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Primary production and biomass on a Dutch salt marsh: emphasis on the below-ground component*, **, ***

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Abstract

The primary production and below-ground biomass of angiosperms were measured in four almost monospecific vegetation stands situated on a salt marsh along the Oosterschelde estuary, The Netherlands.

Maximum below-ground biomass values found for *Spartina anglica, Elymus pycnanthus, Halimione portulacoides* and *Triglochin maritima*, were very high relative to values reported from other European salt marshes: 12586, 9717, 17737 and 16121 g m^{-2} respectively. These relatively high values may be due to the fineness of the sieve used, compared to other studies. The actual values are likely to be even higher because the sample treatment has probably caused loss of fine root material.

Below-ground production estimates, based on the difference between maximum and minimum biomass, yielded: 6044 g m^{-2} yr^{-1} for *Spartina*, 4421 g m^{-2} yr^{-1} for *Elymus*, 7799 g m^{-2} yr^{-1} for *Halimione* and 3475 g m^{-2} yr^{-1} for *Triglochin*. This high production is mainly concentrated in the deeper layers of the root environment (20–60 cm). Although these production figures are considerably higher than those generally reported for comparable species or vegetation types in Europe, statistical evidence suggests that, for the first three species, they are real values rather than figures caused by random fluctuations.

Introduction

Studies on primary production of European tidal salt-marsh communities are relatively few. Although above-ground standing crop values have been published (Ranwell, 1961; Tyler, 1971; Jefferies & Perkins, 1977; Jensen, 1980; Hussey & Long, 1982) only Tyler (1971), Ketner (1972), Wallentinus (1973) and more recently Wolff *et al.* (1980), and Groenendijk (1984) attempted to estimate primary production. Even less information is available on below-ground biomass and primary production. Research on the below-ground primary production has been hampered due to difficulties in devising satisfactory techniques for routine measurement of living and dead material. The change-in-biomass technique applied by Dahlman & Kucera (1965) in a Missouri prairie, a method which is stated to underestimate the primary production (Keefe, 1972; Ketner, 1972; Linthurst & Reimold, 1978), is usually applied. Interest in below-ground biomass may also have been discouraged because it has been assumed that in tidal salt marshes only above-ground vegetation was

* Nomenclature of the plants follows Tutin *et al.* (1980), Flora Europaea, Cambridge.

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subject to export (Teal, 1962; Odum & De la Cruz, 1967; Valiela *et al.*, 1976). Thus only this part of the salt-marsh primary production was considered to contribute to the nutrient- and energy budgets of the adjacent coastal ecosystems, and the below-ground component could be neglected.

However, recent interest in sulfur metabolism of salt marshes pointed to the high level of below-ground primary production and indicated that a significant part of this production may become available to the coastal environment (Howarth, 1979; Howarth & Teal, 1980; Peterson *et al.*, 1980; Howarth *et al.*, 1983).

Present estimates of both above- and below-ground primary production and energy flow within the salt marshes of Europe are almost totally dependent on extrapolation from the results of studies in N. America (reviewed by Turner, 1976) even though the marshes of these two continents are very different with respect to their floristic composition (Chapman, 1974).

Above-ground biomass and primary production of *Spartina* salt marshes in the main estuary of the Netherlands, the Oosterschelde, has been assessed earlier (Groenendijk, 1984). The present study attempts to asses below-ground biomass and primary production of four dominant species of one of the Oosterschelde marshes over a one-year period under normal tidal conditions. Such knowledge can be used to estimate the loss of material input into the coastal ecosystems as a result of a projected 60% reduction of salt-marsh area, following upon the completion of a storm-surge barrier and the connected dams in the near future.

The study area

The study area called Stroodorpe salt marsh, is situated along the Oosterschelde estuary near Krabbendijke (SW Netherlands). The marsh covers ca 30 ha and is frequently immersed by tidal waters (salinity 25–30‰ S). Salt-marsh level is between 1.60 m and 2.54 m above NAP (Dutch Ordnance Level).

Four main vegetation types can be distinguished, (1) *Spartina anglica–Puccinellia maritima* vegetation at the lowest sites, (2) *Puccinellia maritima–Limonium vulgare–Triglochin maritima* in depressions of intermediate level, (3) *Halimione portulacoides* on the banks of the tidal creeks, and (4) *Elymus pycnanthus* dominating on the highest banks of tidal creeks.

Materials and methods

Three monospecific stands of *Spartina anglica*, *Halimione portulacoides* and *Elymus pycnanthus* and one stand of 90% *Triglochin maritima*, 5% *Puccinellia maritima* and 5% *Limonium vulgare* cover (further referred to as the *Triglochin* stand) were chosen as sampling sites. Elevations of the sites were 1.75, 2.21, 2.30 and 2.47 m above NAP respectively. Sites of 24 m^2 each were carefully selected in homogeneous stands.

For detailed data on biomass and above-ground productivity from the stand and a comparison of the yields obtained from several methods for production estimates and data treatment see Groenendijk (1984).

Below-ground samples were taken monthly at the same sites (with intact above-ground vegetation) July–December 1979 and March–June 1980. From each stand 3–70 mm diameter-soil cores were randomly collected to a depth of 60 cm with an auger, divided into two parts, viz. 0–20 cm and 20–60 cm, and subsequently deepfrozen until treatment, as described by Schuurman & Goedewaagen (1971). Roots were separated from soil particles using a 0.106 mm mesh sieve. Subsamples were taken and microscopically examined to estimate the fraction of living and dead root material and non-identifiable organic parts (roots were considered to be living when they were white). The remaining root material was dried at 80 °C for 48 hours and weighed. To correct for attached clay and sand particles the carbon content of a subsample was determined (Coleman carbonanalyser). For each series of samples the mean of the 0–20 cm layer, the 20–60 cm layer and the total root biomass (0–60 cm) was calculated, together with the standard deviations. The actual root biomass was calculated from carbon contents according to Gallagher & Plumley (1979). Below-ground primary production was calculated applying the change of biomass technique (Dahlman & Kucera, 1965) in which maximum and minimum standing crop values are used to calculate increments. Turnover rate was calculated by dividing maximum standing below-ground crop by the net below-ground primary production estimates. Temporal changes in the below-ground biomasses were statistically tested using an analysis of variance on the data of the total root biomass between the sampling dates.

Results

Total root biomass (0–60 cm) of *Spartina anglica*

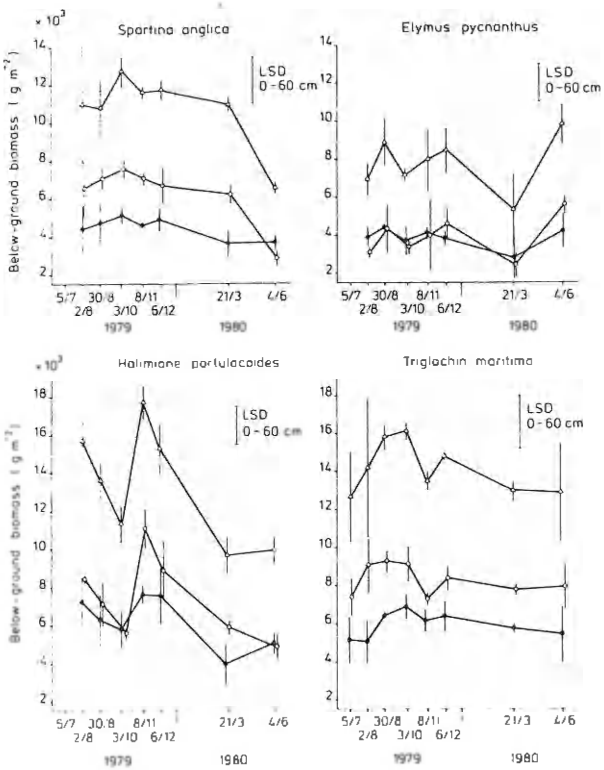

Fig. 1. Change in time for below-ground biomass of *Spartina, Elymus, Halimione* and *Triglochin* (●: 0–20 cm; ○: 20–60 cm; △: 0–60 cm) showing the mean ± S.D. LSD between the means of the sampling dates of the 0–60 cm layer (significance at the 5% level).

showed a peak of 12586 g m^{-2} in autumn, followed by a decrease which lasted until midsummer (Fig. 1). Over the year the the total root biomass showed a statistically significant variation ($p<0.01$). Below-ground primary production amounted to 6044 g m^{-2} yr^{-1} (Table 1).

Total root biomass of *Elymus pycnanthus* was lowest in early spring (5296 g m^{-2}) and reached a maximum of 7917 g m^{-2} in early summer (Fig. 1, Table 1). Seasonal changes in total root biomass were statistically significant ($p<0.05$). Below-ground primary production was 4421 g m^{-2} yr^{-1}.

In *Halimione portulacoides* total root biomass also showed a statistically significant seasonal variation ($p<0.001$) with the highest amount of biomass at 17737 g m^{-2}, in November. Below-ground primary production amounted to 7977 g m^{-2} yr^{-1}.

Highest total root biomass values for *Triglochin maritima* were found in August, September and October. Lowest values were found in July. Seasonal variation in total root biomass was not statistically significant ($p>0.05$). Below-ground production was calculated at 3475 g m^{-2} yr^{-1}.

Turnover rates of the total root biomass did not differ much between *Spartina, Elymus* and *Halimione*: 0.48, 0.45 and 0.45 respectively. For these three species the turnover rates at depth (20–60 cm) were highest. Especially *Spartina* showed a high turnover rate for the 20–60 layer, viz. 0.62. *Triglochin* showed lowest turnover rates, 0.22 for the total root biomass (Table 1).

Discussion

Below-ground biomass values found in this study are very high when compared with their reported above-ground biomass values or those of comparable species (Table 2). Most of the total plant biomass of all four species is found below-ground and the amounts of underground material are likely to be even higher, since the sample treatment has

Table 1. Annual minimum and maximum below-ground biomass, annual primary production and turnover rate of four salt-marsh vegetation types in the Oosterschelde estuary. E = Elymus pycnanthus, H = Halimione portulacoides, S = Spartina anglica, T = Triglochin maritima.

	depth cm	min. biomass g m^{-2} DW	max. biomass g m^{-2} DW	production g m^{-2} yr^{-1} DW	turnover rate prod./max. biom.
E	0–20	2856	4164	1597	0.38
	20–60	2440	5553	3113	0.56
	0–60	5296	9717	4421	0.45
H	0–20	3974	6654	2680	0.40
	20–60	5786	11083	5297	0.47
	0–60	9760	17737	7977	0.45
S	0–20	3725	5064	1339	0.26
	20–60	2817	7522	4705	0.62
	0–60	6542	12586	6044	0.48
T	0–20	5225	6905	1680	0.24
	20–60	7421	9216	1795	0.19
	0–60	12646	16121	3475	0.22

Table 2. Compilation of dry weights (g m^{-2}) of above-ground live and dead plant material from various salt marshes in Europe.

Major species	Locality	Live			Dead			salt m. level*	Source
		min	mean	max	min	mean	max		
Juncus gerardii	Baltic coast, Sweden	–	–	161	–	–	457	L	Tyler, 1971
Juncus gerardii	Baltic coast, Sweden	20	140	280	5	59	26[b]	L	Wallentinus, 1973
Juncus gerardii	Terschelling, The Netherlands	31	197	346	82	129	262	H	Ketner, 1972
Festuca rubra	Schiermonnikoog, The Netherlands	40	–	400[ab]	–	–	–	H	Alberda, 1970
Plantago maritima	Terschelling, The Netherlands	74	297	466	71	205	371	M	Ketner, 1972
Halimione portulacoides	*Jutland, Denmark*	*665*	–	*957*	*156*	–	*406*	M	*Jensen, 1980*
Halimione portulacoides	Zeeland, The Netherlands	503	862	1078	182	391	575	M	Groenendijk, 1984
Triglochin maritima	Zeeland, The Netherlands	15	270	589	6	151	415	M	Groenendijk, 1984
Puccinellia maritima	Essex, England	179	–	495	612	–	1260	M	Hussey & Long, 1982
Puccinellia maritima	Zeeland, The Netherlands	112	272	576	16	180	384[b]	L	Wolff *et al.*, 1980
Puccinellia maritima	Terschelling, The Netherlands	56	252	463	18	84	277	L	Ketner, 1972
Elymus pycnanthus	Zeeland, The Netherlands	64	518	765	256	472	544[b]	L	Wolff *et al.*, 1980
Elymus pycnanthus	Zeeland, The Netherlands	60	454	598	327	455	542	L	Groenendijk, 1984
Spartina townsendii	Somerset, England	–	–	734[a]	–	–	–	L	Ranwell, 1961
Spartina anglica	Zeeland, The Netherlands	64	301	608	–	288	560[b]	L	Wolff *et al.*, 1980
Spartina anglica	Zeeland, The Netherlands	60	579	1122	285	403	573	L	Groenendijk, 1984

[a] dead material included, [b] estimated from graph. H, high marsh; M, middle marsh; L, low marsh.
* These are approximate elevations.

probably caused substantial loss of very fine root particles and dissolved material resulting in an underestimation of the tissue, possibly by as much as 20–40% (Noordwijk & Floris, 1979). Plants in physiologically dry environments, like salt marshes, have been assumed to have high below-ground biomass values (Bray, 1963; Waisel, 1972). Our results show distinctly higher biomass values than hitherto reported before from European marshes, and correspond with values given for the American marshes (Table 3). In our opinion this discrepancy is partly due to the relatively large differences in mesh width of the sieves used by the various authors for separating plant material from soil particles (see Table 4). In a pilot study (Vink-Lievaart, 1982) additional losses of 27% for the 0–20 cm layer and 74% for the 20–60 cm layer were found in a *Halimione* stand when using a 0.3 mm sieve instead of a 0.106 mm. This lack of standardization in mesh width often causes problems when comparing root biomass values from different studies. Therefore, it seems recommendable to unify mesh width for all below-ground biomass sampling (cf. Ketner, 1972).

Another unusual finding is the distribution of the root biomass: on average ca 50% is in the 20–60 cm layer (Fig. 1), while in the literature more superficial rooting systems are reported for salt-marsh species (Tyler, 1971; Ketner, 1972; Gallagher & Plumley, 1979; Livingstone & Patriquin 1981). Ketner (1972) suggested that in salt marshes aeration and soil wetness are the most important factors including root distribution. Beeftink (1965) found that in salt-marsh basins, with 8% air in the upper 8 cm, 80% of the roots appeared in the 0–30 cm layer. In creekbanks with better aeration 80% of the roots were spread over the 0–60 (70) cm layer. A good aeration might be a valid explanation for the high amounts of roots in the 20–60 cm layer of the *Elymus* and *Halimione* stands but does not hold for the distribution of roots in the non-aerated (blue-black coloured) sediments in the low-lying *Spartina* and *Triglochin* stands. Again, these discrepancies could result from the larger mesh sizes used in previous studies and a disproportional amount of fine roots at depth; it may also be due to the relatively shallow sampling in previous studies.

The below-ground production in this study i

Table 3. Compilation of dry weights (g m^{-2}) on below-ground live and dead plant material from various salt marshes in Europe and N. America.

Major species	Locality	Live			Dead			salt m. level*	Source
		min	mean	max	min	mean	max		
Europe									
Juncus gerardii	Baltic coast, Sweden	3810	4200	4400[a]	–	–	–	L	Tyler, 1971
Juncus gerardii	Terschelling, The Netherlands	1438	1848	2477[a]	–	–	–	L	Ketner, 1972
Plantago maritima	Terschelling, The Netherlands	1581	2614	3871[a]	–	–	–	L	Ketner, 1972
Triglochin maritima	Zeeland, The Netherlands	12646	14241	16121[a]	–	–	–	L	This study
Puccinellia maritima	Essex, England	272	364	468	2260	3880	4660	M	Hussey & Long, 1982
Halimione portulacoides	Zeeland, The Netherlands	9760	13338	17737[a]	–	–	–	M	This study
Elymus pycnanthus	Zeeland, The Netherlands	5296	7763	9717[a]	–	–	–	H	This study
Spartina townsendii	Suffolk, England	528	810	1010	520	630	720[b]	M	Dunn, 1981
Spartina townsendii	Lancashire, England	–	940[b]	–	–	–	–	L	Dunn, 1981
Spartina townsendii	Zeeland, The Netherlands	6542	10589	12586[a]	–	–	–	L	This study
N. America									
Juncus roemerianus	North Florida	4000	–	6000[ab]				L	Kruczynski *et al.*, 1978
Juncus roemerianus	North Florida	3000	–	15500[ab]	–	–	–	H	Kruczynski *et al.*, 1978
Juncus roemerianus	North Florida	2700		8000[ab]	–	–	–	H	Kruczynski *et al.*, 1978
Juncus roemerianus	Mississippi	9700	–	12400[a]	–	–	–	L	De la Cruz & Hackney, 1977
Spartina alterniflora	New Yersey	–	11400	12300[a]	–	–	–	M	Smith *et al.*, 1979
Spartina alterniflora	Massachusetts	150	–	1800[b]	8000	–	11000[b]	L	Valiela *et al.*, 1976
Spartina alterniflora	Nova Scotia	–	–	2336[z]	–	–	–	L	Livingstone & Patriquin, 1981
Spartina patens	Massachusetts	100	–	2000	7000	–	11000[b]	H	Valiela *et al.*, 1976
Spartina cynosuroides	Georgia	8000	–	18000[ab]					Gallagher & Plumley, 1979
Distichlis spicata	Delaware	7500	–	12500[ab]					Gallagher & Plumley, 1979

[a] dead material included; [b] estimated from graph, [z] based on living functional biomass. H, high marsh; M, middle marsh; L, low marsh.

* These are approximate elevations.

also considerably higher than reported in some studies for comparable species or vegetation types both in Europe and NE America (Table 4), except for values given by Valiela *et al.* (1976) and Gallagher & Plumley (1979). This high production is concentrated in the deeper layers of the root environment. The strong biomass fluctuations in the 20–60 cm layer suggest a root expansion much deeper than 20 cm. This is also suggested by the relatively high turnover values in the deeper layers (Table 1). Mean turnover times were well within the range given for comparable species or vegetation types: ca. 2–5 yr (cf. Ketner, 1972; Smith *et al.*, 1979).

Are these production estimates reliable? The method used here to estimate below-ground productivity (Dahlman & Kucera, 1965) is an indirect one in that increments of living material are inferred from changes in total macro-organic material including non-living root biomass. A serious shortcoming of this technique is that it does not account for the disappearance of dead material by decomposition between the sampling intervals. Especially when a large portion of the below-ground biomass is dead, the estimated production figures may underestimate the actual values.

Although this aspect cannot be disregarded when considering the reliability of the values found, our

Table 4. Net below-ground production (g m^{-2} yr^{-1}) of halophytes from various salt marshes in Europe and N. America.

Major species	Locality	Production	Salt-marsh level	Mesh width sieves	Source
Europe					
Juncus gerardii	Baltic coast, Sweden	600[y]	H	0.6 mm	Tyler, 1971
Juncus gerardii	Terschelling, The Netherlands	305 – 790[y]	H	0.3 mm	Ketner, 1972
Plantago maritima	Terschelling, The Netherlands	670 – 1515[y]	M	0.3 mm	Ketner, 1972
Spartina anglica	Zeeland, The Netherlands	6044[y]	L	0.106 mm	This study
Triglochin maritima	Zeeland, The Netherlands	3475[y]	L	0.106 mm	This study
Halimione portulacoides	Zeeland, The Netherlands	7977[y]	M	0.106 mm	This study
Elymus pycnanthus	Zeeland, The Netherlands	4421[y]	H	0.106 mm	This study
Puccinellia maritima	Essex, England	1525[by]	L	0.5 mm	Hussey & Long, 1982
N. America					
Spartina alterniflora	Massachusetts	3900 – 6600[y]	L	0.5 mm	Valiela *et al.*, 1976
Spartina alterniflora	New Yersey	2300[y]	L	1 mm	Smith *et al.*, 1979
Spartina patens	Massachusetts	3200 – 6200[y]	H	0.5 mm	Valiela *et al.*, 1976
Juncus roemerianus	Mississippi	1360[y]	L	0.25 mm	De la Cruz & Hackney, 1977
Juncus roemerianus	Nova Scotia	788[bz]	L	–	Livingstone & Patriquin, 1981
Spartina cynosuroides	Georgia	10000[hy]		1 mm	Gallagher & Plumley, 1979
Distichlis spicata	Delaware	5000[hy]		1 mm	Gallagher & Plumley, 1979

[b] estimated from graph; [y] maximum – minimum biomass method, see text; [z] estimation based on measurement of living functional biomass.

microscopical analyses of sub-samples revealed that relatively little (15% at most) non-living roots in winter and early spring, and <5% non-identifiable organic fragments were present. A low humus content of these sediments was also reported by Beeftink (1965). However, the qualitative assessment of roots being alive or dead is arbitrary and large errors may arise. Vital tissue staining techniques (using i.e. tetrazolium compounds) might be of some help in collecting more objective data but this type of work is very time consuming and does not work all that well for the kind and quantity of the material to be processed (Kucera *et al.*, 1967; Smith *et al.*, 1979). The reliability of the results in this study may also be affected by high sampling variation due to the low numbers of soil samples (3 per site) and their limited size (38.5 cm^2). However, standard deviations of the mean biomass values are relatively low, while the statistical significance of the late summer biomass peaks suggest actual values rather than random fluctuations for three of the four stands. Another support for the reliability of the reported changes in below-ground biomass can be found in their good fit to hypothetical predictions: low values in the beginning of the growing season followed by an increase in July-November and a decrease towards the next growing season (cf. Brouwer, 1963; Tyler, 1971; Ketner, 1972).

Our high biomass and primary production values make it clear that for an assessment of the contribution of the salt-marsh primary production to the energy and nutrient levels of the estuarine ecosystems, data on the above-ground component alone give a very incomplete view. The quantity of below-ground biomass as a potential source of nutrients, available to heterotrophs in the salt-marsh itself and in the adjacent estuarine waters, is considerable. Future research should focus on the below-ground processes for a better understanding of the whole estuarine ecosystem.

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