produce less detritus, but a higher percentage of the detritus decomposes annually, and conversely for terrestrial systems. A higher proportion of detrital mass decomposing per unit time in aquatic systems implies faster rates of nutrient recycling through the detrital compartment. Accordingly, turnover rates of nutrients through the detrital pool tend to be faster in aquatic (Legendre and Rassoulzadegan 1995, Urabe et al. 1995, Valiela 1995, Elser and Urabe 1999) than in terrestrial systems (Melillo et al. 1982, Van Cleave et al. 1983, Taylor et al. 1989, Chapin et al. 2002). Moreover, a higher proportion of detrital mass decomposed per unit time in aquatic systems, along with lower levels of detrital production, imply that those systems accumulate smaller pools of detrital carbon on a per m² basis, which is in accordance with past comparisons of detrital storage between terrestrial and aquatic communities (Cebrian and Duarte 1995, Cebrian et al. 1998, Cebrian 1999). In spite of these differences, our analysis shows that the absolute flux of producer carbon transferred annually to Dec + Det does not vary between aquatic and terrestrial systems. Hence, because the efficiency of Dec + Det production (ratio of Dec + Det growth to carbon ingested) does not differ between aquatic and terrestrial systems (Begon et al. 1996), overall the two systems should support similar levels of Dec + Det production.

**Patterns within aquatic and terrestrial ecosystems**

So far we have discussed the extent and some consequences of the differences in herbivory and decomposition between aquatic and terrestrial ecosystems. We now discuss the patterns within each type of ecosystem. Our results first identify a general independence between primary production and producer nutrient concentrations. Increased nutrient availability often leads to increased nutrient concentrations in producer biomass and higher levels of primary production in many aquatic and terrestrial systems (LaPointe and Clark 1992, Valiela 1995, Hauxwell et al. 1998, Ritchie 2000, Rech et al. 2001), but here we show that in general producer nutrient concentrations are unrelated to primary production within either type of system. We think this independence stems from the fact that environmental constraints can generate large variability in net primary production at any given level of producer nutrient concentration. Indeed, many reports have shown that systems composed of producers with similar nutrient concentrations may reach different levels of primary production depending on the extent of environmental stress they endure (e.g., growth limitation by light and temperature, and in terrestrial systems, by water availability, Valiela 1995, Schlesinger 1997, Alongi 1998, Chapin et al. 2002; exposure to wave action in marine systems, Gerard and Mann 1979, Mann 2000).
systems (Schroeder 1981, Elser et al. 2000a), they should also support higher levels of herbivore production.

Within terrestrial systems, however, absolute consumption is only weakly associated with primary production, but the associations with producer nutrient concentration vary from moderate to strong. Again, the reason resides in the interaction between the variability in primary production and that in the percentage consumed within these systems; primary production varies to a lesser extent than does the percentage consumed within terrestrial systems and, as a consequence, absolute consumption remains more closely associated with the percentage consumed and producer nutrient concentration than with primary production. Within terrestrial systems, producer nutritional quality, besides being indicative of the role of herbivores as controls of producer biomass accumulation and carbon and nutrient recycling, is also an indicator of the absolute magnitude of producer carbon transferred to herbivores and potential levels of herbivore production in the system.

Detrital production is unrelated, or only weakly related, to detritus nutrient concentration within both aquatic and terrestrial systems. Hence, within either type of system the quantity of detritus produced annually is generally independent of its nutritional quality. This result is mostly a consequence of the independence between net primary production and producer nutrient concentration. Detrital production is strongly associated with primary production in aquatic and terrestrial systems because most primary production enters the detrital compartment in each type of system. Furthermore, the changes in nutrient concentration that occur with producer senescence are small in comparison with the wide range encompassed by all the concentration values compiled (Vitousek 1982, Thayer et al. 1984, Sterner and Elser 2002). Hence, the fact that net primary production and producer nutrient concentration are independent within either type of system implies that detrital production and detritus nutrient concentration are also unrelated or, at the most, only weakly related.

Our results generalize many past observations that aquatic and terrestrial detritus with higher nutrient concentrations has a larger proportion of its mass decomposed per unit time (Meilillo et al. 1982, Harrison 1989, Enriquez et al. 1993, Schlesinger 1997). That proportion, however, may vary widely for any given nutrient concentration in aquatic or terrestrial detritus. In fact, the associations between a larger proportion of detrital mass decomposed per unit time and higher nutrient concentrations in the detritus vary from weak to moderate. Still, these associations are relevant in view of the many contrasting environmental effects on decomposition encompassed by the data set, such as temperature (Edwards 1975, Van Cleve et al. 1981), soil or sediment redox conditions (Post et al. 1982), and, in terrestrial systems, moisture (Wildung et al. 1977, Santos et al. 1984). As we did for the comparison between aquatic and terrestrial ecosystems, we suggest that, in view of the evidence that Det + Det growth rates are often limited by the nutrient concentrations in their detrital diets (Iversen 1974, Goldman et al. 1987, Yadstein and Olesen 1989, Tezuka 1990, Elser et al. 1996, Sterner and Elser 2002), higher consumption rates per capita and/or large Det + Det standing stocks could be responsible for the higher proportion of detrital mass decomposed per unit time observed in systems with more nutritional detritus.

The association shown here between a higher proportion of detrital mass decomposed per unit time and more nutritional detritus for aquatic and terrestrial systems bears two important corollaries. First, aquatic and terrestrial systems composed of detritus with higher nutrient concentrations should exhibit faster recycling and turnover rates of nutrients through the detrital compartment. This hypothesis is in accordance with past observations of detrital turnover and recycling rates in systems composed of detritus with contrasting nutrient concentrations (Valliela et al. 1984, Elser and Urabe 1999, Reich et al. 2001). Second, there may be a tendency for aquatic and terrestrial systems composed of detritus with higher nutrient concentrations to accumulate smaller detrital pools. It has been shown that larger proportions of detrital mass decomposed per unit time result in smaller detrital pools when aquatic and terrestrial systems are compared (Cebrian and Duarte 1995, Cebrian et al. 1998), but it remains to be seen whether this association also holds within each type of system.

Conversely, absolute decomposition is independent of detritus nutritional quality, but is instead strongly associated with detrital production and primary production, within both aquatic and terrestrial systems. The reason for these patterns lies in the interaction between the variability in annual detrital production and in the percentage decomposed annually within either type of system. The percentage of detrital production decomposed annually varies little relative to the variability in annual detrital production within either type of system. As a consequence, absolute decomposition, which corresponds to the product of detrital production and percentage decomposed, remains closely associated with detrital and primary production, but unrelated to the percentage decomposed and detritus nutritional quality, within either type of system. Thus, aquatic and terrestrial systems that are more productive, and not those having detritus with higher nutrient concentrations, transfer more carbon to Det + Det. Furthermore, because the efficiency of Det + Det production varies relatively little across systems (Beget et al. 1996), aquatic and terrestrial systems with higher primary production should also support higher levels of Det + Det production.
CONCLUSIONS

The results presented identify producer nutritional quality and net primary production as two independent correlates of the variability in herbivory and decomposition between and within aquatic and terrestrial ecosystems. Producer nutrient concentration stands out as a positive correlate of the percentage of primary production consumed by herbivores and the percentage of detritus production decomposed annually regardless of whether the comparison is made between the two ecosystem types or within either type. Thus, producer nutritional quality appears to be a consistent indicator of the extent of top-down control of the accumulation of producer biomass and detritus and nutrient recycling in ecosystems. However, absolute consumption by herbivores and absolute decomposition are often associated with absolute primary production, and independent of producer nutrient concentration, because the variability in net primary production largely exceeds that in the percentage consumed or decomposed across the range of ecosystems compared. Hence, primary production is often an indicator of the absolute flux of producer carbon transferred to consumers and, thus, of the potential levels of secondary production maintained in the ecosystem.

Aside from these important implications, the empirical relationships presented here also point to a series of regulatory mechanisms of herbivory and decomposition in ecosystems. For instance, because the growth rates of herbivores and Dec + Det are often limited by the nutrient concentrations of their diets, it is possible that larger herbivore and Dec + Det standing stocks and/or higher consumption rates per capita are at the base of the consistent associations observed between higher producer nutrient concentrations and larger percentages of primary production consumed by herbivores and decomposed. Demonstrating this hypothesis with ecosystem-level experimental manipulations would certainly improve our understanding of carbon and nutrient cycling in ecosystems. Finally, because the patterns presented here are robust (e.g., based on large data sets), they can also be of use for global change models seeking to predict how anthropogenic impacts on primary production and producer nutrient concentration may alter carbon and nutrient cycling and consumer populations.

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LITERATURE CITED


SUPPLEMENT

The data set and list of references are available in ESA's Electronic Data Archive: Ecological Archives M074-004-S1.