Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies

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Abstract. Many ecosystems are greatly affected by ecosystem engineering, such as coastal salt marshes, where macrophytes trap sediment by reducing hydrodynamic energy. Nevertheless, little is known about the costs and benefits that are imposed on engineering species by the traits that underlie their ecosystem engineering capacity. We addressed this topic by comparing ecosystem engineering efficiency defined as the benefit–cost ratio per unit of biomass investment for two species from the intertidal habitat: the stiff grass *Spartina anglica* and the flexible grass *Puccinellia maritima*. These species were selected for their ability to modify their habitat by trapping large quantities of sediment despite their contrasting growth form. On a biomass basis, dissipation of hydrodynamic energy from waves (a proxy for benefits associated with ecosystem engineering capability as it relates to the sediment trapping capability) was strikingly similar for both salt marsh species, indicating that both species are equally effective in modifying their habitat. The drag forces per unit biomass (a proxy for costs associated with ecosystem engineering ability as it relates to the requirements on tissue construction and shoot anchoring to prevent breaking and/or washing away) were slightly higher in the species with flexible shoots. As a result, stiff *Spartina* vegetation had slightly higher ecosystem engineering efficiency, due to lower engineering costs rather than to a higher engineering effect. Thus, *Spartina* is a slightly more efficient rather than a more effective ecosystem engineer. Ecosystem engineering efficiency was found to be a species-specific characteristic, independent of vegetation density and relatively constant in space. Analyzing ecosystem engineering by quantifying trade-offs offers a useful way toward developing a better understanding of different engineering strategies.

Key words: drag; extended phenotype; niche construction; sediment accretion; trade-offs; waves.

INTRODUCTION

Since the introduction of the concept of ecosystem engineering (Jones et al. 1994, 1997), various studies have demonstrated that biologically mediated modification of the abiotic environment has a major impact on the structure, function, and biodiversity of a wide range of ecosystems (e.g., Crooks 2002, Bruno et al. 2003, Cuddington and Hastings 2004, Gilad et al. 2004, Wright and Jones 2006, Hastings et al. 2007). Despite the well-recognized importance of ecosystem engineering for ecosystem structure and functioning, adaptive significance of ecosystem engineering still has received relatively little attention (Jones et al. 1994, Laland et al. 1999, Day et al. 2003, Odling-Smee et al. 2003, Boogert et al. 2006, Laland and Sterelny 2006). For growth strategies, understanding of potential fitness consequences has benefited greatly from insight in the trade-offs associated with such strategies (Pianka 1970, Grime 1977, 1979, 1988, Grime and Mackey 2002). We expect that studies on trade-offs associated with ecosystem

engineering can equally deepen our understanding of engineering as strategy. However, to our knowledge, studies on the trade-offs associated with ecosystem engineering remain scarce.

Intertidal coastal vegetation proved to be a suitable model system to quantify cost and benefits associated with traits that underlie ecosystem engineering (Bouma et al. 2005). The harsh environmental conditions in the pioneer zone of the marsh make ecosystem engineering (e.g., soil oxygenation, sediment accretion, substrate stabilization) with its associated positive species interactions an important process (e.g., see Bertness and Hacker 1994, Castellanos et al. 1994, Bertness and Leonard 1997, Bruno 2000, Daleo et al. 2007), and hydrodynamic forces can play a critical role in the establishment, survival and expansion of plants (e.g., see Bruno 2000, Houwing 2000, Kennedy and Bruno 2000, Robbins and Bell 2000, van Katwijk and Hermus 2000). Using the biophysical interaction of epibenthic plant structures with hydrodynamic energy as a model system, we were able to demonstrate with *Spartina anglica* and *Zostera noltii*, that the degree of shoot stiffness represents a clear trade-off: Increased shoot stiffness enhances both a species capacity to reduce hydrodynamic wave energy (i.e., proxy for ecosystem engineer-

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ing ability) and the drag that needs to be resisted (i.e., proxy for ecosystem engineering costs); decreasing shoot stiffness restricts both these aspects (Bouma et al. 2005). Field observations suggest that this trade-off may however be more complex.

It has been well described that the stiff pioneer species *Spartina anglica* (a dominant pioneer in the Scheldt estuary, southwest Netherlands) can trap large quantities of sediment (Castellanos et al. 1994, van Hulzen et al. 2007). On the salt marshes of the back-barrier islands of the Waddensea area (northern Netherlands), *Spartina anglica* is nearly absent, because the species reaches its northern distribution limit and grows less well on the sandier substrate that is available there. As a consequence, the pioneer zone occurs at a somewhat higher elevation in the tidal gradient and is dominated by highly flexible *Puccinellia maritima* vegetation, which is also known to trap large quantities of sediment (Andresen et al. 1990). The latter is in contrast to our earlier trade-off analysis, in which we concluded that flexible *Zostera noltii* has a limited ability to modify its environment (Bouma et al. 2005). From the field, it is obvious that *Puccinellia maritima* can reach much higher standing biomass than can *Zostera noltii*. Hence we propose that to further enhance our understanding of ecosystem engineering as a strategy, trade-off analysis of ecosystem engineering should be extended to account for biomass investments related to ecosystem engineering. This would require defining a measure of ecosystem engineering efficiency as a benefit–cost ratio in which both benefits and costs are expressed per unit of biomass investment.

In intertidal vegetation, wave attenuation is caused by the energy dissipation generated by the physical structure of the organism, which causes wave energy to decrease with distance through vegetation (e.g., Fonseca and Cahalan 1992, Moller et al. 1999, Mendez and Losada 2004, Koch et al. 2009). Given the different ecosystem engineering growth strategies that can be found in intertidal coastal vegetation, it may be questioned (1) to what extent the physical laws of energy conservation allow the “stiff” and “flexible” ecosystem engineering strategies to truly differ in their ecosystem engineering efficiency, and (2) if the spatially explicit nature of wave attenuation makes such efficiency dependent on the *scale* over which it is integrated. That is, in stiff vegetation wave energy will attenuate over a relatively short distance, so that the drag forces imposed on the plants are expected to be high at the vegetation edge, but to diminish rapidly with distance. In more flexible vegetation, both wave energy and drag forces may be expected to be lower at the vegetation edge, but also to remain more constant with distance into the vegetation. Regarding the difference in stiffness and comparable sediment trapping capacity, *Spartina anglica* and *Puccinellia maritima* offer an ideal model system to address such questions on ecosystem engineering efficiency.

Our objective in the present study is to determine (1) if ecosystem engineering efficiency, defined as benefit–cost ratio in which both benefits and costs are expressed per unit biomass, differs among ecosystem engineering strategies, (2) how this ecosystem engineering efficiency varies in space, and (3) if this may explain why both stiff *Spartina anglica* and flexible *Puccinellia maritima* pioneer vegetation can trap large quantities of sediment. We addressed these objectives by quantifying, in a flume, for both *Spartina* and *Puccinellia*, the ecosystem engineering efficiency at different locations within the vegetation. To assess the biomass effect, we created three vegetation densities by thinning. Ecosystem engineering efficiency was calculated as the ratio between benefits and costs, using the capacity to attenuate waves as a proxy for engineering benefits and the hydrodynamic drag forces as a proxy for engineering costs (cf. Bouma et al. 2005; details in methods).

MATERIALS AND METHODS

Experimental approach: a rationale

To compare the stiff *Spartina anglica* and flexible *Puccinellia maritima*, we defined ecosystem engineering efficiency (EEF) as the ratio between benefits (B_{EE}) and costs (C_{EE}) with respect to the ecosystem engineering ability of a species:

$$EEF = B_{EE}/C_{EE}. \quad (1)$$

Because biomass is a good measure for investments involved in tissue construction, we derived EEF from biomass based parameters. Hence we determined EEF on three levels of standing biomass, which were similar between the species. Calculating this EEF (details in the next subsections) requires quantitative proxies for engineering benefits and engineering costs. As reduction of hydrodynamic energy is a prerequisite for sediment to settle, wave attenuation was used as quantitative proxy for the ability of these engineering species to enhance sediment accretion (cf. Bouma et al. 2005). Such reduction of hydrodynamic energy by plant tissues, implies that the plant tissues must be able to resist and transform these hydrodynamic forces. This will either put requirements on tissue construction and shoot anchoring or result in enhanced risk of breaking and/or washing away. Hence, drag was used as a quantitative proxy for the costs that may be associated with such ecosystem engineering. Drag is a suitable proxy, as Gaylord (2000) demonstrated that the maximum forces observed in the surf zone were closely related to the calculated drag forces and because inertia forces are unimportant in plants that both lack mass and length of a flexible “tether” (Denny 1999).

Plant material

Wave attenuation and drag was measured on vegetation of *Spartina anglica* Hubbard and *Puccinellia maritima* (Hudson) Parl. Vegetation were obtained

from seeds planted in 1.0 m long, 0.25 m wide, and 0.15 m deep trays and grown in a climate room. Wave attenuation was measured on vegetation of three different densities, which were obtained by thinning the vegetation in two sequential steps. The highest densities were representative for the field situation, whereas the lower densities were artificially created to unravel the importance of biomass investments for trade-off analysis of ecosystem engineering. To not change the size distribution by thinning, we removed randomly selected shoots and had no recovery time after thinning. The flume was emptied and plants illuminated between measurements. At the end of the flume measurements we determined the dry mass of the total standing biomass and the average dry mass per shoot on a representative subsample. This subsample was obtained by harvesting a small vegetation plot and weighing 90 randomly selected shoots that were representative for the size distribution of the vegetation. Dividing the standing biomass by the average shoot dry weight gave the shoot density. Drag measurements were done on a small number of *Spartina* or *Puccinellia* shoots that were attached to a force transducer (details in Bouma et al. 2005). To get a better understanding of the mechanism that determines drag, we also mounted artificial strips with a contrasting stiffness onto the force transducer. We used both strips with a stiffness that is comparable to that of *Spartina* shoots (i.e., strips made from tie-wraps cf. Bouma et al. 2005) and non-bending strips made from 2 mm thick steel.

Measuring wave attenuation and drag

We used a 13.5 m long flume at WL | Delft Hydraulics (Delft, The Netherlands) where regular waves could be generated by a piston system. Between 0.35 m and 1.75 m after the wave generator we placed a smooth plate at a slope, to raise the level of the floor of the flume to the height of our plant trays (0.15 m). After this slope was a 5 m long flat surface, whereafter a 3 m long vegetation section was placed. The vegetation was then followed by a flat surface, with a wave damping rack to minimize wave reflection 1.4 m behind the vegetation. The flume was filled with water to a height of 200 mm, which allowed us to apply regular waves with a wave height up to 70 mm and a period of 1 s. Wave height was measured with three conductivity meters, with one of them mounted onto a sliding carriage that could be moved along the length of the flume. The wave amplitude inside the vegetation was measured at the start of the vegetation, and at 0.25, 0.50, 0.75, 1.0, 1.5, 2, 2.5, and 3.0 m into the vegetation. Measurements of all three conductivity meters were taken at 20 Hz over a period of at least 600 s.

Drag was measured by attaching a number of shoots parallel to each other and perpendicular to the direction of the waves, onto a force transducer. In case of artificial strips, we mounted eight strips that were 0.2 m long and

5 mm wide. This length was comparable to that of the average shoots used in the experiments. The force transducer was developed by WL | Delft Hydraulics (now part of Deltares) and had a design as described by Carrington (1990) and Denny (1988). The voltage output of the force transducer was proportional to the integrated force applied to the shoots, and not the momentum. The drag was measured at 6.1 m behind the wave generator, outside the meadow to eliminate measuring artefacts from touching surrounding vegetation. To relate drag forces and wave heights, a conductivity meter was mounted directly adjacent to the force transducer. Measurements of both sensors were taken at 20 Hz over a period of at least 600 s. During the drag measurements, shoot movement was quantified by marking the most outward positions that the shoots reached. Markings were made onto a transparent sheet attached to the transparent side of the flume, at a height of 0.2 m above the sediment surface. Subsequently, the distance between markings was measured with a ruler. Measurements were repeated for four to five shoots.

Calculating ecosystem engineering efficiency (EEF)

In order to calculate ecosystem engineering efficiency ($EEF = B_{EE}/C_{EE}$; Eq. 1), we defined equations to derive B_{EE} and C_{EE} from our wave attenuation and drag measurements. For regular waves, wave energy (E ; J/m²) is proportional to the square of wave height (H ; m) (Denny 1988):

$$E = 1/8\rho \times g \times H^2 \quad (2)$$

with ρ being the density of seawater (1025 kg/m³) and g being the gravity acceleration (9.8 m/s²). In the presence of vegetation, dissipation of wave energy will be due to drag in the vegetation. For a simplified analysis, we fitted our wave attenuation data according to an equation that assumes dissipation of wave energy conforms to linear wave theory (van Rijn 1994):

$$1/H_x = 1/H_0 + \alpha(x - x_0) \quad (3)$$

with H_0 and H_x being the wave height at given location x_0 and at a distance $x - x_0$ behind location x_0 (m), and α being the wave attenuation coefficient (m⁻²).

To use the wave attenuation as quantitative proxies for engineering benefits, B_{EE} (N/g DM; where DM is dry mass) was calculated by dividing the total amount of wave energy lost between two adjacent locations (E ; J/m² = N/m) by the distance between those locations (Δx ; m) and the standing biomass (SBM; g DM/m²):

$$B_{EE} = (E_{x0} - E_x)/\Delta x \times SBM. \quad (4)$$

Flexible plants are able to reduce drag by reconfiguring their geometry by bending. Quantitative descriptions of this reconfiguration and how it affects drag can be complex (Alben et al. 2002), but in many cases drag in flexible plants is described using a simplified model. The

FIG. 1. Characterization of the *Spartina* (Spa) and *Puccinellia* (Puc) vegetation used in the flume experiments. Contrasting vegetation densities were obtained by two sequential thinning steps. (A) Vegetation dry mass and (B) densities before thinning (all plants), after the first thinning (first cut) and after the second thinning (second cut) are represented by black, gray, and white bars, respectively. The number of shoots per square meter was calculated by dividing the standing biomass by the average ($\pm$ SE) shoot mass of *Spartina* (249 ± 5.5 mg; $n=90$ shoots) and *Puccinellia* (17 ± 0.40 mg; $n=90$). (C) The relatively large plant movement (M ; mm) for *Puccinellia* shoots (solid squares; $M_{\text{Puc}} = 0.0024a^2 + 0.6462a + 1.356$; $R^2 = 0.989$) compared to *Spartina* shoots (open diamonds; $M_{\text{spa}} = 0.0029a^2 + 0.0148a + 2.2327$; $R^2 = 0.985$) as a function of wave amplitude (a ; mm), clearly illustrates that *Puccinellia* shoots have a much higher flexibility than shoots of *Spartina*. Error bars indicate $\pm$ SE.

drag (F_d ; N) of an object is proportional to a power of the velocity (U ; m/s):

$$F_d = 1/2\rho \times A_c \times C_d \times s \times U^\beta \quad (5a)$$

with A_c being the characteristic area of an object (m^2), C_d being the drag coefficient (m/s), s being the sign indicating the direction of the drag (calculated as $s = |U|/U$), and $\beta = 2$ for rigid objects but $\beta < 2$ for flexible objects that are able to reconfigure (Denny 1988, Sand-Jensen 2003, Mendez and Losada 2004, Bouma et al. 2005). For blunt objects, the characteristic area of the object should be equal to the projected area, whereas for streamlined objects the use of the wetted surface is more appropriate (Vogel 1994). When comparing plant growth strategies, it is much more useful to relate drag (F_d ; Eq. 5a) to plant parameters that are relevant either from a more physical (i.e., projected frontal surface area) or a more biological costs (dry plant mass) perspective. Hence, we calculated the drag of an individual shoot per unit of total projected frontal surface area (F'_d ; N/m²):

$$F'_d = F_d/A_c = 1/2\rho \times C_d \times s \times U^\beta. \quad (5b)$$

To derive the drag of an individual shoot per unit of dry mass invested in that shoot (F''_d ; N/g DM), the drag of an individual shoot was divided by the experimentally determined shoot dry mass (M ; g DM):

$$F''_d = F_d/M. \quad (5c)$$

To derive the quantitative proxies for engineering costs that are encountered at that specific location (C_{EE} ; N/g DM), the drag of an individual shoot was multiplied by the shoot density of the population (n ; shoots/m²) and divided by the total standing biomass on an area basis

(SBM; g DM/m²):

$$C_{EE} = (F_d \times n)/\text{SBM}. \quad (6)$$

Note that, because $\text{SBM} = n \times M$, the numerical values and units (N/g DM) of F'_d and C_{EE} are in fact equal, so that the values can be interchanged.

DATA ANALYSIS

Statistics of wave height and wave period were extracted from the data series using Delft-Auke-PC software developed by WL | Delft Hydraulics (now part of Deltares, Delft, The Netherlands). The voltage output of the force transducer was analyzed in a similar way as the waves, as the output of the force transducer had a wave like shape. However, whereas for waves the distance between the maximum positive and minimum negative voltage readings gives the wave amplitude, the maximum drag must be obtained by dividing the “drag amplitude” by two. All presented data are based on estimates of the significant wave height (H_{rms}) in Auke-PC software. For each measurement, at least 600 waves were analyzed. Where suitable, regression lines were compared by ANCOVA.

RESULTS

Wave attenuation as proxy for plant benefits associated with ecosystem engineering

The contrast in shoot characteristics between stiff *Spartina* and flexible *Puccinellia* plants was clearly demonstrated by the huge difference in dry weight per shoot, which results in strongly deviating shoot densities for an approximately similar standing biomass and by the different magnitude of the shoot movement in response to a range of wave amplitudes (Fig. 1). Despite

FIG. 2. Wave attenuation through the vegetation visualized by plotting the wave amplitude (H ; m) as function of distance in the vegetation (x ; m). Vegetation densities for (A) *Spartina* and (B) *Puccinellia* are indicated by the symbols shown within the figure. Eq. 4 was fitted through the data points (dashed line) to estimate α (wave attenuation coefficient; m^{-2}), using the actually observed value for H_0 (wane height at location x_0). The values obtained for α in *Spartina* vegetation were 9.03 ($R^2 = 0.99$; $H_0 = 65.0$ mm) before thinning, 4.82 ($R^2 = 0.99$; $H_0 = 66.6$ mm) after the first thinning, and 2.53 ($R^2 = 0.85$; $H_0 = 69.8$ mm) after the second thinning. The values of α in *Puccinellia* vegetation were 9.34 ($R^2 = 0.95$; $H_0 = 65.9$ mm) before thinning, 3.20 ($R^2 = 0.92$; $H_0 = 67.3$ mm) after the first thinning, and 1.80 ($R^2 = 0.89$; $H_0 = 68.4$ mm) after the second thinning.

the contrasting shoot stiffness, wave attenuation had a comparable magnitude in both vegetation types (Fig. 2). Fitting the theoretical relationship described by Eq. 3 yields a single coefficient to describe the wave attenuation for each vegetation density (α). Plotting this coefficient as function of the standing biomass, shows that wave attenuation is remarkably similar for flexible and stiff vegetation when regarded on a biomass basis (Fig. 3). Expressing the data on such biomass basis is relevant, as this reflects the carbon investments made by both species. The similar wave attenuation per unit of standing biomass, does offer a mechanistic explanation why both species can trap large amounts of sediment despite of their contrast in shoot stiffness.

Drag forces as proxy for plant costs associated with ecosystem engineering

We subsequently quantified the dependence of drag for flexible *Puccinellia* and stiff *Spartina* shoots on wave amplitude, also including measurements on artificial flexible (tie-wrap) and stiff (metal) strips to clarify general patterns. When looking at the drag per unit total frontal surface area (F'_d ; N/m^2), drag on the stiff metal structures that lack reconfiguration is proportional to the wave energy, whereas this proportionality disappears for flexible structures that reconfigure by bending (Fig. 4A). As expected, drag forces per unit total frontal surface area (F'_d ; N/m^2) are smallest for the most flexible species (*Puccinellia*) and higher for the relatively stiff *Spartina* shoots. Differences in drag due to effects of shoot stiffness increase with increasing wave amplitude, but are also present in case of small waves, as can be seen from the initial slopes of the regressions lines (Fig. 4A). A completely different picture is however obtained when considering the drag per unit of shoot dry mass (F''_d ; $\text{N}/\text{g DM}$), as per unit “invested” dry mass, drag was

highest in the most flexible species (*Puccinellia*) and lowest for the relatively stiff *Spartina* shoots (Fig. 4B).

Calculating ecosystem engineering efficiency

Combining the relationship between drag and wave amplitude (Fig. 4) with the measurements of wave amplitude at different positions throughout the vegetation (Fig. 2) allows calculation of the drag imposed on shoots located at different positions within the vegetation. The result of such calculation also strongly depends on how the drag forces are normalized (i.e., per unit shoot dry mass or frontal surface), as the relationship between shoot dry mass and frontal surface area is species specific. When expressing drag per unit frontal surface area (F'_d ; N m^{-2}), drag forces are highest for stiff *Spartina* vegetation (Fig. 5A). When expressed per unit of shoot dry mass (F''_d ; N/g DM), however, drag forces are highest for the flexible *Puccinellia* vegetation (Fig.

FIG. 3. Wave attenuation by vegetation (indicated by α) as a function of standing biomass for two plant species with a contrasting shoot stiffness: relatively stiff *Spartina* (open diamonds) vs. relatively flexible *Puccinellia* (solid squares). The regression line is: $\alpha = 0.030(\text{biomass}) - 1.50$ ($R^2 = 0.97$).

FIG. 4. The dependence of drag on the wave energy (E ; J/m^2 ; Eq. 2) measured on individual structures that differ in stiffness. Drag was expressed both (A) per unit frontal surface area (F'_d ; N/m^2) and (B) per unit of dry mass (F''_d ; N/g DM), to compare physical and biological relevant units. Ranking from flexible to stiff, symbols indicate *Puccinellia* shoots (black squares), *Spartina* shoots (open diamonds), “flexible” artificial strips (gray triangles), and steel artificial strips (gray circles). Regression lines for the drag expressed per unit frontal surface area (N/m^2) are: for *Puccinellia* shoots, $F'_d = 2.77E^{0.50}$ ($R^2 = 0.89$); for *Spartina* shoots, $F'_d = 6.47E^{0.62}$ ($R^2 = 0.98$); for flexible strips, $F'_d = 6.91E^{0.83}$ ($R^2 = 0.999$); and for steel strips, $F'_d = 8.86E^1$ ($R^2 = 0.999$). Regression lines for the drag expressed per unit of dry mass (N/g DM) are: for *Puccinellia* shoots, $F''_d = 0.1327E^{0.50}$ ($R^2 = 0.89$) and for *Spartina* shoots, $F''_d = 0.0812E^{0.62}$ ($R^2 = 0.98$).

5B). Using these spatially explicit drag data of F''_d as substitute for the numerically and dimensionally equal C_{EE} to calculate the ecosystem engineering efficiency (EEF; Eq. 1) for both the stiff *Spartina* and the flexible *Puccinellia* vegetation, yields some surprising results (Fig. 6). First, EEF appears to be relatively independent of vegetation density. Second, EEF is quite similar for both species, with *Spartina* having a slightly but significantly higher EEF than *Puccinellia*. That is, ANCOVA shows that slopes are not different ($P = 0.17$), whereas intercept is significantly higher for

Spartina ($P = 0.0003$). The slightly higher EEF of *Spartina* is primarily due to lower drag costs (F'_d ; Figs. 4 and 5) rather than to a higher wave attenuation (Figs. 2 and 3). Thus, *Spartina* is a slightly more efficient rather than a more effective ecosystem engineer.

DISCUSSION

Despite the well-established importance of ecosystem engineering for the structure, function, and biodiversity of ecosystems, little attention has been given to understanding the trade-offs associated with traits involved in

FIG. 5. Drag imposed on shoots that are located at different positions in the vegetation. Drag was calculated by combining the decreasing wave amplitude with distance in the vegetation (Fig. 2) with the dependence of drag on wave energy (Fig. 4). Similar to Fig. 4, drag was expressed both (A) per unit frontal surface area (F'_d ; N/m^2) and (B) per unit of dry mass (F''_d ; N/g DM), to compare physical and biological relevant units. Large open symbols are for *Spartina*; smaller closed symbols are for *Puccinellia*. Symbols for contrasting vegetation densities are as in Fig. 2.

FIG. 6. The ecosystem engineering efficiency (EEF; Eq. 1) of *Spartina* (large open symbols) and *Puccinellia* (small solid symbols) expresses the ratio between the benefits (i.e., wave attenuation which facilitates sediment trapping in the field) and costs (i.e., drag forces involved in wave attenuation) that are associated with a species ecosystem engineering ability. Symbols for contrasting vegetation densities are as in Fig. 2. Regression lines were $EEF_{Spa} = -0.0141x + 0.0856$ ($R^2 = 0.285$) and $EEF_{Puc} = -0.0054x + 0.0534$ ($R^2 = 0.0787$).

ecosystem engineering. To our knowledge the present study is the first to compare differences between species in terms of ecosystem engineering efficiency (EEF), based on a quantitative analysis of the trade-offs that underlie ecosystem engineering. Present analysis provides us with an explanation for the apparently conflicting observation that despite a major difference in shoot stiffness (see shoot movement Fig. 1), *Spartina anglica* and *Puccinellia maritima* pioneer vegetation are both capable of trapping large quantities of sediment (Andresen et al. 1990, Castellanos et al. 1994, Sanchez et al. 2001). First, our analyses reveal that the stiff *Spartina* and flexible *Puccinellia* pioneer vegetation have remarkably comparable wave attenuation per unit standing biomass (Fig. 3). Second, drag per unit shoot dry mass was highest in the most flexible species (F_d' in Figs. 4 and 5). Finally, despite clear differences in shoot stiffness, EEF was of comparable magnitude for both species and was relatively constant in space (Fig. 6). The slightly higher EEF for stiff *Spartina* than flexible *Puccinellia* was mainly due to slightly lower drag costs per unit biomass (i.e., using F_d' as substitute for C_{EE} as they are numerically equal and share the same units: N/g DM). Hence, *Spartina* appeared to be the most efficient ecosystem engineer, whereas both species are equally effective in that they have comparable wave attenuation per unit standing biomass. Variation in EEF at the leading edge of the vegetation is ascribed to variability in measurements in wave attenuation, which is highest at leading edge.

Two important questions to resolve are (1) how widely such EEF analysis may be applied for species comparisons in other ecosystems, and (2) if such EEF analysis may help explain species distributions in ecosystems. Although

we cannot answer the first question definitively, there are some indications that EEF may be more widely applicable. First, EEF is based on a trade-off analysis, which has proven to be a very powerful tool in understanding growth strategies of species (see *Introduction*). Calculating EEF takes trade-off analysis one step further, by expressing both the costs and benefits of specific engineering traits per unit biomass investments, and subsequently integrating them into a single dimensionless trade-off parameter. As biomass investments are crucial in almost every ecosystem and the resulting EEF is dimensionless, present approach seems applicable for a broad range of ecosystem engineers. Secondly, in the present study EEF appeared to be a species-specific trait, independent of vegetation density. This is likely due to the physical laws of energy conservation that apply to a broad range of bio-physical interactions such as wave attenuation by vegetation. Only for ecosystem engineering processes that depend less strongly on bio-physical interactions, it might be expected that EEF is not a species-specific trait. Resolving this question requires testing on a broader range of organisms.

Regarding the second question, if EEF analysis may help explain species distributions in ecosystems, it is important to keep in mind that ecosystem engineers often occur in stressful environments (Jones et al. 1997), where persistence in space and time may be more important than efficiency-related characteristics such as productivity and competitive ability (e.g., see Hay 1981, Hacker and Gaines 1997). If ecosystem engineering is regarded as a special kind of stress coping strategy, comparing EEF might offer a useful method to describe the efficiency by which organisms are able to alleviate stress. It may be expected that the latter might help explaining the species distribution in stressful habitats, but this remains to be tested, and cannot be answered by the present study. We selected the stiff *Spartina anglica* and flexible *Puccinellia maritima* as model for studying EEF, because of their comparable ecosystem engineering capacity by sediment trapping despite their difference in shoot stiffness. We do not want to translate their difference in EEF as indicative of competitive strength, as their competitive interaction will be affected by many abiotic (e.g., inundation frequency, sediment type, climate) and biotic (e.g., grazing intensity) factors that we did not take into account in the present study.

In line with current theory, present results clearly show how drag per unit frontal surface area (F_d' ; N/m²) depends on wave energy and the ability of shoots to reconfigure by bending (Fig. 4A). For macro algae, this is a well described characteristic, with exact relations depending on a complex combination of wave size, shoot length and shoot stiffness (e.g., see Koehl 1996, Denny 1999, Helmuth and Denny 2003). Present results add two important new insights to the existing knowledge. First, drag forces may actually be the highest for the most flexible vegetation types that are typically able to reconfigure, when drag is regarded per

unit of dry mass invested in a single shoot (i.e., F_d' in N/g DM; see Fig. 4B). This observation is highly relevant for regarding the efficiency of stress avoidance. A full analysis of stress avoidance should however include calculations on the probability of dislodgement (Denny 1995). Second, in a wave-dominated environment, drag forces are strongly dependent on the location of an individual plant within a vegetation stand (Fig. 5). This is ignored in the majority of the available plant studies (e.g., Ennos 1999, Sand-Jensen 2003), except for a single study by Fonseca et al. (2007) who reported comparable effects. Drag analysis in a spatial context shows that drag is highest at the vegetation edge and reduced within the vegetation. However, the high hydrodynamic stress at the border of the vegetation must be tolerated for it to survive. This may perhaps partly explain why many higher plant species that inhabit coastal environment are clonal species, where stress reduction at the vegetation edges represents intra-specific facilitation. Such facilitation could be a special kind of division of labor, a process that has been well documented for many other process in clonal species (e.g., see De Kroon et al. 1998, Charpentier and Stuefer 1999, Van Kleunen and Stuefer 1999, Pennings and Callaway 2000).

Apart from increasing understanding of ecosystem engineering as a strategy, present results also provide new insight in current understanding of wave attenuation by vegetation, which is of growing interest in this age of global change (Barbier et al. 2008, Koch et al. 2009). Despite the gradual growth of available data sets on wave attenuation by vegetation (e.g., see Fonseca and Cahalan 1992, Yang 1998, Koch and Gust 1999, Moller et al. 1999, Verduin and Backhaus 2000, Tschirky et al. 2001, Mendez and Losada 2004, Koch et al. 2009), there remains a remarkable lack of studies comparing plant species with contrasting stiffness and shoot density (Bouma et al. 2005, Koch et al. 2009). Present species comparison at three different vegetation densities addresses this gap by providing simple across species relationships based on standing biomass (Fig. 3). Such process knowledge is needed for understanding the role of vegetation in coastal protection.

In conclusion, calculating EEF for two autogenic ecosystem engineers that both modify the habitat via their own physical structure (stiff *Spartina* and flexible *Puccinellia*), showed that contrasting engineering strategies may have quite comparable engineering efficiency. Differences were due to differences in resisting drag (costs) rather than to differences in attenuating wave energy (benefits), indicating that *Spartina* is a more efficient rather than more effective engineer. EEF may offer a good way to characterize engineering species, as in our study EEF was independent of vegetation density, and appeared to be a species specific descriptor for a specific biophysical interaction. The small differences in EEF between species may indicate that evolution might lead to functionally similar groups (Scheffer and van Nes 2006). Uncovering simple costs-benefits relation-

ships and translating them in EEF seems important to further developing a general theory of (autogenic) ecosystem engineering.

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