

# Chapter 7

## Carbon Flux in Seagrass Ecosystems

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### I. Introduction

Understanding matter circulation in the biosphere constitutes one of the fundamental research objectives for ecologists. Stocks of materials, their distribution, and their fluxes between different compartments are basic parameters that need to be characterized to explain the functioning of any ecosystem. Their study is usually arduous owing to the variety of routes that materials can follow, and to the complexity of the processes that are involved. Leopold (1949) described matter flux in ecosystems in a brief but elegant way in what he named '*The odyssey of the atom X*': "*An atom at large in the biota is too free to know freedom; an atom back to the sea has forgotten it. For every atom lost to the sea, the prairie pulls another one out of the decaying rocks. The only certain truth is that its creatures must suck hard, live fast, and die often, lest its losses exceed its gains.*" When an atom abandons its long rest in the lithosphere and joins the organic com-

partment of the biosphere, it enters in that fast cyclic dynamic that characterizes life. Autotrophic organisms bring an atom to life, while the organism's death leaves it at the mercy of decomposers that return it to the inorganic compartment where it waits to join a new cycle. The persistence of an ecosystem relies on both the optimization of carbon and nutrient acquisition and on the minimization of carbon and nutrient losses (Hemminga et al., 1991). In other words, persistence requires a continuous effort to prevent the atoms essential for life from escaping the fast cycles that enable the high production we observe on our planet. Therefore, a fine tuned balance between production and remineralization (and the fluxes between sources and sinks) govern the rhythm of the ecosystems.

This chapter, far from pretending to be an exhaustive examination or reassessment of what is known about carbon fluxes in seagrass ecosystems, is an attempt to put a picture of carbon flux in focus by combining equal parts of literature review, personal achievements (including some recent unpublished and submitted results), a critical appraisal, and

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Table 1. Comparison between average seagrass and other marine and terrestrial ecosystems. NPP (net primary production). Simplified and modified from Margalef, 1986 and Duarte and Cebrián, 1996.

System	Area covered (10 <sup>6</sup> km <sup>2</sup> )	NPP (gC m <sup>-2</sup> year <sup>-1</sup> )	Total NPP (PgC year <sup>-1</sup> )
Marine phytoplankton			
Oceanic waters	332	130	43
Coastal waters	27	167	4.5
Coastal macrophytes			
Mangroves	1.1	1000	1.1
Seagrasses	0.6	817	0.49
Macroalgae	6.8	375	2.55
Microphytobenthos	6.8	50	0.34
Terrestrial ecosystems			
Forests	41	400	16.4
Crops	15	350	5.25
Deserts	40	50	2
Terrestrial ecosystems	148	200	29.6
Continental waters	1.9	100	0.19
Oceans	359	132	47.5

thought-provoking estimates. Our goal is to provide a critical summary of the current knowledge of the topic and identify relevant areas of seagrass research for the coming decade.

## II. Seagrass Production

### A. Seagrass Standing Stocks and Productivity

Since the pioneering work of Petersen (1914), we have accumulated a vast amount of knowledge on seagrass productivity. The 1973 International Seagrass Workshop held in Leiden resulted in one of the first comprehensive and integrative summaries of seagrass ecosystems (McRoy and Helfferich, 1977). Based on a synopsis of existing literature at the time, McRoy and McMillan (1977) concluded that seagrass beds were among the most productive and complex of oceanic ecosystems. Most importantly, they recognized that seagrasses themselves were often just one component of a highly diverse ecosystem that also included significant contribu-

tions of other primary producers, including benthic micro- and macroalgae, epiphytic algae, and phytoplankton.

For seagrasses, net primary production is extremely variable (see Table 1, Larkum et al., Chapter 14) and only tentative ranges and average values can be provided. The compilation of Duarte and Chiscano (1999) indicates that above-ground production ranges from 0.003 to 15 gDW m<sup>-2</sup> day<sup>-1</sup>. In terms of carbon, estimates range from 0.1 to 18.7 gC m<sup>-2</sup> day<sup>-1</sup>, but average 0.5–2.0 gC m<sup>-2</sup> day<sup>-1</sup> for most beds with above-ground biomass >50 gDW m<sup>-2</sup> (Stevenson, 1988; Dawes, 1998). These rates roughly correspond to productivity:biomass ratios (P:B ratios) of about 1–5 for populations in subtropical and temperate latitudes (Duarte, 1989) and are equivalent to 300–1500 gC m<sup>-2</sup> year<sup>-1</sup> based on the wide range in seagrass standing stocks and productivity rates reported in the literature. This high annual productivity demonstrates that seagrasses stand out when compared with other aquatic and terrestrial producers (Table 1).

An important realization over the last decade was that previous seagrass production assessments using leaf marking techniques (e.g. Zieman, 1974; Vermaat et al., 1987) probably underestimated total production. Below-ground to above-ground ratios of seagrass biomass are often >1, ranging from 2 to 5 for many systems and species (McRoy, 1974; Kirkman and Reid, 1979; West and Larkum, 1979; Zieman, 1982; Sand-Jensen and Borum, 1983; Kenworthy and Thayer, 1984; Brouns, 1985; Dunton,

Abbreviations:  $\delta^{13}\text{C}$  – ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  based on a belemnite standard;  $\delta^{15}\text{N}$  – ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$ ;  $\delta^{34}\text{S}$  – ratio of  $^{34}\text{S}$  to  $^{32}\text{S}$ ; DIC – dissolved inorganic carbon; DOC – dissolved organic carbon; DP – detrital production; GC – grams carbon; GDW – grams dry weight; NPP – net primary production; PAM – pulse amplitude modulated (fluorometer); PLFA – polar lipid-derived fatty acid; P:R ratio – photosynthetic rate to respiration rate ratio; RA – refractory accumulation; RPD – redox potential discontinuity.

1996). Thus, below-ground production ranges from 0.001 to 20 gDW m<sup>-2</sup> day<sup>-1</sup> (Duarte et al., 1998; Duarte and Chiscano, 1999; Kaldy and Dunton, 2000). Only recently, however, have the importance of below-ground tissues for carbon storage and in-sediment biogeochemical processes been recognized in plant production models.

### *B. Contribution of Epiphytes and Other Primary Producers*

In addition to understanding the factors that control carbon flow through food webs, it is necessary to determine the trophic importance of components of the seagrass food web, which are often overlooked. On a broad level, the extent to which these food webs depend on locally-derived food resources vs. more transient planktonic resources needs to be quantified. Although locally-generated production is high in seagrass systems, organic matter flux through the planktonic and filter-feeding pathways may be significant as well. At a finer level, and as will become evident below, the relative contribution of the resident producers must be better understood: algal epiphytes and other primary producers (e.g. drift macroalgae, benthic macroalgae, and phytoplankton) have long been recognized as significant contributors to total seagrass bed primary production (McRoy and McMillan, 1977), yet their quantitative role has been neglected (Fry et al., 1987). Because sediments within and between seagrass beds constitute a large area in the seagrass landscape, it is likely that the role of sediment microalgae may have been largely underestimated. Algal epiphyte contribution alone has been reported to range from 20 to 60% (see review by Borowitzka and Lethbridge, 1989; see also Borowitzka et al., Chapter 19). More recently, Moncreiff et al. (1992) reported algal production (including epiphytes, benthic diatoms, and phytoplankton) to be 87% of total system production in Mississippi Sound. As described in detail later, Moncreiff and Sullivan (2001), Dauby (1989), and Yamamuro (1999) have recorded the large contributions of algae in seagrass beds, and stand in contrast to many studies which concentrate only on the importance of seagrass carbon both within and outside seagrass communities (see review by Stevenson, 1988 and Section 3.4.1).

Kaldy et al. (2002), for example, showed that benthic macroalgae accounted for most of system

net primary production (33–42%), followed by seagrasses (33–38%) and other microalgae (23–56%). Furthermore, this is a role that may be increasing in coastal and estuarine systems that are becoming increasingly more eutrophic due to nitrogen loadings from adjacent watersheds (Hauxwell et al., 2003). By incorporating the sediment microalgae into future studies, a more complete picture of trophic dynamics can be developed that will allow us to generate a landscape perspective (see Bell et al., Chapter 26) of the flux of carbon and nutrients, related to variables such as depth, irradiance, nutrient availability, and sediment type.

### *C. Seagrass Production Measurements*

For decades, seagrass productivity estimates have been based on the hole-punching (Zieman, 1974). Alternatively, for plants with very narrow blades, cut and harvest approaches have been employed (Virnstein, 1982). Neither method accounts for below-ground production, which as mentioned earlier, can be greater than 50% of total seagrass production. Other problems include tissue loss by grazing or mechanical damage and physiological disturbance associated with clipping (Tomasko and Dunton, 1995; Kowalski et al., 2001).

More sophisticated approaches to net production measurements have included *in situ* measurement of whole plant photosynthetic oxygen evolution and respiration using chambers in combination with continuous measurements of underwater irradiance at canopy level (Herzka and Dunton, 1997, 1998). This approach is not only extremely labor intensive but requires comprehensive knowledge of seagrass photosynthetic response to temperature and light. Alternatively, various researchers have employed a whole plant approach based on laboratory determinations of plant photosynthetic parameters (Zimmerman et al., 1989; Fourqurean and Zieman, 1991). In either case, the method is labor intensive and requires continuous *in situ* measurement of underwater irradiance to calculate daily or annual net production. These physiological measurements normally measure oxygen evolution or carbon uptake, and the inherent errors related to internal recycling or storage of gases, contributions by other organisms (such as bacteria, epiphytes, and macroalgae), and the photosynthetic quotient make either approach problematic (see Mateo et al., 2001).

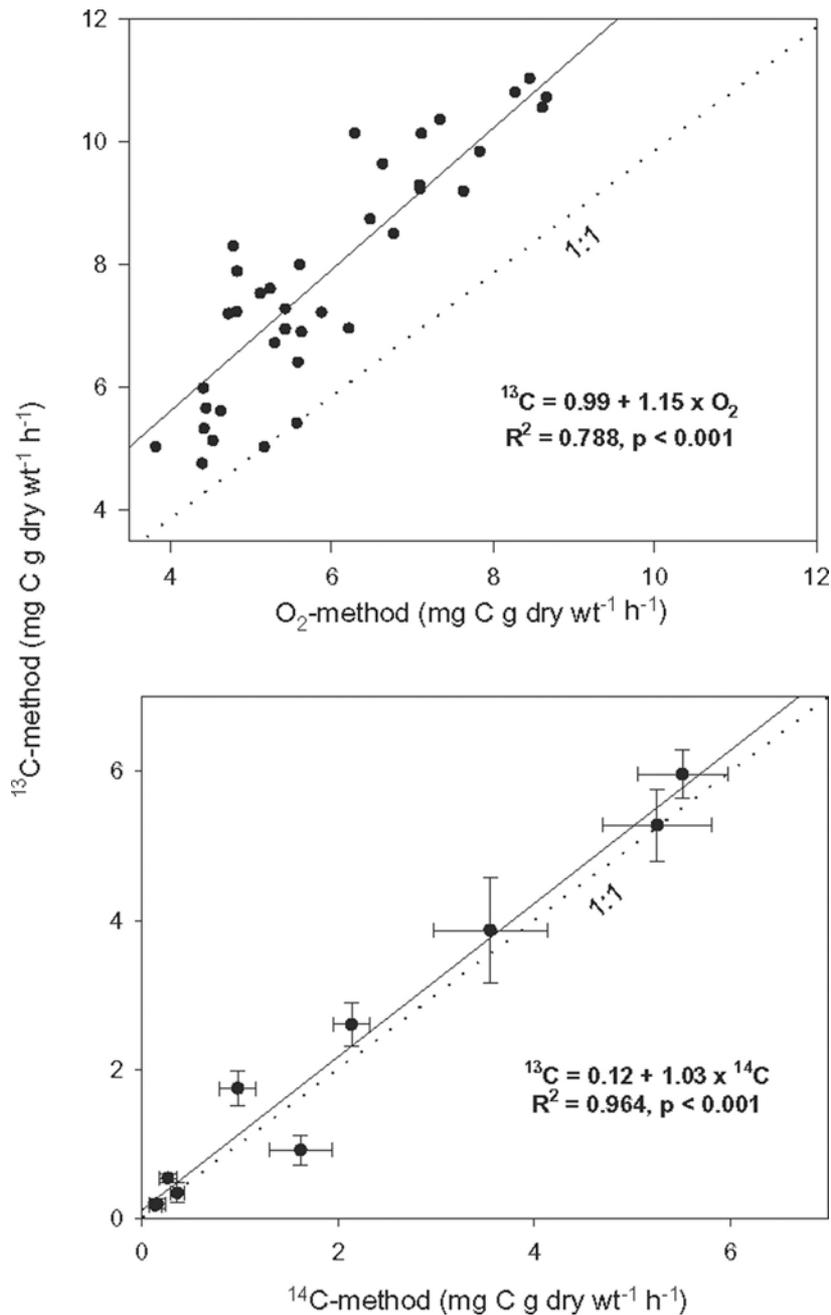


Fig. 1. Comparison of the  $^{13}\text{C}$ ,  $^{14}\text{C}$ , and  $\text{O}_2$  methods for estimating carbon uptake rates in *Zostera marina* (modified from Mateo et al., 2002).

Recent advances in both mass spectrometric analyses of stable isotopes and chlorophyll fluorescence measurements have presented some promising opportunities for seagrass biologists. Direct measurement of carbon uptake by seagrasses and other large

macrophytes has always proved difficult, using  $^{14}\text{C}$  uptake methods, due to expense and hazards associated with its use and disposal. However, both Mateo et al. (2001) and Miller and Dunton (2003) have recently demonstrated the application of  $^{13}\text{C}$  to

measurement of carbon uptake rates in both seagrasses, and large macroalgae (kelp), respectively (Fig. 1). Challenges with the  $^{13}\text{C}$  method include access to an isotope ratio mass spectrometer (IRMS), accurate knowledge of the  $\delta^{13}\text{C}$  ratio of the dissolved inorganic carbon (DIC) pool, and the labor associated with sample preparation. Despite these limitations, isotopic labels of  $^{13}\text{C}$  and  $^{15}\text{N}$  can provide substantial insights to critical processes affecting seagrass productivity including carbon and nitrogen cycling and storage, epiphytic effects on seagrass photosynthesis, and carbon translocation within various tissue compartments.

Pulse-amplitude modulated (PAM) fluorescence has been used to examine seagrass photosynthetic characteristics (Ralph et al., 1998; Beer and Bjork, 2000; Durako and Kunzleman, 2002; Larkum et al., Chapter 14). Currently, PAM fluorescence not only measures leaf photosynthetic potential ( $F_v/F_m$ ), but provides a non-invasive opportunity to assess photosynthetic electron transport (approx. equivalent to gross photosynthesis). Although PAM fluorescence facilitates photosynthetic response determinations, the method does not allow linkage between photosynthetic electron transport rates and net productivity, because respiratory rates are not measured. Consequently, PAM fluorescence has been limited in its application to primary productivity measurements, and awaits further development of reliable  $P/R$  ratios.

#### *D. Light and Carbon Metabolism in Seagrasses: Whole Plant Models*

Seagrass distribution and productivity are largely regulated by variations in light attenuation through the water column (Fig. 2). This is especially true in coastal regions, where declines in water quality from human encroachment have caused worldwide losses of seagrasses (Dennison et al., 1993; Walker et al., Chapter 23). Decreased water transparency from river discharge, devegetation (causing higher resuspension of sediments), dredging activities, excess phosphorus and nitrogen loading, which promotes pelagic, epiphytic, and benthic algal blooms, etc., reduces light availability for photosynthesis, ultimately causing significant loss of productivity and biomass as plants retreat from deeper waters (Onuf, 1994; Hauxwell et al., 2003; see Walker et al., Chapter 23).

Negative effects of nutrient enrichment on submerged aquatic vegetation in eutrophic systems through algal overgrowth have been widely observed (Duarte, 1995). However, a recent study by Heck et al. (2000) contradicted this accepted notion. Based on well-designed field experiments that combined the effects of top predators and nutrient additions in a *Thalassia testudinum* community, Heck et al. (2000) found that nutrient enrichment had no significant effect on epiphyte biomass or *T. testudinum* productivity (see also Heck and Orth, Chapter 22). Instead, Heck et al. (2000) determined that the manipulation of top predators in the system resulted in the most significant effects on epiphyte biomass and seagrass productivity, complicating the simple paradigm between nutrient enrichment, light alteration, and seagrass productivity proposed by Duarte (1995). This example suggests that the paradigm of eutrophication always having negative effects needs to be closely scrutinized (see also Marbà et al., Chapter 6).

The critical role of below-ground tissues as carbohydrate storage organs, sinks for photosynthetically evolved oxygen and osmoregulation sites was summarized by Touchette and Burkholder (2000). The below-ground tissues of seagrasses are often a major component of the total biomass and serve as a photosynthetic reservoir that supports growth and maintenance of other tissues during periods of low photosynthetic production (Pirc, 1989; Burke et al., 1996; Alcoverro et al., 2001) and also  $\text{CO}_2$  generated in the roots and rhizomes may be a significant source of carbon for the leaves (Borum et al., Chapter 10).

Reliable seagrass biomass and productivity models have been generated based on both above- and below-ground tissues and mass carbon balance calculations (Wetzel and Neckles, 1986; Alcoverro et al., 2001; Burd and Dunton, 2001). Zimmerman (2003) (see also Zimmerman, Chapter 13) took another approach and developed a sophisticated model that predicts seagrass canopy photosynthetic performance in response to a variety of variables, including canopy architecture, leaf orientation, and water quality (although the model so far does not incorporate epiphytes). It is apparent that the development of predictive seagrass productivity models requires further research on carbon partitioning among seagrass compartments, especially under light-limited conditions, and long-term in situ measurements of seagrass productivity under recorded light and water quality conditions.

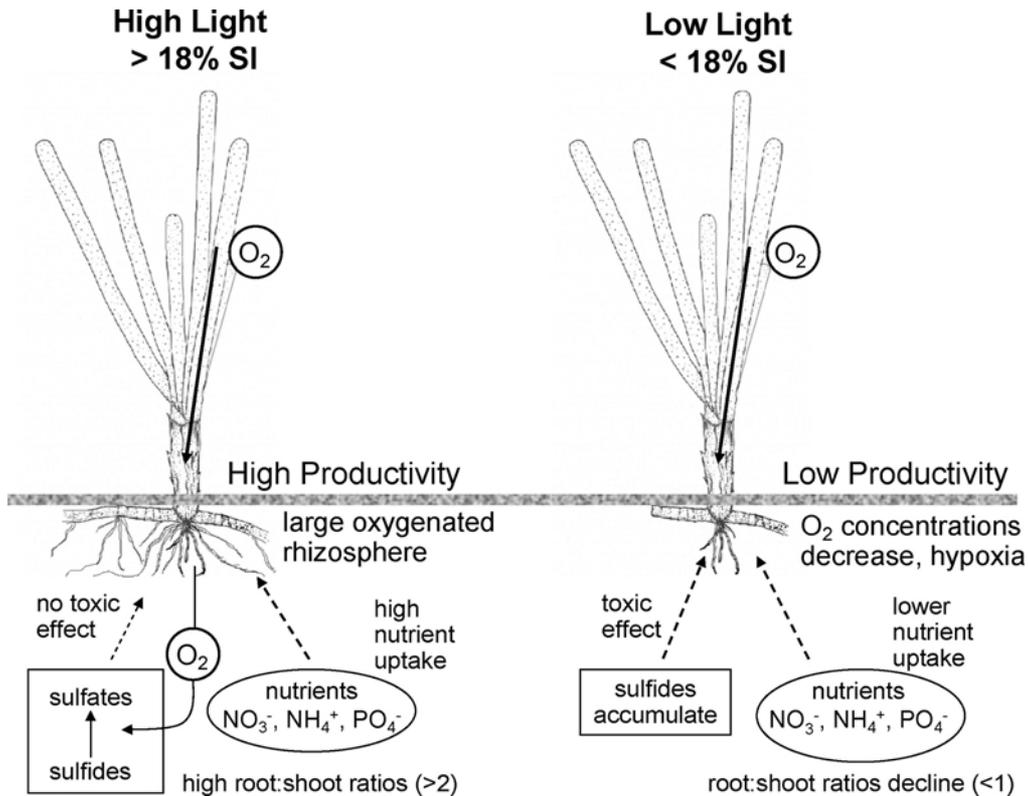


Fig. 2. Effect of light attenuation on seagrass productivity, sediment chemistry, and root:shoot biomass ratios. Photosynthetic oxygen transported into seagrass roots and rhizomes plays a significant role in the maintenance of aerobic conditions in the rhizosphere. Light attenuation that drops the percent surface irradiance (SI) to less than 18% (for seagrasses in the northwestern Gulf of Mexico) produces less oxygen for below-ground tissue respiration, which can result in build-up of sulfides and ammonium, toxic to seagrasses at high concentrations.

### III. The Fate of Seagrass Production

As an essential part of the ecological approach to material cycles in the biosphere, the study of the fate of organic matter is of equal importance to the study of primary production itself. For instance, the amount of seagrass production that is consumed by herbivores and decomposers sets limits to the level of secondary production that can be maintained by the bed (Cebrián and Duarte, 1998). Similarly, the capacity of seagrass beds to act as sinks of organic matter depends on how much production is left over by herbivores and decomposers and subsequently accumulated as refractory matter in the bed (Duarte and Cebrián, 1996; Mateo and Romero, 1997).

The fates that seagrass production may endure are related by the following mass-balance equations:

$$\Delta B_t = \text{NPP} - \text{H} - \text{DP} \quad (1)$$

$$\Delta \text{DM}_t = \text{DP} + \text{I} - \text{D} - \text{E} - \text{RA} \quad (2)$$

where  $\Delta B_t$  (the living compartment) and  $\Delta \text{DM}_t$  (the detrital compartment) are the changes in seagrass biomass and degradable detrital mass per unit time, respectively, and the other terms are NPP—the temporal rates of net primary production, H—herbivory, DP—detrital production, I—import, D—decomposition, E—export, and RA—refractory accumulation. Units for all these fates are usually reported in gDW per square meter per unit time. Equation (1) corresponds to the living compartment, and it states that any temporal change in seagrass biomass corresponds to the difference between production and the loss processes of herbivory and detrital production. Detrital production, in turn, includes wasteful removal by herbivores, exudation of dissolved organic matter, natural mortality through senescence and infectious mortality. Equation (2) corresponds to the detrital compartment, and states that any temporal change in degradable detrital mass is the difference between the gain processes of detrital

production and import and the loss processes of decomposition, export, and refractory accumulation. The following sections contain a selective discussion of the variability, controls, and consequences of the routes listed in Eqs. (1) and (2). The two main objectives of this discussion are to (i) summarize some important patterns in our current knowledge and (ii) identify gaps that merit further research.

## A. Herbivory

### 1. The Extent of Herbivory in Seagrass Beds

Herbivory may vary widely both within and among seagrass species. Some species, such as the mediterranean Neptune grass (*Posidonia oceanica*), tend to have modest levels of herbivory (i.e. <10% of aboveground production consumed by herbivores; Pergent et al., 1994; Cebrián et al., 1996a), although occasionally this species has been shown to support substantial herbivory (Kirkman and Young, 1981; Shepherd, 1987). Other species, such as turtle grass (*T. testudinum*), often support larger levels of consumption, although this may have been more important in pre-columban (ca. 1500 AD) times when abundances of turtles, manatees, dugongs, and other large grazers were high, before the current centuries of heavy human exploitation. Indeed, intense grazing on turtle grass does not seem uncommon (Valentine and Heck, 1991; Heck and Valentine, 1995; Valentine et al., 2000; Valentine and Duffy, Chapter 20). However, even for species that often show large losses to herbivores, the spatial and temporal variability in herbivory within the species can be substantial. For instance, Cebrián and Duarte (1998) compared four turtle grass populations in the Caribbean and found that the percentage of primary production consumed by herbivores ranged between <1 and 30% among the populations. Many other examples of large within-species variability in herbivory exist (Cebrián et al., 1996b; Valentine and Heck, 1999; Valentine et al., 2000).

So what generalities can be made about the magnitude of herbivory for seagrasses? Figure 3A and B includes an extensive compilation of published values of herbivory made for this chapter (data set and further explanations are available at <http://ecosystemslab.disl.org> under 'data sets'). It can be seen that the percentage of above-ground pro-

duction removed by herbivores is skewed to the right, with most populations losing <10% of the above-ground production to herbivores. While herbivory is an inherently variable process, the number of studies reporting modest levels of herbivory largely exceeds those reporting intense herbivory (but see Valentine and Duffy, Chapter 20).

An important difference emerges depending on whether herbivory is regarded as absolute consumption or as the percentage of seagrass production consumed. While the percentage formulation tends to be modest, because of the high levels of above-ground production that seagrasses often reach, the values of absolute consumption tend to be higher and similar to those observed for many other aquatic and terrestrial producers (Cebrián and Duarte, 1994; Cebrián et al., 1998; Cebrián, 1999, 2002).

Thus, in general, seagrasses transfer a significant quantity of biomass to herbivores despite appearing to have only a modest percentage of production removed. This dichotomy suggests two important corollaries. First, it appears that herbivores generally have a limited role in constraining seagrass biomass since they often remove <10% of the plant production. Second, and despite the seemingly modest role of herbivores, seagrasses seem to have the capacity to fuel significant levels of herbivore production in comparison to the levels supported by other aquatic and terrestrial producers. The large variability in herbivory found within and among seagrass species indicates that numerous mechanisms can influence this process. One such mechanism is herbivore abundance. The influence of herbivory abundance has been particularly well demonstrated for sea urchins. Sea urchin densities are often strongly regulated by the intensity of predation on young recruits (Sala, 1997; Sala et al., 1998). Under relaxed predation, sea urchins may become abundant and inflict substantial damage in nearby seagrass beds (Keller, 1983; Larkum and West, 1990; Klumpp et al., 1993; Greenway, 1995; Rose et al., 1999). The increase in sea urchin density may be enormous, leading to population outbreaks and the subsequent decimation of large seagrass areas (Camp et al., 1973; Larkum and West, 1990; Macia and Lirman, 1999; Rose et al., 1999).

Another well-known source of variability is the 'cultivation' feeding pattern that some vertebrate herbivores, such as green turtles (Bjorndal, 1980; Zieman et al., 1984) and dugongs (De Iongh et al., 1995; Preen, 1995) exhibit. These herbivores feed

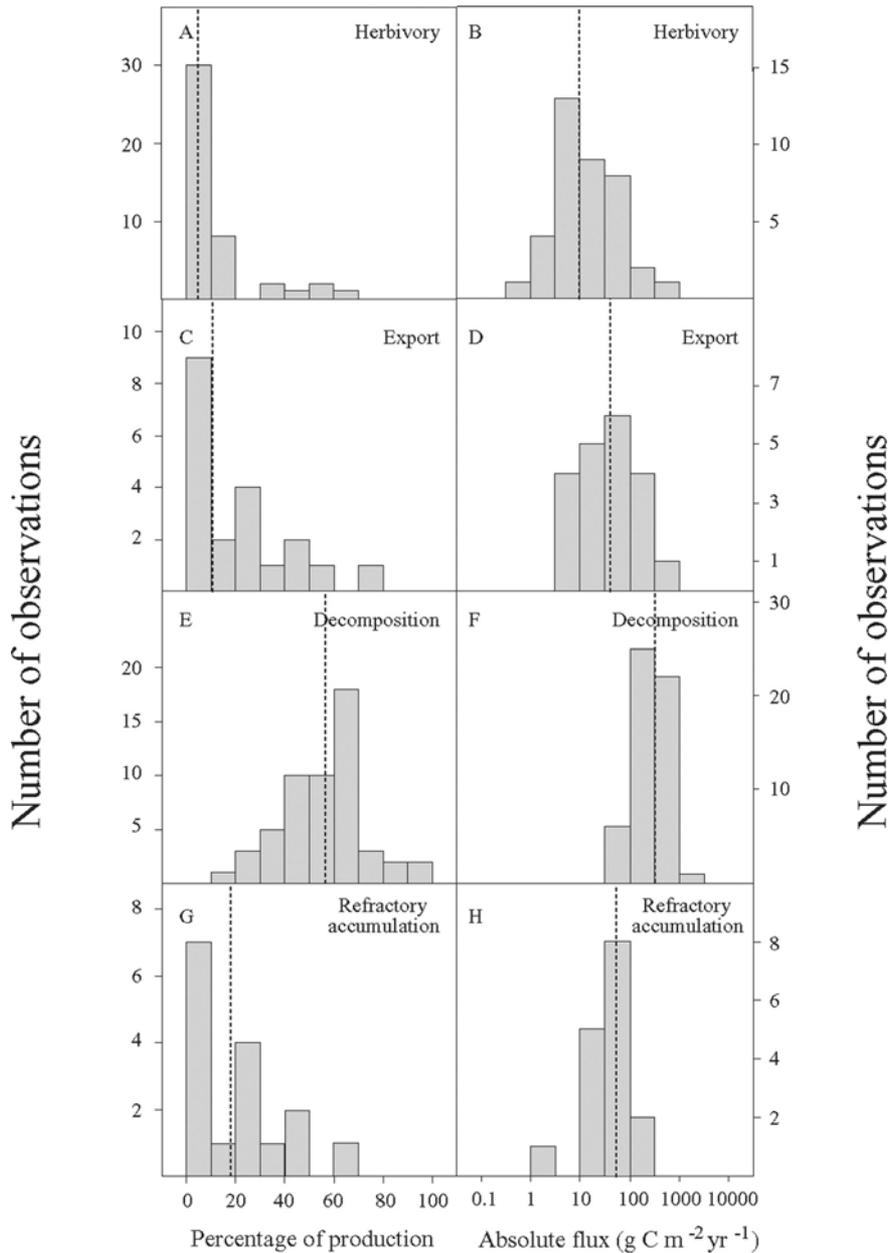


Fig. 3. The histograms of (A) the percentage of seagrass leaf production consumed by herbivores, (B) absolute consumption, (C) the percentage of leaf production exported, (D) absolute leaf litter export, (E) the percentage of total (sum of below- and aboveground) seagrass production decomposed, (F) absolute decomposition, (G) the percentage of total seagrass production accumulated as refractory detritus, and (H) absolute seagrass refractory accumulation. Dashed lines represent the medians.

recurrently on the same seagrass plots for a sustained period of time, thereby keeping the blades tender and young and maximizing the intake of nutrients and energy. After a variable period of time, the herbivores abandon those plots and start ‘cultivating’ new ones.

## 2. The Role of Nutrients in Herbivory

One regulating factor that has received considerable attention is the nutrient content of seagrass leaves with the suggestion by several authors that the extent of herbivory is limited by the nutrient

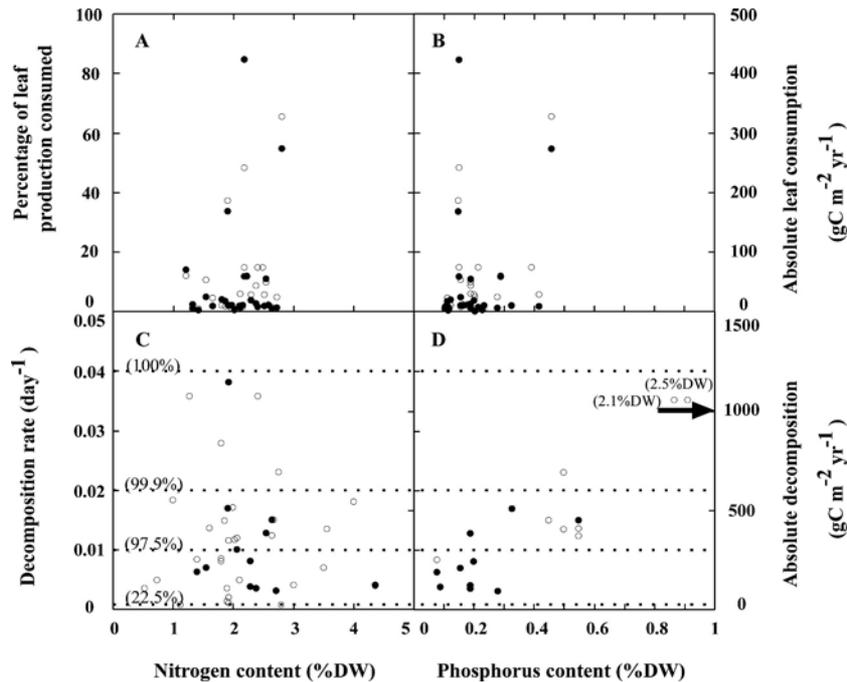


Fig. 4. The relationships between (A) the percentage of leaf production consumed by herbivores and absolute consumption, and leaf nitrogen content; (B) the percentage of leaf production consumed by herbivores and absolute consumption, and leaf phosphorus content; (C) decomposition rates and absolute decomposition, and detritus nitrogen content; (D) decomposition rates and absolute decomposition, and detritus phosphorus content. Open circles correspond to the percentage of leaf production consumed or decomposition rates, and closed circles to absolute consumption or absolute decomposition. The dashed lines in (C) and (D) correspond to the percentage of detritus production decomposed within 1 year for that given decomposition rate, which has been calculated as  $(1 - e^{-k \cdot 365}) \times 100$  and where  $k$  is the given decomposition rate (Olson, 1963). Values in (A) and (B) correspond to leaves, and in (C) and (D) most values correspond to leaves and a few of them to below-ground (rhizomes and roots) organs. The relationships between decomposition rates and nitrogen and phosphorus content are mostly redrawn (i.e. we just include a few more values) from Enriquez et al. (1993), whereas the rest of relationships are original to this contribution. The two points right above the arrow in (D) correspond to the highly questionable values of detritus phosphorus content (in parenthesis) reported by Pellikaan (1984) (see text). Those values are off the scale used in the panel, as is indicated by the arrow.

content of the leaves, with higher nutrient content being conducive to greater herbivory (Bjornald, 1980; Lalli and Parsons, 1993; Duarte, 1995; Valiela, 1995). This contention is primarily based on observations that grazing rates by selective vertebrate herbivores, such as parrotfish, green turtles, and dugongs, are positively correlated to higher nutrient contents (Zieman et al., 1984; Williams, 1988; McGlathery, 1995; Preen, 1995). However, as recent research has shown, greater herbivory pressure is not always associated with higher nutrient contents (see also Valentine and Duffy, Chapter 20). For instance, Cebrián and Duarte (1998) compared several populations of nine seagrass species encompassing a broad latitudinal range and found no significant relationship between herbivory and leaf nitrogen and phosphorus content across species and, with the ex-

ception of *Cymodocea nodosa*, across the populations of any given species, possibly because a substantial fraction of the nutrients may be bound to fibrous compounds (i.e. lignin) and thus indigestible to many herbivores (Thayer et al., 1984; Choat and Clements, 1998). In addition, Valentine and Heck (2001) have shown that the intensity of grazing by the pink sea urchin (*Lytechinus variegatus*) on turtle grass does not increase with leaf nutrient content.

Figure 4 gives values of leaf nutrient content for a subset of the herbivory values. There appears to be very little correlation between leaf nitrogen and phosphorus contents and herbivory, either expressed in absolute terms or as the percentage of production consumed. The correlation coefficients between the percentage consumed and leaf nutrient content ( $R = 0.29$ ,  $p = 0.14$  for nitrogen content

and  $R = 0.37$ ,  $p = 0.05$  for phosphorus content; Fig. 4A and B, respectively) are possibly suggestive, but they do not allow for any robust conclusion. Clearly, more work is needed to understand the existing controversial observations of the association between seagrass leaf nutrient content and the intensity of herbivory. Given the high spatial and temporal variability that herbivory may show in nature (see above), it seems possible that the different spatial and temporal scales covered by these studies confounds any firm conclusion.

An important point to be made is that, of the carbon consumed by herbivores, only a very small fraction will be assimilated and effectively incorporated in the secondary production compartment. For example, it has been shown that the carbon assimilation efficiency of the main grazer of Neptune grass in the Mediterranean, the fish *Sarpa salpa*, is as low as 0.2% (Velimirov, 1984). In fact, it is not uncommon to observe entire, green fragments of Neptune grass leaves (ca. 0.8 cm<sup>2</sup>) being defecated to the bed sediments from schools of this fish (personal observation). For *P. australis* on the East coast of Australia, the value was 3% for the main grazing fish, *Monacanthus chinensis* (Conacher et al., 1979). In tropical seagrass stands, grazing by macro-invertebrates can be substantial. Gammarids of the genus *Ampithoe* in Fiji grazed half the leaf carbon production of *Syringodium isoetifolium*, but assimilated only 10% of it (Mukai and Iijima, 1995). More than half of the carbon grazed was respired and the rest excreted and defecated. Thus, most grazing rates given in the literature may be large overestimates of the actual carbon flux from producers to consumers. A detailed knowledge of assimilation rates for the various herbivores should be acquired and used to correct the fluxes accordingly.

## B. Export

The export of materials from seagrass beds has many important implications for surrounding communities and ecosystems (Romero et al., Chapter 9; Kenworthy et al., Chapter 25; Bell et al., Chapter 26). Since most exported detritus is decomposed in downstream systems (Mann, 1988), the quantity of detritus exported sets the limits to the levels of secondary production that the bed can support beyond its boundaries (i.e. allochthonous secondary production; see Chapters 25 and 26). Since export represents a nutrient loss for the bed, these losses

must be compensated by exogenous nutrient inputs (Duarte and Cebrián, 1996; Mateo and Romero, 1997; Romero et al., Chapter 9).

Despite the importance of export in seagrass-dominated coastal ecosystems, few reports exist on its impact on bed economy. This oversight may be due to three inherent technical difficulties.

First, and most importantly, seagrass beds are often open systems and have widespread exchange with offshore waters, driven by the interaction of several forces, including wind, tides, and waves. This renders measurement of detrital export difficult. Most measurements of detrital export are limited to specialized systems connected to open waters through narrow outlets (e.g. coastal lagoons).

Second, the boundaries of seagrass beds, which define the location at which export measurements are taken, are sometimes difficult to define with certainty, making measurements somewhat arbitrary.

Third, detrital traps used to derive direct estimates of export are difficult to deploy.

These methodological limitations have discouraged researchers from quantifying detrital export from seagrass beds and have resulted in a scarcity of publications on the issue. These problems emphasize the importance of developing alternative methods. Romero et al. (1992) proposed an indirect method: in the hypothetical absence of export, litter stocks in the bed depend on inputs from leaf fall (the main source of variation being depth) and outputs due to remineralization. Leaf fall rates can be estimated as the difference between primary production (using the method described in Zieman, 1974) and biomass increase. Decay rates can be approximated using the classical in situ litter bag incubations. This can be expressed mathematically in order to predict litter accumulation in a given moment and a given place in the bed.

$$L'_i = F_i e^{(-kt/2)} + L_{i-t} e^{(-kt)} \quad (3)$$

where  $L'_i$  is the predicted standing litter at time  $i$ ,  $F_i$  is the weight of leaf fallen between times  $i$  and  $i - 1$ ,  $t$  is the time interval between consecutive samplings,  $k$  is the decay rate for this period and area (e.g. depth), and  $L_{i-t}$  is the standing litter observed in situ at time  $i - t$  (i.e. before the initiation of the period). Knowing the standing litter stock at the end of the

period  $L_i$  (sampled in the field), export ( $E_i$ ) can be calculated as the difference

$$E_i = L'_i - L_i \quad (4)$$

Such an approach entails intensive field effort, requiring estimates of leaf input, litter decay, and litter stocks throughout the year, and it possibly underestimates discontinuous export events. Nevertheless, all the methods required are robust, easy to apply, and integrate changes over long time. Therefore, this should be a useful integrative approach for future studies.

The few reports indicate that export can vary from 0 to 100% of total production (e.g. Bach et al., 1986; Hemminga and Nieuwenhuize, 1990; Stapel et al., 1996; Mateo and Romero, 1997; Ochieng and Erfte-meijer, 1999; Hemminga and Duarte, 2000). This large variability results from the high variability of the intensity of physical energy in the bed, the major driving force (Josselyn et al., 1983; Bach et al., 1986; Fry and Virnstein, 1988; Mateo et al., 2003; Mateo and Rossi, submitted; Section II.A of Koch et al., Chapter 8). Weather, tides, and the degree of bed exposure (i.e. area of open water or fetch and openness to offshore waters) dictate this intensity. The crucial role of physical energy is shown by supralittoral deposits in different ecosystems. The largest accumulations of seagrass leaf litter cast on beaches have been reported in a small Mediterranean exposed bay (Tabarca Island, Alicante, Spain) for the species *P. oceanica* (Mateo et al., 2003; Fig. 5, left and top right); the distribution and height of the deposits ('banquettes') accurately described the water energy reaching the perimeter of the bay, with leaf litter accumulation in amounts from 18 to 500 kg of dry wt.(m shoreline)<sup>-1</sup>, at both ends and in the center of the bay, respectively (see also Kuo and den Hartog, Chapter 3 for *P. australis* examples). The authors estimated for the *P. oceanica* example that the total supralittoral deposits represented 50.7, 71.0, 27.2, and 8.7% of the annual bed dry weight, carbon, nitrogen, and phosphorus production, respectively. They concluded, however, that the deposits were only temporary sinks because the accumulated material can eventually return to the water (Fig. 6). At the other extreme, export figures for *C. nodosa* leaf litter in a semi-enclosed estuarine bay (Alfacs, Tarragona, Spain) were found to be almost negligible due to the rapid wave energy dissipation against the embayment shore (the relative proportions be-

ing 0.26, 0.27, 0.27, and 0.16% of the annual bed dry weight, carbon, nitrogen, and phosphorus production, respectively; Mateo and Rossi, submitted). Some seagrass species have long, bulky leaves that sink soon after shedding, whereas others produce light, thin leaves that can float for long periods before sinking and are thus, more likely to be exported. Zieman et al. (1979) provided the first example of the importance of leaf buoyancy. They compared adjacent beds of the relatively broad-leaved turtle grass (*T. testudinum*) with beds of the thin-leaved manatee grass (*Syringodium filiforme*), and showed that, whereas turtle grass exported 1% of its leaf production, manatee grass exported 75%.

Export of below-ground parts is rarer and only strong storms can carry significant amounts out of the bed or throw them onto the beach (Bach et al., 1986; Fig. 5, bottom right).

In many temperate systems, autumn is characterized by high absolute amounts of litter export because many seagrass species shed most of their leaf biomass at this time (Cebrián et al., 1997; Mateo and Romero, 1997; Hauxwell et al., 2003). Accordingly, Bach et al. (1986) surveyed leaf export from an eelgrass bed in Phillips Island (NC, USA) monthly over 1 year and found the greatest levels of absolute export in late August, which was also the period of maximum leaf shedding. However, ecologically meaningful export rates are those relative to detritus production or to plant requirements. In a seasonal study of leaf litter export in a *P. oceanica* bed, Mateo and Romero (1997) found that the highest export losses relative to detritus production occurred from February–May although maximal litter stocks were recorded during July–October.

The nutritional quality of seagrass leaf litter is often strongly correlated with decomposition rates, which in turn influence export (Mateo and Romero, 1997; Pérez et al., 2001). Thus, seagrass leaf litter nitrogen content is often positively correlated with decomposition rates although contradictory results abound (see Section III.C): if decomposition is slow there is the greater likelihood of export or burial (see Section IV.B.1). Two *P. oceanica* beds, one off Medes Islands (NW Mediterranean, Spain) and another off the Island of Ischia (Naples, Italy), both located in open areas and at similar latitudes, had a three-fold difference in export rates (higher at Ischia). The effect of waves and currents affecting both beds seemed to be different, and the different export rates were most probably associated



Fig. 5. Supra-littoral deposits of *Posidonia oceanica*. Left: Old 'banquettes' of *P. oceanica* leaf litter along the coast of Nueva Tabarca Island (Alicante, Spain). The banquettes shown are ca. 1.5 m high (photograph by J. L. Sánchez-Lizaso). Top right: Recently formed banquettes 0.5 m high from Corsica, France (photograph by M. Manzanera). Bottom right: Beach-cast detritus from *P. oceanica* below-ground organs. Rhizomes and a sheath-derived aegagropile can be distinguished (photograph by M. Manzanera).

with the different nutrient content of the leaf litter (Table 2). Nitrogen and phosphorus contents of the coarse leaf litter in Ischia were on average 0.42 and 0.039%, respectively. Equivalent figures for Medes were 1.24 and 0.067%, respectively, which are 3.0 and 1.7 times higher than those at Ischia, suggesting that leaf litter 'palatability' may be an important factor governing export rates in seagrass beds.

In comparing nutrient-rich and nutrient-poor *C. nodosa* stands growing in a semi-enclosed bay (Alfacs, Ebro River estuary, Spain), Pérez et al. (2001) obtained differences in export rates that largely support the previous contention (Table 2). Around 53% of the total annual production of plant biomass was exported in poor stands, while in rich stands this value was 3.4 times lower (15.5%). Nutrient losses were much higher in nutrient-poor stands when compared to plant nutrient requirements (Table 2).

The large variability found in the percentage of leaf production exported suggests that seagrass beds may also vary widely in their levels of dependence on imported nutrients, from negligible (i.e. beds that

export <10% of leaf production) to high (i.e. beds that export >80% of leaf production) levels. On the other hand, when export is regarded as an absolute flux (Fig. 3D), another important corollary arises: in spite of substantial variability, most values of absolute export tend to be large when compared with the amount of seagrass biomass that is consumed by herbivores (Fig. 3B).

### C. Decomposition

Decomposition in situ seems to be the most probable fate for seagrass leaf detritus (Fig. 3E and F) and even more so for below-ground production. Seagrass rhizomes and roots are consumed by few herbivores (Valentine and Heck, 1999) due to the compactness of the tangled web that these organs form and because they are usually buried (particularly in large bodied species) (but see Valentine and Duffy, Chapter 20) for another viewpoint on the recent geological past and evolutionary considerations). As a consequence, in the absence of sirenians, etc, most

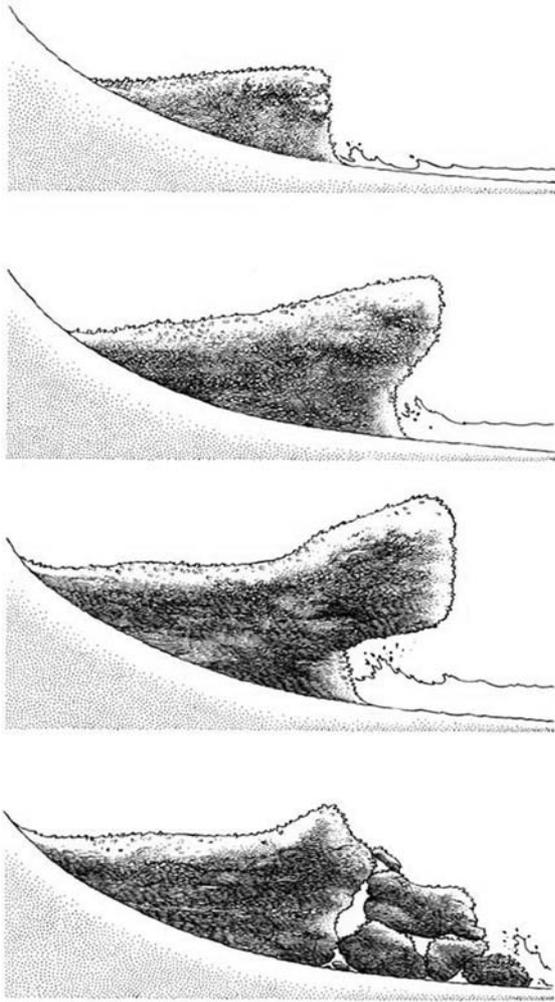


Fig. 6. Formation and destruction of *Posidonia oceanica* 'banquettes' in the Mediterranean Sea. Leaf litter accumulates on the shore by the action of strong waves forming deposits more than 2 m high. Once the maximum height has been attained, moderate wave action erodes the base of the banquette that partially collapses, returning material to the water (from Mateo et al., 2003).

below-ground production becomes detritus and decomposes within the bed, with a usually modest fraction being accumulated as refractory material (see section IV.B).

In general, the total (the sum of above- and below-ground) seagrass production that is decomposed in situ is large. The absolute amount of seagrass detritus transferred to decomposers and detritivores tends to be much larger than for many other aquatic and terrestrial producers (Cebrián, 1999, 2002). These patterns suggest two important corollaries. First, assuming that seagrass production is in steady-state

(i.e. no noticeable changes across years), these results suggest that most seagrass production is supported through internal nutrient recycling. Second, seagrass beds seem to maintain high levels of secondary production by microbial decomposers and invertebrate detritivores. Thus, the abundant faunal populations that are normally associated with seagrass beds are supported mainly through the detritus-based food chain (see Section II.D.1); notice, however, that this neglects herbivory on algal epiphytes and benthic micro- and macroalgae, rich sources of food for fish in their nursery stages (see below and Borowitzka et al., Chapter 19; Valentine and Duffy, Chapter 20; and Gillanders, Chapter 21).

Seagrass decomposition can be highly variable, accounting for 15–95% of plant production (Fig. 3E) and the absolute flux to decomposers varies from 55 to 1150 gC m<sup>-2</sup> year<sup>-1</sup> (Fig. 3F). Harrison (1989) examined the extent of decomposition variability within and among seagrass species and discussed some factors responsible for that variability. His analyses pointed to three major factors (see next sections).

### 1. Environmental Physical Conditions

Water temperature, sediment oxygen content, water nutrient content, and desiccation are important in decomposition. Harrison, however, gathered conflicting results as to the explicit effect of each of those physical conditions. Water temperature, contrary to what models of microbial metabolism predicted (Melillo et al., 1984), did not always stimulate decomposition rates of seagrass detritus (Walker and McComb, 1985). Some workers found higher seagrass degradation rates under anaerobic conditions (Pellikaan, 1984; Josselyn et al., 1986), consistent with the belief that most cellulose-degrading bacteria are anaerobic (Kenworthy and Thayer, 1984; Roth and Hayasaka, 1984), but contrary results have also been found (Godshalk and Wetzel, 1978; Pellikaan, 1984). Water nutrient content is important because the activity of decomposers is frequently limited by nutrient availability (Melillo et al., 1984), but again, higher nutrient concentrations in the water column did not always enhance degradation (Harrison and Mann, 1975; Fenchel and Harrison, 1976). Available reports on the effect of desiccation on the decomposition of seagrass detritus also showed discrepancies (Harrison and Mann, 1975; Zieman, 1975; Josselyn and Mathieson, 1980).

*Table 2.* Leaf litter nutrient content and biomass, and export of carbon, nitrogen, and phosphorus in nutrient-rich and nutrient-poor *Posidonia oceanica* and *Cymodocea nodosa* meadows. Export % is referred to annual leaf-blade production. Nutrient content % expressed on a dry weight basis. Values for Ischia Island (Naples, Italy) calculated from Romero et al. (1992); Values for Medes calculated from Mateo and Romero (1997). Values for Alfacs Bay (Ebre River estuary, Spain), calculated using data from Pérez and Camp (1986), Pérez and Romero (1994), and Pérez et al. (2001). Values have been rounded for the sake of clarity.

Species	Location	Nutrient content (%)		Decay rate (day <sup>-1</sup> )	Export (%)				Depth (m)
		N	P		DW	C	N	P	
<i>Posidonia oceanica</i>	Ischia	0.4	0.04	0.009	60	56	30	21	1–30
	Medes	1.1	0.07	0.022	10	6	6	4	5–15
<i>Cymodocea nodosa</i>	Alfacs-poor	2.0	0.05	0.009	53	50	42	21	0.5–1
	Alfacs-rich	2.5	0.15	0.015	16	15	15	20	0.5–1

## 2. Nutrient Content of Detritus

From the foregoing, it would be expected that detritus with higher nutrient contents would decompose faster. That hypothesis had been supported for certain types of producers, such as shrubs and trees (Melillo et al., 1982) and marsh plants (Valiela et al., 1984). However, Harrison's attempt to generalize as to whether seagrass detritus with higher nutrient concentrations decomposes faster yielded contradictory results. When comparing four reports on eelgrass, he found a significant correlation between faster decomposition rates and higher nitrogen content in leaf detritus; however, when studying four reports on turtle grass the correlation was not significant. Later, Enríquez et al. (1993) compiled a larger data set including several seagrass species and tested whether higher nutrient concentrations in the detritus were associated with faster decomposition rates across the species gathered. For 24 records encompassing six seagrass species (*Thalassia hemprichii*, *T. testudinum*, *P. oceanica*, *Zostera marina*, *Z. noltii*, and *Syringodium filliforme*), no significant correlation between faster decomposition rates and higher nitrogen content was found (Fig. 4C), but for seven records encompassing three species, they found a strong correlation between faster decomposition rates and higher phosphorus content (Fig. 4D). That strong correlation, however, was entirely driven by two anomalously high values of phosphorus content reported by Pellikaan (1984; see Fig. 4D). When those two anomalous values were eliminated, the relationship between decomposition rates and detritus phosphorus content became non-significant (Pearson correlation coefficient = 0.68,  $P = 0.09$ ).

More recently, Mateo and Romero (1996) reported the results of several in situ litter bag experiments on a seasonal basis using two clearly different types of material in terms of nutrient quality, senescent and detrital *P. oceanica* leaves. The first type was 1.5 and 1.2 times richer in nitrogen and phosphorus, respectively, than the latter. For all seasons, senescent leaves decomposed faster than leaf litter (15% faster on average). In this case, a multiple variance analysis confirmed a highly significant effect of nutrient content in decay rates either in field or in laboratory incubations.

## 3. The Methodological Approach Used

It is obvious, as already noticed by Harrison (1989), that the type of material selected for litter bag experiments (senescent, detrital, entire, fragmented, fresh, frozen, with or without epiphytes, etc.) may strongly affect the decay rates to be obtained. Also, he noted that the length of detritus incubation was one of the most important methodological differences among existing reports. Detritus decay normally follows a decreasing exponential pattern that comprises leaching, decomposition, and slow breakdown of refractory phases (Olson, 1963; Valiela, 1995). Thus, the length of the incubation period can greatly affect the pattern obtained if it is not long enough to capture the three phases. Another important methodological disparity among studies was whether the incubation was done in field or laboratory conditions and, if done in the field, the pore size of the litter bags employed (Fig. 7, top left). Mateo and Romero (1996) evaluated in detail the extent of error attributable to particle losses

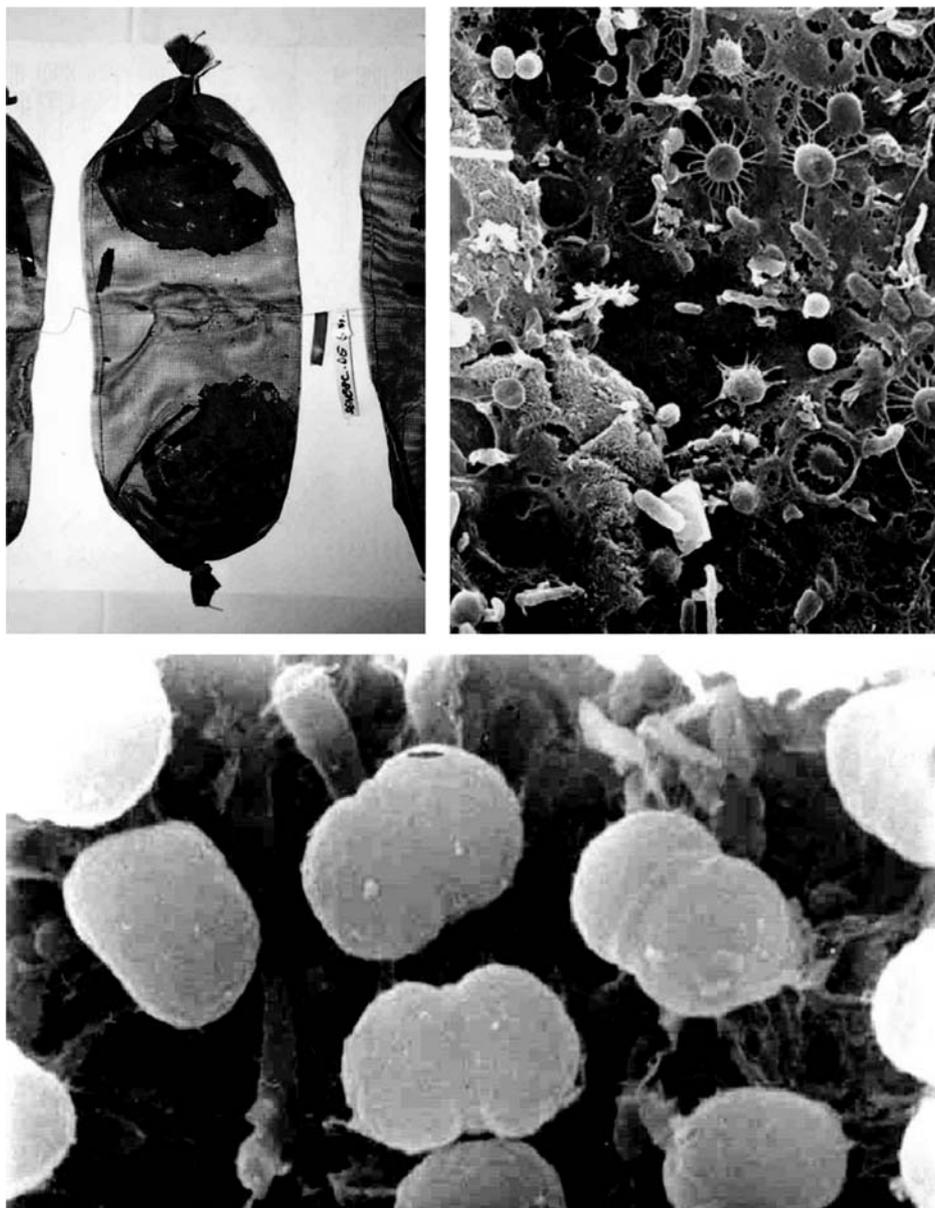


Fig. 7. Seagrass leaf litter decomposition. Top left: Typical litter bags used in the classical experiments for determining seagrass leaf litter in situ decay rates. The mesh size of the bags, as in the image, is usually 1 mm. The bags in the picture contain *Posidonia oceanica* senescent leaf litter. Top right: Round-shaped bacteria growing on *P. oceanica* leaf litter adhering by extracellular polymers. Bottom: Bacteria dividing on *P. oceanica* leaf litter (photographs by M. A. Mateo).

through the bag pores in *P. oceanica*. When comparing the results from both methods on a carbon basis, it was found that only 40% of the weight lost from the bags was actually attributable to micro-decomposer activity (Figs. 7 right and bottom and 8) and the rest would seem to have been lost through the bag pores. This conclusion, however, has to be

taken with caution because of the well-known limitations of microcosm experiments. However, it is also possible that respiration rates in situ may have been much higher owing to a higher water nutrient renewal.

Despite the fact that decay rate estimates using litter bags are not the most adequate for ecosystem

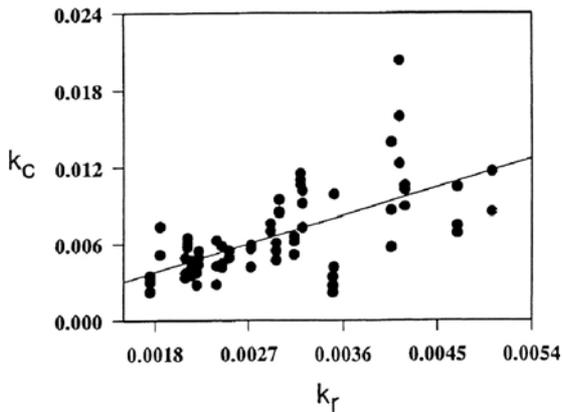


Fig. 8. Relationship between rates of carbon loss during *Posidonia oceanica* leaf litter decomposition using in situ litter bags ( $k_c$ ) and litter respiration ( $k_r$ ) methods ( $k_c = 2.46 \cdot k_r - 0.0006$ ;  $r = 0.63$ ; from Mateo and Romero, 1996).

budget studies, they have been kept for comparative purposes because of their methodological simplicity and the valuable amount of historical and recent data available in the literature derived from this approach (Short and Coles, 2001).

The work showing the prevalence of decomposition over herbivory in seagrass beds, has been the basis since the 1960s for the view that high secondary production fueled a detrital pathway using seagrass-derived carbon. Later tests, particularly using stable isotopic tracers in food web studies, have revealed that this old assumption appears to be unfounded in a growing number of cases as discussed in the following section.

#### D. Seagrass Food Web Studies: The Stable Isotope Approach

##### 1. Algal vs. Seagrass Carbon Source

Stable isotope analyses have proved increasingly valuable for the study of trophic interactions within seagrass ecosystems over the past 30 years. The premise underlying their use is that the isotopic composition of an organism will reflect the composition of its food source(s) (after accounting for fractionation). Based on this simple relationship, stable isotope studies have been conducted to identify primary trophic pathways within seagrass systems from the  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{34}\text{S}$  signatures of the resident organisms. Fry et al. (1987) reviewed stable isotopic

investigations in seagrass systems and recognized that ambiguities of the  $\delta^{13}\text{C}$  method could often be resolved by also using nitrogen and sulfur isotopic values. In particular, it was noted that benthic (i.e. epiphytic and sediment-associated) microalgae can have carbon isotopic values similar to those of seagrass, making it difficult to assess the relative contribution of these primary producers to carbon flow through the food web. At the same time, the relative contribution of algal and seagrass organic matter to food webs differs among seagrass systems. While seagrass detritus is the dominant source of carbon in some systems, benthic and microalgal carbon dominates others.

Since Fry et al. (1987), researchers have attempted to address some of the problems inherent in stable isotope studies. Recently, Connolly et al. (2004) highlighted the effectiveness of sulfur isotopes to distinguish primary producers with similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. As such, it appears that concurrent analysis of carbon, nitrogen, and sulfur may maximize the utility of the stable isotope approach. Indeed, Moncreiff and Sullivan (2001) used stable carbon, nitrogen, and sulfur isotopic composition to trace the flow of organic matter through *Halodule wrightii* beds of Mississippi Sound, USA, and showed that benthic microalgae were the primary food source in these seagrass beds. These and other stable isotope studies conducted over the past decade have resulted in a paradigm shift in our view of seagrass trophic dynamics, from one where seagrasses were thought to be the most important material for secondary production to one in which the benthic microalgae are the major source of organic matter to higher trophic levels in seagrass food webs (Kenworthy et al., 1987; Dauby, 1989, 1995; Loneragan et al., 1997; Yamamuro, 1999; Lepoint et al., 2000).

One important advance in this direction was that achieved by Boschker et al. (1999, 2000). In an attempt to study carbon sources for bacteria they labeled, branched polar lipid-derived fatty acids (PLFAs) of bacteria to study the role of *Z. marina* carbon in several European beds. If bacterial PLFA carbon were obtained from seagrass detrital carbon, carbon isotopic ratios ( $\delta^{13}\text{C}$ ) of both materials should be similar. Instead,  $\delta^{13}\text{C}$  values of bacterial PLFA fell between those of *Z. marina* (leaves or roots) and sediment organic matter (Fig. 9), suggesting that bacteria used a combination of both sources of carbon. However, the authors also observed that bacteria from nearby barren areas and from laboratory

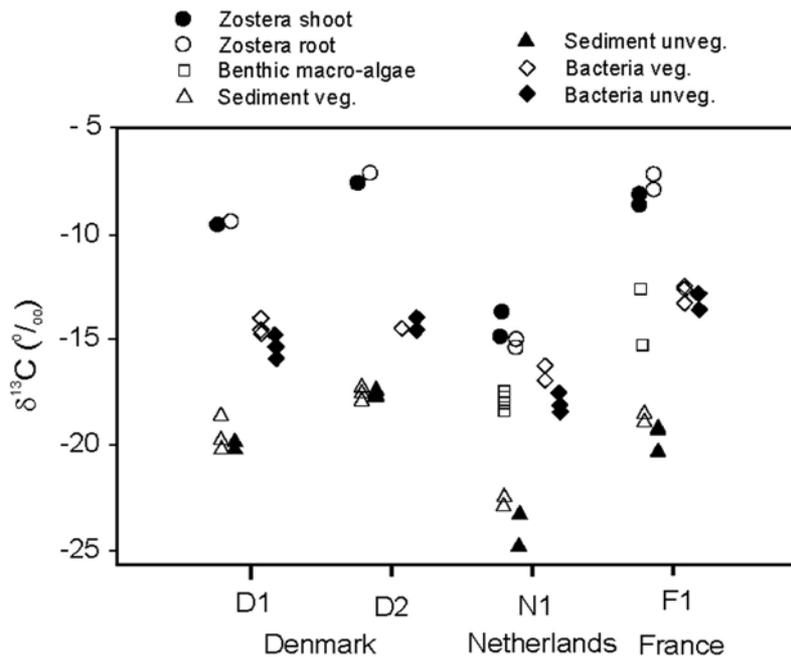


Fig. 9. Stable isotopes approach to assess the possible sources of bacterial carbon in *Zostera marina* and unvegetated sediments. Stable carbon isotope ratios in bacteria were determined in specific bacterial polar lipid-derived fatty acids (PLFAs) using specific-compound isotopic ratio mass spectrometry. D1, D2, N1, and F1 correspond to different study sites in Denmark, The Netherlands, and France, respectively (redrawn from Boschker et al., 2000).

sediment incubations had similar  $\delta^{13}\text{C}$  values to those in vegetated areas. This paradox was resolved by comparing isotope ratios of benthic microalgae and bacterial biomarkers: the two being highly correlated, with the conclusion that autochthonous benthic microalgal production accounts for the abundant secondary production in these *Z. marina* beds.

Such a conclusion seems consistent with the scenarios shown in Section II.A, where seagrasses were not the dominant producers in the system (as also seen in Section II.B). Other studies have also provided evidence that seagrass contribution of organic carbon to bed sediments is only around 25–30% of the total (Simenstad and Wissmar, 1985; Dauby, 1989; Hemminga et al., 1994; Fourqurean et al., 1997; Gacia et al., 2002).

Although the relative contribution of carbon by seagrasses is lower than initially assumed, intuitively it seems that it should be substantial enough to be reflected in bacterial carbon. In another study of stable isotope ratios in PLFAs of sedimentary bacteria, Jones et al. (2003) found that the majority of sedimentary organic carbon originated from *T. testudinum* shoots and that there is tight coupling of the sedimentary bacteria and seagrass-derived or-

ganic matter. The contrasting results of Jones et al. (2003) and Boschker et al. (2000) leads one to think that there may be strong variability owing to various environmental and biological factors, as follows:

- i. *Seasonality*. First, it has to be born in mind that the measurements made by Boschker et al. (2000), correspond to single sampling events. As discussed earlier, seagrass production and, therefore, detritus inputs to the sediments is seasonal and in temperate seas, with maximum production rates in summer and minimum rates in late autumn and winter (e.g. Alcoverro et al., 1998, 2001). Accordingly, leaf litter stocks in the sediment are maximum in autumn (right after leaf abscission) and minimum in early summer (Mateo and Romero 1997; see more details in Section IV.A). Thus, in autumn large inputs of fresh seagrass leaf litter may constitute the main carbon source for bacterial activity.
- ii. *Export*. In Section III.B, export has been discussed in detail. Depending on seasonality, basin morphology, bed depth, hydrodynamic forces, leaf buoyancy capacity, and leaf nutrient content export can be negligible or account for the

transport of virtually the entire seagrass production out of the bed.

- iii. *Low palatability of seagrass carbon.* Lower mineralization rates are shown by microbes on seagrass detritus than on macro- and microalgal detritus and this might explain why it has been observed that seagrass carbon is not the dominant carbon source for bacterial metabolism. On the other hand, Del Giorgio and Cole (1998) found that bacterial growth efficiencies were similar for macrophyte and microalgal material.
- iv. *Redox conditions in sediments.* Oxygen transport from seagrass leaves to the rhizosphere oxidizes the upper few centimeters of the seagrass sediments (Figs. 2 and 10; see also Marbà et al., Chapter 6 and Borum et al., Chapter 10). Unless actively bioturbated, sediments receiving significant loads of organic matter tend to be highly reducing from the uppermost layer. Oxidizing conditions can promote rapid and dominant aerobic decomposition of fresh labile carbon (oxygen sensitive material, Hulthe et al., 1998; Kristensen, 2000). The consequence of this can be that highly palatable algal detritus is always attacked preferentially by bacteria, while seagrass detritus persists for a longer time, making it more susceptible to export or burial.
- v. *Enhanced microalgal carbon sedimentation.* While seagrass leaf litter is easily exported from the originating bed, the seagrass canopies enhance microalgal carbon sedimentation from the overlying water column by reducing flow over the bed (Gambi et al., 1990; Gacia and Duarte, 2001). This augments the labile carbon supply to the sediment.

In conclusion, the algal-based detrital pathway could be a major mechanism for carbon and energy transfer to upper trophic levels in seagrass-dominated ecosystems. Seasonal studies identifying the source of bacterial carbon are needed in order to provide a robust annual estimate of the relative contributions of the various sources of carbon. Such studies should be complemented with other studies focusing on the dynamics of the bacterial populations associated to the decomposing material. Estimates of bacterial activity and production would help to support the hypothesis of seagrass-dominated ecosystem being fueled via the detrital pathway (see discussions in Kenworthy et al., 1987 and in Velimirov and Walenta-Simon, 1993; Fig. 7, bottom).

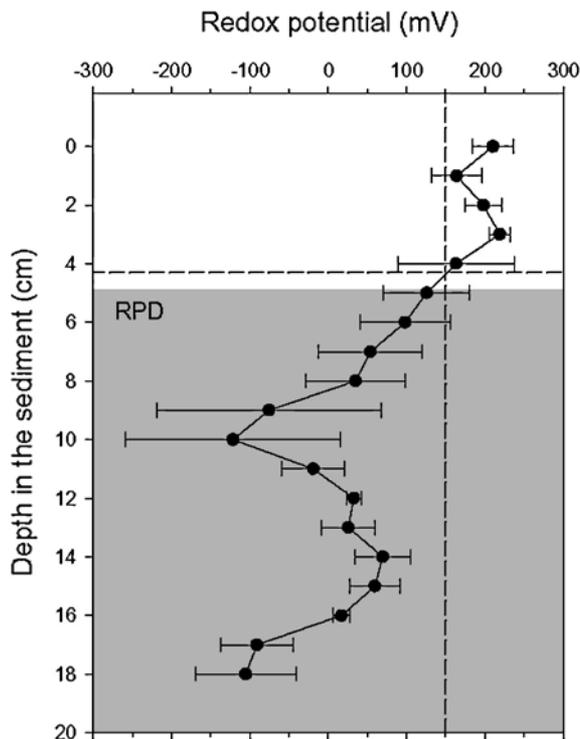


Fig. 10. Sediment average redox potential measured in a *Posidonia oceanica* meadow off Medes Islands (NW Mediterranean, Spain). The dashed lines cross to show the depth in the sediment where a redox potential of 150 mV is attained. The shaded area starts at the redox potential discontinuity (RPD). Error bars represent the standard error of the mean of six redox profiles (redrawn from Mateo, submitted).

## 2. Nutrients and Food Web Dynamics: Isotope Addition Experiments

Stable isotope studies have identified the benthic algae as the primary carbon source in some seagrass systems. However, it is still not known what factors determine the relative importance of phytoplankton, seagrass, and benthic micro- and macroalgal production in trophic dynamics. Fry et al. (1987) hypothesized that nutrient availability may determine which primary producers supply the bulk of the organic matter to food webs, suggesting that, under eutrophic conditions, ample nutrients would foster extensive growth by the benthic microalgae and phytoplankton, leading to a food web driven by algal production. This prediction is supported by the responses of some primary producer to elevated nutrients (Short and Burdick, 1996; see also Walker et al., Chapter 23 and Ralph et al., Chapter 24). However, in view our lack of understanding of mechanisms

that affect food web dynamics and the current threat of eutrophication to seagrass systems, it is essential that the much more thorough investigations be carried out.

The role of nutrients is also important because, with eutrophication, the growth of epiphytes and phytoplankton are favored at the expense of seagrass production, typically resulting in the loss of seagrass cover at high nutrient inputs when phytoplankton and epiphytes shade out seagrass systems (Kemp et al., 1983; Borum, 1985). However, the effects of nutrients on epiphytes and phytoplankton are complex (see Borowitzka et al., Chapter 19 and Walker et al., Chapter 23). Analyzing the isotopic compositions of seagrass residents under various nutrient regimes may permit identification of differences in the flow of N and C through the food web, as changes in the nutrient dynamics may be expected to cause shifts in the relative contribution of organic matter by various primary producers to higher trophic levels. The isotope addition experiments magnify differences in the isotopic composition among producers and allow better resolution of C and N flows from primary producers to consumers (Peterson et al., 1985, 1993). Employing an experimental manipulation to generate distinct  $\delta^{15}\text{N}$  values for seagrass and its epiphytes, Winning et al. (1999) were the first to use isotope additions. By adding  $^{15}\text{N}$ -enriched potassium nitrate to mesocosms containing *Z. marina* and its epiphytes, they were able to produce significantly changed  $\delta^{15}\text{N}$  values for these two primary producers. This demonstrated the potential of manipulating isotope values in the field to resolve trophic relationships and such an approach can actually solve another serious problem that limits the use of  $\delta^{15}\text{N}$  as a tracer of organic matter through simplified food webs in mesocosm studies (see next three paragraphs).

Fry et al. (1987) observed that the sulfur and carbon isotopic compositions for consumers and their diets were similar, but the  $\delta^{15}\text{N}$  values of consumers were on average 3.2‰ greater than that of their diet (as a consequence of excretion of  $^{15}\text{N}$ -depleted nitrogen). In many subsequent studies, this average value was subtracted from consumers to infer potential diets; however, this practice is ill advised as the range of variation is very wide (from 0 to 6‰; Fry et al., 1987). While it is tempting to simplify, a careful study of seagrass associated food webs based on stable isotopes requires detailed knowledge of (i) fractionation phenomena associated with metabolic

assimilation, (ii) seasonal variability in isotopic ratios, and (iii) variability in isotopic ratios between plant parts (see Vizzini et al., 2003 for the two last items).

Mutchler et al. (2004) have developed a field methodology for the isotope addition experiments, based on the mesocosm work of Winning et al. (1999). In these experiments,  $^{14}\text{N}$ -labeled (i.e.  $^{15}\text{N}$  depleted), slow-release fertilizer is used to both simulate eutrophication and generate differential isotopic compositions of *H. wrightii* and its epiphytes. After only 20 days of exposure to water column enrichment, the  $\delta^{15}\text{N}$  values of the epiphytes were significantly different from those of the seagrass (−78‰ vs. −31‰, respectively, Fig. 11).

Although this methodology was developed to address food web dynamics under eutrophic conditions, the approach could easily be modified to generate isotopic tracers under ambient nutrient conditions. By actively ‘labeling’ organisms within seagrass beds, one can trace not only the flow of organic matter to higher trophic levels, but through creative isotope additions, investigate the degree of movement of ‘labeled’ organisms and assess the extent to which these organisms facilitate the retention or export of organic matter within and between seagrass beds and other habitats.

### 3. Partitioning of Ecosystem Autotrophic Components

There are a number of components of the seagrass food web that are often overlooked. For example, the extent to which food webs depend on locally-derived food resources vs. more transient planktonic resources needs to be quantified. Although locally-generated production is high in seagrass systems, organic matter flux through the planktonic and filter-feeding pathways may be significant as well. At another level, the relative contribution of the resident producers must be better understood. Until recently, the role of the sediment microalgae has been largely neglected (Fry et al., 1987), despite the fact that sediments within and between seagrass beds constitute a large area in the seagrass landscape (see Bell et al., Chapter 26). Broadly, the contribution of sediment microalgae within seagrass beds (~18–35%) (see also Sections II.B and II.D.1) may be as great or greater than the contribution by the seagrass (~24%), epiphytes (~21%), and phytoplankton

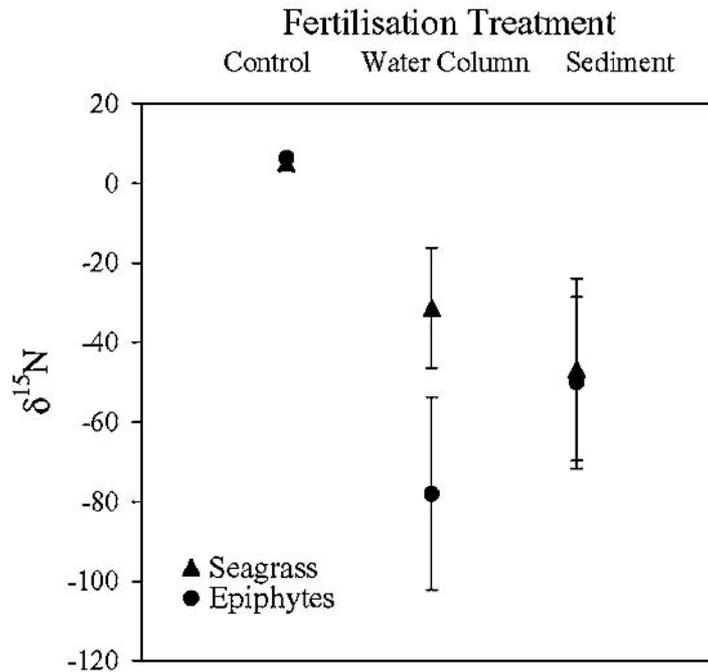


Fig. 11.  $\delta^{15}\text{N}$  values (%; mean  $\pm$  95% confidence intervals) of *Halodule wrightii* and epiphytic algae in seagrass beds exposed to control, water column, and sediment fertilization during 20 days (see text).

(~31%; averages calculated from a compilation by Daehnik et al., 1992).

#### 4. From the Individual to the Landscape Level

Also overlooked in traditional studies of food web dynamics is the contribution of individual species in a community: measurements of primary production, biomass, and isotopic composition are often performed on samples containing complex assemblages of species, where the measurements integrate the functional properties as single points on a graph and ignore the individual contribution of each species. This practice is most common with microalgae and small invertebrates, both of which have been shown to be functionally important (Klumpp et al., 1992; Moncreiff et al., 1992). Although this 'guild-level' approach is a necessary starting point, much ecological information is lost when groups of species are combined; measuring the production, biomass, turnover time, density, consumption rate, and assimilation efficiency of individual species would permit quantification of the contribution by each species to the overall flux of matter within the system.

Addressing questions at larger scales is also possible: for example, in the trophic pathways between beds and other communities. Thus, stable isotopes

will be useful in evaluating the residency time of individuals in particular beds (Fry et al., 2003). Knowing how organisms move between seagrass beds, unvegetated sediments, salt marshes, and other nearshore habitats as well as the degree to which they feed in each habitat will help to elucidate how organic matter production in these habitats is linked (see Valentine and Duffy, Chapter 20; Heck and Orth, Chapter 22; Kenworthy et al., Chapter 25; and Bell et al., Chapter 26). Landscape-level maps of production could be generated to relate areas of high productivity and carbon flux to landscape variables so that areas of greatest value to fisheries and the health of coastal ecosystems can be identified (see Bell et al., Chapter 26).

#### 5. Stable Isotopes: Future Developments

A particularly strong approach for the future is a balanced combination of natural abundance analyses and isotope addition experiments. Natural abundance analyses can provide an assessment of the background conditions while creatively targeted isotope additions would afford opportunities to resolve trophic ambiguities, monitor changes in trophic dynamics in response to environmental factors (e.g. nutrient enrichment, fragmentation, and disturbance),

or examine export of organic matter to other habitats. Despite the numerous difficulties of applying isotope additions in such open systems, advances continue to be made to permit isotope additions in the field. Along with direct isotope additions via spraying (Ottosen et al., 2001; Carman and Fry, 2002; Fry et al., 2003) or incorporation into fertilizer (Mutchler et al., 2004), organisms themselves could be labeled in the laboratory and 'released' into the field. Isotope signatures of specific beds (Stapel et al., 2001) or unvegetated sediments could be manipulated and the fate of the tracer monitored. Indeed, multiple isotope additions (e.g.  $^{13}\text{C}$ ,  $^{15}\text{N}$ , and  $^{34}\text{S}$ ) may be applied (Carman and Fry, 2002).

#### *E. Other Carbon Fates—Translocation and Seagrass Exudates*

Retranslocation of carbon resources from senescent to young leaves, between above- and below-ground organs (e.g. Alcoverro et al., 2001) or between adjacent shoots (Marbà et al., 2002), are mechanisms apparently used by seagrasses for an efficient use of their resources. A maximum of 11% of the carbon gain by the *P. oceanica* leaves can be accumulated as non-structural carbohydrates in the whole plant (above- and below-ground organs, Alcoverro et al., 2001). The fraction of this amount that is actually stored in roots and rhizomes cannot be easily determined at this time due to different criteria by different authors concerning the size of the living below-ground compartment. The relevance of this possible fate for leaf carbon is also difficult to ascertain since the carbon accumulated during periods of positive plant carbon balance can be later mobilized to support the growth of new leaves during periods of negative plant carbon balance (Alcoverro et al., 2001). It has been shown that the use of stable isotopes may have a potential in the study of carbon reserves in seagrasses (see discussion in Vizzini et al., 2003).

Concerning clonal resource sharing, Marbà et al. (2002) found that from 27.1 to 80.6% of the carbon incorporated by the leaves of different seagrass species could be exported to adjacent shoots to contribute to the growth of new and colonizing shoots. For instance, the value estimated for *P. oceanica* was 26% in June at 11–15 m of depth (NW Mediterranean). During periods of reserve mobilization, carbon export to other shoots could be substantially higher. Since an asymmetrical transport between

clones has been demonstrated (and not only in seagrasses) preferential transport of resources to pioneer ramets would, in effect, represent an important net carbon and nutrients loss from the source individuals.

Dissolved organic compounds have been recognized as a potentially important component of carbon transfer. In an early study, Moriarty et al. (1986) reported that the amount of dissolved carbon released into the water column by the leaves of *H. wrightii* was 1% of the carbon fixed. Carbon exuded from roots and rhizomes into the sediments was estimated as 6–17% of the  $^{14}\text{C}$  fixed by the leaves. Leaf uptake, translocation to roots and rhizomes, and exudation into the sediment occurred within 6 h. Using two different methods to determine bacterial production, Moriarty et al. (1986) concluded that all the excreted  $^{14}\text{C}$  was utilized by bacteria growing in the sediment. For the same species, Koepfler et al. (1993) found that dissolved inorganic carbon (DOC) concentration in pore-water was 25% higher in vegetated than in bare sediments. In *T. testudinum*, benthic net fluxes of DOC ranged from 0 to 216 mgC m<sup>-2</sup> day<sup>-1</sup> and were attributed mainly to seagrass exudation (Ziegler and Benner, 1999). Strong correlations between benthic DOC release and water column respiration suggested that water column heterotrophy was largely fed by seagrass exudation. Finally, an ecosystem model in Chesapeake Bay assigned to eelgrass-derived DOC an important role as a carbon source, accounting for up to 30% of littoral primary production (Buzzelli et al., 1998, 1999).

#### **IV. Ecosystem Carbon Budgets and Carbon Sinks**

The concept of ecosystem carbon budgets deserves a brief comment here to better focus the problem. Such a budget may compare the stocks of net or gross carbon incorporated by a producer compartment to the amount of carbon evolved from the detrital compartment during remineralization. Fates other than remineralization (such as grazing, export, and immediate release of DOC) need also to be known in order to account for all the carbon synthesized. Notice that ecosystem budgets can take into account (i) all producers of all compartments of the ecosystem, (ii) part of them, (iii) a single producer, or (iv) a part of a producer. The individual budget of a certain seagrass species can be largely positive, while growing in a globally heterotrophic ecosystem. It is suggested

*Table 3.* Summary of the annual budget and fate of leaf-derived carbon in *Posidonia oceanica* meadows in Medes Islands (Girona, Spain), the Bay of Calvi (Corsica, France), and Ischia Island (Naples, Italy). The values are the average for the range of depths indicated. The potential sink is the difference between leaf production and all known fates (remineralization, export and grazing). P:R accounts for the quotient between annual leaf net growth and leaf litter respiration. Values expressed in  $\text{gC m}^{-2} \text{ year}^{-1}$ . The values in parentheses represent the percentage of annual leaf production (modified from Mateo, submitted).

	MEDES (5–13 m)	CALVI (1–30 m)	ISCHIA (5–20 m)
Production	153.5 (100)	155 (100)	96.9 (100)
Remineralization	61.3 (39.9)	68.7 (44.3)	23.2 (23.9)
Budget	92.3 (60.1)	86.3 (55.7)	73.7 (76.1)
Export	9.8 (6.4)	38.8 (25.0)	47.9 (49.5)
Grazing	10.0 (6.5)	31.0 (20.0)	6.3 (6.5)
Known fate	81.0 (52.8)	138.5 (89.3)	77.4 (79.9)
Potential sink	72.5 (47.2)	16.6 (10.7)	19.5 (20.1)
P:R	2.5	2.3	4.2

that these aspects be taken into account when interpreting budget results and comparing budgets from different studies.

### A. Carbon Budgets

As mentioned in Section II.C, the available information on carbon budgets in seagrass beds comes from oxygen exchange experiments (Bay, 1982; Smith and Hollibaugh, 1997; Ziegler and Benner, 1998; Welsh et al., 2000). Almost all of these budgets provide global estimates for the ecosystem, distinguishing major compartments but without addressing the individual contribution of the different compartment components.

From Frankignoulle and Bouquegneau (1987) an annual P:R of 1.09 can be estimated for a *P. oceanica* bed in Calvi (Corsica, France). This would suggest that some seagrass beds, like coral reefs, are nearly in balance in terms of carbon balance. In a *Z. marina*-dominated bay (Tomales Bay, Ca, USA), Smith and Hollibaugh (1997) obtained a net heterotrophic carbon budget for the entire bay, with P:R = 0.9. They inferred that terrestrial and marine carbon sources each accounted for about half the heterotrophy of the system. Ziegler and Benner (1998), working in the seagrass-dominated Laguna Madre (Tx, USA) found that, while the water column was highly heterotrophic (P:R = 0.27), the benthos was net autotrophic with a P:R ratio of 1.16 (annual average). It was suggested that the benthos, dominated by *T. testudinum*, could be responsible for an important part of the heterotrophic activity of the water column and that this was a common situation for other temperate and tropical seagrass-dominated ecosys-

tems (Ziegler and Benner, 1998, 1999 and references therein). In an intertidal *Zostera noltii* bed on the French Atlantic coast, Welsh et al. (2000) estimated a P:R of 1.6–2.8, values in the same order as those found in an earlier study in a *Halophila stipulacea* bed in the Gulf of Aqaba (P:R = 2.36; Bay, 1982). Clearly, we need more studies of whole seagrass beds to resolve the range of P:R ratios.

Currently, we also need to examine the carbon budget for individual components of the ecosystem to identify relevant factors governing the balance and to assess the relative contribution of each component (Kemp et al., 1997). In three *P. oceanica* beds encompassing depths from 0 to 30 m, the P:R ratio for leaves (net leaf production vs. leaf detritus respiration) ranged from 1.5 at the deep limit of plant distribution (in Medes Islands) to 4.9 at 10 m at Ischia Island (intermediate bed depth; see summary in Table 3). During 10 months of the yearly cycle studied in Medes Islands, the budget was positive (Fig. 12). This seasonal pattern is consistent with what is generally known of *P. oceanica* beds: plant productivity approaches its yearly minimum in late summer due to the greatest ambient nutrient deficiencies (Pirc, 1989; Alcoverro et al., 1997). Additionally, a massive leaf detachment takes place in late summer–autumn (Bay, 1984; Pirc, 1986; Romero et al., 1992; Mateo and Romero, 1997). These leaves enter the detrital compartment. Both meiofaunal and bacterial activity in this period of the year is high owing to the abundant fresh (nutrient-rich) organic matter available (López et al., 1995a,b; Danovaro, 1996; Mateo and Romero, 1997) and to the maximum annual water temperatures (23–25°C; Velimirov and Walenta-Simon, 1993). From the aforementioned,

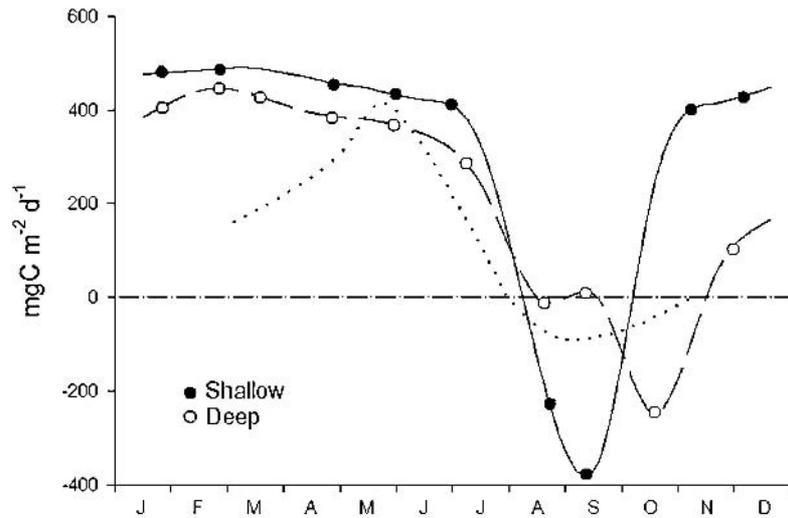


Fig. 12. Seasonal changes in *Posidonia oceanica* leaf carbon budget (Medes Islands, NW Mediterranean, Spain). The dotted line is the carbon budget estimated by Frankignoulle and Bouquegneau (1987) also for *P. oceanica* (Bay of Calvi, Corsica, France) assaying DIC and O<sub>2</sub> evolution within benthic chambers. The budget in Medes was estimated for the shallow and deep limits of plant distribution (from Mateo, submitted).

it appears that seagrass-dominated ecosystems are, with exceptions, somewhat autotrophic systems on an annual basis. However, as mentioned in Section II.B, it is often found that seagrasses are not the major contributors to this autotrophy. Based on these observations, several authors have suggested a structural rather than a trophic role for seagrasses (e.g. Frankignoulle and Bouquegneau, 1987, *P. oceanica* in Calvi, Corsica, France; Pollard and Kogure, 1993, *S. isoetifolium* in Dravuni Island, Fiji; Kaldy et al., 2002; *H. wrightii* and *T. testudinum* in Low Laguna Madre, Tx, USA).

### B. Carbon Sinks

Once all the known fates of organic material have been accounted for, it is often found that there is an excess component, which is put down to refractory carbon. When the latter material is buried, it is in a highly decay-resistant chemical form, and the term 'refractory accumulation' has become widespread.

Information on burial of refractory carbon is very limited since the estimates available for seagrasses are indirect. Often refractory carbon is taken as deriving from below-ground organs, since leaf-derived carbon has a low residence time in the detrital compartment. However, a pool of refractory carbon origi-

inating from seagrass leaves has been found to be potentially very important as a short-term sink (see below).

Depending on the species, the time span for below-ground detritus to reach the refractory phase may range from a few months (e.g. eelgrass, Kenworthy and Thayer, 1984) to several years (e.g. Neptune grass, Romero et al., 1994). Degradation of refractory detritus occurs at a very slow rate and it may take many years, even millennia, to get measurable degradation (Mateo and Romero, 1997; Mateo et al., 1997). The following classification is proposed in order to provide some unifying guidelines when addressing the phenomenon of refractory accumulation. Two time scales are considered:

*Short-term accumulation or sink* refers to the pool of carbon that remains in the organic form after the first year (plant life cycle) of decomposition. In relation to the annual ecosystem budget, this pool has not been remineralized and hence represents a net accumulation. The residence time of this sink is therefore longer than 1 year and shorter than 2 or 4–6 years for above- and below-ground production, respectively (see below). The organic carbon in this sink is still susceptible to biological degradation processes. Assuming a steady-state for carbon accretion into this pool, the size of this sink should remain constant over time periods relevant to the biology of the plant.

*Long-term accumulation or sink* accounts for material with a biomass and nutrient content (C/N ratio) that no longer exhibit a change with time. In the best documented case, long-term accumulation of *P. oceanica* applies only to the carbon derived from below-ground organ production, starting 4–6 years after tissue death and lasting for decades, centuries, or millennia (Romero et al., 1994; Mateo and Romero, 1997; Mateo et al., 1997). The dynamics of this long-term sink is only affected by geochemical diagenetic phenomena. In the biospheric context, these kinds of sinks are usually named ‘reservoirs’ because they are considered virtually permanent. For periods comparable to a plant’s biological cycle, this sink would increase in size.

### 1. Keys Processes for Material Accumulation

There is general agreement that the two main factors leading to an accumulation of carbon in sediments are (i) incorporation of carbon into refractory geomacromolecules or humic substances and (ii) oxygen availability (turnover) in the sediments (e.g. Henrichs, 1992, 1993). This means on the one hand, that carbon trapped in seagrass sediments does not necessarily have to be highly refractory provided the redox potential of the sediments is low enough, and on the other hand, that highly refractory material can remain intact even in oxidizing environments. A number of biological and environmental agents will modulate the extent of these two factors.

### 2. Chemistry of Refractory Material

Among all vascular plant components, lignin is considered to have the highest preservation potential (Klap, 1997 and references therein). The presence of this polymer in aquatic plants seems largely unnecessary and in fact, of all aquatic plants, seagrasses are the only ones that contain lignin (Lewis and Yamamoto, 1990; Kuo and den Hartog, Chapter 3). One possible reason is the terrestrial origin of seagrasses (Larkum and den Hartog, 1989), allied to the fact that decay-resistant material is useful at the leaf base and in rhizomes.

Despite the pioneering studies of Klap (1997) and Klap et al. (2000), in *P. oceanica*, the importance of lignin in making seagrass below-ground organs particularly decay-resistant still needs to be adequately addressed.

Evidence suggests that one cause for the refractory accumulation of seagrass below-ground detritus could be the progressive impoverishment of nutrients in the detritus and resulting slower decomposition (Melillo et al., 1984; Romero et al., 1992; Mateo and Romero, 1997; Sterner and Elser, 2002). López et al. (1998) found that in several *P. oceanica* beds in the NW Mediterranean, fertilization significantly increased bacterial activity. They found that in the fertilized plots, organic matter content was reduced by about 33% with respect to the controls, which suggested a potential role of nutrients.

The increasing tannin content of seagrass material during aging (Pergent, 1987) has also been proposed as another important factor that impairs microbial activity (Crouzet, 1984). Also, it has been demonstrated that this secondary compound can act against herbivory either by deterring herbivores or by reducing total protein availability (e.g. Robbins et al., 1987; Bernays et al., 1989).

### 3. Redox Potential and Anoxia

Anoxic conditions and oxidation reduction (redox) potential in sediments may also play a role in preservation of refractory carbon (Harrison, 1989). However, this is the subject of much current debate. For instance, it is known that many bacteria that possess cellulase activity seem to be strict anaerobes (Kenworthy and Thayer, 1984; Roth and Hayasaka, 1984) and numerous studies have reported partial or complete lignin degradation by both aerobic and anaerobic decomposers (Klap, 1997 and references therein). In two reviews of the topic, Henrichs and Reeburgh (1987) and Henrichs (1993) conclude that organic matter decomposition rates are not substantially different under oxic or anoxic conditions. The situation is obviously complicated by the fact that seagrass sediments are highly structured with a variety of different environments (Kristensen, 2000).

Lepidochronological dating (i.e. dating rhizome remains from the number of leaf bases present), elemental analysis, and sediment redox measurements provide evidence suggesting an important role of anoxia in helping to retain the organic carbon from below-ground production (Mateo, submitted). In a *P. oceanica* bed, the redox potential discontinuity (RPD) was found to be located at 5 cm from the sediment surface (range 4–6 cm, in March) which is close to the 150 mV of redox potential limit (Fig. 10), i.e. the potential at which it is assumed that

sediments are reduced and therefore bacterial efficiency for remineralization drops drastically (e.g. Stumm and Morgan, 1981; Kristensen, 2000). From the fact that  $t$ , the elongation rate of recent rhizomes was found to be  $0.95 \text{ cm yr}^{-1}$  and this must be matched by the sediment accretion rate, since the rhizomes do not become exposed, it can be estimated that a reducing environment will arise within 5–7 yr; at which point decay rates would fall drastically. From Mateo and Romero (1997) the C:N ratio of dead rhizome sheaths stabilizes at  $\sim 6$  yr, which may well be the result of anoxia and changed redox conditions. Although the foregoing suggests that anoxia and redox potential in seagrass sediments promotes organic matter preservation, the considerable amount of contradictory evidence makes it advisable to further investigate the effect of oxygen depletion on below-ground refractory material.

#### 4. Other Factors

The situation is made more complex by the influence of other factors especially the four following ones, which clearly favor low redox potential in marine sediments and therefore help material preservation: (i) high temperatures, (ii) high organic supply, (iii) low water motion, and (iv) small sediment grain size.

It has been repeatedly demonstrated that high temperatures increase bacterial activity in seagrass sediments (e.g. López et al., 1995a,b; Mateo and Romero, 1997) with concomitant oxygen consumption. On the other hand, low temperatures may promote material accumulation by reducing bacterial activity. In terrestrial ecology, it is well established that cold biomes present the largest accumulation of organic matter in the soil as a consequence of reduced decomposition rates (e.g. Swift et al., 1979).

An abundant organic matter supply not only from seagrass production but from micro- and macroalgal detritus (Section II.D.1) accelerates oxygen depletion in the sediment.

Reduction of water velocity over a bed due to water friction of the seagrass canopy (Gambi et al., 1990; Koch et al., Chapter 8) leads to seagrass vegetated areas having a sediment retention capacity up to 15 times higher than barren areas (Gacia et al., 1999) and accelerates burial. Also, low water motion and a small grain size of the sediment lead to a reduction of pore-water renewal and oxygenation,

very effectively helping to maintain a low redox potential in the sediment.

Finally, Cebrián et al. (2000) examined the formation refractory material throughout the development of *C. nodosa* beds and found that refractory accumulation increased from small patches, to large patches, to climax beds.

#### C. Refractory Carbon: The Potential Seagrass Carbon Sink

Refractory accumulation has two main consequences for the ecology of seagrass beds. First, the capacity of climax beds to sequester organic carbon is indicative of their role as sinks in oceanic and global models. Second, the accumulation of refractory detritus entails a loss of nutrients from the bed since a significant amount of nutrients remain bound to fibrous compounds (i.e. lignin, cellulose) in the detritus (Romero et al., 1994; Mateo and Romero, 1997; Mateo et al., 1997). Hence, refractory accumulation also needs to be added to the export of dead leaves out of the bed when estimating the bed's total dependence on imported nutrients. Yet, despite its importance, refractory accumulation is clearly the least studied of all the routes of seagrass production listed in Eqs. (1) and (2).

Information on organic matter burial in seagrass sediments began to be studied in detail during the 1990s, and the only direct estimations available so far are basically limited to the below-ground-derived production of the species *P. oceanica* (Romero et al., 1994; Mateo et al., 1997, 2002; Mateo, submitted). The two different time scales for seagrass carbon sinks, described at the beginning of this section, will be distinguished below.

#### 1. Short-Term Sinks (i.e. Material Broken Down Over a Period of a Year or so)

The preliminary compilation made for this chapter showed that the percentage of seagrass production accumulated as refractory material varies from ca. 1 to 62% and the absolute value from 3 to  $207 \text{ gC m}^{-2} \text{ year}^{-1}$  (Fig. 3G and H). The studies on *P. oceanica* presented in this chapter (for beds off the islands of Medes, Calvi, and Ischia; Table 3) and estimates from two other available studies (Cebrián et al., 1997; Gacia et al., 2002), indicate that the average potential carbon sink (short-term) from leaf-derived material for this species can be estimated as

**Table 4.** Estimates of the potential annual carbon sink in *Posidonia oceanica* meadows and other environments in absolute values and relative to net primary production (% NPP; adapted and simplified from Mateo, submitted). Estimates are presented separately for leaves, below-ground organs, total plant and total ecosystem (see text for details).

	Depth (m)	Potential sink	
		gC m <sup>-2</sup> year <sup>-1</sup>	% NPP
<i>Posidonia oceanica</i>			
Aboveground			
Medes	5	123	59
Medes	13	22	23
Calvi	20	17	11
Cala jonquet	4	66	17
Fanals point	15	40–55	36–50
Ischia	5–20	20	20
Average	12	57	29
Range	4–20	17–123	17–59
Belowground			
Short-term			
Medes	5	84	91
Medes	13	24	96
Long-term	5–20	9–112	4–51
Total plant			
Medes	5	207	63
Medes	13	46	42
Ischia	5–20	58	43
Total ecosystem			
Fanals point	15	182	43
Calvi	20	56	45
<i>Others</i>			
Peatlands	–	26–99	14–52
Coastal areas	–	62	50
Oceanic areas	–	0.02–4	0.01–2
Seagrass ecosystems	0–40	3–182	1–62

57 gC m<sup>-2</sup> year<sup>-1</sup> (ranging 17–123 gC m<sup>-2</sup> year<sup>-1</sup>) representing 29% of the annual leaf production (17–59%, Table 4). This estimate accounts for a substantial part of the range estimated for all seagrasses, suggesting that the phenomenon of refractory accumulation may present large between- and within-species variability.

As discussed above, carbon from below-ground organs may also contribute to the sediment refractory pool. The carbon stored in a *P. oceanica* bed after the first year of decay (short-term sink) was estimated to be 84 and 24 gC m<sup>-2</sup> year<sup>-1</sup> at the shallow and deep limits of the bed, respectively (Mateo and Romero, 1997); this represents 91 and 96% of the total below-ground production, respectively (Table 4). Adding up both above- and below-ground sinks for the *P. oceanica* bed in Medes Islands, the total potential sink for the studied year amounted to 207 and

46 gC m<sup>-2</sup> year<sup>-1</sup> at 5 and 13 m, respectively (63 and 42% of total plant production, Table 4). Comparable estimates were only possible for the bed in Ischia Island that yielded an average of 58 gC m<sup>-2</sup> year<sup>-1</sup> (43% of total plant production; average for 5–20m depth).

## 2. Long-Term Sinks (i.e. Accumulations Over a Period of 4 to Many Years)

The accumulation of refractory organic matter in below-ground deposits is a phenomenon exclusive to a very few species in the biosphere. Ecosystems dominated by peat lands (e.g. Gorham, 1991; Clymo, 1992), mangroves (e.g. Macintyre et al., 1995; Middleton and Mckee, 2001), and seagrasses (Lipkin, 1979, *Thalassodendron ciliatum*; Shepherd and Sprigg, 1976, *Posidonia australis* and related species; Boudouresque et al., 1980; Romero et al., 1994 and Mateo et al., 1997, *P. oceanica*) are, to our knowledge, the only plants generating important refractory deposits with a very high residence time (from decades to millennia). The long-term below-ground carbon stocks of peat lands are well studied, with estimates up to 12 × 10<sup>4</sup> gC m<sup>-2</sup> (e.g. Warner et al., 1993). This value falls well within the average range, obtained for several *P. oceanica* deposits (usually known as ‘mattes’) studied by Mateo et al. (1997), of 4–16 × 10<sup>4</sup> gC m<sup>-2</sup>. Long-term annual carbon burial rates are also similar for peat lands and *P. oceanica* below-ground deposits, 26–99 gC m<sup>-2</sup> year<sup>-1</sup> and 9–112 gC m<sup>-2</sup> year<sup>-1</sup> (Table 4), representing 14–52% and 17–59% of the production, respectively.

The reason why *P. oceanica*, and possibly *P. australis*, seem to be the only seagrasses that form such thick long-term organic reservoirs (at least 5 m thick, Fig. 13), lies most likely in the combination of the multiple factors: (i) a low palatability of the below-ground tissues, (ii) the fact that sheaths remain attached after leaf-blade abscission, (iii) the increasing concentration of highly refractory carbon compounds (e.g. lignin; Klap et al., 2000) and herbivore deterrents (Crouzet, 1984) during tissue aging, (iv) the long life span of this species, (v) the rapid burial capacity promoted by high sedimentation rates enhanced by reduced water velocity, and (vi) the low redox potential maintained by (a) an intense organic matter accretion, (b) a relatively high bacterial activity, and (c) a low hydraulic



Fig. 13. A reef-like formation of *Posidonia oceanica* ‘matte’ of the island of Formentera (Balearic Islands, Spain). The millenary accumulation of *P. oceanica* detritus derived from its below-ground organs (roots and rhizomes) results in the elevation of the sea bottom forming a highly organic sediment that resembles terrestrial peat formations. In the upper part of the picture, the living shoots of *P. oceanica* can be recognized. The matte in the picture is more than 5 m high (photograph by M. San Félix).

conductivity of the sediment. All these factors converge to make a substantial part of *P. oceanica* below-ground detritus unavailable for decomposers.

Applying a model proposed by Clymo (1984) for terrestrial peat, the residence time of the *P. oceanica* matte has been estimated between 2800 and 12,500 years (Mateo et al., 1997, 2002). This old continuous organic reservoir constitutes a unique feature in the marine environment. Apart from its implications in the context of biospheric carbon sinks (Smith, 1981), it should be regarded as a valuable repository of paleo-ecological information of a seagrass ecosystem during, at least, the second half of the Holocene (Mateo et al., 2002).

## V. Summary and Future Work

### A. Production

Together with coral reefs, mangrove forests, and some macroalgae, seagrass beds are responsible

for some of the most productive and complex marine ecosystems. They show highly variable above-ground production rates ranging from  $0.003$  to  $15 \text{ gDW m}^{-2} \text{ day}^{-1}$  ( $0.1$  to  $18.7 \text{ gC m}^{-2} \text{ day}^{-1}$ ) with average values probably around  $1\text{--}2 \text{ gC m}^{-2} \text{ day}^{-1}$ . More recently, it has been demonstrated that below-ground production can be as substantial as 50% of total plant production, although covering a wide range from  $0.001$  to  $20 \text{ gDW m}^{-2} \text{ day}^{-1}$  (carbon content in below-ground tissues is still too scattered to attempt an estimate).

The increasing number of different methods currently coexisting to measure seagrass production points to the need for an intense effort of exploration of new approaches able to provide accurate values.

It is becoming clear that seagrass productivity is not always the major contributor to secondary production in seagrass ecosystems; the few reports available seem to place seagrasses as a lesser contributor (24–38%), exceeded by benthic macroalgae (33–42%), and seagrass epiphytes (20–60%)

and with sediment microalgae apparently sometimes accounting for the highest part of the productivity (18–56%). Areas which need much attention are the role of below-ground parts as producers, consumers or storage organs, canopy structure, and light dynamics.

### B. Fate

The preliminary review attempted in this chapter shows that overall, most seagrass production is decomposed within the bed (~65%) while the rest is exported (~15%), grazed (<10%), or accumulates in a refractory pool (~10%). Detritus nutrient content may be a controlling factor on decomposition rates, alongside the oxygen status of the sediment. The importance of certain chemical constituents (e.g. lignin and tannins) of seagrass detritus in influencing microbial attack still needs to be explored in almost all seagrass species.

Seagrass leaf nutrient content and the intensity of herbivory is a controversial topic and studies are needed of how different field spatial (i.e. cultivated patches vs. entire beds) and temporal scales (i.e. seasonality) affect the relationship. Along with these manipulations, specific assimilation rates for the major grazers need to be determined because most grazing rates given in the literature may represent large overestimates of the actual carbon flux from producers to consumers.

Given our lack of understanding of mechanisms that affect food web dynamics and the current threat of eutrophication to seagrass systems, it is recommended that the role of nutrients in determining the fluxes of carbon and nitrogen be investigated. Both surveys of natural abundances of stable isotopes and isotope addition experiments will be useful in these investigations.

The lack of a method that adequately covers the entire ecosystem and integrates export rates over time has been identified as the main reason behind the scarcity of export estimates.

### C. Budgets and Sinks

Based on the relatively limited information available, seagrass ecosystems appear to be net producer systems, with P:R ratios ranging from 1 to 4.9; this range is mainly a consequence of the quantitative importance of export and refractory accumulation and

needs detailed investigation. If true, it would confirm the role of seagrass-dominated areas as food sources for downstream ecosystems. At the same time, we need more efforts to study single ecosystem components to avoid losing important information of bed functioning.

The percentage of the production accumulated as refractory materials has often been shown to be modest; however, the high productivity of seagrasses results in a substantial absolute amount of carbon fluxing to this pool. In the context of a world with an increase in atmospheric CO<sub>2</sub>, global estimates suggest that seagrass ecosystems may be relevant carbon sinks, not only at a local scale, but also in a biospheric context; 0.08 PgC year<sup>-1</sup>, representing 20% as much as for phytoplanktonic communities.

### Acknowledgments

This chapter has been improved by the critical comments of Jack Middelburg, Tony Larkum, and two anonymous referees. The authors are grateful to Brian Fry and Mike Sullivan for their valuable comments on stable isotopes and seagrass food webs. Heather Alexander contributed to improve the linguistic quality of the text. Part of the original material presented in this chapter has been obtained and prepared in the framework of the project PALEOMED, financed by the Spanish Ministry of Science and Technology (project reference: BOS2002-02247).

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