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Microorganisms on macrophyte debris: Biodegradation and its implication in the food web

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Abstract

In a Mediterranean seagrass ecosystem (*Posidonia oceanica*) around Ischia (Gulf of Naples) an attempt was made to study the fate of *Posidonia* derived particulate matter in wrack beds around and within the seagrass stands, on the shore and in the water column. Changes in total soluble carbohydrate concentrations from green and brown parts within one leaf vary from 70.7 to 25.7 $mg.g^{-1}$ dry weight. Minimum values of 0.2 $mg.g^{-1}$ dry weight consisting mainly of saccharose are detected for brown wrack particles. All other components found in green leaf parts, e.g. fructose, glucose and myo-inositol probably leach rapidly into the water or are transported into the rhizome prior to the loss of the brown leaf region. Only in the rhizome the trisaccharide raffinose was detected in addition to the components found in the leaves. The importance of the brown leaf fraction as a substrate for microheterotrophs is indicated by bacterial densities up to 4×10^4 $cells.mm^{-2}$. This is correlated with nitrogen and carbon values, showing a decreasing C/N ratio with decreasing particle size, but increasing 0_2 uptake with maximum values of 10 $mg.g^{-1}.h^{-1}$ for the particle size fraction of 0.1 – 1 mm. The role of the brown dead *Posidonia* derived leaf fractions as energy source for consumers is discussed and attempts are made to redefine the terms ''debris'' and ,,detritus''.

Introduction

Particulate organic matter in the water column of nearshore systems and macrophyte productivity are of increasing interest to ecologists since the importance of the decomposer food chain for marine ecosystems has been recognized (ODUM and De la CRUZ 1967; FENCHEL 1972; SIEBURTH 1976; WANGERSKY 1977). The interrelationships between productivity of macrophytes and nutrient regeneration, as well as between the actively metabolizing bacteria and particle content of the water, indicate that studies on the dynamics of particle formation and on the particle content in the water column are of major importance in view of the filter and particle feeders which usually dominate such systems (MARSHALL 1970; MANN 1972; MILLER and MANN 1973; VELIMIROV et al. 1977; KIKUCHI and PÉRÈS 1977 and TENORE and RICE 1980). Recent studies on seagrass stands of *Posidonia oceanica* (L.) DELILE at the island Ischia (Gulf of Naples) dealt with the productivity and export of the organic matter produced, as well as with energy transfers from the macrophyte to the consumer levels (OTT and MAURER 1977; OTT 1980). In the present study an attempt is made to describe the dynamics of particle formation, and the changes in the soluble carbohydrates which take place in the aging leaf of a *Posidonia* shoot until it is torn off and exported to the adjacent wrack beds or enters the water column in the form of a small particle. The importance of these particles for different consumer levels is discussed and an attempt is made to overcome definition problems.

Material and Methods

Shoots of *Posidonia* were collected in a bay near Punta Vico on the northern shore of the island Ischia, Italy. The seagrass bed extends from 1m down to 33m depth over a distance of 500m from the shore. Samples were taken at 5, 15 and 30 m depth by clearing quadrates of 1/16 m² using SCUBA. Sampling always took place between 11^{00} and 12^{00}h. The shoots were uprooted with the rhizomes, transferred into plastic bags and kept in light-tight cooling boxes during transport to the laboratory. Samples of uprooted, torn off and fractionated brown *Posidonia* leaves were taken randomly from wrack beds on the sea bottom within a depth range of 10 to 15m and from wrack beds on sandy beaches. The samples were treated as described above.

In the laboratory, shoots from each station were layed out on soft paper, and arranged according to their position in the shoot, which is related to age (OTT 1980). Each leaf was split up into brown distal part, green part and bases, the rhizomes being treated separately. Subsamples of these fractions (approximately 20 g wet weight) were transferred into acetone and kept at 5°C for determination of soluble sugars. The acetone was boiled off at 70°C followed by desiccation of the samples at 80°C over two days and subsequent grinding to a fine powder. A hot water extract of the powder was centrifuged and the supernatant (10 ml) passed through an ion-exchanger to separate organic acids from the liquid phase. The supernatant was then dried in a rotorvapor, kept in a desiccator overnight and dissolved in double distilled water (3 ml) to be filtered and prepared for analysis on a Hewlett-Packard 5835-A terminal operated gas liquid chromatograph with flame ionization detectors (JANAUER and ENGLMAIER 1978).

Subsamples of the above fractions were dried at 80°C for carbon and nitrogen determination. Carbon values were obtained from a carbon-analyzer (Coulomat-Ströhlein) and nitrogen was determined following the method of KJELDAHL. Brown dead leaves from wrack bed samples were analyzed as described above. Leaf particles from wrack beds were split into size classes using sieves of 100 μm, 1 mm, 2 mm, 3 mm and 8 mm mesh width. Metabolic activity of microorganisms on the above particle fractions was estimated by measuring 0_2 consumption using polarographic oxygen sensors in closed systems. Scanning Electron Microscopy (Cambridge Mark 2A Stereoscan) was used to determine bacterial densities on different parts of the leaf. Samples of 0.5 cm² were taken from freshly collected *Posidonia* shoots fixed immediately in 4% buffered formalin-seawater, starting 1 cm above the leaf base (lunula) in different growth regions. Only the morphological ''under'' side of the leaves was examined. Bacterial density was estimated from 24 – 39 samples lying on a transect crossing the leaf surface, each sample amounting to an area of 3466 μm².

Results

Changes in concentrations of soluble carbohydrates in a set of leaves from a *Posidonia* shoot from winter over spring to summer are illustrated for 15 m depth in Fig. 1. Lowest concentrations are found in February followed by peak values in April and a relative drop in June. This indicates highest photosynthetic activity in spring, supporting the assumption (OTT 1980) that the high leaf production values per gram leaf tissue in winter actually reflect conversion of storage material from the rhizomes into leaf material. In all months total soluble carbohydrate concentrations increase from young leaves to mature leaves and drop towards senescent leaves regardless of absolute concentrations. This pattern is most pronounced in April. In June the youngest leaves of the bundle (I – III) are already mature (OTT 1980) and therefore only the drop towards senescent leaves (IV – V) is evident. The soluble carbohydrate

dynamics during the aging of a leaf becomes even more evident, when the values for corresponding leaves – which change their position in the bundle from young inner leaves over mature middle to senescent outer leaves – are connected. A sharp increase in total soluble carbohydrate content is noted especially towards those leaves which have reached their maximum development of leaf tissue and have almost stopped growing. A rapid drop follows, probably reflecting transport towards the rhizome of carbohydrates which in these leaves have not been used to add more tissue prior to leaf decay.

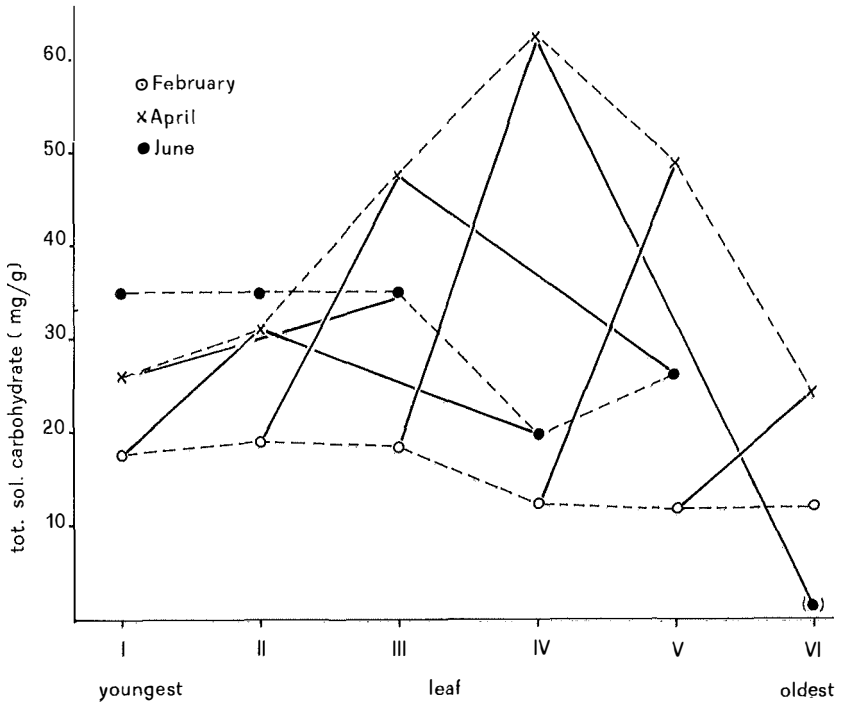

Figure 1

Change in total soluble carbohydrate content of the green parts of leaves in *Posidonia oceanica* shoots collected in February, April and June (15 m depth). Dashed lines connect values for leaves collected at the same time in a sequence from youngest (innermost) to oldest (outermost) leaf. Solid lines connect values of corresponding leaves (which change place in a shoot in a time sequence), thus approximating the actual change in soluble carbohydrate concentrations during the life span of an individual leaf. The data point in parentheses for leaf VI represents the soluble carbohydrate content from a brown wrack bed sample.

Similar changes in soluble carbohydrates to those observed during the aging of a whole leaf occur from base to tip (youngest to oldest part) of a single representative mature leaf from a *Posidonia* shoot. Fig. 2 shows concentrations in 3 leaf regions and the rhizome over the same seasons. Low concentrations in February are agaln in contrast with April and June, but within each month a clear concentration gradient is seen from the base having the highest values up to the leaf tips with lowest values, reflecting the process of dying off at the end of the plant. It should be noticed that

soluble sugar concentrations in the base, with 134.12 mg.g^{-1} dry weight, are more than twice as high as the concentrations in the leaves (63.93 mg.g^{-1} dry weight in April) and more than 4 times higher than in leaves in June. A trend similar to the April one is noticed in February but absolute values are 3 times lower than in spring.

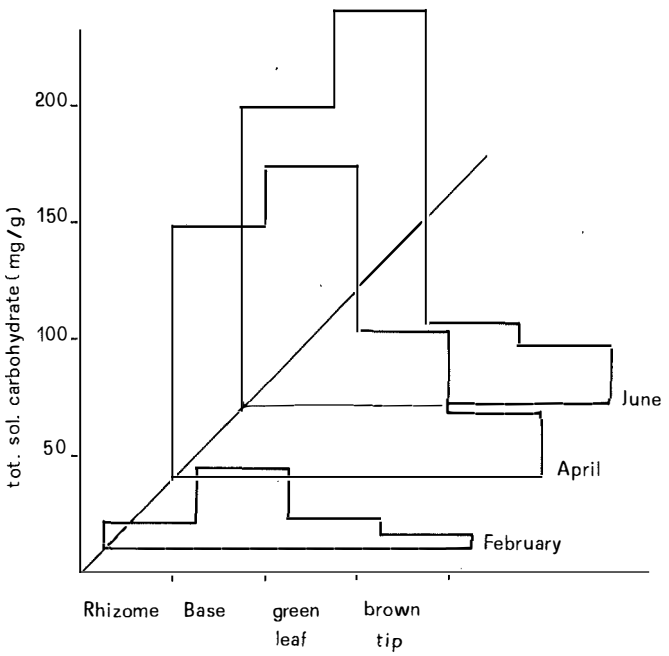

Figure 2

Change in total soluble carbohydrate content in a mature leaf of *Posidonia oceanica* (leaf III) from February, April and June (15 m depth). The leaf is divided into the chlorophyll free base, the green photosynthesizing blade and the dead brown tip. Values for the rhizomes are given for comparison.

Detailed information on total soluble carbohydrates and on individual components for the month of April (highest photosynthetic activity) and over three depth ranges (Table 1) indicates the presence of considerable concentrations of saccharose, compared to fructose, glucose, myo-inositol and raffinose. These compounds are detected over all seasons (unpublished data). The trisaccharide raffinose is only found in the leaf bases in concentrations of 0.6 to 1.2 mg.g^{-1} dry weight. Saccharose accounts for 60 to 95 % of all soluble carbohydrates in most leaves, only in leaf V in 15 m depth, it drops to 47 % while fructose and glucose amount to 32.6 and 18.4 % respectively. In all other leaves fructose and glucose vary from 0.6 to 8 % and 1.4 to 11 % respectively. Myo-inositol is present in the lowest concentrations varying between 0.03 and 1.1 %. An increase in all components is noticed from leaf I to leaf III for shoots at 5m depth, and up to leaf IV at 15 and 30 m depth. Of special interest for the dynamics of particle formation are the older leaves where the total soluble carbohydrates decrease again. At 5 m depth leaf IV shows a clear decrease in all sugar components and in the oldest leaf (V) the net loss of total soluble carbohydrates is reflected as a decrease in saccharose, while fructose

Table 1
Total soluble sugar (including inositol) and sugar components concentration (mg · g^{-1} dry weight) in leaves and bases of a *Posidonia oceanica* shoot over 3 depth ranges. Leaf I is the youngest and most inner leaf of the shoot, leaf VI is the oldest and outermost leaf of the shoot.

Month	Plant Unit	Σ sol. Sugar	Fructose	Glucose	Inositol	Saccharose	Raffinose
				Depth 5 m			
	Base I–III	99.29	3.55	2.60	1.09	92.05	–
	Base IV–VI	109.76	7.08	8.90	0.67	91.91	1.20
	Leaf I	24.83	1.93	2.50	0.14	20.26	
April	Leaf II	25.48	6.13	2.77	0.10	16.48	
	Leaf III	28.64	7.69	3.29	0.11	17.55	
	Leaf IV	65.02	0.49	1.10	0.02	63.41	
	Leaf V	19.44	6.34	3.59	0.34	9.15	
	Leaf VI	–	–	–	–	–	
				Depth 15 m			
Month	Plant Unit	Σ sol. Sugar	Fructose	Gluctose	Inositol	Saccharose	Raffinose
	Base I–III	134.10	4.45	4.95	0.95	123.14	0.61
	Base IV–VI	77.34	7.35	12.30	0.44	55.41	1.84
	Leaf I	25.02	–	0.51	0.32	24.19	
April	Leaf II	31.87	0.19	0.46	0.30	30.92	
	Leaf III	47.36	0.22	0.95	0.31	45.88	
	Leaf IV	63.91	0.59	1.03	0.36	61.93	
	Leaf V	49.56	1.06	1.62	0.32	46.56	
	Leaf VI	24.86	0.52	0.78	0.12	23.42	
				Depth 30 m			
Month	Plant Unit	Σ sol. Sugar	Fructose	Glucose	Inositol	Saccharose	Raffinose
	Base I–III	168.59	7.33	7.88	1.33	149.26	2.79
	Base IV–VI	92.66	4.79	6.43	0.70	80.10	0.64
	Leaf I	22.75	0.16	0.43	0.37	21.79	
April	Leaf II	36.05	0.47	0.89	0.28	34.41	
	Leaf III	54.24	1.38	1.26	0.36	50.88	
	Leaf IV	70.70	1.38	1.68	0.29	67.35	
	Leaf V	35.53	1.05	1.51	0.42	54.55	
	Leaf VI	27.71	0.79	1.11	0.26	25.54	

and glucose increase. At 15 m depth leaf V shows a net loss of total soluble carbohydrates with a comparable decrease in saccharose while fructose and glucose increase. Leaf VI indicates again an overall loss of all components as compared to leaf IV and V. At 30 m depth a slow but steady decrease of all components is noticed for leaves V and VI.

Leaf VI, being the oldest leaf of the shoot, is in most cases entirely brown and eroded and is lost by breaking off at the lunula. At this stage the leaf is lost from the seagrass stand, enters the water column after fractionation as particulate organic matter and

may be washed upon the beach. The chemical reduction and simplification which takes place on the living plant while aging and eroding at the tips continues when exported from the system (Table 2). Brown tips over 3 depth ranges and over 3 seasons

Table 2

Total soluble sugar (including inositol) concentration in the brown distal parts of live *Posidonia* leaves from the seagrass bed and dead wrack leaves from sea bottom and beach with percentage of the sugar components.

SACC = SACCHAROSE GLU = GLUCOSE
FRU = FRUCTOSE INOSIT = INOSITOL

	FEBRUARY				
	mg/g	%			
	Σ sol. SUGAR	FRU	GLU	INOSIT	SACC
Tips brown					
5 m	9.90	6.06	5.05	2.02	86.87
15 m	17.30	2.89	2.31	0.58	92.49
30 m	5.00	–	–	2.40	97.40
Wrack brown					
sea bottom	0.80	–	–	12.50	87.50
beach	0.15	–	–	–	100.00

	APRIL				
	mg/g	%			
	Σ sol. SUGAR	FRU	GLU	INOSIT	SACC
Tips brown					
5 m	19.44	32.61	18.47	1.75	47.07
15 m	24.86	2.09	3.14	0.49	94.21
30 m	27.71	2.85	4.01	0.94	92.17
Wrack brown					
sea bottom	0.21	–	–	–	100.00
beach			no wrack		

	JUNE				
	mg/g	%			
	Σ sol. SUGAR	FRU	GLU	INOSIT	SACC
Tips brown					
5 m	17.52	38.64	6.34	–	54.97
15 m	25.71	22.17	18.28	0.19	59.51
30 m			no brown tips		
Wrack brown					
sea bottom	0.91	27.91	57.80	–	13.85
beach			no wrack		

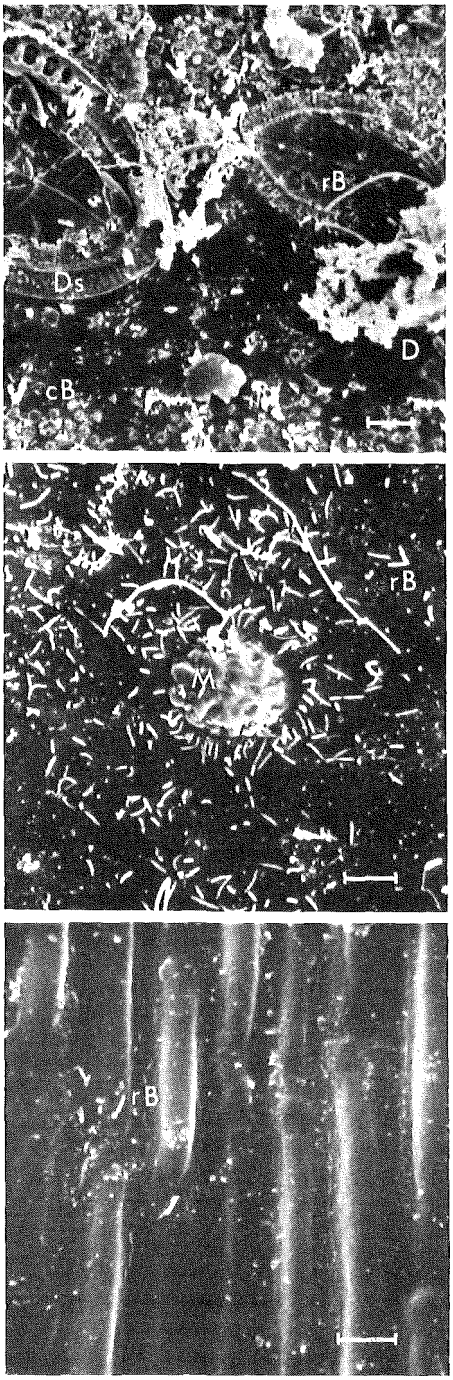

Figure 3

Microbial community on a *Posidonia oceanic* leaf. Leaf surface areas of different age and distance from the base are illustrated.

a) 1 cm above the base, age of region approximately 0.5 weeks.
b) 11 cm above the base, on the green blade of the leaf, age approximately 9 weeks.
c) 26 cm from the base, near the brown dead leaf tip, age approximately 13 weeks.

Abbrevations:
rB: rod-shaped Bacteria
cB: coccoid Bacteria
Ds: Diatom shell
D : unidentified particulate matter
M : *Melobesia* sp.
scale in all figures 5 μm

show that the soluble carbohydrate fraction consists of the same components with similar proportions in the concentrations as the green leaves, but the absolute values represent only 20 to 50% of the former. Exceptions are samples from 30 m depth in February, where fructose and glucose are missing and in June, where brown tips could not be found in sufficient quantities.

In wrack bed samples from the sea bottom at 10 – 15 m depth the soluble carbohydrate fraction in February is reduced to 1/20 of corresponding brown tips of the same depths, myo-inositol and saccharose being the only components. In April the soluble sugar fraction is less than 1/100 of the corresponding tips, the sole component being saccharose, whereas in June the fraction is 1/28 of the brown tips, with relatively high concentrations in fructose and glucose, a low saccharose concentration, while myo-inositol is missing. Only in February had significant wrack beds accumulated on the beach, indicating with 0.15 mg-g^{-1} dry weight minimum absolute values in soluble carbohydrate concentrations, consisting only of saccharose. The predictable and orderly process of growth, change in position and soluble carbohydrate content during leaf aging are now reflected in the changing value of the leaf as a substrate for microbial colonization, which is anything but uniform throughout the leaf. Fig. 3a shows the relatively bare surface area of a freshly exposed leaf part near the lunula, Fig. 3b illustrates a clear increase in rod shaped bacteria for a leaf surface which is fully photosynthesizing, while Fig. 3c illustrates the epigrowth on a leaf surface towards the brown tip of a leaf.

Fig. 4 shows densities of bacteria on the leaves of a *Posidonia* shoot. In young leaves and the basal (younger) parts of mature leaves bacterial density is mainly a function of age (exposure time). In distal (older) parts bacterial densities stabilize around 2 – 5 x 10^4 cells.mm^{-2} and even drop, probably as a result of increased spatial competition with algae. In older leaves, which have stopped growing, even the basal parts have high bacterial densities according to their relative age. Since wrack beds are washed back into the sea and are only found on the beach in late fall and winter, one can expect *Posidonia* particles to be subject to leaching, with extremely low values of soluble sugars throughout the year, offering a settling surface for microorganisms, which can still use these particles for nutrition.

For an estimation of microbial activity on debris of different mean particle size, oxygen uptake and carbon and nitrogen content was determined on natural particles. Two samples were investigated, one in November, approximately one month after the leaf fall in early autumn, and another in April during the main growing season. In each case both oxygen consumption and % – nitrogen values increase with decreasing particle size. This is most pronounced in the November samples, when values up to

$$10 \text{ mg } 0_2\, 1^{-1}\, h^{-1}$$

at 16°C in the fraction smaller than 0.1 mm and 1.2% N in the fraction 0.1 – 1 mm particle size were reached. At the same time carbon showed little variability and generally low figures for all size classes. In April both carbon and nitrogen values are higher for the coarse fraction, carbon decreases strongly towards the finer size classes and nitrogen increases, but less drastically than in November. Correspondingly oxygen uptake is higher in the coarser and lower in the smaller fraction than in November. The coarse fraction in November consists mainly of the material from the autumn leaf fall, which is poor in soluble carbohydrates. The fine fraction may be aged remains of the erosion in previous months. In April new debris has originated starting at higher carbon levels from which the fine fraction may have been newly formed and which has been quickly depleted from easily metabolized carbohydrates to a level comparable to autumn debris.

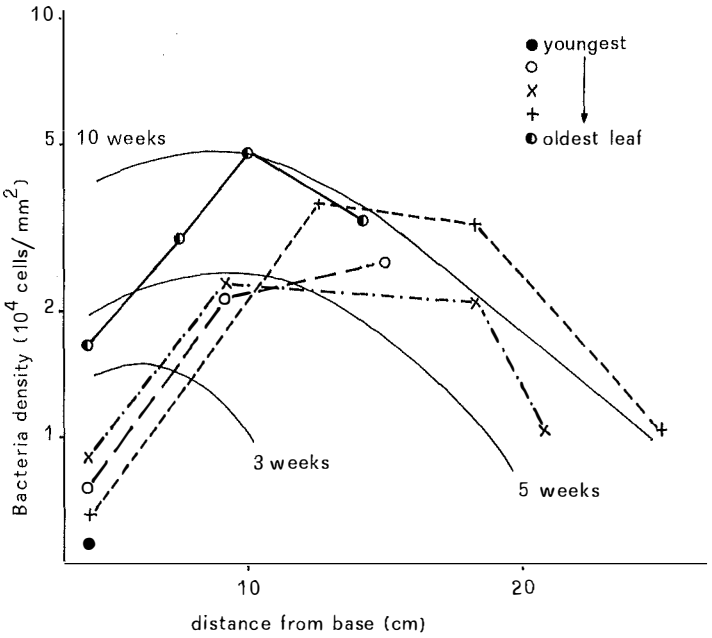

Figure 4

Density of bacteria on the surface of *Posidonia* leaves (collected in September) in relation to the distance of the leaf region from the base and age of the leaf region.

Discussion

The *Posidonia* derived particulate matter found in wrack beds and in the water column may be exported from the seagrass stands 1) as dead eroded brown tips, 2) as brown leaves breaking off at the lunula and manifesting no or very little metabolic activity, or 3) as whole shoots, displaying no or intense metabolic activity according to leaf age and region.

When a brown tip is lost from the *Posidonia* system only little amounts of easily metabolizable sugar, varying between 5 and 27 $mg.g^{-1}$ dry weight, enter the neighbouring consumer system, since most of the sugar components may have been used by microorganisms settled on the leaf surface (Fig. 3) or have been transported into lower leaf regions during senescence. It is assumed that in this case (Table 1) the relatively high amounts of saccharose are mobilized in form of glucose and fructose to be stored in bases and rhizomes .The same is true for those leaves lost during the leaf fall. When a whole shoot is uprooted, considerable amounts of soluble carbohydrates are potentially available to the consumers. To which extend the difference in soluble sugar between a green leaf IV in April (15 m depth) with 63.91 $mg.g^{-1}$ dry weight and a corresponding wrack particle with 0.21 $mg.g^{-1}$ dry weight is used directly by benthic consumers or leaches into the water can not be decided at this stage, but nearly all of these easily metabolizable sugars are directly or indirectly (VELIMIROV 1980) available for consumer use. Since a particle nearly totally depleted of soluble sugars except for saccharose (Table 2) has a carbon concentration varying between 24 and 33 % (Fig. 5), which represents mainly structural carbohydrates, its importance as a substrate for microheterotrophs is obvious.

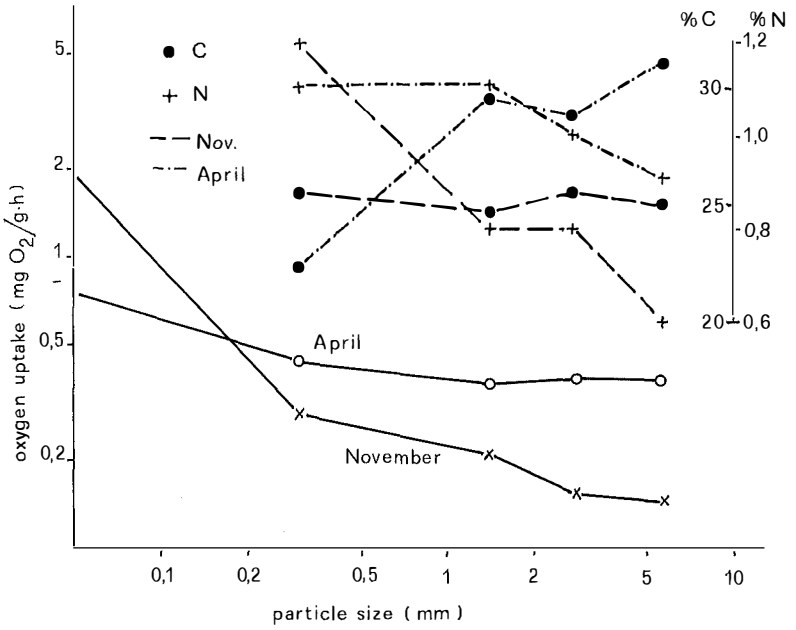

Figure 5

Oxygen uptake of different size fractions of particles derived from *Posidonia oceanica* leaves at a temperature of 15 – 16 °C. Particles were collected in November and April. Carbon and nitrogen values expressed as percentage of dry weight are given for particles down to the 0.1 – 1 mm fraction for the corressponding months.

This is demonstrated by the clear correlation between increasing oxygen uptake towards the finer particle fraction, and increase of the nitrogen content of the smaller particles, which is a reflection of microheterotrophs and microbial exudates which are rich in nitrogen (HOBBIE and LEE 1980). The respiration data for the different particle size fractions compare well with the oxygen measurements of particles derived from *Spartina* leaves (ODUM and De la CRUZ 1967) and from *Thalassia* leaves (FENCHEL 1970). At the present state of knowledge about detritus dynamics (MANN 1972; HARRISON and MANN 1975; LENZ 1977; FENCHEL 1972 and TENORE and PRICE 1980) it is well established that most of the macrophyte production enters the detritus food chain, and that the particle itself, as shown by our study, is rather poor in nutritive substances, becoming attractive to the consumers because of microorganisms settling on this substrate and processing this substrate to make it attractive (HANSON 1980). From the similar respiration figures for similar-sized leaf particles derived from different macrophytes, and the fact that *Posidonia* particles are nearly devoid of nutritional substances, it can be speculated that from a certain particle size or age class on, the source of the particles is of no importance any more for the consuming filter or particle feeders.

High densities of bacteria, up to 4×10^4 cells.mm^{-2}, are counted on brown and mostly dead parts of leaves which are still alive and connected proximally the *Posidonia* shoot. These brown parts could be considered as detritus according to DARNELL (1964), since it is biogenic material in various stages of microbial decomposition. Earlier studies (OTT and MAURER 1977) showed that sea urchins feed preferentially

on these parts of the leaves. Such brown parts or whole leaves found in wrack beds are referred to as debris (OTT 1980). Similarily, in other macrophyte systems such as kelp beds, torn off fronds which are partly eroded at the distal end are also referred to as debris, and urchins feeding on these are classified as debris feeders rather than grazers or detritus feeders (VELIMIROV et al. 1977).

Since no satisfactory definitions of the terms debris and detritus are yet available, an attempt is made to define the terms, taking into consideration the functional concepts seen from the consumer and the plant. We call debris living or dead particulate organic matter which is not active any more in maintenance and propagation of the population it is derived from, whether or not it is still part of the organism or stand it originated from, and it has to be fractionated before ingestion by the consumer. We call detritus dead (only) particulate organic matter which is never part of the stand where it orginated from; it does not need to be fractionated before ingestion by the consumer and it is not recognizable where it is derived from. Both detritus and debris may be colonized by microheterotrophs and are decomposed microbially in a process referred to as biodegradation.

Acknowledgements

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