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Seagrass biomass and production: a reassessment

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Abstract

The biomass and production of seagrass populations were reassessed based on the compilation of a large data set comprising estimates for 30 species, derived from the literature. The mean ($\pm$ SE) above- and below-ground biomass in the data set were very similar, 223.9 ± 17.5 and $237.4 \pm 28\,\mathrm{g\,DW\,m^{-2}}$, respectively, indicating a general tendency for a balanced distribution of biomass between leaves and rhizomes + roots (mean ratio ($\pm$ SE) = 1.11 ± 0.08). The biomass development and the ratio of above- to below-ground biomass varied significantly with latitude and was species-specific, with a significant tendency for large-sized seagrass species to develop high below-ground biomass. Maximum daily seagrass production differed significantly among species, but averaged 3.84 ± 0.34 and $1.21 \pm 0.27\,\mathrm{g\,DW\,m^{-2}}$ per day for above- and below-ground organs respectively, with an average ratio of above- to below-ground production of 16.4 ± 8.5. The biomass turnover rates averaged 2.6 ± 0.3 and $0.77 \pm 0.12\%$ per day for the above- and below-ground material respectively, and tended to be faster for temperate species. The average annual seagrass production found here, $1012\,\mathrm{g\,DW\,m^{-2}}$ per year, exceeds previous estimates by 25%, because the average excedent carbon produced by seagrasses must be revised upwards to represent 15% of the total surplus carbon fixed in the global ocean.

Keywords: Seagrass; Comparative analysis; Above- and below-ground biomass; Above- and below-ground production

1. Introduction

Seagrass meadows are prominent components of the littoral zone of tropical and temperate seas, where they provide habitat and food for organisms and modulate sedimentary and biogeochemical processes (McRoy and Helfferich, 1977). These roles are so important

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that seagrass meadows are considered to be the most valuable ecosystems in terms of the value-added benefits of the services they provide (Costanza et al., 1997). In addition to their local importance, seagrasses are significant contributors to the primary production of the global ocean (Smith, 1981; Charpy-Roubaud and Sournia, 1990). They are present in 0.15% of the ocean surface only (Charpy-Roubaud and Sournia, 1990) and contribute a modest 1% of the net primary production of the global ocean (Duarte and Cebrián, 1996). Yet, their role in the oceanic carbon budget is proportionally more significant than expected from their cover or primary production alone, for seagrasses are estimated to contribute 12% of the net ecosystem production in the ocean (Duarte and Cebrián, 1996).

The empirical basis on seagrass biomass and production supporting the estimates of their role in the ocean is, however, limited and biased towards the coastal waters of Europe, Australia, and Southeast United States. Previous reviews of seagrass biomass and production have been based on the examination of limited data sets, typically including data on the biomass and production of <10 species, and with most species being represented by only one stand (e.g. McRoy and McMillan, 1977; Zieman and Wetzel, 1980; Hillman et al., 1989). Indeed, the average biomass reached by the seagrasses is a source of disagreement, for the values often quoted in the past (e.g. McRoy and McMillan, 1977; Zieman and Wetzel, 1980; Hillman et al., 1989) have been claimed to be a factor of three-fold too high (Brouns, 1994). Yet, considerable progress in estimating seagrass biomass and production has been made over the past two decades (Phillips, 1996), when about 100 papers on seagrass ecology have been published annually (Duarte, 1999). The empirical basis available to assess the distribution of seagrass biomass and production exceeds by at least a factor of 10 that contained in previous assessments, so it is now possible to present a more balanced estimate of the average biomass and production of seagrass communities.

We provide here an overview of the available information on biomass and production (above- and below-ground) of seagrass populations aimed at reassessing the average values and, accordingly, the estimates of the role of seagrasses in the global ocean derived from these values. In addition, we test for differences in biomass and production (above-ground and below-ground) among seagrass species and for latitudinal differences in these important properties of seagrass meadows.

2. Methods

We searched the literature published until 1996 for reports on biomass and production (both above- and below-ground) of seagrass communities distributed world-wide. The majority of seagrass literature reports only standing crop values, which we referred to as above-ground biomass. We recorded the maximum seasonal biomass, the annual mean and maximum production, whenever possible. Biomass values are expressed as grams dry weight, assuming, when necessary, ash-free dry weight to be 80% of dry weight (Westlake, 1974), and organic carbon to be 33.5% of dry weight (Duarte, 1990).

The examination of the possible size-dependence of differences in the average biomass and production of different seagrass species was based on the use of the average diameter of the rhizomes as an indicator of size (Duarte, 1991a). Data on average rhizome diameter for the seagrass species was derived from the data compiled by Duarte (1991a), complemented with additional data by Marbá and Duarte (1998) (submitted).

3. Results

The data set compiled included 423 and 250 estimates of above- and below-ground biomass, respectively, and 128 and 60 estimates of maximum daily above- and below-ground production rates, respectively. Estimates of annual production were available for only 52 and 12 estimates of above- and below-ground rates, respectively. Root biomass and production were estimated in a small fraction of the studies of below-ground biomass (14% of the studies) and production (29% of the studies). The average values described here, therefore, underestimate the total biomass and production of the below-ground compartment. The data set comprised estimates for 30 species, thus representing more than half of the global seagrass flora. The fact that no estimates were found for the remaining species reveals a substantial unevenness in our knowledge of these properties for seagrasses as a whole. The geographical origin of the estimates was unbalanced, comprising a dominance of estimates in the northern Atlantic, where two species, *Thalassia testudinum* and *Zostera marina*, comprised 1/4 of all the reports (Table 1). The uneven distribution of effort reflects the geographic distribution of marine research institutions, and implies that our knowledge on the biomass and production of some seagrass floras is adequate (e.g. N. temperate Atlantic coasts), whereas this knowledge is very sparse for other areas (e.g. African coast). Most of the samples were derived from relatively shallow (mean ($\pm$ SE) sampling depth = 3.22 ± 0.24 m, median depth = 1.6 m), and the deepest biomass estimate was derived from a population of *Posidonia oceanica* growing at a depth of 22 m in the Mediterranean.

The mean ($\pm$ SE) above- and below-ground biomass in the data set were very similar, 223.9 ± 17.5 and 237.4 ± 28 g DW m^{-2}, respectively, suggesting a tendency towards a roughly equal allocation of biomass to above- and below-ground organs. The distribution of biomass estimates in the data set were, however, skewed by the presence of a few very lush meadows (skewness coefficient = 9.61 and 4.62 for above- and below-ground biomass respectively, Fig. 1), so that the number of observations in the data set declined exponentially as the biomass increased. As a result, the median biomass was much lower than the mean (100 and 105 g DW m^{-2} for above- and below-ground biomass, respectively).

There was a strong positive relationship between above- and below-ground biomass of seagrass populations (Fig. 2). This relationship was best described by the regression equations

$$\text{Above-ground biomass} = 1.55\ \text{Below-ground biomass}^{0.81\pm0.04}$$

$$(R^2 = 0.65,\ F = 406,\ P < 0.0001,\ N = 229)$$

which indicated a weak, albeit significant, tendency for the above-ground biomass to increase somewhat faster than the below-ground biomass does (H_o: slope = 1, t-test, $P < 0.001$). The ratio of above- to below-ground biomass varied greatly (0.005–8.56) among populations ($N = 229$) and averaged 1.11 ± 0.08.

Table 1
Average maximum biomass and production, both above- (Abg) and below-ground (Blg), of different seagrass species[a]

Species	Biomass (Abg)	g DW m^{-2}(Blg)	Production (Abg)	g DW m^{-2}per day (Blg)
Amphibolis antarctica	1005.0 (6)	NA	6.2 (2)	NA
Amphibolis griffithii	736.7 (3)	NA	NA	NA
Cymodocea nodosa	146.7 (37)	285 (22)	1.3 (9)	0.17 (11)
Cymodocea rotundata	33.2 (20)	62.5 (20)	0.45 (2)	0.18 (2)
Cymodocea serrulata	69.7 (22)	37.9 (18)	0.46 (2)	0.14 (2)
Enhalus acoroides	72.0 (29)	392.4 (18)	1.05 (4)	1.35 (4)
Halodule uninervis	27.0 (25)	60.8 (25)	0.1 (3)	NA
Halodule wrightii	253.5 (19)	193.3 (12)	7.4 (2)	0.87 (1)
Halophila decipiens	77.5 (2)	66.0 (1)	NA.	NA
Halophila hawaiana	104.0 (1)	NA	7.1 (1)	NA
Halophila johnsonii	43.0 (2)	53.5 (2)	NA	NA
Halophila ovalis	54.8 (34)	21.1 (11)	0.03 (1)	0.01 (1)
Halophila stipulacea	2.3 (1)	2.6 (1)	NA	NA
Heterozostera tasmanica	NA	NA	1.54 (4)	NA
Phyllospadix scouleri	615.2 (1)	418.1 (1)	13.7 (1)	10.5 (1)
Phyllospadix torreyi	586.4 (1)	485.9 (1)	14.2 (1)	11.3 (1)
Posidonia angustifolia	471.4 (11)	840.0 (2)	3.0 (2)	NA
Posidonia oceanica	501.0 (25)	1610.7 (6)	2.4 (17)	0.23 (6)
Posidonia sinuosa	575.0 (2)	NA	NA	NA
Syringodium filiforme	368.2 (6)	450.8 (4)	3.8 (2)	0.96 (2)
Syringodium isoetifolium	86.6 (13)	94.2 (12)	1.1 (3)	0.92 (2)
Thalassia hemprichii	86.9 (29)	209.9 (29)	3.7 (5)	0.5 (5)
Thalassia testudinum	519.0 (62)	582.5 (22)	5.0 (29)	1.8 (2)
Thalassodendron ciliatum	NA	NA	7.3 (3)	NA
Zostera capricornii	191.4 (7)	176.0 (5)	1.9 (3)	0.44 (1)
Zostera japonica	130.0 (2)	NA	NA	NA
Zostera marina	298.4 (49)	149.7 (29)	5.2 (29)	1.7 (18)
Zostera muellerii	342.0 (4)	NA	NA	NA
Zostera noltii	82.5 (8)	66.1 (8)	1.1 (2)	NA
Overall	239.4 (423)	235.6 (250)	3.8 (128)	1.21 (60)

[a] Values in parentheses represent the number of observations. NA = no estimates available.

Differences in biomass among seagrass populations were largely the result of species-specific differences in biomass development (Kruskal–Wallis test, $P < 0.00001$), with a tendency for large-sized seagrass species to develop high below-ground biomass ($r = 0.61$ between rhizome diameter, as a descriptor of seagrass size, and below-ground biomass, $P = 0.0068$, data not shown). In particular, the populations of species of the genera *Amphibolis*, *Phyllospadix* and *Posidonia* tended to develop very high above-ground (about 500 g DW m^{-2} or higher) biomass, and the below-ground biomass developed by *Posidonia* sp. by far exceeded (about 1000 g DW m^{-2} or higher) those developed by other seagrasses (Fig. 3(a), Table 1). Populations of the genus *Halophila* were characterised by low biomass (Fig. 4 (a)) with the densest *Halophila* meadow reported corresponding to SW Thailand. The distribution of biomass values was also skewed within species, particularly so for the above-ground biomass, with most populations having relatively low biomasses and one or a few of them developing a biomass well-above the average for the species (Fig. 3(a), Table 1).

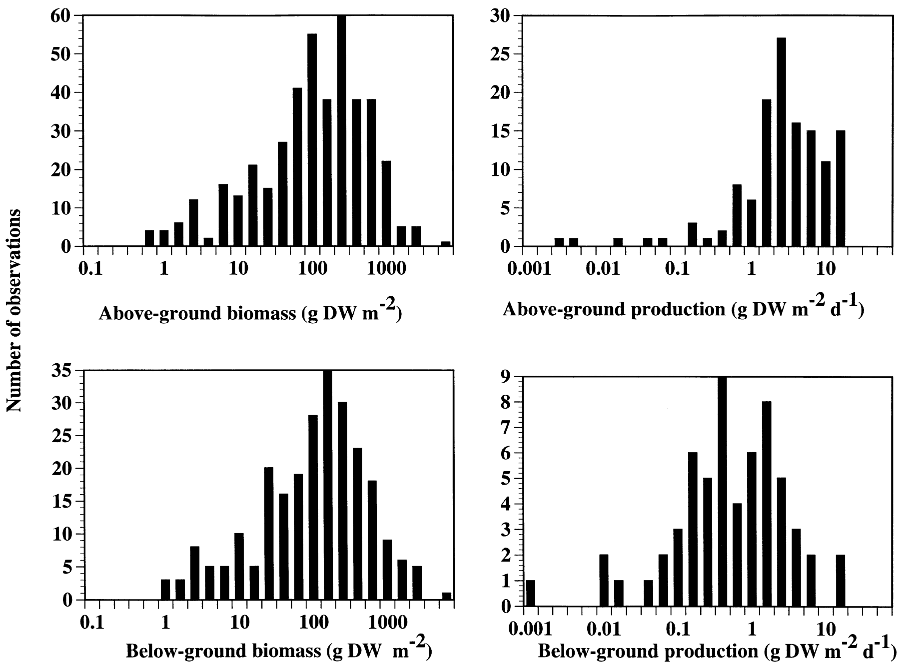


Fig. 1. Frequency distribution of maximum seagrass biomass and production.

As a result of the significant differences in above- and below-ground biomass among species, the ratio of above- to below-ground biomass was also, to a large extent, a species characteristic (Kruskal–Wallis test, $P < 0.00001$). Above-ground exceeded below-ground biomass for most of the species (i.e. ratios > 1, Fig. 3(c), Table 1). However, species of the genera *Zostera*, *Halophila*, and *Halodule* were characterised by a particularly high biomass allocation to above-ground relative to below-ground biomass compared to other species, while *Enhalus acoroides* and *Posidonia* sp. had the largest share of below-ground biomass (Fig. 3(c), Table 1). There was, therefore, a significant tendency for the ratio of above-ground to below-ground biomass to decline ($r = -0.56$, $P = 0.024$) with increasing seagrass size, as represented by the average diameter of the species rhizome.

Examination of the data set revealed a significant (Kruskal–Wallis test; $P < 0.0001$) tendency for the average above-ground biomass developed by seagrass populations to increase with increasing latitude (Fig. 4). This tendency, however, accounted for only 18% of the variance observed. The below-ground biomass developed by seagrass populations also varied significantly across latitudinal ranges (Kruskal–Wallis test; $P < 0.0001$), although this variation did not follow a monotonous trend with latitude (Fig. 4). The ratio of biomass allocated to above- and below-ground material also showed a significant tendency to increase with increasing latitudinal range (Kruskal–Wallis test; $P < 0.0001$; Fig. 4).

The perception that seagrass meadows are highly productive ecosystems is supported by our data set, for maximum seagrass production averaged 3.84 ± 0.34 (range 0.002–15.5) g DW m^{-2} per day and 1.21 ± 0.27 (range 0.008–11.34) g DW m^{-2} per day for above- and below-ground organs, respectively. Maximum below- and above-ground production (both

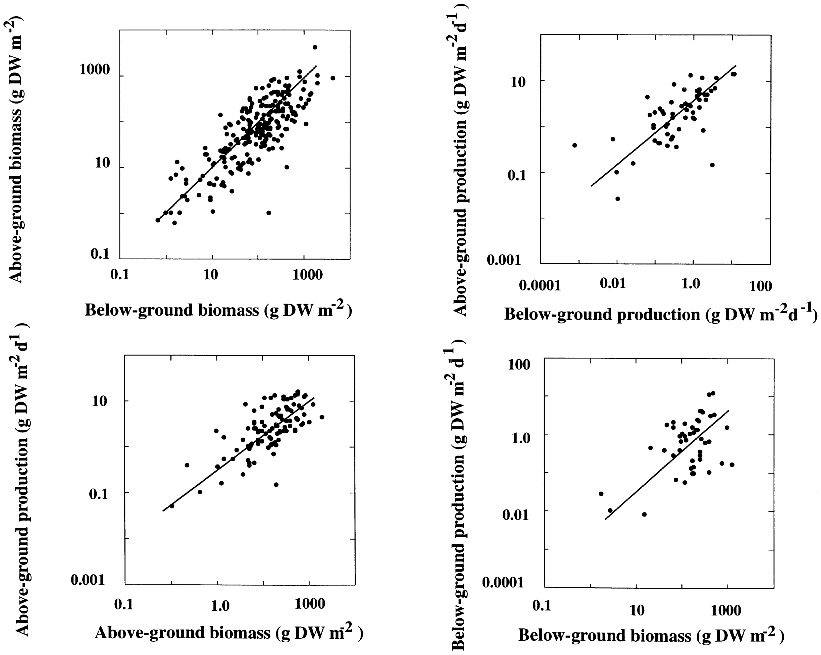


Fig. 2. The relationship between above- and below-ground maximum seagrass biomass and production, and the relationship between maximum production and biomass for the above- and below-ground compartments.

in g DW m^{-2} day) were found to be significantly correlated (Fig. 2) as described by the regression equation,

$$\text{Above-ground production} = 2.81\ \text{Below-ground production}^{0.50\pm0.07}$$

$$(R^2 = 0.45,\ F = 39,\ P < 0.0001,\ N = 57)$$

which indicates that above-ground production increases as the 1/2 power of below-ground production. This observation implies a shift towards a greater relative allocation of resources to below-ground production as the populations become more productive. The relative allocation of resources to production of above- and below-ground material varied greatly among populations (range 0.04–486), with a mean ratio of 16.4 ± 8.5 and a median value of 3.55.

The annual mean daily production increased slower than maximum daily production does (both in g DW m^{-2} per day), as described by the regression equations:

$$\text{Log above-ground production}_{\text{mean}} = -0.16 + 0.86\ \text{Log above-ground production}_{\text{max}}$$

$$(R^2 = 0.83,\ P < 0.0001,\ N = 52)$$

and,

$$\text{Log below-ground production}_{\text{mean}} = -0.28 + 0.81\ \text{Log below-ground production}_{\text{max}}$$

$$(R^2 = 0.70,\ P < 0.0001,\ N = 12)$$

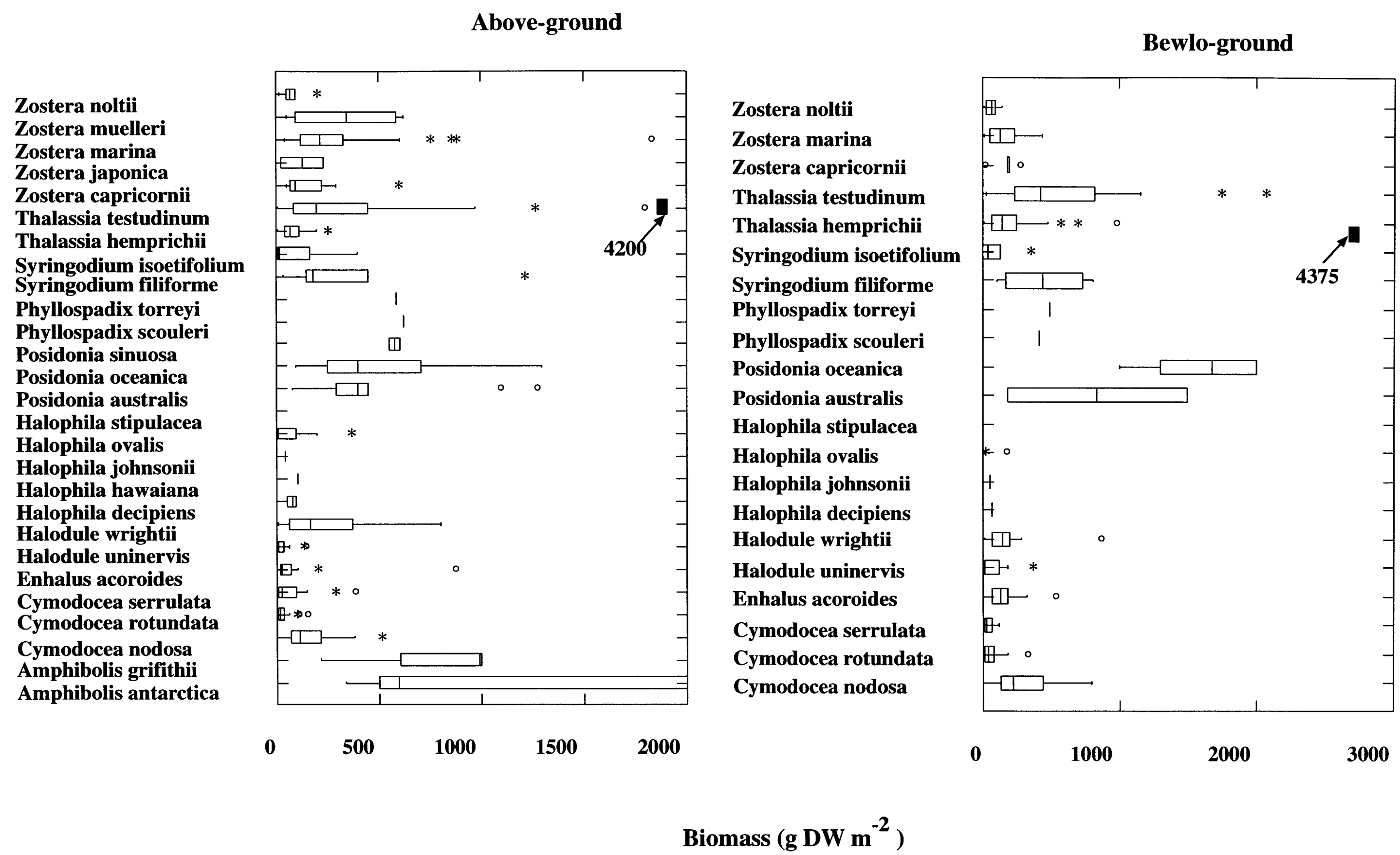
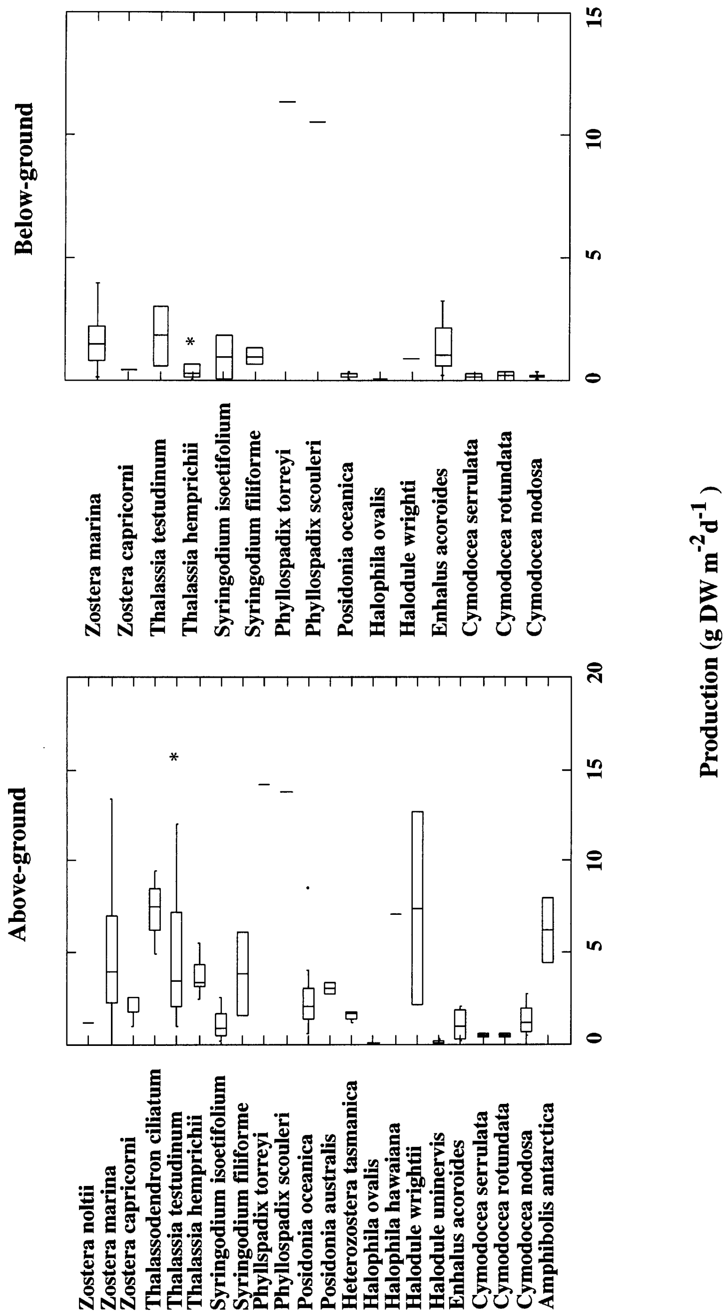


Fig. 3. The distribution of maximum seagrass biomass (a), production (b), their above- to below-ground allocation (c), and the turnover of below- and above-ground material (d). Boxes encompass 25 and 75% quartiles, and the central line represents the median, and bars encompass 95% of the values. Asterisks and open circles indicate observations outside the 95% limits. Some extreme values outside the range of the axis are indicated in the figure.



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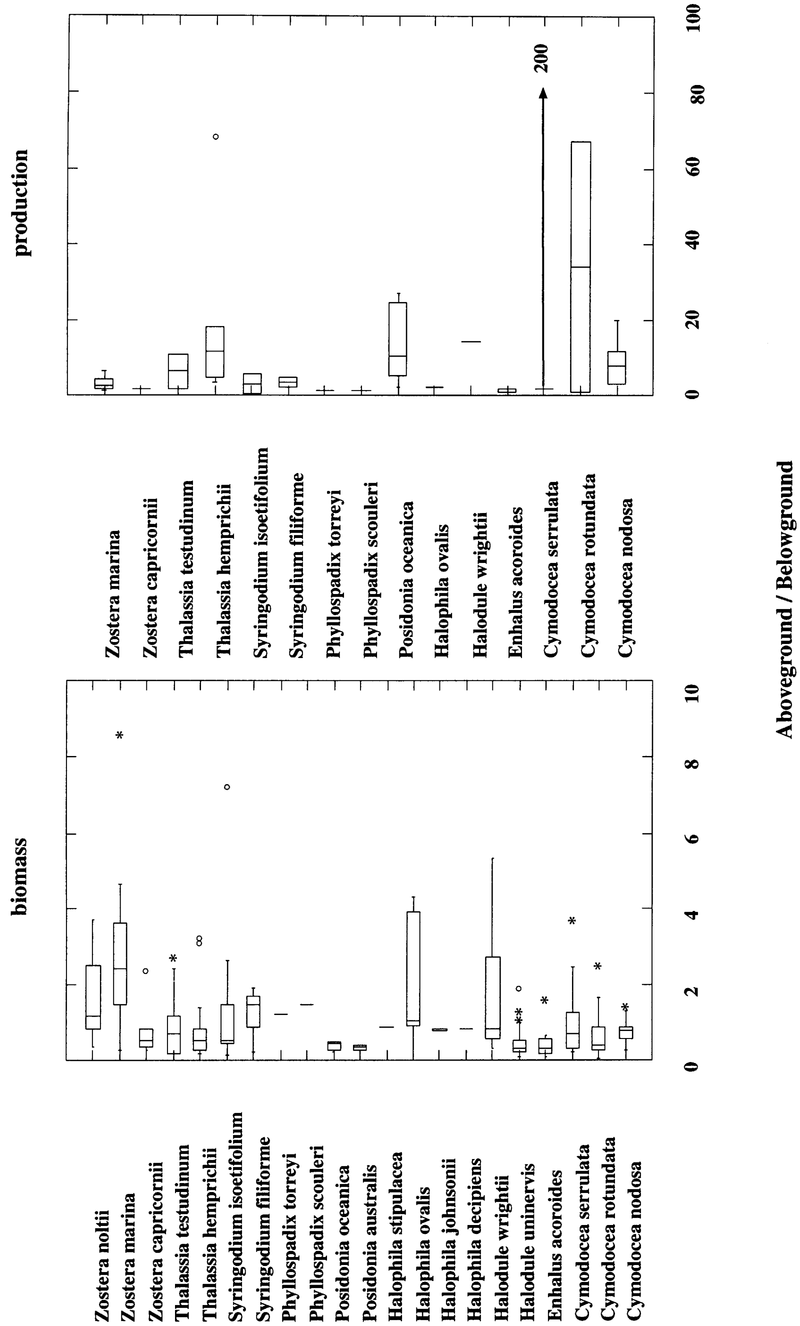

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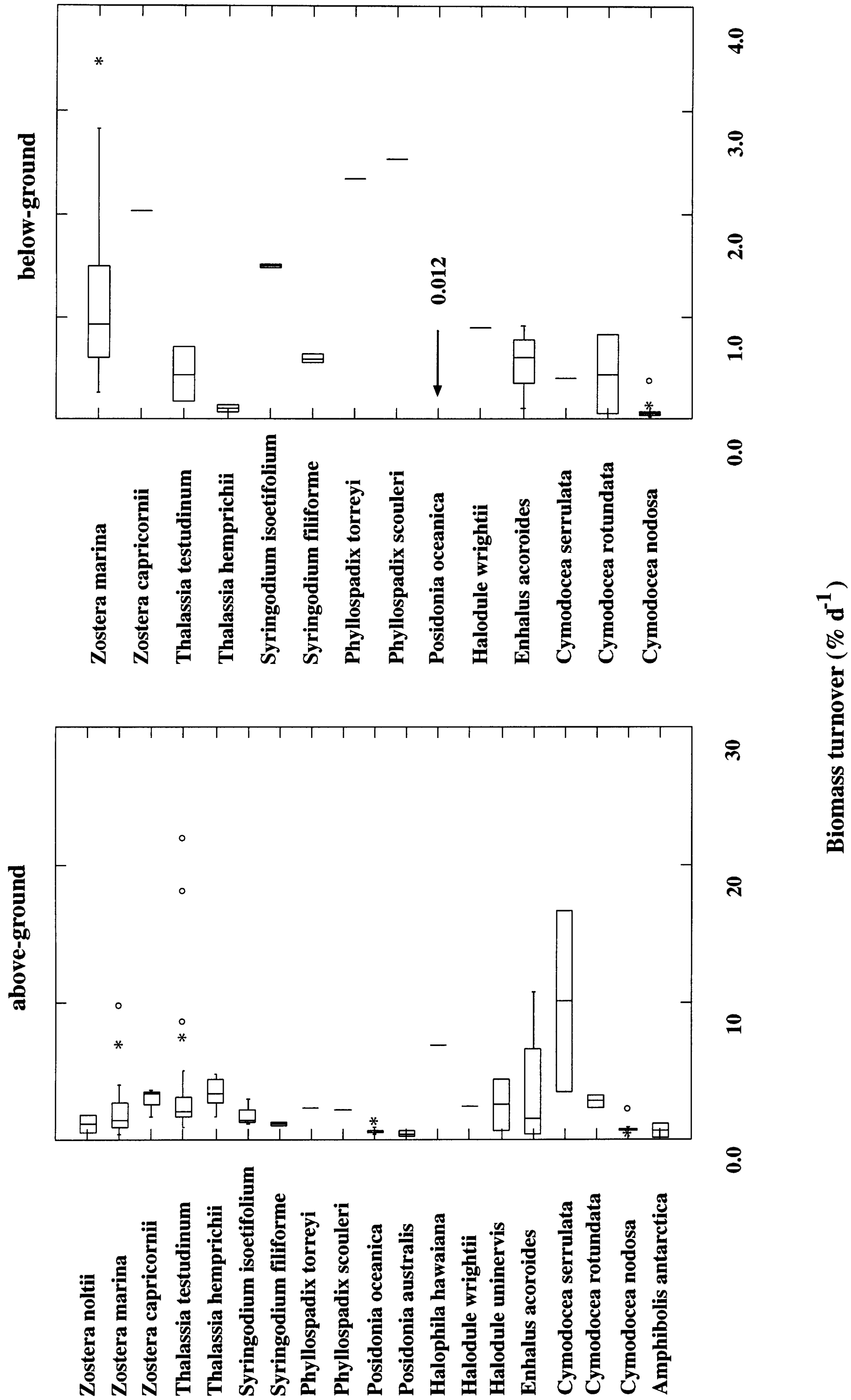

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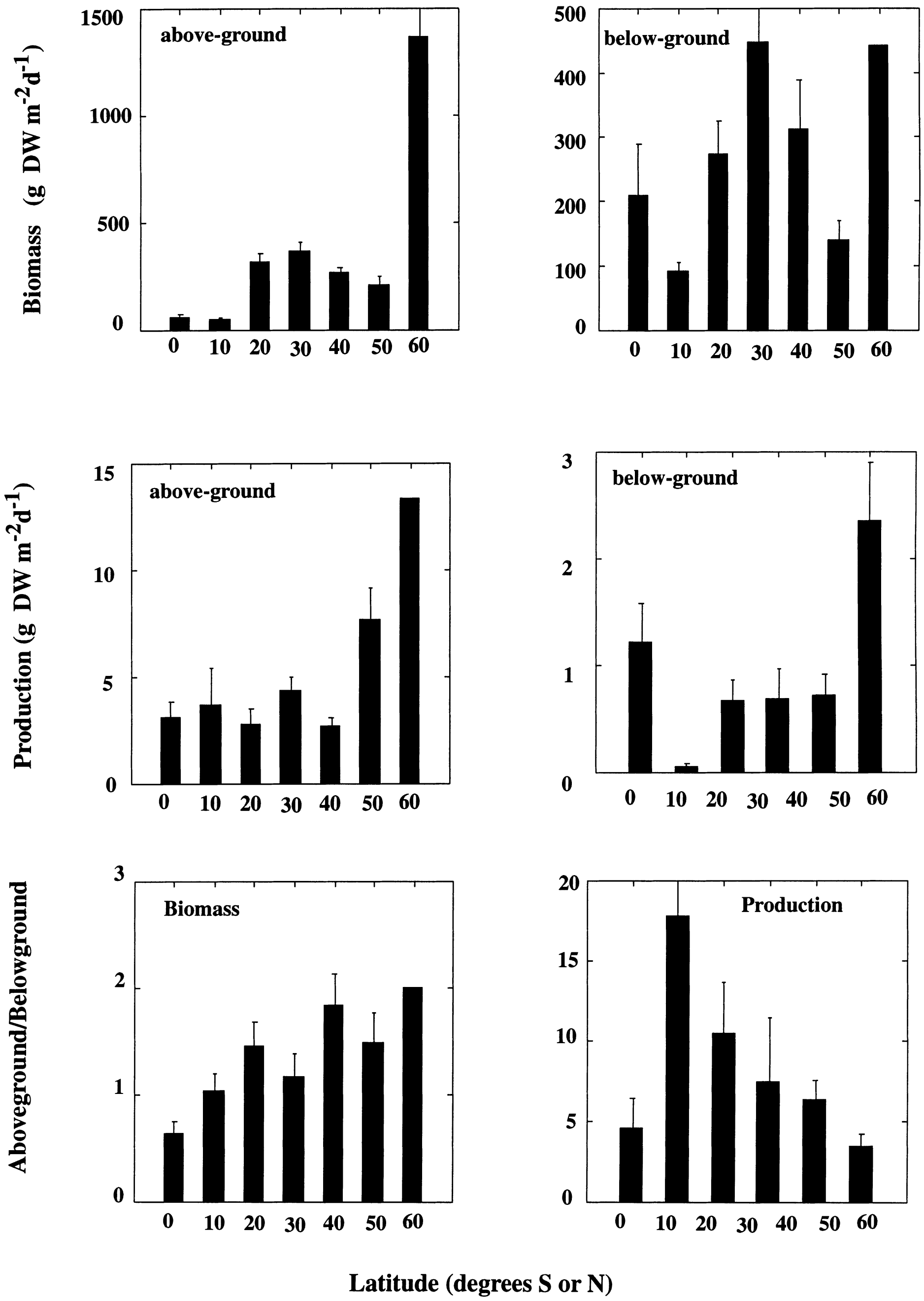

Fig. 4. The latitudinal distribution of maximum seagrass biomass, production and their above- to below-ground allocation. Bars depict the mean (± SE) of the observations comprised within 10 degree bins (whether South of North) of latitude.

Differences among species were found to be a significant source of differences in above-ground (Kruskal–Wallis, $P = 0.00006$) and, to a lesser extent, below-ground (Kruskal–Wallis, $P = 0.0023$) production among the populations (Fig. 3(b)). These differences were, however, independent of seagrass size ($P > 0.05$), and pointed to *Phyllospadix* sp., in particular, along with *Amphibolis antarctica*, *Zostera marina*, *Halodule wrightii*, *Thalassia* sp., and *Thalassodendron ciliatum* as species able to develop highly productive populations. The growth of the massive roots and rhizomes of *Enhalus acoroides*, the largest of the seagrass species, leads to a relatively high below-ground production for this species. In addition, there were significant differences in above and below-ground production (Kruskal–Wallis, $P = 0.00048$ and 0.00186, respectively) across latitudinal ranges. The variation in seagrass production with latitude involved a tendency towards greater above-ground production with increasing latitude and no clear monotonous latitudinal trend in below-ground production (Fig. 4), as also observed for the distribution of below-ground seagrass biomass.

The turnover rates of seagrass biomass averaged $2.6 \pm 0.3\%$ per day (median value = 1.7, $N = 104$) and $0.77 \pm 0.12\%$ per day (median value = 0.57, $N = 47$) for the above- and below-ground material, respectively. Hence, leaf biomass turns over almost three times faster than below-ground biomass does. The relationships between the production and biomass of the above- and below-ground compartments were not linear (Fig. 2), as described by the regression equations,

$$\text{Above-ground production} = 0.1\ \text{Above-ground biomass}^{0.64 \pm 0.06}$$

$$(R^2 = 0.51,\ P < 0.0001,\ N = 104)$$

and,

$$\text{Below-ground production} = 0.02\ \text{Below-ground biomass}^{0.67 \pm 0.12}$$

$$(R^2 = 0.25,\ P = 0.0002,\ N = 47)$$

which indicate that both above- and below-ground seagrass production increase as the 0.6 power of their biomass. Accordingly, seagrass production increases slower than population biomass, so that the biomass of dense seagrass stands turns over slower than that of thin stands. Species-specific differences in above- and below-ground turnover rates were, however, important (Kruskal–Wallis test, $P = 0.00008$ and 0.00095, respectively). There was a tendency for some tropical species to sustain faster above-ground turnover rates than temperate (Fig. 3(d)), but there was no clear latitudinal pattern in above or below-ground turnover rate.

4. Discussion

The results clearly place seagrass populations amongst the most productive autotrophic communities on the planet (Table 2). This reassessment of the biomass and production of seagrass populations confirms the perception that seagrasses tend to form lush, productive ecosystems. The conclusion is based, however, on data unevenly distributed, both in space and across species. Sampling effort has been greatest along the coasts of Europe, North

Table 2
Average biomass and net primary production of different plant communities

Community	Biomass (g DW m^{-2})	Production (g DW m^{-2} per day)	Reference
Forests			
Tropical	45000	5.2	Whittaker (1975)
Temperate	35000	3.4	Whittaker (1975)
Boreal	20000	2.2	Whittaker (1975)
Grasslands			
Savanna	4000	2.4	Whittaker (1975)
Temperate	1600	1.6	Whittaker (1975)
Tundra and alpine	600	0.4	Whittaker (1975)
Swamp and marshes	15000	5.5	Whittaker (1975)
Cultivated land	1000	1.8	Whittaker (1975)
Phytoplankton	9.2	0.35	Cebrián and Duarte (1994)
Microphytobenthos		0.13	Charpy-Roubaud and Sournia (1990)
Coral reefs	2000	0.8	B = Whittaker (1975) P = Crossland et al. (1991)
Macroalgae	40.7	1.0	B = Cebrián and Duarte (1994) P = Charpy-Roubaud and and Sournia (1990)
Marsh plants	767	3.0	B = Cebrián and Duarte (1994) P = Woodwell et al. (1973)
Mangroves		2.7	P = Lugo et al. (1988)
Seagrasses	461	2.7	This study

America and Australia, although there has been a recent increase in the availability of estimates for SE Asian populations (e.g. Terrados et al., 1998). Yet, our knowledge of seagrass biomass and production in some areas is still underrepresented, notably along the African and South American coasts.

The high biomass and production of seagrass populations is directly linked to the important role they play in the ecosystem, and explain why seagrass meadows have been reported to rank amongst the most valuable ecosystems in the world in terms of the value-added services they provide, estimated at 1994 – US$ 19,004 ha^{-1} per year (Costanza et al., 1997). Even so, the skewed distribution of above-ground biomass and production, both when examined for the entire data set and within species, strongly suggest that observed seagrass biomass and production are generally below the maximum values possible. This observation implies that the biomass and production of seagrass meadows are kept below their potential by resource limitation and/or due to heavy losses caused by physical disturbance. Nutrient limitation of seagrass production has been demonstrated experimentally for populations located in contrasting regions of the world (e.g. Short et al., 1990; Perez et al., 1991; Alcoverro et al., 1997; Agawin et al., 1996), although it does appear to be more important in oligotrophic, tropical areas (but see Erftemeijer et al., 1994) than in the comparatively nutrient-rich temperate coasts (e.g. Short, 1987; Pedersen and Borum, 1993), parallel to an increase in porewater phosphate concentrations from tropical to temperate meadows (Hemminga, 1998).

The above-ground material of seagrasses turns over relatively fast (about once every 2 months on average). This rapid turnover implies a limited capacity to accumulate material in above-ground organs despite a moderate (20–25%) efficiency for internal recycling (e.g. Hemminga et al., 1991; Pedersen and Borum, 1993; Hemminga et al., 1999 this volume). Light availability imposes an ultimate limit to the biomass and production of seagrasses, particularly towards the light-imposed depth limit of the populations (Duarte, 1991b). Grazing losses are, in general, relatively unimportant (about 18% on average, Cebrián and Duarte, 1994), but can be high in tropical areas (Cebrián and Duarte, 1997). Grazing losses may reduce biomass somewhat, but they have been reported to stimulate production in some instances (e.g. Tomasko and Dawes, 1989; Cebrián et al., 1997). Disturbance reduces the cover of seagrasses and can, therefore, limit both biomass and production. The greater prevalence of nutrient limitation and the greater losses experienced by seagrasses in tropical areas may account for the observed tendency for both seagrass biomass and production to increase with increasing latitude.

The distribution of below-ground biomass and production was much less skewed than that for above-ground biomass, suggesting below-ground biomass and production to be less controlled by resource availability or losses. The comparatively slow turnover of the below-ground organs of seagrasses allows for a greater capacity for the long-term accumulation of materials. This capacity reaches reef-building capacity in the long-lived seagrass *P. oceanica* (Romero et al., 1994), which large below-ground biomass turns over at the slowest rates observed for any seagrass species. At the same time, grazing losses of below-ground material are negligible for most seagrass species, although it is grazed by vertebrates in *Halophila* sp. (e.g. Supanwanid, 1996). Below-ground material is also less prone to losses derived from disturbance. These factors allow seagrasses to maintain a relatively high below-ground biomass (about equal to that maintained above-ground), despite a generally modest production. The 4-fold greater above-ground production compared to the below-ground production, based on median values, is, however, likely to be an overestimation. Below-ground production is generally underestimated, because the estimates available in the literature often exclude root production, which represent, on average, some 15–50% of the total production (Duarte et al., 1998). Future efforts to assess the role of seagrasses in the carbon economy of the ecosystem should, therefore, include, and examine the fate of the below-ground production.

Previous estimates of the global seagrass production (0.49 Gt C per year, Duarte and Cebrián, 1996) represent, when scaled to the estimated area covered by seagrass communities ($0.6 \times 10^6\ \mathrm{km}^2$), an average production of $816\ \mathrm{g\,DWm}^{-2}$ per year. The average annual seagrass production derived from the data compiled here is $1012\ \mathrm{g\,DW\,m}^{-2}$ per year (including above- and below-ground production), which is 25% higher than the previous estimate. This revised estimate is a conservative one, since root production (15–50% of total production, Duarte et al., 1998) is underrepresented here. Hence, recent estimates of the average surplus carbon produced by seagrasses (16% of seagrass production, cf. Duarte and Cebrián, 1996), should also be revised to yield 0.16 Gt C per year, which implies that seagrasses should be responsible for 15% of the total excess carbon produced in the global ocean (i.e. the net CO_2 uptake by oceanic biota, cf. Duarte and Cebrián, 1996). Seagrasses are, therefore, significant components of its carbon budget.

In summary, this reassessment of the biomass and production of seagrass populations confirms the perception that they often form lush, productive ecosystems. Observations are, however, sparse for some areas, notably in the coasts of Africa and South America, and species, particularly for non-dominant ones. These imbalances in our knowledge of seagrass biomass and production point to a need of greater efforts in poorly studied areas and species in order to achieve an improved inventory of seagrass resources around the world. In addition, the selection of sampling sites within specific areas has not been made at random, and is likely to have been biased, in some cases, towards particularly lush and shallow populations, adding uncertainty as to the accuracy of these estimates. Despite these uncertainties, the present estimates of average seagrass biomass and production provide a faithful synthesis of current knowledge on the subject. The estimates are also based on a thorough compilation of hundreds of estimates obtained world-wide, and are, therefore, likely to remain relatively unchanged when additional data are incorporated. In fact, incomplete knowledge on the world-wide distribution and areal cover of seagrass populations adds considerable uncertainty as to the area seagrass meadows cover at the global scale, and is likely to be the most important source of imprecision in current estimates of global seagrass biomass and production.

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