

Fate of production of the seagrass *Cymodocea nodosa* in different stages of meadow formation

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ABSTRACT: Many seagrass species can be found in different stages of meadow formation, from recently established patches to fully developed meadows. However, little is known about how the fate of seagrass production (i.e. herbivory, decomposition, export and carbon storage), and its ecological implications, vary across meadow development. Here we examine the fate of production of the seagrass *Cymodocea nodosa* (Ucria) Ascherson across increasing stages of meadow formation in a Spanish Mediterranean coastal lagoon, Alfacs Bay. Differences in time elapsed since seagrass establishment explained only a modest fraction of the variability in the fate of production, with most production routes ranging over 1 order of magnitude for any given time. However, on the whole, leaf consumption by herbivores increased by 5-fold, and decomposition and export of detrital leaves by almost 2-fold from young (i.e. 0 to 2 yr since seagrass establishment) to old (i.e. 5 to 7 yr since establishment) stages of meadow formation. Below-ground decomposition also increased by almost 1 order of magnitude from young to old stages. These results indicate that longer-established *C. nodosa* patches transfer greater fluxes of production to consumers, and should thus support greater levels of secondary production. Moreover, seagrass biomass and detritus increased by 3-fold from young to old stages, showing that longer-established patches may act as greater sinks of organic carbon. These results suggest that generalizations about the extent of carbon storage and secondary production maintained by seagrasses must consider the stage of meadow formation typically exhibited by the species concerned.

KEY WORDS: *Cymodocea nodosa* · Meadow formation · Herbivory · Decomposition · Export · Biomass storage

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INTRODUCTION

The ecological role of seagrass meadows in coastal ecosystems is partially determined by the interplay between the magnitude and the fate of seagrass production. For instance, highly productive seagrass species with low rates of decomposition usually store large detrital pools, thereby acting as significant carbon sinks in the communities they inhabit (Lipkin 1979,

Romero et al. 1994). Species exporting large amounts of detrital leaves off the meadow may fuel substantial levels of secondary production in receiving communities (Zieman et al. 1979, Josselyn et al. 1983, Bach et al. 1986, Fry & Virnstein 1988, Romero et al. 1992). In addition, highly productive seagrass species normally support high levels of herbivore production in spite of the modest percentages of production consumed (Thayer et al. 1984, Cebrián & Duarte 1998). While reports of the magnitude of seagrass production are abundant, evaluations of the fate of production are still scanty.

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Many seagrass species are often encountered in different stages of meadow formation, from recently established patches to climax meadows with steady carbon pools. For instance, permanent patchy distributions of species growing on mobile sediments may result from the migration of sand waves. Seagrass growth is stimulated at the wave front—an adaptive response—aimed at overcoming burial, whereas in the wave troughs the seagrass dies when horizontal rhizomes are exposed and subsequently epiphytised (Marbà & Duarte 1994, 1995, Marbà et al. 1994). Conversely, seagrass patches coalesce to form extensive, steady meadows on more stable sediments (Patriquin 1975, Fonseca et al. 1983, Duarte 1991, Marbà & Duarte 1995). Moreover, pioneer species with a fast turnover in heterogeneous meadows dominated by climax species with a slower turnover (e.g. *Halodule wrightii* or *Halophila ovalis* in meadows dominated by *Thalassia testudinum*) continuously accrue biomass because they rapidly colonize bare zones created by micro-perturbations within the meadow, but are eventually outcompeted by the slower growing dominant species (Den Hartog 1971, Zieman 1982, Zieman et al. 1989, Williams 1990, Fourqurean et al. 1995). In addition, natural disturbances, such as hurricanes (Patriquin 1975, Preen et al. 1995) or overgrazing (Camp et al. 1973, Supanwanid 1996), and anthropogenic large-scale perturbations, such as boat activity (Walker et al. 1989, Dawes et al. 1997) and sewage outfalls (Burkholder et al. 1994, Pergent-Martini & Pergent 1996), may entail different degrees of seagrass loss and subsequent recolonization.

Various lines of evidence suggest that the fate of seagrass production may change across increasing stages of meadow formation. Older stages exhibit increased plant production and structure, which, in turn, entail enhanced food and refuge availability for herbivores and, in turn, greater herbivore abundance (Heck & Wetstone 1977, Heck & Orth 1980, Orth et al. 1984, Stoner & Lewis 1985, Irlandi 1997). Larger numbers of herbivores could remove higher percentages of production, thus becoming a more important controlling factor of seagrass biomass at older stages of meadow formation. Moreover, enhanced above-ground structural complexity (i.e. higher shoot density) with increasing meadow development may reduce water friction within the seagrass canopy (Ward et al. 1984, Irlandi & Peterson 1991, Fonseca & Cahalan 1992), thereby depressing the export of sloughed leaves. Nevertheless, the influence of increasing stages of meadow formation on the fate of seagrass production remains to be examined.

Cymodocea nodosa (Ucria) Ascherson is an abundant seagrass species in the Mediterranean (den Hartog 1970) that is often dominant in shallow coastal lagoons (Perez & Romero 1992, 1994, Terrados & Ros

1992). Several reports have addressed the magnitude of biomass and production of *C. nodosa* (Gessner & Hammer 1960, Drews 1978, Peduzzi & Vuckovic 1990, Vant Lent et al. 1991, Terrados & Ros 1992, Perez & Romero 1994), but its ecological role is poorly known because only a few aspects of the fate of its production have been examined (Mateo 1995, Cebrián et al. 1996, 1997). Moreover, meadows of *C. nodosa* often comprise different stages of development (Duarte & Sand-Jensen 1990a, Marbà et al. 1994, Marbà & Duarte 1995), thereby providing a good scenario for examining the effects of meadow development on the fate of seagrass production. Here, we quantify herbivory, detrital production, detrital export, decomposition and accumulation of biomass and detritus in *C. nodosa* patches of increasing age (i.e. from young to older stages of meadow formation) in Alfacs Bay, a shallow protected lagoon within the Ebro Delta (Spain).

METHODS

Study area and field sampling. The study was carried out during July 1994 on the southern edge of Alfacs Bay (Spain; 40° 36.15' N, 0° 43.08' E) on the bay side of the 5 km long, 300 m wide sand bar which separates the bay from the open sea (Fig. 1). Depth at the study site ranged from 0.1 to 0.8 m (Marbà et al. 1994, Marbà & Duarte 1995, Vidondo et al. 1997). The hydrographical properties of the bay generate submerged sand dunes that migrate from offshore into the bay at an average speed of $13 \pm 0.6 \text{ m yr}^{-1}$ (Marbà et al. 1994). The distance between 2 consecutive dunes ranges from 7 to 29 m, and their height varies from 0.07 to 0.65 m (Marbà et al. 1994). *Cymodocea nodosa* (Ucria) Ascherson appears in patches scattered throughout the area covered by the dunes. Patch size varies from a few cm (i.e. a single seedling) to 80 m in diameter (Duarte & Sand-Jensen 1990a). The passage of dune crests over *C. nodosa* stimulates the growth rates and flowering frequency of the vertical shoots—an adaptive response to overcome burial (Caye & Meinesz 1985, Marbà & Duarte 1994, 1995). Exposure of horizontal rhizomes and roots in dune troughs leads to fast, intense coating with epiphytes and subsequent death (Duarte & Sand-Jensen 1990a). New patches are generated from the seeds produced during the passage of dune crests (Marbà & Duarte 1995). Hence, sand dune migration is responsible for the occurrence of *C. nodosa* patches of different sizes (Marbà & Duarte 1995), the variability in patch size arising from heterogeneity in dune size and migration speed, success in seed germination, and coalescence of smaller patches into larger ones. Larger patches are generally older and thus representative of a later stage of meadow for-

mation (Duarte & Sand-Jensen 1990a, Marbà & Duarte 1995, Vidondo et al. 1997).

To examine the variability in the fate of *Cymodocea nodosa* production at different stages of meadow formation, we chose 14 patches ranging in size from a few cm to 80 m. Patch size was determined as the length of the longest axis between 2 edges across the geometrical center of the patch. Samples were taken at regular intervals from 1 edge to the geometrical center in some patches, and from edge to edge in the rest of patches. The number of samples per patch ranged from 1 to 10 depending on patch size. Samples consisted of 20 cm diameter aluminum cores dug into the sediment down to a depth of ca 30 cm. After retrieval, the samples were rinsed through a 1 mm sieve, stored in plastic

bags, and carried to the laboratory. There, we separated *C. nodosa* from the other organisms collected (mainly macroalgae), counted shoot density, and determined the oldest shoot age in each sample. Shoot age was estimated as number of PIs (i.e. plastochrone intervals, with 1 PI corresponding to the time elapsed between the appearance of 2 consecutive leaves; Erickson & Michellini 1957) by summing the number of internodes along the vertical rhizome and the number of standing leaves (Duarte et al. 1994). Shoot age was used as a conservative estimate of the time elapsed since seagrass establishment (Duarte & Sand-Jensen 1990a, b), and translated to years through knowledge of the mean number of leaves produced per shoot per year in the patches studied (i.e. 13 leaves shoot⁻¹ yr⁻¹; Perez 1989, Perez & Romero 1994). We took a total of 52 samples ranging from 5 mo to 7 yr since seagrass establishment.

In each sample, we measured the width and length of all the leaves in the shoots collected, and registered whether the leaf blades were intact or had been torn by grazers or physical agents. Each sample was then partitioned into leaves and alive and dead below-ground parts, and the biomass (g dry wt m⁻²) of each compartment and leaf-specific area (g dry wt cm⁻²) was quantified. In addition, prior to core-harvesting, we sampled the *Cymodocea nodosa* detrital leaves enclosed in 0.25 m² quadrats adjacent to the location of core sampling. To do so, we vacuumed the area covered by the quadrat with a suction pump and sieved the sucked samples through a 1 mm mesh. The samples were then stored in bags and carried to the laboratory. Detritus samples were taken only from patch edges to their geometrical centers. For each sample, detrital leaf fragments >0.5 cm (the limit of visual resolution) were sorted out from all other material and their mass (g dry wt m⁻²) quantified.

Magnitude and fate of leaf production. At every location sampled, we estimated leaf production, removal of leaf apices by herbivores and physical agents (e.g. waves and currents), leaf shedding by senescence, decomposition of leaf detritus, and export of leaf detritus off the location. The seasonality in leaf appearance and growth rates of the population studied is well documented (Perez 1989, Perez & Romero 1992, 1994). This information, in conjunction with the mean number of leaves (\pm SD) per shoot found in July (4 ± 0.6), allowed us to estimate that, on average, 3 of the 4 leaves had been formed ('born') since May and that the 4th leaf was 2 mo old. Furthermore, the existing reports document that the mean number of leaves per shoot in May is 4, and, therefore, we estimated that, on average, 3 leaves per shoot had been shed since then. Based on these estimates, we calculated the cumulative leaf production per shoot (LPS) from May to July in

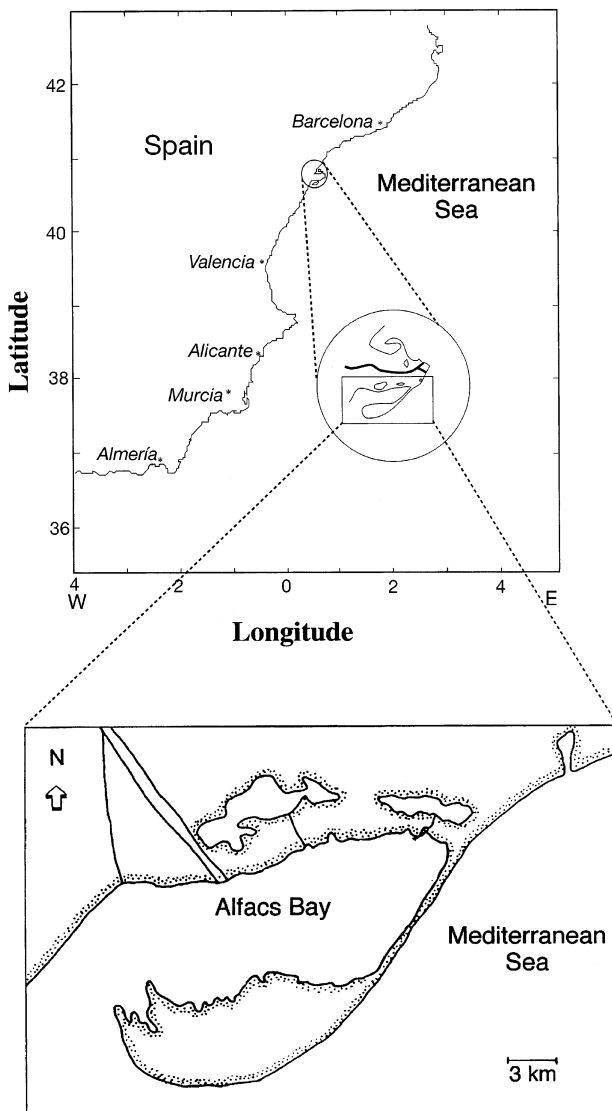


Fig. 1. Map of study site on the southern edge of Alfacs Bay, Spain

each location sampled (mg dry wt shoot⁻¹) as the sum of production by born leaves ($B_{1i} + B_{2i} + B_{3i}$), the leaves remaining through the 60 d period ($B_{4i} - B_{1i}$) and shed leaves [$(B_{4i} - B_{2i}) + (B_{4i} - B_{3i}) + (B_{4i} - B_{4i})$]:

$$\text{LPS} = B_{1i} + B_{2i} + B_{3i} + (B_{4i} - B_{1i}) + (B_{4i} - B_{2i}) + (B_{4i} - B_{3i}) + (B_{4i} - B_{4i}) \quad (1)$$

where B_{1i} , B_{2i} , B_{3i} and B_{4i} = mean biomass of the 1st, 2nd, 3rd and 4th intact leaves (not torn by grazers or physical agents) in the sampling location in July, respectively. This approach assumes that the mean biomass for any given leaf number remains constant throughout the 60 d period. The bias introduced is, however, small, since the growth of born leaves, unaffected by this assumption, contribute most (>75%) to the LPS. Leaf production was converted to an areal and daily basis (g dry wt m⁻² d⁻¹) by multiplying by the shoot density measured at the respective locations (shoot m⁻²) and dividing by 60 d.

Cymodocea nodosa has narrow leaves, and only a single or (rarely) a few herbivore bites are present on the leaf blades regardless of grazing intensity. Moreover breakage of partially grazed leaf tips by waves and currents may be substantial. Hence, calculation of herbivory on *C. nodosa* from bite marks on the blades could lead to severe underestimation (Cebrián et al. 1996). To rule this out, we applied the rationale developed by Cebrián et al. (1996) and Cebrián & Duarte (1998), and estimated the cumulative removal of leaf apices by herbivores and other physical agents (e.g. waves and currents) per shoot from May to July (apical leaf removal, ALR, mg dry wt shoot⁻¹) in each location as the sum of the differences in mean biomass between intact and torn leaves for the born [$(B_{1i} - B_{1t}) \times F_{1t} + (B_{2i} - B_{2t}) \times F_{2t} + (B_{3i} - B_{3t}) \times F_{3t}$], remaining [$(B_{4i} - B_{4t}) \times F_{4t} - (B_{1i} - B_{1t}) \times F_{1t}$], and shed [$(B_{4i} - B_{4t}) \times F_{4t} - (B_{2i} - B_{2t}) \times F_{2t}$] + [$(B_{4i} - B_{4t}) \times F_{4t} - (B_{3i} - B_{3t}) \times F_{3t}$] + [$(B_{4i} - B_{4t}) \times F_{4t} - (B_{4i} - B_{4t}) \times F_{4t}$] leaves:

$$\begin{aligned} \text{ALR} &= (B_{1i} - B_{1t}) \times F_{1t} + (B_{2i} - B_{2t}) \times F_{2t} + (B_{3i} - B_{3t}) \times F_{3t} \\ &+ [(B_{4i} - B_{4t}) \times F_{4t} - (B_{1i} - B_{1t}) \times F_{1t}] \\ &+ [(B_{4i} - B_{4t}) \times F_{4t} - (B_{2i} - B_{2t}) \times F_{2t}] \\ &+ [(B_{4i} - B_{4t}) \times F_{4t} - (B_{3i} - B_{3t}) \times F_{3t}] \\ &+ [(B_{4i} - B_{4t}) \times F_{4t} - (B_{4i} - B_{4t}) \times F_{4t}] \\ &= 3 \times (B_{4i} - B_{4t}) \times F_{4t} \end{aligned} \quad (2)$$

where B_{1i} , B_{2i} , B_{3i} and B_{4i} are as in Eq. (1); B_{1t} , B_{2t} , B_{3t} and B_{4t} = mean biomass of the 1st, 2nd, 3rd and 4th torn leaves in the sampling location in July; and F_{1t} , F_{2t} , F_{3t} and F_{4t} = frequencies of 1st, 2nd, 3rd and 4th leaves out of the total number of 1st, 2nd, 3rd and 4th leaves in the sampling location in July. This approach assumes that the biomass difference between intact and torn leaves for any given leaf number is constant

between May and July. Hence, our estimates of ALR may be somewhat skewed.

Therefore, we first compared the mean biomass of intact 4th leaves with that of torn 4th leaves in each population and used Eq. (2) to derive ALR if these were different (Student's *t*-test, H_0 : mean values are equal, $p < 0.05$). Otherwise, we assumed that all torn leaves had been bitten by herbivores at least once and arrived at a conservative estimate of ALR by multiplying the mean leaf biomass covered by 1 herbivore bite by the number of leaves shed during May to July (i.e. 3), and by F_{4t} . In each population, the mean leaf surface covered by 1 herbivore bite was calculated by digitizing the area covered by each discernable bite encountered and transforming to biomass using the leaf-specific area for that population. ALR was expressed on an areal and daily basis (g dry wt m⁻² d⁻¹) by multiplying by shoot density (shoot m⁻²) and dividing by 60 d. The 2 approaches assume that intact and torn leaves have similar growth rates, which was supported by a parallel study (Cebrián et al. 1998).

The cumulative leaf shedding per shoot from May to July (mg dry wt shoot⁻¹) was calculated for each location sampled by multiplying the mean biomass of both intact and torn 4th leaves in the location by 3 (i.e. by the average number of leaves shed). This approach may involve a certain degree of overestimation, since 4th leaves are longer in July than in May. The values obtained were converted to an areal and daily basis (g dry wt m⁻² d⁻¹) by multiplying by shoot density (shoot m⁻²) and dividing by 60.

For each location sampled, the cumulative decomposition (D) of leaf detritus from May to July (g dry wt m⁻²) may be calculated following the procedure presented by Romero et al. (1992):

$$D = DM_{\text{may}} \times (1 - e^{-k \times 60}) + LS \times (1 - e^{-k \times (60/2)}) \quad (3)$$

where DM_{may} = detrital leaf mass (g dry wt m⁻²) in May, and LS = cumulative leaf shedding from May to July (g dry wt m⁻²) at a given location; k = average decomposition rate of leaf detritus (d⁻¹) during the period, which has been estimated as 0.011 d⁻¹ by Mateo (1995). DM_{may} was unknown, but could be removed from the equation without compromising the results because LS is >1 order of magnitude larger than DM_{may} in the population studied (Mateo 1995). D was thus estimated as:

$$D = LS \times (1 - e^{-k \times (60/2)}) \quad (4)$$

The values obtained were converted to g dry wt m⁻² d⁻¹ by dividing by 60.

The cumulative export (E) of detrital leaves from each sampling location from May to July (g dry wt m⁻²)

can be derived from the following equation (Romero et al. 1992):

$$DM_{\text{july}} - DM_{\text{may}} = LS - D - E \quad (5)$$

where DM_{july} = detrital mass (g dry wt m⁻²) at the given location in July, and DM_{may} , LS and D are as in Eq. (3). The increment in detrital mass from May to July ($DM_{\text{july}} - DM_{\text{may}}$) should be similar to the detrital mass in July (DM_{july}) because LS is >1 order of magnitude higher than DM_{may} (Mateo 1995). Therefore, DM_{may} can be disregarded in Eq. (5), and E estimated as:

$$E = LS - D - DM_{\text{july}} \quad (6)$$

The values obtained were converted into g dry wt m⁻² d⁻¹ by dividing by 60.

Magnitude and fate of below-ground production.

Because the rhizomes and roots of the *Cymodocea nodosa* population studied have a turnover longer than 1 yr (Perez & Romero 1994), we examined the fate of below-ground production across increasing stages of meadow formation by calculating the changes in below-ground production, mortality and decomposition over 1 yr increments since seagrass establishment. To do so, we averaged the below-ground (rhizomes and roots) biomass of all the locations established within the same year. Hence, any annual increment in below-ground biomass (ΔBB , g dry wt m⁻² yr⁻¹) and detrital biomass (ΔDB , g dry wt m⁻² yr⁻¹) corresponds to:

$$\Delta BB = \frac{BB_{n+1} - BB_n}{1 \text{ yr}} = BP - M \quad (7)$$

$$\Delta DB = \frac{DB_{n+1} - DB_n}{1 \text{ yr}} = M - BD \quad (8)$$

where BB_{n+1} and DB_{n+1} = mean below-ground biomass and detrital mass (g dry wt m⁻²) at Year $n+1$, BB_n and DB_n = mean below-ground biomass and detrital mass (g dry wt m⁻²) at Year n , and BP , M and BD = mean below-ground production, mortality and decomposition from Years n to $n+1$ (g dry wt m⁻² yr⁻¹). In turn, BD corresponds to (Romero et al. 1992):

$$BD = DB_n \times (1 - e^{-k}) + M \times (1 - e^{-k/2}) \quad (9)$$

where k = decomposition rate (yr⁻¹) of below-ground detritus, estimated as ~1 yr⁻¹ by Romero et al. (1990) in the area studied. BD in Eq. (8) can be replaced by its equivalent in Eq. (9); rearranging, we obtain:

$$M = \frac{DB_{n+1} - DB_n \times e^{-k}}{e^{-k/2}} \quad (10)$$

This equation allowed us to estimate the annual changes in M across increasing stages of meadow formation. Subsequently, we combined the annual M estimates with Eqs. (7) & (8) to calculate the annual changes in BP and BD .

Statistical analyses. We examined the changes in the magnitude and fate of *Cymodocea nodosa* leaf production across increasing stages of meadow formation by least-square regression of leaf production, apical removal, shedding, and decomposition and export of leaf detritus versus time since seagrass establishment (oldest shoot age) for all the locations sampled. Changes in below-ground biomass and detrital mass with increasing stages of meadow formation were analyzed by regressing yearly averaged values (i.e. mean values for all the locations established within the same year) versus number of years elapsed since colonization. Data were log-transformed when needed to meet the assumptions of least-square regression techniques. The variability in the estimates of yearly below-ground production, mortality and decomposition was evaluated with techniques of error propagation (Tsokos 1972), assuming that k was known without error.

RESULTS

Leaf biomass *Cymodocea nodosa* ranged over 2 orders of magnitude across the locations sampled (Table 1). Leaf production, apical removal and shedding by senescence also varied widely, with leaf production and shedding varying by 2 orders of magnitude and apical removal varying by 3 orders of magnitude across locations (Table 1). This variability was partially associated with differences in the time elapsed since seagrass establishment. Leaf biomass tended to increase with increasing time since establishment (Fig. 2, Table 2). Leaf production, apical removal and shedding also tended to be higher at older stages of meadow formation (Fig. 2, Table 2). Yet, differences in time since establishment only explained a modest fraction of the variability in leaf biomass, production, apical removal and shedding across locations (Table 2), with these variables ranging over 1 order of magnitude for any given time (Fig. 2).

The magnitude and fate (i.e. decomposition and export) of leaf detritus also varied by ~2 orders of magnitude across locations (Table 1). Only 1 of the sampled locations showed a negative value of detrital export (i.e. -0.05 g dry wt m⁻² d⁻¹), indicative of a net import of detritus over the 2 mo considered. Longer established locations tended to store larger amounts of leaf detritus (Fig. 3a, Table 2), and to have higher values of decomposition and export (Fig. 3b, Table 2). Yet these tendencies were weak, with differences in time since

Table 1. *Cymodocea nodosa*. Sample sizes (n), ranges, means and standard deviations (SD) of above- and below-ground biomass and detrital mass, and of magnitude and fate of above-ground production. DW: dry weight

Variable (units)	n	Range	Mean	SD
Above-ground compartment				
Leaf biomass (g DW m ⁻²)	52	1.4–272.1	103.6	82.7
Leaf production (g DW m ⁻² d ⁻¹)	47	0.1–8.7	2.8	2.2
Leaf apical removal (g DW m ⁻² d ⁻¹)	47	0.003–3.3	0.4	0.6
Leaf shedding (g DW m ⁻² d ⁻¹)	47	0.07–6.4	2.0	1.5
Leaf detrital mass (g DW m ⁻²)	38	0.2–12.6	4.8	3.0
Leaf decomposition (g DW m ⁻² d ⁻¹)	47	0.02–1.8	0.6	0.4
Leaf export (g DW m ⁻² d ⁻¹)	35	-0.05–4.6	1.4	1.1
Below-ground compartment				
Rhizome biomass (g DW m ⁻²)	52	7.1–456.5	136.8	116.1
Root biomass (g DW m ⁻²)	52	3.7–254.4	84.6	56.7
Below-ground detrital mass (g DW m ⁻²)	52	3.2–665.2	187.9	171.6

Table 2. *Cymodocea nodosa*. Results of least-square regressions of leaf biomass, detrital mass and routes of the fate of leaf production versus time since *C. nodosa* establishment for all locations sampled. To comply with assumptions of least-square regression techniques, all regressions refer to log-transformed variables except that between leaf detrital mass and time. Prior to log-transformation, 1.05 was added to all values of export to eliminate the negative value of -0.05 dry wt m⁻² d⁻¹ found in 1 location (Wall 1986)

Variable regressed vs time since establishment	n	R ²	F-ratio	p
Leaf biomass	52	0.28	20.8	<0.0001
Leaf production	47	0.36	27.2	<0.00001
Leaf apical removal	47	0.14	8.6	<0.01
Leaf shedding by senescence	47	0.36	27.1	<0.00001
Leaf detrital mass	38	0.11	5.6	<0.05
Leaf decomposition	47	0.36	27.2	<0.00001
Leaf export	35	0.11	5.4	<0.05

establishment explaining only a small fraction of the variability in the magnitude and fate of leaf detritus (Table 2).

Both rhizome and root biomass ranged over 1 order of magnitude across locations (Table 1). Below-ground detrital mass also varied considerably (i.e. over 2 or-

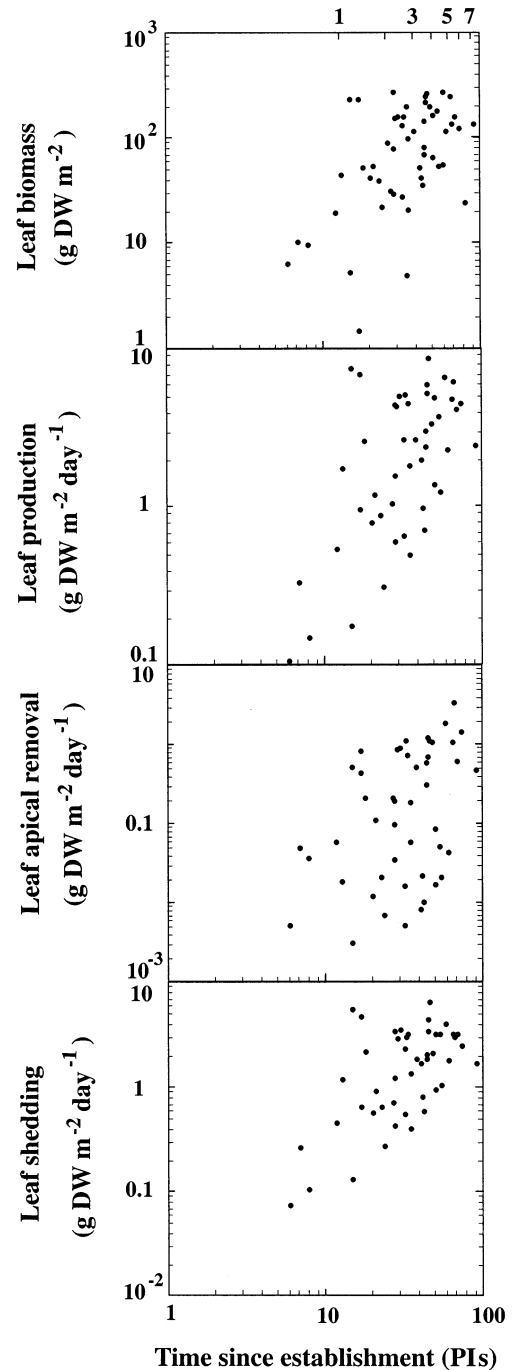


Fig. 2. *Cymodocea nodosa*. Relationships between leaf biomass, leaf production, leaf apical removal and leaf shedding, and time since sea-grass establishment for all locations sampled. DW: dry wt, PIs: plastochrone intervals

ders of magnitude), and showed a similar range to that of total (i.e. rhizomes + roots) below-ground biomass (Table 1). Differences in yearly averaged values of below-ground biomass and detrital mass were strongly

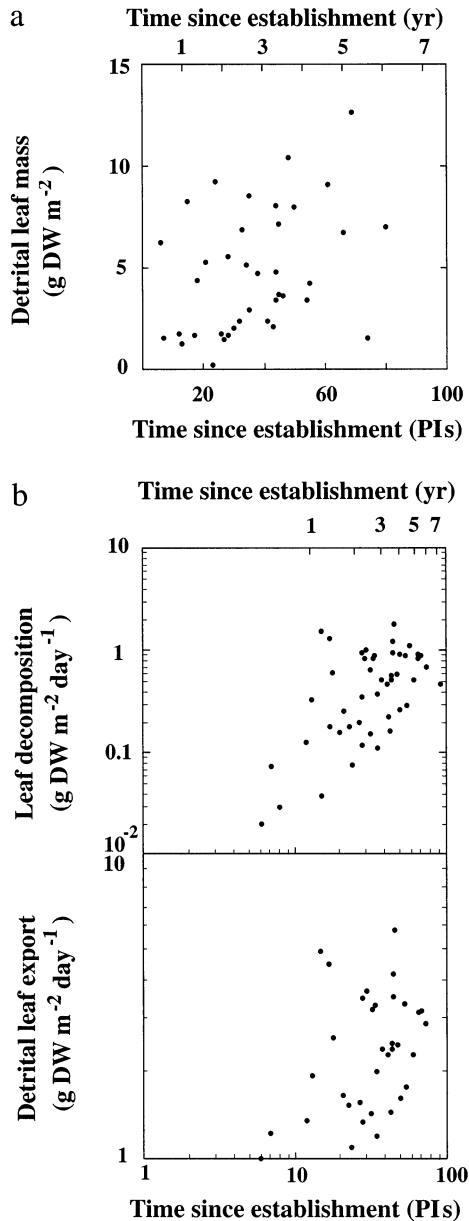


Fig. 3. *Cymodocea nodosa*. Relationships (a) between detrital leaf mass and time since seagrass establishment for all the locations sampled, and (b) between leaf decomposition and detrital leaf export, and time since seagrass establishment for all the locations sampled. Prior to log-transformation, 1.05 was added to all export values to eliminate the negative value of -0.05 dry wt $m^{-2} d^{-1}$ found in 1 location (Wall 1986)

associated with the variability in time since establishment, with the tendencies towards a larger biomass and detrital mass with increasing time explaining ca 85% of these differences (Fig. 4, Table 3). The increase in below-ground biomass and detrital mass with time since establishment was not linear, with little increase after 4 yr since establishment (Fig. 4).

During the first 4 yr since establishment, the increase in detrital mass (Figs. 3a & 4) was disproportionately larger than that in total biomass (i.e. leaves + rhizomes + roots; Figs. 2 & 4) and, as a result, the ratio of total biomass to detrital mass tended to decrease during that period (Fig. 5). This ratio, however, reached a constant value of ca 2 after 4 yr since establishment (Fig. 5) because both below-ground biomass and below-ground detrital mass (which largely dominate over leaf biomass and leaf detritus, respectively) increased at similar rates after 4 yr since establishment (Fig. 4). The ratio of above- to below-ground biomass remained close to 0.4 throughout meadow development (Fig. 5).

Below-ground production, mortality and decomposition increased during the first 4 yr since establishment, with production always exceeding mortality and mortality always exceeding decomposition (Fig. 6). These differences resulted in an accumulation of below-ground biomass and detrital mass during that period (Fig. 4). After 4 yr, however, below-ground production, mortality and decomposition displayed similar values and, as a consequence, biomass and detrital mass increased little with further meadow development.

DISCUSSION

Our estimates of magnitude and fate of above-ground production in *Cymodocea nodosa* are similar to previous measurements obtained in the same population and season but using different methods. Our values of leaf production agree well with those reported by Perez (1989), Perez & Romero (1994) and Perez et al. (1994), and the range in apical removal is similar to previous estimates by Cebrián et al. (1996). The values of leaf export and decomposition lie within the ranges reported by Romero et al. (1990) and Mateo (1995). Our estimates of below-ground production, mortality and decomposition are, albeit variable, also similar to previous measurements in the same location and season (Romero et al. 1990, Perez & Romero 1994, Mateo 1995). Finally, the values of above- and below-ground biomass and detrital mass are in a similar range to previous estimates reported for the same area (Duarte & Sand-Jensen 1990b, Romero et al. 1990, Perez et al. 1991, 1994, Perez & Romero 1994, Mateo 1995). These similarities suggest that the assumptions and bias of the methods employed here do not greatly affect the results.

Our results allow some general conclusions on the fate of *Cymodocea nodosa* production in the area studied:

First, apical leaf removal by herbivores and physical agents represents, on average, only ~15% of the production. Assuming that herbivores ingest half of this

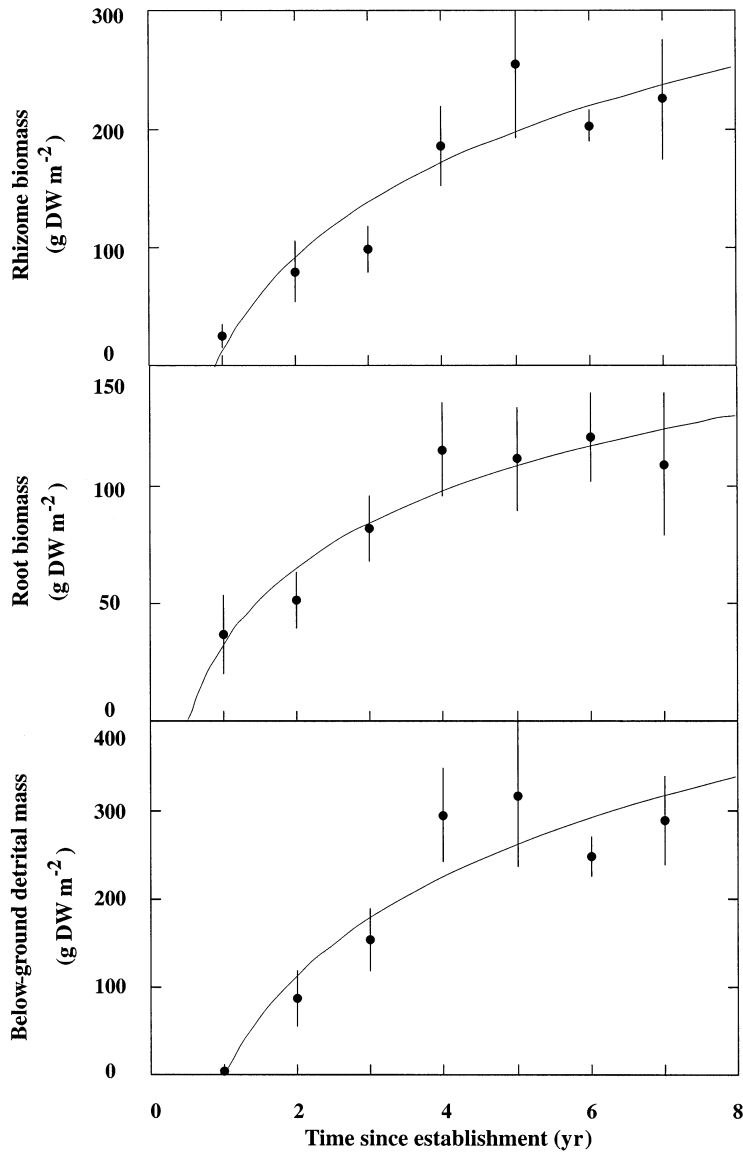


Fig. 4. *Cymodocea nodosa*. Relationships between rhizome biomass, root biomass and below-ground detrital mass, and time since establishment. Data are means for all locations established within same year, and bars their SEs. Curves depict adjusted regression equations (Table 3)

percentage (Cebrián et al. 1996, 1997), we suggest a mean consumption of $0.2 \text{ g dry wt m}^{-2} \text{ d}^{-1}$ during May to July. This is relatively high compared with consumption of other temperate seagrass species (Cebrián & Duarte 1998). Hence, although herbivores remove only a small fraction of the *Cymodocea nodosa* leaf production in the study area, the total consumption is fairly large, because of the high values of production attained.

Second, most leaf production is shed as leaves turn senescent, in agreement with the current belief that most seagrass production is transferred to higher

trophic levels in the form of detritus (Ott 1981, Zieman 1983, Thayer et al. 1984, Cebrián & Duarte 1998). Furthermore, in the population studied, a large percentage of detrital leaf production (mean = 70%) was exported off the sampled locations during May to July, with nearly all the remainder being decomposed within the locations. Our results suggest that most exported detritus are carried out of the patch boundaries, since we would have found much larger standing stocks of detrital leaves had the detritus exported from a given location been deposited within other sampled locations. The high export rates observed are probably due to the fact that the patches studied grow in a shallow area (depth range 15 to 80 cm) that is often exposed to substantial wind shear and intense water friction (Camp & Delgado 1987, Falques 1989, Camp et al. 1991). These high export rates have 2 corollaries. First, export represents a nutrient loss for the patches since exported detritus is decomposed and recycled elsewhere. Therefore, the estimated average of 70% detrital leaf production exported off the patches implies that these patches must import substantial amounts of nutrients from allochthonous sources. Inputs of nutrients from sedimented phytoplankton or from crop fields in the northern edge of the bay have been previously suggested as such sources (Prat et al. 1988, Pedersen et al. 1997). Second, an average of $1.4 \text{ g dry wt leaf detritus m}^{-2} \text{ d}^{-1}$ is exported off the patches, indicating that these patches can fuel substantial levels of secondary production in neighboring systems, as described for other seagrass species (Zieman et al. 1979, Bach et al. 1986, Fry & Virnstein 1988).

Nevertheless, we have shown that the magnitude of the routes followed by *Cymodocea nodosa* production is dependent, to a certain extent, on the time elapsed since seagrass establishment. On average, leaf production and shedding increase by 2-fold, and apical removal by 5-fold, from the youngest (i.e. 0 to 2 yr old) to the oldest (5 to 7 yr old) stages of meadow formation encountered (Fig. 7). Breakage of leaf tips by water turbulence should be smaller in older plots because their higher above-ground biomass attenuates water friction within the leaf canopy to a greater degree (Ward et al. 1984, Irlandi & Peterson 1991, Fonseca & Cahalan 1992). Therefore, higher levels of apical removal in older plots should represent larger levels of consumption and herbivore production. The hypothesis is consistent

Table 3. *Cymodocea nodosa*. Results of least-square regressions between yearly averaged values of below-ground biomass and detrital mass and number of years since establishment. RB: rhizome biomass, ROB: root biomass, BDM: below-ground detrital mass

Variable	Equation	n	R ²	F-ratio	p
RB	RB = 11.4 (± 27.8) + 268.0 (± 46.7) log age	7	0.84	32.9	<0.01
ROB	ROB = 32.9 (± 10.1) + 106.7 (± 17.0) log age	7	0.87	39.4	<0.01
BDM	BDM = 1.3 (± 39.7) + 372.4 (± 66.6) log age	7	0.83	31.2	<0.01

with the observation that older seagrass patches, through enhanced refuge and food, frequently support larger herbivore abundances (Heck & Wetstone 1977,

Heck & Orth 1980, Orth et al. 1984, Stoner & Lewis 1985, Irlandi 1997). Moreover, older plots lose, albeit non-significantly (Student's *t*-test, $p > 0.05$), greater percentages of leaf production through

apical removal than do younger and middle-aged plots (Fig. 7). If this hypothesis is confirmed, it would suggest that herbivores remove greater percentages of leaf production in older patches, thereby exerting greater control over seagrass biomass.

Mean values of detrital leaf export and decomposition increased by almost 2-fold from young to old plots (Fig. 7). Below-ground decomposition increased by almost 1 order of magnitude across the gradient of meadow development covered (Fig. 7). Thus, older patches should maintain larger levels of detritivore production within and outside the patches. The relatively low mean percentage of detrital production exported from young plots (i.e. 48.1 ± 14.5 ; Fig. 7) was strongly influenced by the only location where a negative value (i.e. $-0.05 \text{ g dry wt m}^{-2} \text{ d}^{-1}$) was derived. When this location is not considered, the average percentage exported from young plots is 61.6 ± 6.1 , a value very similar to the percentages exported from middle-aged and old plots (Fig. 7). This suggests that the higher shoot density and structural complexity in the oldest plots sampled do not reduce water friction enough to significantly decrease detrital export. This could be due to the intense wind and water motion characteristic of the area studied (Camp & Delgado 1987, Falques 1989, Camp et al. 1991), which may override any influence of enhanced seagrass structure on detrital export. Moreover, because the percentage of

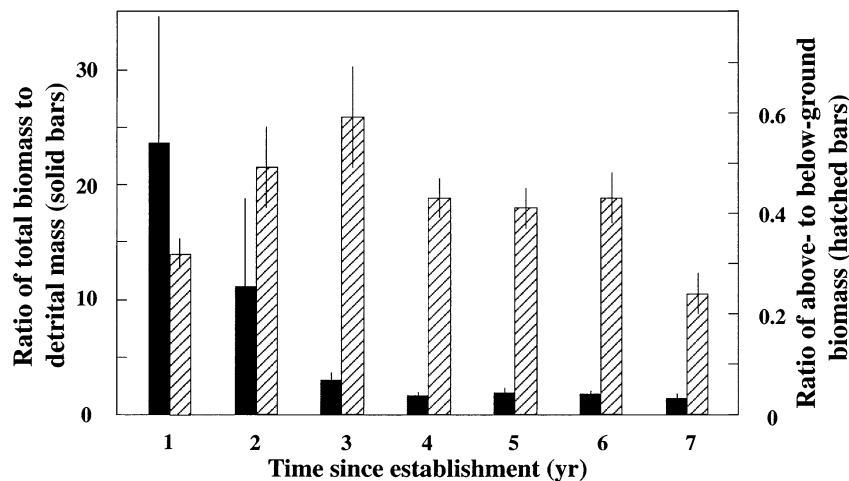


Fig. 5. *Cymodocea nodosa*. Variability in ratio of total biomass (above- and below-ground) to detrital mass and in the ratio of above- to below-ground biomass across the gradient of meadow development covered. Columns are means for all locations established within same year, and bars their SEs

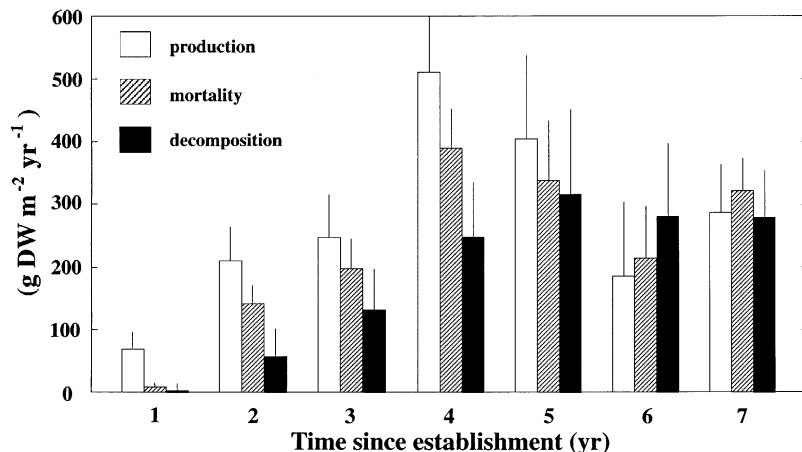


Fig. 6. *Cymodocea nodosa*. Variability in below-ground production, mortality and decomposition across the gradient of meadow development covered. Columns are means for all locations established within same year, and the bars their SEs

detrital production exported remains similar among patches of different age, we suggest that the degree of dependence of *Cymodocea nodosa* patches on imported nutrients is unrelated to development stage.

We have shown that older plots of *Cymodocea nodosa* accumulate larger pools of biomass and detrital mass, acting therefore as greater sinks of organic carbon. Our results allow us to estimate total storage (i.e. above- and below-ground biomass and detrital mass) as 227.5 ± 54.4 , 575.8 ± 71.4 and 776.6 ± 96.8 g dry wt m^{-2} (mean \pm SE) at young, middle-aged and old stages of meadow formation, respectively. These estimates are conservative because seagrass microdetritus (<0.5 cm) is unaccounted for. Furthermore, our results help to characterize the nature of carbon storage across meadow development. More than 90% of the seagrass carbon is stored as biomass during the first 2 yr after establishment, as would be expected from

the preferential allocation of seagrass photosynthates into fast-growing rhizomes and new leaf clusters during the young stages of meadow development (Duarte & Sand-Jensen 1990a). However, during the middle-aged and old stages of development, when both below-ground biomass and below-ground detrital mass increase slowly at similar rates, the ratio of total biomass to total seagrass carbon remains about 60%. The constant increases in leaf biomass and leaf detrital mass during middle-aged and old stages do not change this ratio, because they represent a modest percentage of total seagrass carbon. Moreover, the fact that the ratio of leaf to below-ground biomass remains similar with increasing time since establishment suggests that the seagrass allocates similar fractions of CO₂ fixation into the photosynthetic (i.e. leaves) and storage (i.e. rhizomes) compartments throughout meadow development.

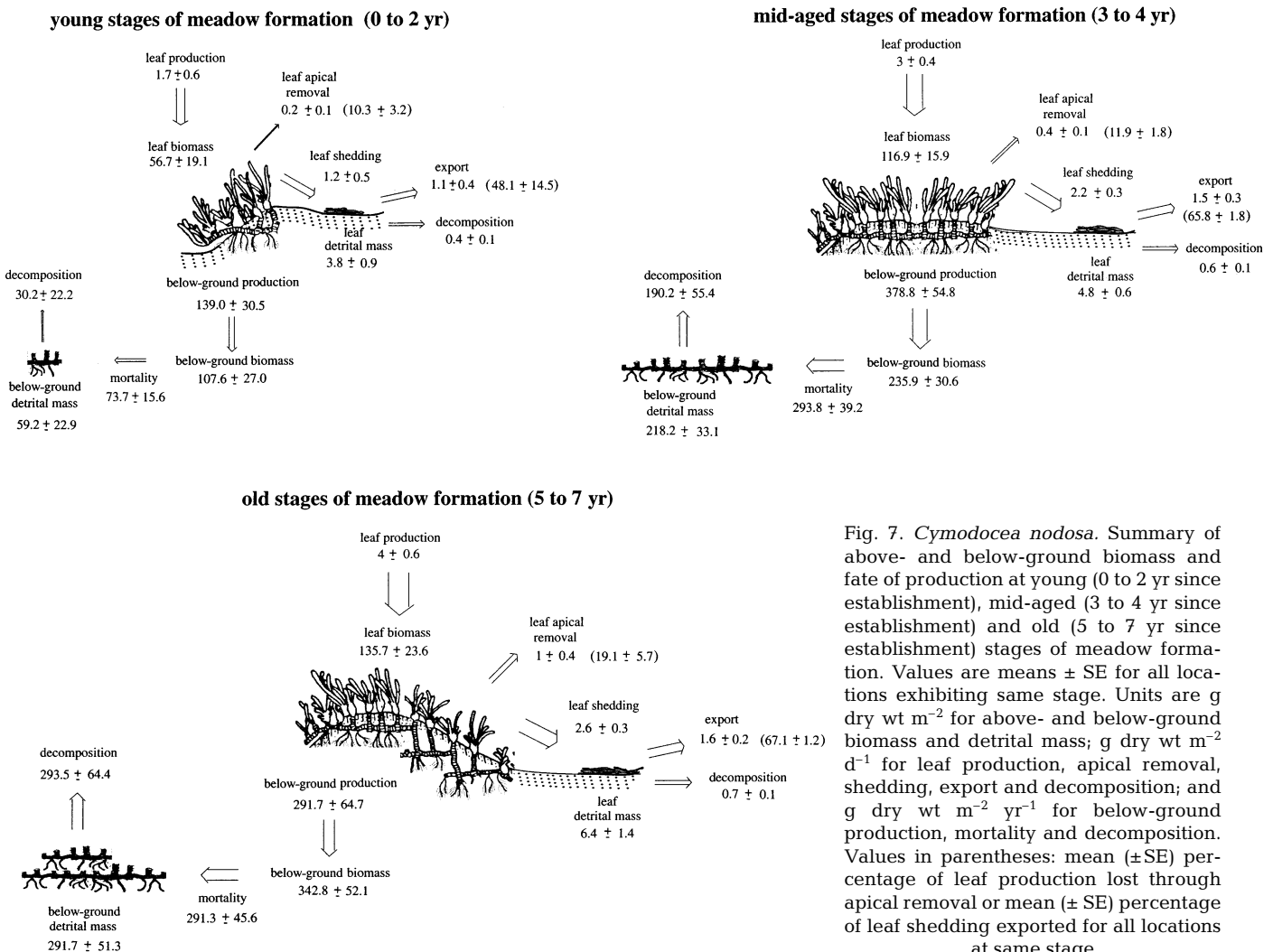


Fig. 7. *Cymodocea nodosa*. Summary of above- and below-ground biomass and fate of production at young (0 to 2 yr since establishment), mid-aged (3 to 4 yr since establishment) and old (5 to 7 yr since establishment) stages of meadow formation. Values are means \pm SE for all locations exhibiting same stage. Units are g dry wt m^{-2} for above- and below-ground biomass and detrital mass; g dry wt $m^{-2} d^{-1}$ for leaf production, apical removal, shedding, export and decomposition; and g dry wt $m^{-2} yr^{-1}$ for below-ground production, mortality and decomposition. Values in parentheses: mean (\pm SE) percentage of leaf production lost through apical removal or mean (\pm SE) percentage of leaf shedding exported for all locations at same stage

In conclusion, we have shown that the magnitude of the carbon pools and trophic routes of *Cymodocea nodosa* production is dependent on the stage of meadow formation: older plots channel larger fluxes of production towards heterotrophs both within and outside (through increased export) the plots, and accumulate larger pools of carbon. Therefore, the importance of *C. nodosa* stands as trophic resources for heterotrophs and as carbon reservoirs is related to stand age. Seagrass meadows are maintained in different stages of formation as a result of physical and anthropogenic disturbances and successional competition with other producers. Hence, generalizations about the ecological role of any seagrass species as a food resource for secondary producers or as a carbon reservoir should consider the stage of meadow formation typically exhibited by that species.

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