Article details

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Growth of pioneer beach plants is strongly driven by buried macroalgal wrack, whereas macroinvertebrates affect plant nutrient dynamics

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ABSTRACT

Sandy beach food webs depend heavily upon marine organic input, such as macroalgae, as internal organic matter productivity is low. The fate, however, of this marine organic material (termed wrack) after being deposited onto the beach and its relation to pioneer vegetation, consisting of annual and perennial beach plants, needs to be further elucidated. In particular, the effect of various drivers, such as wrack burial and macroinvertebrate presence, on wrack decomposition is largely unknown on sandy beaches. Also, the subsequent effects of decomposition-driven nitrogen and phosphorus availability on beach pioneer plant growth are not yet understood. We performed a mesocosm experiment manipulating *Fucus vesiculosus* wrack access to the supratidal amphipod *Talitrus saltator*, and used *Cakile maritima* and *Elytrigia juncea* as phytometers to estimate decomposition-driven, wrack-derived nutrient supply. Buried wrack had a strong positive effect (2–3 fold increase) on plant mass, N and P content of *C. maritima* compared to surface wrack, while effects on *E. juncea* were largely absent. In addition, macroinvertebrate-facilitated decomposition was important for increasing nutrient availability, but this did not result in an increase in plant growth. We conclude that the burial of wrack by a thin layer of sand is a crucial driver of beach pioneer plant growth, which is most likely due to an increase in moisture availability. This supports the importance of management practices that allow deposited wrack to remain and be buried on the sandy beach for a long period of time, which will have positive effects on beach pioneer plant growth and possibly embryo dune formation.

1. Introduction

Sandy beaches receive large amounts of marine exogenous organic matter that has been produced by primary and secondary producers, and they are therefore considered to be primarily recipient ecosystems (McLachlan and Brown, 2006; Liebowitz et al., 2016). Sea grasses and macroalgae are important primary producers that grow attached to a substratum, but become detached as a result of severe hydrodynamic conditions and are consequently deposited onto the beach (Suursaar et al., 2014). Drift lines mainly contain stranded sea grasses and macroalgae (collectively termed wrack), but may also include other organic components, such as carrion or faeces (Colombini and Chelazzi, 2003). Wrack supply to the beach is highly variable in time and space and is driven by, among others, the buoyancy capacity of the wrack, hydrodynamic forces and beach type and geomorphology (Orr et al., 2005).

Moreover, the location of wrack on the beach, i.e., the distance to the mean sea level isocline, is strongly determined by tidal amplitudes that change monthly to annually (e.g., Plag and Tsimplis, 1999) resulting in several drift lines parallel to the water line.

The initial quality of freshly deposited wrack depends on the identity of the macroalgal species and the anatomical, physiological and chemical traits at the moment of detachment and transportation (Oldham et al., 2014), as well as on the relative contribution of carrion in the wrack. Together, this results in a spatiotemporally diverse drift line composition at the sandy beach. As the internal primary production of sandy beaches is very low and the ecosystem is generally bottom-up controlled (Schlacher and Hartwig, 2013), the input and subsequent pathway of wrack-bound energy and nutrients is crucial to the functioning of the sandy beaches. Wrack significantly contributes to the total amount of energy and nutrients available on sandy beaches

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(Colombini and Chelazzi, 2003). Therefore, understanding the fate of marine-derived organic matter that enters sandy beaches is key for understanding its ecosystem functioning.

Once wrack is stranded on the beach, this material decomposes through a variety of abiotic and biotic processes (Colombini and Chelazzi, 2003). Abiotic processes that work on freshly deposited wrack resulting in its degradation include photodegradation, erosion by wind-blown sand and coverage of wrack by a layer of sand. Over time, wrack in drift lines higher up the beach generally becomes buried by sand through aeolian transportation and other natural processes, where it locally enhances organic matter content and changes the physical structure of the sand, which is especially relevant in sandy beaches (Rossi and Underwood, 2002). The aging and burial of wrack change the microclimate and habitat properties for microbial decomposers and macroinvertebrates, making wrack an ephemeral but stabilised habitat in terms of temperature and moisture content for supratidal macro-invertebrates (Ince et al., 2007; Ruiz-Delgado et al., 2015). An important biotic process influencing wrack decomposition is the swift colonisation of wrack by microbes and invertebrates, after which a succession of species starts (Olabarria et al., 2007). As the volume and quality of wrack alter over time, changes in macroinvertebrate abundance, richness and community composition occur (Jędrzejczak, 2002; Olabarria et al., 2007). Macroinvertebrates that feed on wrack, and its associated biofilm (Porri et al., 2011), fragment the organic material (Salathé and Riera, 2012). By decreasing wrack particle size and mixing of bacteria and fungi with organic matter through feeding, the surface area for microbial activity increases and decomposition is stimulated (Robertson and Mann, 1980; Colombini and Chelazzi, 2003). Also, the burrowing activities of some macroinvertebrates incorporate wrack fragments within the sand, stimulating an increase in decomposition, due to enhanced activity of decomposers by more favourable abiotic conditions (Inglis, 1989). All these (a)biotic processes potentially affect the decomposition of wrack and the release of organically-bound nutrients, but how these are interacting remains largely unknown. Specifically, the relationship between natural sand burial of wrack and macroinvertebrate-facilitated decomposition has not been previously studied.

During and after the processing of organic material by detritivores, nutrients may flow back to the sea where they support marine primary production (McLachlan, 1980; Dugan et al., 2011) or create nutrient hot spots and locally support terrestrial primary (Hemminga and Nieuwenhuize, 1990; Del Vecchio et al., 2013) and secondary (Polis and Hurd, 1996; Schlacher et al., 2017) production. As sandy beach communities depend more heavily on marine subsidies than vice versa (Liebowitz et al., 2016), our focus in this study was on the role of macroinvertebrate-facilitated decomposition of wrack on beach plant growth. The supratidal zone provides adverse conditions for most plant species due to among others high salinity, low moisture content and low nutrient availability (Pakeman and Lee, 1991a). Wrack patches, however, are a unique micro-habitat for beach pioneer plants and an important nutrient and habitat source for animals within sandy beaches (Williams and Feagin, 2010; Del Vecchio et al., 2013). Indeed, beach pioneer plants benefit in terms of growth from a pulse in nutrient availability, especially nitrogen (Pakeman and Lee, 1991b). However, the role of abiotic (burial by sand) and biotic (macroinvertebrate activity) factors, influencing wrack decomposition and nutrient availability, for beach pioneer plant growth needs to be further experimentally tested.

Hence, the aims of this study were to test the effects of 1) wrack burial, 2) macroinvertebrate presence and 3) their interaction, on decomposition-driven nitrogen and phosphorus supply and beach pioneer plant growth. We hypothesised that 1) buried wrack would have a more positive effect on decomposition-driven nutrient supply and beach pioneer plant growth than wrack on the surface, as buried wrack has a higher moisture content and can more easily be decomposed. We further hypothesised that 2) macroinvertebrate presence would have a

positive effect on decomposition-driven nutrient supply and beach pioneer plant growth. The common semi-terrestrial amphipod *Talitrus saltator* used in this experiment was expected to play an important role in decomposition by feeding on and thereby fragmenting the wrack and by burrowing wrack fragments. As the wrack decomposes, more nutrients become available in the sand below the wrack. This in turn is expected to enhance pioneer beach plant growth as nutrient-limitation for beach plant growth is removed when growing in a drift line. Finally, we hypothesised that 3) there is an interaction effect between wrack burial and macroinvertebrate presence on decomposition-driven nutrient supply and beach pioneer plant growth. We expected that wrack on the surface would be less palatable to *T. saltator* as it holds less moisture (see Ruiz-Delgado et al., 2015) and a lower microbial biomass, hence food. Thus, exposed wrack would negatively impact the facilitation by macroinvertebrates of decomposition and subsequent beach pioneer plant growth.

2. Methods

To test the effect of macroinvertebrate presence and wrack burial on wrack decomposition and beach pioneer plant growth, we conducted a climate room experiment for which we assembled mesocosms consisting of pots of sand with different combinations of wrack burial, macroinvertebrate presence and plant species.

2.1. Wrack and animal collection

We used the brown macroalga *Fucus vesiculosus* as wrack, as it is a major component of wrack found upon Dutch sandy beaches (personal observation; see also Nienhuis, 1970). It is a preferential food source for the terrestrial amphipod *Talitrus saltator* (Lastra et al., 2008), which is used in this experiment as the macroinvertebrate species. Fresh *F. vesiculosus* was collected in May 2016 from the rocky pier near IJmuiden, the Netherlands (52.46 N, 4.55 E) during low tide, two weeks prior to the experiment. Sea weeds were cut loose with a pair of scissors at the stipe, ± 2 cm above the holdfast and stored in a plastic bucket. Directly after collection, *F. vesiculosus* was spread out on tables in the laboratory to dry at room temperature (20 °C) for three days to ensure a similar moisture content at the start of the experiment and to prevent any decay from occurring before the start of the experiment. *Fucus vesiculosus* was stored in a dry place until the start of the experiment seven days later.

Talitrus saltator is a common inhabitant of wrack on Dutch sandy beaches (see e.g., Van Colen et al., 2006). We collected *T. saltator* individuals from the beach near Scheveningen, the Netherlands (52.05 N, 4.19 E) not more than two weeks before the start of the experiment. Animals were collected from bare sand in the intertidal zone with visible holes (entrance to burrows of *T. saltator*) and from fresh wrack patches deposited during receding tide. Upon arrival in the laboratory the same day, collected animals were transferred to a terrarium filled with an 8–10 cm thick layer of quartz sand (Multiquartz, Lelystad, the Netherlands) and ad libitum *F. vesiculosus* as food. The last 24 h before the start of the experiment all food was removed to starve the animals and to empty their guts. For more details concerning animal collection and storage see Supplementary material.

2.2. Plant cultivation

We used two common pioneer plant species of Dutch sandy beaches: *Cakile maritima* and *Elytrigia juncea* (see e.g., Doing, 1995; Speybroeck et al., 2008). *Cakile maritima* is an annual forb that typically grows on buried wrack lines (Davy et al., 2006), while *E. juncea* is a perennial grass that can be found at the dune foot and initiates embryo dune formation by capturing sand, or within stabilised stands of *C. maritima* (Davy et al., 2006; Speybroeck et al., 2008). *Cakile maritima* seeds were collected by hand at the beach near Scheveningen, the Netherlands

(52.05 N, 4.19 E) in November 2014 and December 2015, after which they were stored cool (5 °C) and dark upon arrival in the laboratory until sowing commenced. We grew *C. maritima* plants from these seeds five weeks before the start of the experiment. Seedlings were watered once a week with 50 mL half-strength Hoagland solution (3 mM KNO$_3$, 2 mM Ca(NO$_3$), 1 mM NH$_4$H$_2$PO$_4$, 0.5 mM MgSO$_4$, 25 μM H$_3$BO$_3$, 1 μM KCl, 2 μM MnSO$_4$, 2 μM ZnSO$_4$, 0.1 μM CuSO$_4$, 0.1 μM (NH$_4$)$_6$Mo$_7$O$_{24}$ and 10 μM Fe(Na)EDTA) and once a week with 50–100 mL demineralised water, depending on the size of the plants, until the start of the experiment. For details about seedling cultivation, see Supplementary materials.

As we were insufficiently successful in growing *E. juncea* seedlings from root stocks collected in the field, we collected mature *E. juncea* plants (with a shoot length of at least 20 cm) and used these directly in the experiment. Approximately 100 *E. juncea* plants were collected seven days before the start of the experiment on the beach 'De Hors', Texel, the Netherlands (53.00 N, 4.74 E) and maintained in the laboratory (see Supplementary material). As we collected more *E. juncea* plants than necessary, we randomly selected 47 individuals to be used in the experiment.

2.3. Experimental design

We used a 2-way design to study the effect of wrack burial (surface or buried) and macroinvertebrates (present or absent) on the growth of two individual beach pioneer plant species (*C. maritima* and *E. juncea*). For each treatment we had eight replicates that were divided over eight blocks (Table 1). In addition, we performed a nutrient addition test to determine if a potential positive effect of wrack addition on plant growth could be related to nutrient limitation. For this purpose, we used three treatments for both *C. maritima* and *E. juncea*: nutrient addition, inoculum addition and no nutrient addition (plant only). An inoculum addition treatment was included to account for the effect of indirectly adding extra nutrients in treatments that received wrack and inoculum. The inoculum was a soluble extract of wrack, prepared by soaking *F. vesiculosus* in water (see below for details). For each of these three treatments we had five replicates that were divided over five blocks (Table 1). The number of treatments was dissimilar between the wrack x macroinvertebrate test and the nutrient addition test due to a lack of sufficient material for the latter test, but as these tests were

Table 1
Summary of the experimental design indicating the mesocosms included for both testing the main treatments and the nutrient addition test. Within brackets it is indicated how many mesocosms were included in the subset excluding mesocosms where no animals were retrieved upon harvest.

Main treatments	Wrack burial	Macroinvertebrates	Plant species	*n*	Total *n*
	Surface	Present	*C. maritima*	8 (6)	
			E. juncea	8 (6)	
		Absent	*C. maritima*	8 (8)	
			E. juncea	8 (8)	
	Deep	Present	*C. maritima*	8 (3)	
			E. juncea	8 (3)	
		Absent	*C. maritima*	8 (8)	
			E. juncea	8 (8)	
					64 (50)
Nutrient addition test	Addition		Plant species	*n*	Total *n*
	Nutrients		*C. maritima*	5	
			E. juncea	5	
	Inoculum		*C. maritima*	5	
			E. juncea	5	
	None (control)		*C. maritima*	5	
			E. juncea	5	
					30

analysed separately, this did not cause statistical problems. In a climate room, all mesocosms were placed within combined blocks (eight in total). This finally resulted in five blocks with fourteen mesocosms (combining main treatments and the nutrient addition test treatments) and three blocks with eight mesocosms (remaining mesocosms of main treatments). Blocks and mesocosms within blocks were moved around randomly twice a week. In total, there were 94 mesocosms and each mesocosm was randomly assigned to one of the above treatments.

Each mesocosm (plastic pot, diameter: 14 cm; height: 14 cm) was filled with a 9 cm layer of quartz sand. Each mesocosm assigned to a wrack treatment received 14 ± 0.3 g of dry *F. vesiculosus*, which corresponds to a potential nutrient addition (if all nutrients would be released from wrack) of 0.37 g N and 0.05 g P (data not shown). In treatments with surface wrack, this resulted in a 2.5–3 cm thick layer of loosely packed wrack placed on top of the sand, covering the entire surface of the mesocosm. In treatments that contained buried wrack, this resulted in a layer of 2.5–3 cm loosely packed wrack placed on top of the sand and covered with approximately 150 g sand so that the top of the wrack was just visible (Fig. 1). Before placing wrack in the mesocosm, 50 mL of wrack inoculum (see below) was added onto the wrack to re-establish populations of wrack-associated decomposer microorganisms that may have died-off while air-drying. For those treatments with macroinvertebrates present, we randomly added eight individuals of *T. saltator* (± 0.3 g total fresh biomass or 52 individuals m^{-2}) corresponding to field densities encountered in wrack (19 ± 24 individuals m^{-2} (Bessa et al., 2014); 91 ± 18 individuals m^{-2} (Ruiz-Delgado et al., 2016)). Females with brood sacks were omitted. Animals were placed on top of the sand, after which most of them started burying themselves into the sand. Each mesocosm contained either one *C. maritima* or *E. juncea* plant. All mesocosms were covered with a nylon mesh (mesh size 0.5 mm), secured by tape on the pot edges, and had a hole (square of 1 cm^2) in the middle to allow the stem of the plant to pass while keeping the animals in the mesocosms. A piece of white nylon wool was wrapped around the stem to protect it from the sharp edges of the plastic mesh, and to prevent animals from escaping. All mesocosms were placed in a climate room with a 12:12 h light/dark regime (light intensity: 500 μmol m^{-2} s^{-1}; lamp type: Philips CDM-TMW 315 W/942), a 20:15 °C day/night temperature regime and an 85:75% RH day/night air humidity. These circumstances correspond to late spring/early summer conditions in the Netherlands. The bottom of the mesocosms was lined with tightly woven plastic root canvas, which allowed water and solutes to pass but kept all other material inside the mesocosm. The experiment was run for four weeks in June–July 2016.

The day before the start of the experiment, each mesocosm received 250 mL demineralised water and 50 mL 50 mM NaCl to ensure equal starting conditions in moisture and salt content. A low salt content has a positive effect on beach pioneer plant growth (Lee and Ignaciuk, 1985; Debez et al., 2004). Wrack inoculum was prepared by adding 3.7 kg of freshly collected *Fucus vesiculosus* wrack to 3.5 L demineralised water. After 3 h of soaking, the inoculum was strained to remove larger wrack particles (> 1 mm). All main treatments and the inoculum treatment of the nutrient addition treatments were given 200 mL demineralised -water and 50 mL inoculum at the start of the experiment, while the nutrient addition treatment without inoculum was given 250 mL demineralised water. All mesocosms received 125 mL demineralised water twice a week during the experiment. The nutrient addition treatments that received nutrient solution instead were watered twice a week with 125 mL nutrient solution that contained 0.03 g N (0.43 mL of 5 M NH$_4$Cl stock solution) and 0.004 g P (0.13 mL of 1 M NaH$_2$PO$_4$ stock solution). In total, plants in these treatments received 0.24 g N and 0.03 g P, which is in the same range as the amount of N and P available in the amount of wrack added in this experiment.

2.4. Measured variables

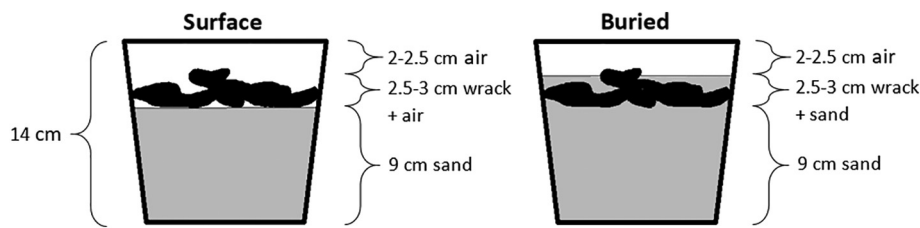For a subset of specimens (*n* = 10), we collected the fresh and dry

mass (to the nearest 0.001 g) at t = 0 for the roots, shoot (*E. juncea* only) and stem (*C. maritima* only) and leaves (*C. maritima* only). We determined the fresh mass of the total plant for all individual plants at the start of the experiment and we measured fresh mass of wrack for all mesocosms. Upon harvest, we collected the fresh and dry mass of the roots, shoot (*E. juncea* only), stem (*C. maritima* only), flowering heads (*C. maritima* only), green leaves (*C. maritima* only) and (shedded) brown leaves (*C. maritima* only). In addition, we determined the fresh and dry mass of remaining wrack and the numbers of *T. saltator* found dead or alive. For wrack, the moisture content (%) at harvest was calculated. Total shoot mass of *C. maritima* consisted of the stem, green and brown leaves and flowering head combined. *Elytrigia juncea* plants, on the other hand, were all in the vegetative stage and without entire leaves browning. Upon harvest, samples were oven-dried for 72 h at 70 °C. Dried samples were ground into a fine powder in a ball mill (MM400, Retsch, Haan, Germany) and homogenised by mixing the ground sample. Total N concentration of plant parts were determined by dry combustion with a Flash EA1112 elemental analyser (Thermo Scientific, Rodana, Italy). For P content, a 50 mg subsample was digested in 1 mL of a 1:4 mixture of 37% (by volume) HCl and 65% (by volume) HNO_3, in a closed Teflon cylinder for 6 h at 140 °C. Samples were then diluted with 4 mL demineralised water and total P content was measured colorimetrically (Murphy and Riley, 1962). To correct for sand trapped between plant roots, a homogenised root subsample was combusted at 550 °C to obtain mass loss on ignition. Total N concentration was used to determine the total N content of the plants, which can be considered as a measure of total N uptake. Finally, the N/P ratio based on dry mass upon harvest was calculated as a measure for the type of nutrient limitation in the plant and its organs (see Supplementary for results on the N/P ratio).

2.4.1. Data and statistical analysis

Given the large number of non-retrieved individuals (see Supplementary material) and the unknown time of death and how this affects the processes measured (while individuals found dead will at least have contributed to wrack decomposition and mineralisation for part of the experimental period), we decided to include only those mesocosms in which macroinvertebrates were retrieved upon harvest, either dead or alive, in further analysis. Exclusion of mesocosms without retrieved animals upon harvest resulted in 18 out of 32 mesocosms remaining for the macroinvertebrate treatment (n = 6 for shallow buried wrack and n = 3 for deep buried wrack, for each of the two plant species, see Table 1).

We chose to present the absolute final mass, nutrient content and N/P ratio of the different plant organs as plants grew large quickly: the relative increase of total plant biomass was on average 317% (± 278%) and 70% (± 101%) for *C. maritima* and *E. juncea*, respectively. Biomass at t = 0 was therefore considered small relative to the biomass increase and focussing on the absolute final biomass simplifies both the analysis and interpretation of the results. Prior to analysis, all data were tested for homogeneity of variances (Levene's test) and normal distribution (Shapiro-Wilk test). When these assumptions were not met (main treatments: dry mass (total shoot), P content (total plant, total shoot and roots), N/P ratio (total plant, total shoot and roots) of *C. maritima*; dry mass (total plant, total shoot and roots), N content (total plant, total shoot and roots), P (total shoot), N/P ratio (total plant and

roots) of *E. juncea*; nutrient addition treatments: N content (total shoot) of *E. juncea*), a log transformation was performed on the original data. To test the effect of both wrack and macroinvertebrates on each of the variables plant mass, N and P content and N/P ratio, a two-way ANOVA was performed for each plant organ (total plant, total shoot and roots) and for each plant species, separately. We performed a Kruskal-Wallis test, as the data did not meet the assumptions of a parametric test after transformation, to test the effect of macroinvertebrate presence and plant species on wrack moisture percentage separately. To evaluate the nutrient addition treatments (three levels: nutrient addition, inoculum addition and plant only) on each of the variables plant dry mass, N and P content and N/P ratio, we performed a one-way ANOVA for each plant organ (total plant, total shoot and roots) and for each species, separately. The results of the nutrient addition treatments can be found in the Supplementary. ANOVAs were followed up with Tukey's post hoc tests if relevant. All statistical analyses were done in R, version 3.2.3 (R Core Team, 2015).

3. Results

3.1. Wrack moisture content

Surface wrack had a lower moisture content than buried wrack (61.3 ± 6.4% and 81.7 ± 3.3%, respectively; Kruskal-Wallis test, df = 1, χ^2 = 47.3, p < 0.001). There were no significant differences in wrack moisture content between pots with different plant species (Kruskal-Wallis test, df = 1, χ^2 = 0.27, p = 0.60) or macroinvertebrate treatments (Kruskal-Wallis test, df = 1, χ^2 < 0.1, p = 0.98).

3.2. Plant biomass

For *Cakile maritima*, wrack burial resulted in a strong and significant increase in the dry mass of the total plant, total shoot and roots (Table 2, Fig. 2). Plant dry mass was approximately two times as high when wrack was buried as opposed to surface wrack. No significant effects were found for macroinvertebrate presence on the dry mass of the total plant, total shoot or roots. For *Elytrigia juncea*, there were no significant differences of either wrack burial or macroinvertebrate presence on the dry mass of either the total plant, total shoot or roots (Table 2, Fig. 2).

3.3. Plant nitrogen content

The overall pattern for N content, for both plant species and all plant organs, was highly similar to the pattern of dry mass (Table 3, Fig. 3), except that for *C. maritima* there was a significant negative effect of macroinvertebrate presence on the N content of the total plant. When macroinvertebrates were present, the N content of the total plant was lower than when macroinvertebrates were absent, both for buried and surface wrack. Moreover, the N content was approximately three times as high when wrack was buried as opposed to surface wrack (Fig. 3).

3.4. Plant phosphorus content

The overall pattern for P content, for both plant species and all plant

Table 2
Overview of the two-way ANOVA results on the effect of wrack burial (Wrack) and macroinvertebrate presence or absence (Macroinvertebrates) on plant dry mass, for two species (*Cakile maritima* and *Elytrigia juncea*) and plant organs separately. Significant *p*-values (p < 0.05) are indicated in bold.

		df	F	p
C. maritima				
Total plant	Wrack	1	20.2	**< 0.001**
	Macroinvertebrates	1	1.8	0.19
	Wrack * Macroinvertebrates	1	0.0	0.87
Total shoot	Wrack	1	17.8	**< 0.001**
	Macroinvertebrates	1	2.2	0.15
	Wrack * Macroinvertebrates	1	0.0	0.98
Roots	Wrack	1	21.7	**< 0.001**
	Macroinvertebrates	1	0.3	0.60
	Wrack * Macroinvertebrates	1	0.5	0.47
E. juncea				
Total plant	Wrack	1	0.1	0.74
	Macroinvertebrates	1	0.1	0.74
	Wrack * Macroinvertebrates	1	1.3	0.26
Total shoot	Wrack	1	0.3	0.61
	Macroinvertebrates	1	0.5	0.48
	Wrack * Macroinvertebrates	1	2.0	0.18
Roots	Wrack	1	0.0	0.98
	Macroinvertebrates	1	0.5	0.50
	Wrack * Macroinvertebrates	1	0.0	0.93

Table 3
Overview of the two-way ANOVA results on the effect of wrack burial (Wrack) and macroinvertebrate presence or absence (Macroinvertebrates) on N content, for two species (*Cakile maritima* and *Elytrigia juncea*) and plant organs separately. Significant p-values (p < 0.05) are indicated in bold.

|		df	F	p
C. maritima				
Total plant	Wrack	1	88.2	**< 0.001**
	Macroinvertebrates	1	5.3	**0.03**
	Wrack * Macroinvertebrates	1	0.6	0.46
Total shoot	Wrack	1	78.1	**< 0.001**
	Macroinvertebrates	1	3.7	0.07
	Wrack * Macroinvertebrates	1	0.6	0.45
Roots	Wrack	1	52.6	**< 0.001**
	Macroinvertebrates	1	1.6	0.21
	Wrack * Macroinvertebrates	1	0.8	0.37
E. juncea				
Total plant	Wrack	1	0.7	0.43
	Macroinvertebrates	1	0.2	0.69
	Wrack * Macroinvertebrates	1	0.1	0.76
Total shoot	Wrack	1	1.4	0.26
	Macroinvertebrates	1	1.1	0.30
	Wrack * Macroinvertebrates	1	0.2	0.67
Roots	Wrack	1	0.1	0.71
	Macroinvertebrates	1	0.4	0.56
	Wrack * Macroinvertebrates	1	0.0	0.94
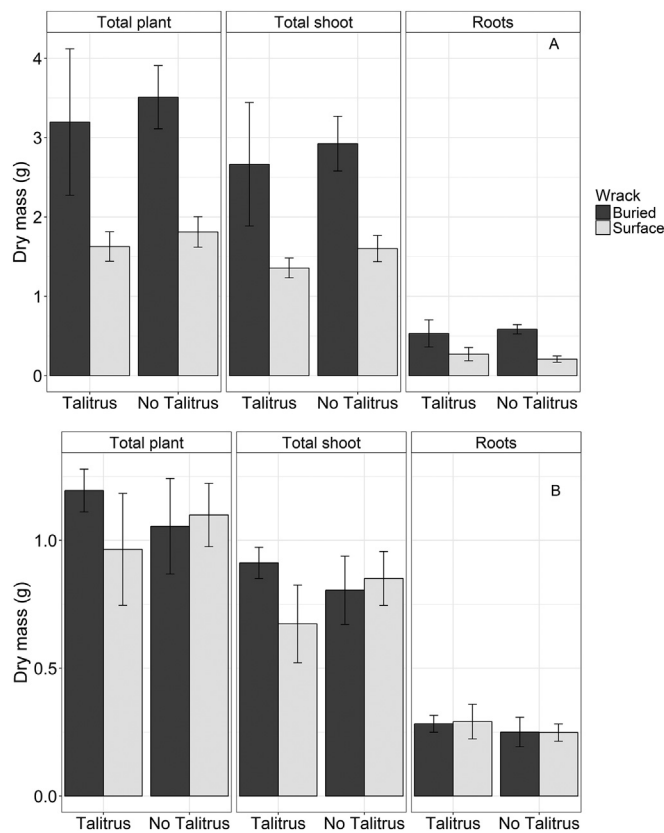
Fig. 2. Dry mass of the total plant (roots and shoot), total shoot (stem and leaves) and roots of A) *Cakile maritima* and B) *Elytrigia juncea* at harvest shown for both buried or surface-exposed wrack and in the presence or absence of the amphipod *Talitrus saltator*. For buried wrack n = 3, while n = 6 for surface-exposed wrack in the presence of *T. saltator*. For all other treatment combinations n = 8. Error bars indicate the standard error from the mean.

organs, was also highly similar compared to the pattern of dry mass (Table 4, Fig. 4), except there was an interaction effect between wrack burial and macroinvertebrate presence for both the P content of the
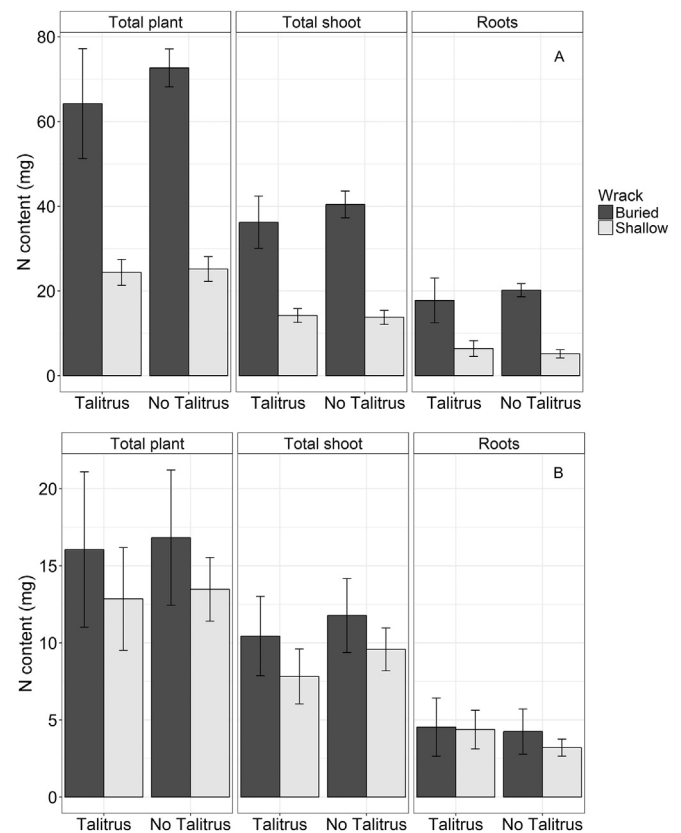
Fig. 3. N content of the total plant (roots and shoot), total shoot (stem and leaves) and roots of A) *Cakile maritima* and B) *Elytrigia juncea* at harvest shown for both buried or surface-exposed wrack and in the presence or absence of the amphipod *Talitrus saltator*. For buried.

total plant and the total shoot: if wrack was buried, P content of the total plant and the total shoot was higher in the presence of macroinvertebrates, while the opposite was the case when wrack was placed on the surface. The P content was approximately two to three times as high when wrack was buried as opposed to surface wrack (Fig. 4).

Table 4

Overview of the two-way ANOVA results on the effect of wrack burial (Wrack) and macroinvertebrate presence or absence (Macroinvertebrates) on P content, for two species (*Cakile maritima* and *Elytrigia juncea*) and plant organs separately. Significant p-values (p < 0.05) are indicated in bold.

|		df	F	p
C. maritima				
Total plant	Wrack	1	27.9	**< 0.001**
	Macroinvertebrates	1	0.1	0.71
	Wrack * Macroinvertebrates	1	4.5	**< 0.05**
Total shoot	Wrack	1	18.5	**< 0.001**
	Macroinvertebrates	1	1.6	0.22
	Wrack * Macroinvertebrates	1	8.8	**< 0.001**
Roots	Wrack	1	20.4	**< 0.001**
	Macroinvertebrates	1	2.5	0.13
	Wrack * Macroinvertebrates	1	0.2	0.63
E. juncea				
Total plant	Wrack	1	0.7	0.41
	Macroinvertebrates	1	0.0	0.84
	Wrack * Macroinvertebrates	1	0.6	0.43
Total shoot	Wrack	1	0.0	0.96
	Macroinvertebrates	1	0.5	0.50
	Wrack * Macroinvertebrates	1	0.5	0.48
Roots	Wrack	1	2.3	0.14
	Macroinvertebrates	1	0.6	0.46
	Wrack * Macroinvertebrates	1	0.7	0.40
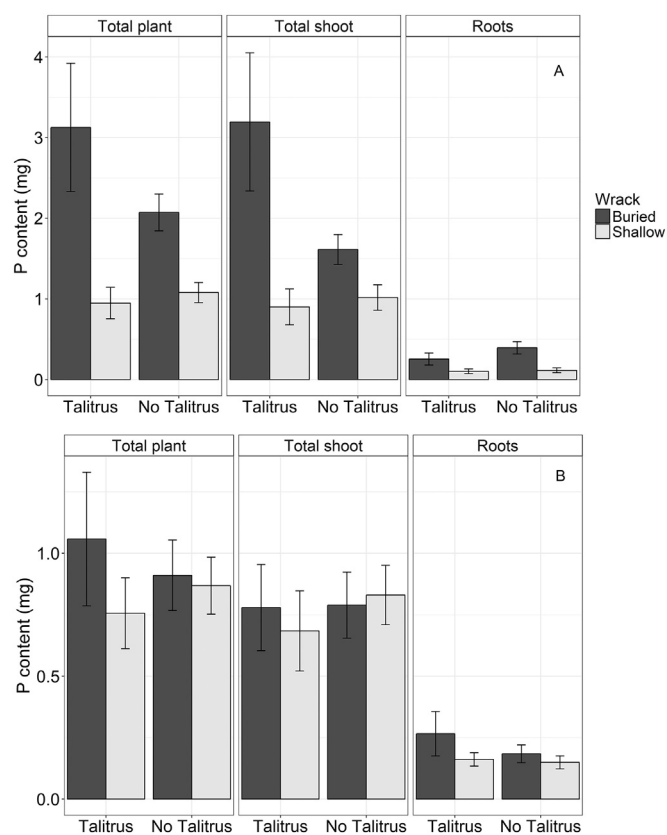
Fig. 4. P content of the total plant (roots and shoot), total shoot (stem and leaves) and roots of A) *Cakile maritima* and B) *Elytrigia juncea* at harvest shown for both buried or surface-exposed wrack and in the presence or absence of the amphipod *Talitrus saltator*. For buried wrack n = 3, while n = 6 for surface-exposed wrack in the presence of *T. saltator*. For all other treatment combinations n = 8. Error bars indicate the standard error from the mean.

4. Discussion

We focused on the effect of wrack burial and macroinvertebrate presence on decomposition and nutrient availability for beach pioneer plant growth. We found that while burial of wrack had a strong positive effect on the growth of *Cakile maritima*, no significant effect was found for *Elytrigia juncea*. For *C. maritima*, the N content of the total plant was lower in the presence of macroinvertebrates. For buried wrack, P content was higher for both the total plant and total shoot of *C. maritima* in the presence of macroinvertebrates. Differences in N and P content of *C. maritima* plants due to macroinvertebrate presence did however not result in differences in plant dry mass. Together, this suggests that macroinvertebrates enhance decomposition of wrack but that released inorganic N is not available for *C. maritima* plants. Excess P on the other hand was incorporated in *C. maritima*. We conclude that the burial of wrack is of paramount importance for *C. maritima* growth, which may support embryo dune formation and sandy beach and dune ecosystem functioning. Below these findings are discussed in more detail.

4.1. Buried wrack is a strong driver of Cakile maritima growth

As to our first hypothesis, buried wrack had indeed a strong positive effect on beach pioneer plant growth, but only for *C. maritima*. *Cakile maritima* plants not only accumulated more nutrients both in the total shoot and roots, but also grew larger when wrack was buried. Although the age of the plants differed in this experiment, which might have impacted plant growth, it is expected that the differences in plant growth between *C. maritima* and *E. juncea* are mainly species-specific and related to differences in growth and habitat requirements. *Cakile maritima* is an annual herb, and annual plant species are known to exhibit taller and faster growth of both the shoot and roots than perennial species (Gross et al., 1992). In contrast, *Elytrigia juncea* is a perennial grass (Hanlon and Mesgaran, 2014) and may thus exhibit lower plant growth. Buried wrack may thus promote the growth of some plant species more profoundly than other species on the beach, which ultimately may result in an altered plant community structure on sandy beaches.

Our findings suggest that the positive effect of buried wrack on *C. maritima* growth is primarily due to an increase in moisture availability rather than an increase in nutrient availability. To discriminate between the moisture and nutrient effect of wrack on plant growth, we included nutrient addition treatments (see Supplementary, Section 3 and 4). These indicated that nutrients are not a limiting factor for plant growth. Only when buried wrack was added as opposed to solely nutrients in solution, the increased accumulation of N and P did result in higher plant growth, suggesting that the physical properties of buried wrack had an additive positive effect.

In our study, buried wrack had a higher moisture content than wrack placed on the surface. This finding suggests that a higher soil moisture content is an important wrack-mediated factor, positively influencing *C. maritima* plant growth. The decay of litter is greater when the material is fresh and moist (Coûteaux et al., 1995), thereby releasing more dissolved organic carbon and increasing microbial activity (Coupland et al., 2007; Lavery et al., 2013). By retaining moisture, wrack forms an organic band of easy-to-reach moisture in the sand column (Adair et al., 1990), which benefits beach pioneer plant growth (Del Vecchio et al., 2013), most likely by lifting moisture limitation and promoting N and P transport and uptake (Aerts and Chapin III, 1999). This is opposed to rain water entering the sand and quickly moving downwards beyond the reach of the roots, as sand has a low moisture holding capacity (Pakeman and Lee, 1991a).

There may have been other wrack-related factors, such as an increase in the interstitial space of the sand (Rossi and Underwood, 2002), that could have an effect on plant growth, but these are expected to be small compared to the effect of moisture and nutrient availability, which are more directly related to plant growth. We conclude that

burial of wrack has a positive effect on *C. maritima* plant growth mainly through enhancement of sediment moisture content.

4.2. Macroinvertebrate presence affects plant nutrient content, but not plant growth

Macroinvertebrate presence had an effect on N and P content in plant tissue but not on beach pioneer plant growth, which is in contrast to our second hypothesis. In addition, we found some interactive effects between wrack burial and macroinvertebrate presence for N and P content in plant tissue only, which is partly in line with our final hypothesis. Thus, macroinvertebrates were important in decomposition-driven nutrient availability. Previous studies on the effect of supratidal macroinvertebrates on wrack decomposition reported mixed results, ranging from large positive (Lastra et al., 2008; Salathé and Riera, 2012) to small or no effects (Inglis, 1989; Jędrzejczak, 2002; Catenazzi and Donnelly, 2007) and our findings are mainly in agreement to the former studies.

For *C. maritima*, a negative effect of macroinvertebrate presence on the N content of the total plant was observed, which appears to be in contrast to our second hypothesis. In other nutrient-poor ecosystems, such as northern peatlands, high decomposing activities, however, result in an initial immobilisation of N by the microbial community (Dorrepaal et al., 2007). Macroinvertebrates enhance decomposition via fragmentation of wrack (Ince et al., 2007; Salathé and Riera, 2012; Lastra et al., 2015), but the additionally released N may initially be incorporated in microbial instead of plant biomass (Dorrepaal et al., 2007). In addition, phenolic compounds, which are present in high amounts in *Fucus* spp. (Targett et al., 1992), may be released during decomposition. This released carbon may have acted as a carbon source for the microbial community, enhancing its activity (Lavery et al., 2013) and consequently N immobilisation (Michelsen et al., 1995). Released phenolic compounds may also bind to inorganic N thereby forming insoluble complexes and causing chemical immobilisation of N (Hättenschwiler and Vitousek, 2000).

On the other hand, P content was higher for both the total plant and total shoot in the presence of macroinvertebrates when wrack was buried, while the opposite was the case in the presence of macroinvertebrates when wrack was placed on the surface. Macroinvertebrates thus had a positive effect on decomposition-driven P availability, supporting a higher P content in *C. maritima* plants, but only when moisture was not limiting.

Differences in N and P content of *C. maritima* were only observed when wrack was buried and sand moisture content was increased, which is likely due to an increase in microbial activity (Coupland et al., 2007; Lavery et al., 2013) as opposed to drier surface-facing wrack. In addition, moist wrack was probably more palatable to *T. saltator* resulting in a higher consumption (see Ruiz-Delgado et al., 2015). The findings for P further suggest that the microbial community associated with wrack may be principally N (or C) limited and less limited by P (e.g., Heuck et al., 2015), resulting in an increased uptake of N when this became available during wrack decomposition. Plants appeared to be P limited in the absence of macroinvertebrates when wrack was buried, as the N/P ratio of *C. maritima* shoots was relatively high (Fig. S1, Table S1) and well above a N/P ratio of 16, which indicates a P limitation (Aerts and Chapin III, 1999). Plants may in that case have competed more strongly with the microbial community for P than N, resulting in a higher P content and lower N/P ratio (Fig. S1, Table S1) when macroinvertebrates were present and nutrient availability was enhanced.

Nevertheless, neither for N or P an effect of macroinvertebrate presence was found on plant dry mass. This suggests that lifting P limitation is not sufficient to result in an increase in plant growth, even though total moisture availability increased when wrack was buried. Moisture was either still limiting or an additional factor had been limiting plant growth (e.g., salt, micronutrients). Macroinvertebrates

may have had a positive effect on plant growth when decomposition and nutrient release, due to macroinvertebrate feeding activity, would have exceeded the nutritional needs of the microbial community, or when nutrients are finally released from the microbial community via remineralisation. Therefore, our study highlights the complexity of macroinvertebrate-mediated processes that result in the degradation of wrack and subsequent uptake of nutrients by beach pioneer plants.

4.3. Limitations to our study

As we have performed a laboratory experiment, there are limitations to the conclusions that can be drawn regarding the sandy beach ecosystem as a whole, even though the natural complexity on Dutch exposed sandy beaches is low. Finally, it should be noted that the effects of biotic factors were likely underestimated in our experiment due to the considerable mortality of *T. saltator*. The effects of macroinvertebrate presence were even smaller when mesocosms in which no macroinvertebrates were retrieved upon harvest were included in the analysis (see Supplementary, Fig. S6-S9 and Table S3-S6). Although we had used a representative *T. saltator* density in this experiment, the effect of *T. saltator* on decomposition-driven nutrient availability may be larger in the field where *T. saltator* densities can locally become very high (up to 3500 individuals m^{-2} (Van Colen et al., 2006) or even 7900 individuals m^{-2} (Ruiz-Delgado et al., 2016)). The effect of macroinvertebrate presence on decomposition-driven nutrient availability may thus be amplified when more individuals are present and active. Nevertheless, this will likely not result in an increase in plant growth as other factors appear to limit plant growth.

4.4. Conclusions

We conclude that wrack burial enhances nutrient availability and stimulates the growth of the beach pioneer plant species *C. maritima*, but not *E. juncea*. Beach pioneer plants appeared to be mainly limited by moisture rather than nutrients. Decomposition of wrack by macroinvertebrates was an additional factor that increased nutrient availability, but this did not result in an increase in plant growth. Leaving wrack on the beach and allowing it to be covered by sand and subsequently decomposed, is expected to provide a moisture and nutrient hot spot for beach pioneer plants on sandy beaches. Buried wrack can provide preferable microclimate conditions for plant growth and possibly support embryo dune formation, e.g., for *C. maritima* (Davy et al., 2006), while also having a positive effect on dune vegetation in terms of plant diversity (Del Vecchio et al., 2017). It is therefore recommended to allow wrack to be deposited and buried on the sandy beach to promote the sandy beach ecosystem in future coastal management strategies.

Author contributions

EME, PMB, MPB and RA conceived and designed the experiment. EME, JRH, RSPL and RAB performed the experiment. EME, PMB, MPB and RA analysed the data. EME wrote the manuscript with the other authors providing editorial advice.

Data accessibility

Data can be obtained by contacting the corresponding author directly.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2019.03.015.

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