CONSERVATION ECOLOGY – ORIGINAL RESEARCH

Ecosystem engineering creates a new path to resilience in plants with contrasting growth strategies

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Abstract

Plant species can be characterized by different growth strategies related to their inherent growth and recovery rates, which shape their responses to stress and disturbance. Ecosystem engineering, however, offers an alternative way to cope with stress: modifying the environment may reduce stress levels. Using an experimental study on two seagrass species with contrasting traits, the slow-growing *Zostera marina* vs. the fast-growing *Zostera japonica*, we explored how growth strategies versus ecosystem engineering may affect their resistance to stress (i.e. addition of organic material) and recovery from disturbance (i.e. removal of above-ground biomass). Ecosystem engineering was assessed by measuring sulphide levels in the sediment porewater, as seagrass plants can keep sulphide levels low by aerating the rhizosphere. Consistent with predictions, we observed that the fast-growing species had a high capacity to recover from disturbance. It was also more resistant to stress and still able to maintain high standing stock with increasing stress levels because of its ecosystem engineering capacity. The slow-growing species was not able to maintain its standing stock under stress, which we ascribe to a weak capacity for ecosystem engineering regarding this particular stress. Overall, our study suggests that the combination of low-cost investment in tissues with ecosystem engineering to alleviate stress creates a new path in the growth trade-off between investment in strong tissues or fast growth. It does so by being both fast in recovery and more resistant. As such low-cost ecosystem engineering may occur in more species, we argue that it should be considered in assessing plant resilience.

Keywords Recovery from disturbance · Resistance to stress · Seagrass · Sulphide intrusion

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Introduction

Based on spatial distribution over habitat types, resource competition and ability to respond to disturbances, plants have been broadly classified into different growth strategies. Several models have been defined to classify plants depending on their capacity to respond to their environment [Grime's CSR theory (Grime 1974), Westoby's L–H–S strategy (Westoby 1998)], on resource limitation [Tilman's R rule (Tilman 1990)], on their life history and reproductive strategies [r/K selection (MacArthur and Wilson 1967; Pianka 1970)]. In Grime's CSR theory and depending on their environment, plants can be divided into three growth strategies: competitive, ruderal and stress-tolerant species (Grime 1974, 1977). Competitive species, which are adapted to low stress and low disturbance, and ruderal species, which are adapted to low stress and high disturbance, typically exhibit high capacity to extend in space through vegetative growth. They thus show high growth rates to better

compete for light and other resources (competitors) or to recover from disturbances and improve chances for survival (ruderals). Unlike competitors, ruderal species also exhibit rapid seedling production and establishment (Grime 1974). Generally, for these two strategies, the energy invested in plant tissues are relatively low resulting in cheap tissues. In contrast, stress-tolerant species (adapted to high stress and low disturbance) typically show a relatively low growth rate with long-lived, relatively expensive leaves and a capacity to store resources for extended growth (Grime 1977), which allows for more robust structure and better defence of their tissues (higher C:N, lignin and secondary metabolites).

Grime's growth strategy theory (1977) has proven to be important in understanding a species' resilience in terms of resistance to stress and recovery from disturbance, and remains an important research topic in current ecology (Jabot and Pottier 2012; Mumby and Anthony 2015). A species' resistance to stress can be defined as the ability to maintain consistent standing stock under stress (Wissel 1984). Resistance represents both a species' capacity to tolerate stress (stress-tolerant strategy) or to avoid stress (stress-avoiding strategy) by morphological, physiological and/or developmental adaptations (see Touchette et al. 2009; Puijalon et al. 2011 and references therein). A species' recovery capacity from disturbance can be defined as its ability to regenerate after a local disturbance back to its original state.

A completely different way to cope with stress may come from an organisms' ability to modify its abiotic environment. This is often referred to as niche construction [predominantly considered as an evolutionary concept (Matthews et al. 2014)] and/or ecosystem engineering. Ecosystem engineering is a term used to indicate a species' ability to drive changes in the state of the biotic or abiotic environment (Jones et al. 1994) via their own physical structure (autogenic, e.g. trees) or via the transformation of non-living or living material (allogenic, e.g. beavers creating dams). Ecosystem engineers often—but not exclusively—occur in relatively stressful environments (Crain and Bertness 2006).

To our knowledge, the concepts of plant growth strategies (Grime 1977) and ecosystem engineering (Jones et al. 1994) have not been thoroughly linked to each other. Grime's CSR theory displays a trade-off between resilience mechanisms: stress-tolerant species are typically slow-growing and depend on their ability to resist stress, whereas the fast-growing ruderals and competitors typically present high recovery rates after disturbances either via high seed production (ruderals) or high leaf turnover rate (competitors) and fast vegetative growth (both) (Grime 1977; Kilminster et al. 2008). It is unknown to which extent this resilience trade-off might be affected by a species' ability to modify its environment by ecosystem engineering. Thus, we aim at identifying the importance of a species' resistance to stress

and recovery from disturbance to both its growth rate and its ecosystem engineering capacity, using a fast- and a slow-growing seagrass species as a model system.

There are various species of seagrasses worldwide, representing different growth strategies as a function of their size and rhizome elongation rate (i.e. fast-growing or slow-growing species). This difference in growth rates has been related to seagrass allometry (Duarte 1991; Hemminga and Duarte 2000): slow-growing seagrasses are large, long-lived plants with strong tissues while fast-growing seagrasses are generally small with relatively high rhizome elongation rates (Marbà and Duarte 1998). Both fast- and slow-growing seagrass species have been recognized as autogenic ecosystem engineers (Jones et al. 1994) that attenuate hydrodynamic energy and stabilize sediment (Fonseca and Fisher 1986; Bos et al. 2007; Widdows et al. 2008; Ganthy et al. 2013). As photosynthetic organisms, seagrasses also have the capacity as allogenic engineers to alter sediment chemistry by releasing oxygen via their root system (Greve et al. 2003), thereby escaping sulphide toxicity in organically rich sediments (Marbà et al. 2009; Frederiksen et al. 2006; Jovanovic et al. 2015; Pedersen and Kristensen 2015). In the case that the oxygen leakage is too low, however, there is a risk of sulphide intrusion into the relatively permeable tissues. Alternatively, seagrass may escape sulphide toxicity by producing relatively impermeable roots, which are protected from toxin intrusions. This morphological adjustment also reduces radial oxygen loss (ROL), thus resulting in lower intensity of sediment engineering (Frederiksen et al. 2006; Hasler-Sheetal and Holmer 2015; Jovanovic et al. 2015; Pedersen and Kristensen 2015). Note that seagrasses and most plants face many different stresses, and resilience traits may differ regarding these stresses.

The present study aims at evaluating whether ecosystem engineering capacity would affect the expected resilience trade-off between resistance to stress on the one hand, and recovery from disturbance on the other, as predicted from Grime's theory (Grime 1977). We compared the slow-growing eelgrass *Zostera marina* with the fast-growing dwarf eelgrass *Zostera japonica*. Based on Grime's theory, we expect that the slow-growing, 'stress-tolerant' *Z. marina* will be more resistant to stress (i.e. anoxic sediment) compared to the fast-growing, 'ruderal' or 'competitive' *Z. japonica*. However, and based on ecosystem engineering capacity (i.e. detoxification of anoxic sediment by oxygen loss from the roots), our hypothesis is that the fast-growing species will also become more resistant to stress due to a strong capacity for ecosystem engineering through oxygen release, related to low investment in plant tissues. To test this hypothesis, we assessed, along a gradient of organic material addition, the capacity of the two species: (1) to maintain standing stock under increasing addition of organic matter (resistance); (2) to recover from disturbances such as above-ground removal

along the stress gradient; (3) to engineer their habitat via sediment detoxification (quantified through porewater sulphide measurements). Finally, we will (4) discuss whether our hypothesis (fast growth resulting in cheap tissues and high resistance through ecosystem engineering) may also potentially occur in other vegetation types and whether our results can be generalized.

Materials and methods

Study site

This experiment was implemented simultaneously in stands of *Zostera marina* and *Zostera japonica* co-occurring in the "Yuehu lagoon" or "Swan Lake" (N37° 20′48.6″; E122° 34′10.9″). This is a sheltered lagoon located in Shandong province (China) close to the city of Weihai (Fig. 1). The lagoon has a small tidal inlet (86 meters wide) and shallow waters (< 2 m). The two seagrass species inhabit different tidal depths, though sometimes overlapping: mid to low intertidal for *Z. japonica*; to subtidal for *Z. marina* (van Katwijk and Hermus 2000). However, inside this lagoon,

the two seagrass stands are located within the same area and are thus subject to similar environmental conditions. At low tide, both species are submerged under 20–50 cm of water. Both meadows were extensive and presented healthy plants during our study. The presence of both species has been observed for years by local fishermen (pers. com.). Therefore, we could postulate that the environment they were both sharing and developing in was not a source of stress that may override our experimental design. Organic carbon content in the sediment was previously measured at $0.66 \pm 0.19\%$ (Han et al. 2017). Water temperatures oscillate between 18 and 21 °C in summer with a salinity of $31.45 \pm 0.03‰$. Hydrodynamics were not measured during the experiment, but the geographical situation, wind fetch and average granulometry (D50 of 119 ± 26 μm, i.e. fine sand) of the co-occurring seagrass stands allowed us to define their relative exposure as sheltered (see Soissons et al. 2014, for more information on the field site).

Experimental design

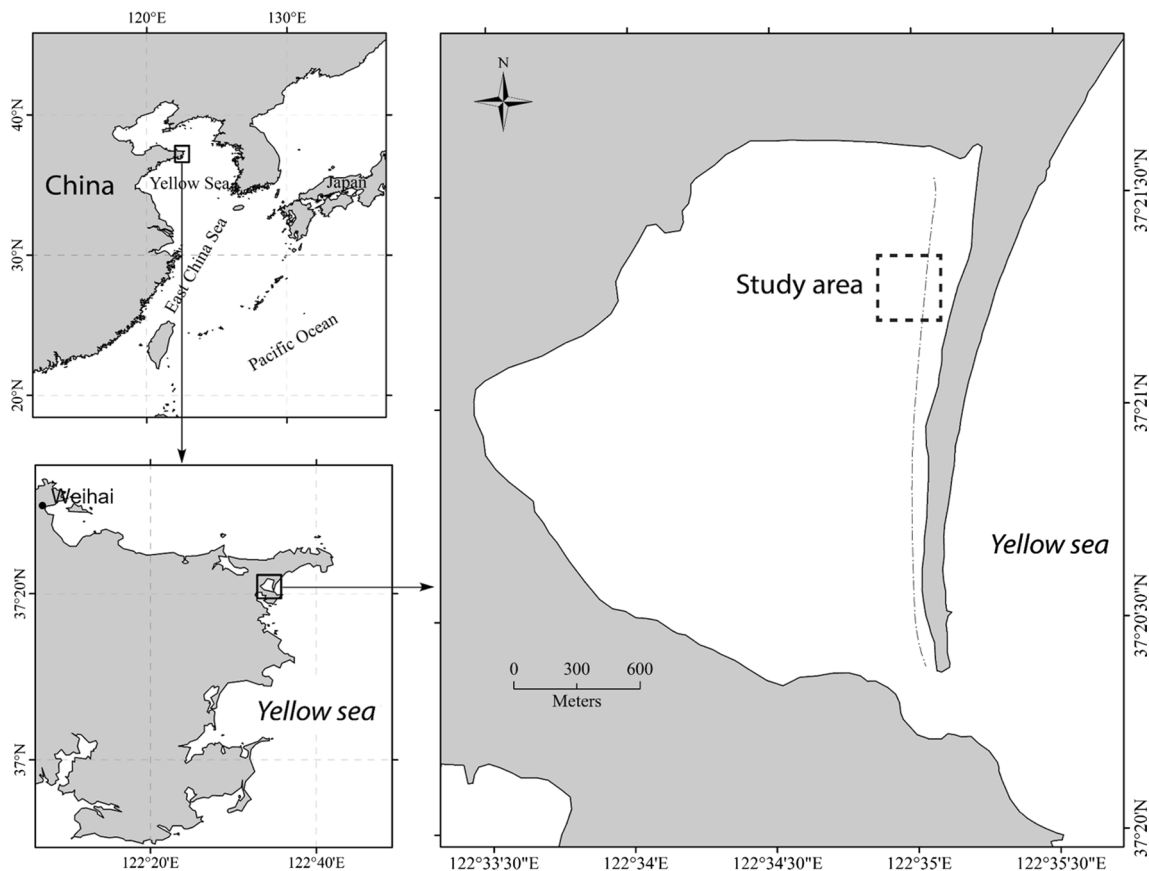Stress gradient: To apply a stressor, an organic matter (OM) gradient was created with a range of increasing sulphide

Fig. 1 Map of the study area within the 'Moon Lake' lagoon, Shandong province, China

levels in the sediment and porewater within the rhizosphere. For each seagrass stand, four levels of OM were added to the sediment ($n = 10$ per OM addition level). The OM contained only carbon (cellulose) to avoid the additional effects of nutrients contained in some other organic matter substrates (Govers et al. 2014). Hence, a mixture comprising equal parts of shredded coffee filters and potato starch (i.e. 1 g of coffee filter for 1 g of potato starch) was used in different quantities to create the four levels: no OM [no OM added]; $1 \times$ OM [100 g C m^{-2} = 3.5 g (starch) + 3.5 g (filters) per plot]; $4 \times$ OM [400 g C m^{-2} = 14 g (starch) + 14 g (filters) per plot] and $10 \times$ OM [1000 g C m^{-2} = 35 g (starch) + 35 g (filters) per plot]. The OM was added to the sediment in all the randomly allocated plots within each seagrass stand, which were all areas of homogeneous density. Mean shoot densities were 433 ± 62 and 6366 ± 609 m^{-2} for the *Zostera marina* and *Zostera japonica* meadows, respectively. Mean below-ground biomass at the start of the experiment was 28 ± 4 and 30 ± 4 g m^{-2}, respectively.

Disturbance: To measure recovery from disturbances, we removed the above-ground biomass of the plants by clipping all the leaves in a circle (0.3 m diameter, 0.07 m^2 area) at the centre of the plots, leaving below-ground parts and sheaths in place to allow for regrowth over the short-term. This disturbance was imposed on half of the OM addition plots (i.e. 5 randomly selected plots out of 10 per treatment) 10 days after OM addition. Leaf clipping was chosen to mimic grazing from birds (swans migrating in this region), or the effect of boat anchoring and shell collection by local fishermen, which results in removal of parts of the seagrass. Rhizomes around the disturbed and undisturbed 0.3-m-diameter plots were cut to limit recovery by colonization from the edges on the basis of their reserves outside the gap, to measure regrowth independently from the surrounding meadow.

A total of 80 plots were thus created: 2 seagrass species and 8 treatments (OM addition = 4 levels, disturbance = 2 levels) replicated 5 times, resulting in a fully balanced experiment that ran for 30 days after gap creation, from the 22nd of July until the 20th of August, 2013.

Sampling and analysis

Seagrass samples

During gap creation (i.e. 10 days after OM addition), seagrasses were randomly sampled from a surface of 0.07 m^2 in the experimental area, but outside the plots, to obtain control samples for biomass and morphological measurements, and this was replicated five times for both *Zostera marina* and *Zostera japonica* meadows. At the end of the experiment, all plots were sampled using 0.07 m^2 cores so that all plants in the gaps were collected. After sampling, seagrasses were directly cleaned with seawater in the field before being transported to the laboratory for measurements. In the laboratory, all plants were carefully rinsed and scrapped with a razor blade to remove epiphytes and any remaining sediment. The total number of shoots per sample was directly recorded. Then subsamples of 5 shoots per sample were randomly selected for morphological measurements (number of leaves per shoot, leaf length and width). The leaf surface per shoot was calculated from the mean values of the morphological measurements. The leaf area index of the standing crop (LAI$_{standing}$ = m^2 of leaf surface per m^2 of soil surface area; dimensionless) was calculated as the product of leaf surface per shoot (m^2) and the shoot density (m^{-2}) from undisturbed plots, and was used to estimate the plant's resistance to the stress gradient. To assess the relative resistance to stress, a relative LAI$_{standing}$ (RLAI %) was also computed by dividing the LAI$_{standing}$ values of the treated plots ($1 \times$ OM, $4 \times$ OM and $10 \times$ OM) by the LAI$_{standing}$ in the plots with no OM addition (undisturbed plots). Relative recovery from disturbance (RC %) was calculated by dividing LAI$_{regrowth}$ (LAI measured in the disturbed plots) by LAI$_{standing}$ for each OM addition level.

Porewater samples

Porewater was sampled to quantify sulphide concentration as a result of OM addition and disturbance for both plant species. Sampling was done both during gap creation to observe the effect of OM addition after 10 days, as compared to the control, and at the end of the experiment (i.e. 40 days after OM addition, which was 30 days after gap creation). Porewater samples were obtained using 20-ml syringes connected to a Rhizon MOM 5 cm female luer (19.21.22F) (Rhizosphere research products, Wageningen, the Netherlands). The Rhizon was inserted into the upper sediment layer, and the syringe was left on top of the sediment while the Rhizon progressively extracted porewater from the first 5 cm of sediment. Sulphide measurements were conducted directly after field sampling. Collected porewater samples were directly transferred into a plastic bottle after being filtered with pinhole filters (25 mm diameter and 0.45 μm pore size) connected to the syringe. To measure sulphide concentrations, we used an Ion selective electrode Ag–S (AGS15XX Electrode, Consort, Turnhout, Belgium) connected to a voltmeter (pH–mV–ion-conductivity meter C6030, Consort, Turnhout, Belgium). The samples were first fixed with a sulphide antioxidant buffer solution (SAOB) in a 1:1 proportion (4 ml of sample + 4 ml of SAOB) to fix the sulphides. The SAOB was prepared in the laboratory and stored in airtight sealable bottles prior to the measurements. The electrode was calibrated prior to field measurements and mV measurements were converted into mM for sulphides.

Statistical analysis

Differences between species in terms of $LAI_{standing}$ at the start and the end of the experiment in untreated (undisturbed, no OM added) plots were checked using a one-way ANOVA (factor = species). For porewater sulphide levels, an ANOVA was used to test differences between the start and the end of the experiment in untreated (undisturbed, no OM added) plots, per species (fixed factor = time; random factor = Replica, for repeated measures). Treatment effects (OM addition and disturbance) were also tested on porewater sulphide for both seagrass species together using a three-way ANOVA (factors: seagrass species, OM addition, disturbance) and per species individually using two-way ANOVAs (factors: OM addition, disturbance). The influence of two factors (seagrass species and OM addition) and their interactive effect on $LAI_{standing}$, relative resistance to stress (RLAI %) and relative recovery from disturbances (RC %) were checked with a two-way ANOVA. The effect of OM addition on $LAI_{standing}$, relative resistance to stress (RLAI %) and relative recovery from disturbances (RC %) was also checked for each seagrass species individually with a one-way ANOVA. Statistically significant differences between means were estimated per species using the Tukey post hoc tests only for 'OM addition'. Normality and homogeneity

of the data were checked before testing. All tests were conducted using SPSS (IBM® SPSS® Statistics Version 21). Data are presented as means (± SE).
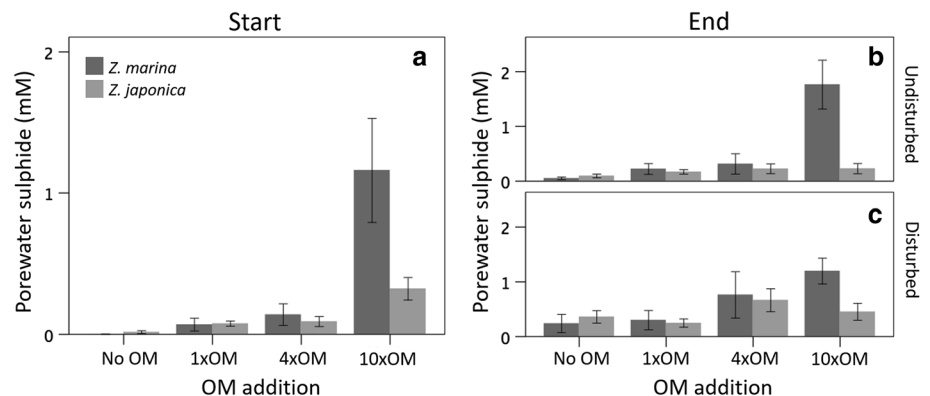
Results

Ecosystem engineering capacity: ability to suppress sulphide buildup

The porewater sulphide concentrations showed differences with respect to treatment (Table 1, Fig. 2). In the untreated plots, no significant increase was observed in the porewater sulphide concentrations over the experimental period (ANOVA: $F = 4.410$; $P = 0.069$; $F = 5.21$; $P = 0.055$ for *Z. marina* and *Z. japonica*, respectively). However, the addition of organic matter led to higher sulphide concentrations in most treatments by the end of the experiment (i.e. day 40). This increase in sulphide content was the highest and fastest for the high OM level ($10 \times OM$), especially in plots of the slow-growing species, *Zostera marina* (Tukey: $P < 0.001$ in all instances). In general, the fast-growing species *Zostera japonica* showed lower sulphide concentration in the sediment/rhizosphere, indicating better detoxification (i.e. ecosystem engineering) than the slow-growing species *Zostera*

Table 1 Statistical values (*df* (numerator, denominator), *F* and *P* values) for the effect of treatments (disturbance and organic material (OM) addition gradient) on porewater sulphide levels either including species as a factor (three-way ANOVA) or for each species individually (two-way ANOVA)

| | Three-way ANOVA | | | Two-way ANOVA | | | | | |
| | | | | *Zostera marina* | | | *Zostera japonica* | | |
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Species	1, 64	8.982	0.004	–	–		–	–	
Disturbance	1, 64	2.059	0.156	1, 32	0.04	0.843	1, 32	9.551	0.004
OM addition	3, 64	10.911	< 0.001	3, 32	10.896	< 0.001	3, 32	1.831	0.161
Species*Disturbance	1, 64	1.147	0.288	–	–		–	–	
Species*OM addition	3, 64	7.901	< 0.001	–	–		–	–	
Disturbance*OM addition	3, 64	1.658	0.185	3, 32	1.38	0.266	3, 32	0.838	0.483
Species*Disturbance*OM	3, 64	0.925	0.434	–	–		–	–	

Fig. 2 Porewater sulphide concentration in plots along the organic material (OM) addition gradient for both *Zostera* species: **a** at the start of the experimental period (i.e. at gap creation, 10 days after OM addition), and at the end of the experimental period in **b** the control plots (undisturbed) and **c** disturbed plots. Error bars represent the standard error of the mean ($n = 5$)

marina, even at the high OM level (Fig. 2). For the fast-growing species, disturbance strongly decreased the detoxification capacity. At the two higher OM levels, porewater sulphide was 0.5–0.7 mM, which is more than double the value of 0.2–0.3 mM found in the undisturbed plots. In contrast, the disturbance had no significant effect on the porewater sulphide levels of the slow-growing species, where sulphide levels were consistently high.

Standing stock dynamics: proxies for resistance to stress and recovery

Leaf area index of the standing stock (LAI$_{standing}$) was the same for both species at the start of the experiment (ANOVA: $F = 1.632$, $P = 0.237$), as well as at the end of the experimental period for untreated plots (ANOVA: $F = 0.07$, $P = 0.798$) (Fig. 3a). OM addition resulted in the reduction of LAI$_{standing}$ and relative resistance to stress (RLAI %) for the slow-growing species, *Zostera marina*, even when OM additions were low (Table 2, Fig. 3a). For *Zostera japonica*, LAI$_{standing}$ and the relative resistance to stress (RLAI %) both significantly decreased only at the highest OM level ($10 \times OM$) (Tukey: $P = 0.03$ for both). Relative recovery from disturbance (RC % for leaves clipped) was significantly higher with respect to the control for the fast-growing than for the slow-growing species (Table 2, Fig. 3b). The fast-growing species showed lower recovery when OM was added (i.e. significantly reduced RC % and LAI$_{regrowth}$) for all three levels of addition compared with the control treatment (Table 2, Fig. 3b).

Fig. 3 **a** LAI$_{standing}$ values and **b** relative recovery from disturbances (RC %) at the end of the experimental period along the organic material (OM) addition gradient for both *Zostera* species. Error bars represent the standard error of the mean
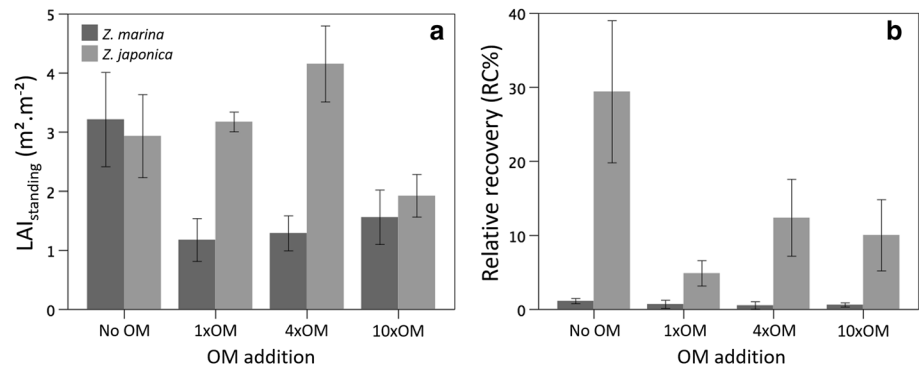
Table 2 Statistical values (*df* (numerator, denominator), *F* and *P* values) for the influence of the organic material (OM) addition on LAI$_{standing}$, LAI$_{regrowth}$, relative resistance (RLAI %) and relative recovery (RC %) either including species as a factor (two-way ANOVA) or for each species individually (one-way ANOVA)

	Two-way ANOVA			One-way ANOVA					
				Zostera marina			*Zostera japonica*		
	df	*F (df)*	*P*	*df*	*F (df)*	*P*	*df*	*F (df)*	*P*
LAI$_{standing}$									
Species	1, 32	11.45	0.002	–	–		–	–	
OM addition	3, 32	2.59	0.07	3, 16	3.37	0.045	3, 16	3.16	0.054
Species*OM addition	3, 32	3.93	0.017	–	–		–	–	
LAI$_{regrowth}$									
Species	1, 30	17.77	< 0.001	–	–		–	–	
OM addition	3, 30	2.96	0.048	3, 14	3.45	0.046	3, 16	3.17	0.053
Species*OM addition	3, 30	2.57	0.073	–	–		–	–	
RLAI %									
Species	1, 40	15.89	< 0.001	–	–		–	–	
OM addition	3, 40	2.58	0.07	3, 20	3.37	0.045	3, 24	3.15	0.054
Species*OM addition	3, 40	3.92	0.017	–	–		–	–	
RC %									
Species	1, 38	17.46	< 0.001	–	–		–	–	
OM addition	3, 38	2.79	0.058	3, 18	0.32	0.81	3, 20	3.11	*0.056*
Species*OM addition	3, 38	2.57	0.073	–	–		–	–	

LAI leaf area index, *standing* standing crop

Growth rate vs. ecosystem engineering: testing our hypothesis

To evaluate whether ecosystem engineering capacity would affect the expected resilience trade-off of two co-occurring seagrass species with contrasting strategies, we compared the expected and observed (data points in Fig. 4) plant responses for both relative resistance to stress (i.e. RLAI % expressed as the $LAI_{standing}$ of OM-stressed plots relative to control plots; X-axis Fig. 4) and relative recovery from disturbances (i.e. RC % representing regrowth into gaps; Y-axis in Fig. 4). In our experiment, we observed that the fast-growing species showed high resistance to low- and medium-OM addition (i.e. same position along X-axis in Fig. 4) but not to high OM levels (i.e. shifted position along X-axis in Fig. 4). As expected, the fast-growing species showed a relatively high recovery from above-ground removal, as long as OM levels were low (Y-axis in Fig. 4). When OM addition was high, the recovery of the fast-growing plants decreased, although it remained higher than that of the slow-growing species at all levels of OM addition, including the control. In contrast to our expectations based on Grime's theory, the slow-growing species did not show high resistance to stress; both the resistance to OM addition and recovery of the slow-growing species were very low compared with the fast-growing species. The high resistance to stress and high recovery of the fast-growing species are consistent with our hypothesis of strong capacity for ecosystem engineering, which alters the expected response to stress and disturbance based on Grime's theory (Fig. 4).

Discussion

In our study, the fast-growing species showed both higher resistance to stress and higher recovery from disturbances than the slow-growing species. This result does not support our expectation based on Grime's theory (1977) that the slow-growing species would be more stress resistant. This indicates that ecosystem engineering may in some cases change the expected outcome of the well-recognized trade-off between growth strategies identified by Grime (Fig. 4). We postulate that the combination of low-cost investment in tissues with the capacity for ecosystem engineering to alleviate stress creates a new path in the predicted trade-off between investment in strong tissues or fast growth (Fig. 5). Therefore, such plants with high growth rates and high ecosystem engineering capacities may be capable of developing in both stressful and disturbed environments.
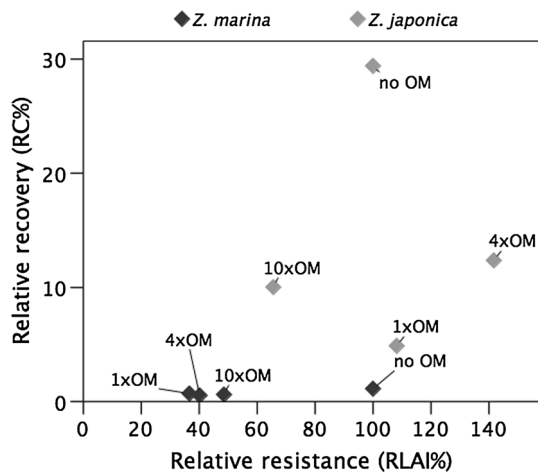

Fig. 4 Correlation between relative resistance to stress by organic (OM) addition (RLAI, calculated as a function of the control so that 'no OM' is set at 100%) and relative recovery from disturbances by clipping for both *Zostera* species. Labels represent the different levels of OM addition used to create the anoxia gradient. Grime's trade-off suggests slow-growers would have high resistance and low recovery, while fast-growers would have low resistance to stress but high recovery. Our results show that the slow-growers (dark shading) have a low recovery from disturbances and a low resistance under stress because of a weak ecosystem engineering strategy. With a strong ecosystem engineering strategy, the fast-growers (light grey shading) can increase their resistance to stress while maintaining a relatively high recovery from disturbances
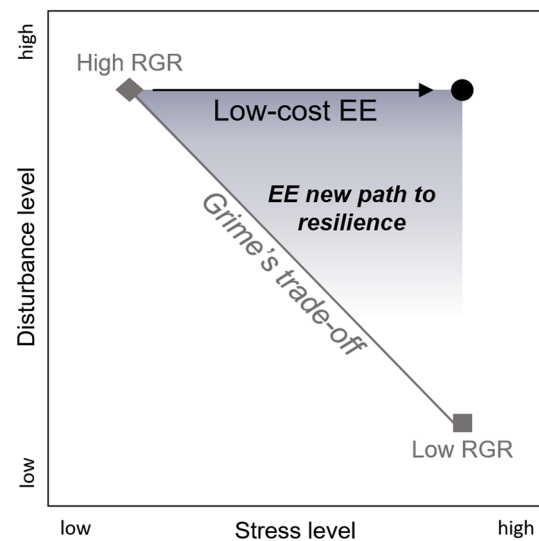

Fig. 5 Conceptual model illustrating the relationship between Grime's growth trade-off and ecosystem engineering along increasing disturbance (*y*-axis) and stress (*x*-axis) levels. Light grey lines represent the current state of knowledge based on Grime's plant trade-offs. The dark solid lines represent this study's findings. This explains how ecosystem engineering (EE) can create a new path towards a stronger capacity to resist to stress and to recover from disturbance, at low cost for the plant

Growth rates and ecosystem engineering as strategies for resilience

The construction of relatively impermeable roots by the slow-growing species (*Zostera marina*, Pedersen and Kristensen 2015) seems to fit a slow-growth strategy of investing in expensive tissue (Grime 1977; Klap et al. 2000; Lamers et al. 2013). As the plant also presents a low growth rate, this 'impermeability strategy' allows it to better preserve its resources by keeping toxins out (e.g. sulphide) and retaining assets (e.g. oxygen) (Hasler-Sheetal and Holmer 2015; Pedersen and Kristensen 2015). Sensu Grime (1977), this strategy may thus increase success in stressful environments by making the plant more resistant. These adaptations, however, also inherently restrict the species' ecosystem engineering capacity by radial oxygen loss (Jovanovic et al. 2015). For this slow-growing species (*Zostera marina*), oxygen leakage can only be measured at its root tips (about < 8% of the root surface; ROL = 2.32 ± 0.30 nmol h^{-1}) as opposed to other species that can release oxygen through 33% of their root surface (e.g. for *Ruppia maritima*: ROL = 2.89 ± 0.38 nmol h^{-1}; note that to our knowledge, no ROL data are available for *Z. japonica*), thereby providing a much better potential for detoxification (Frederiksen et al. 2006; Jovanovic et al. 2015; Pedersen and Kristensen 2015). If the stress increases, such slow-growing, resource-efficient species may be less resistant to stress due to the limited ecosystem engineering potential for detoxification. As seen in our study, the resistance of the slow-growing species, as well as its recovery, was very low, showing neither an effective stress tolerance (i.e. tolerance for sulphide-rich sediments by impermeable roots; cf. Frederiksen et al. 2006; Pedersen and Kristensen 2015) nor a stress-avoiding strategy (i.e. detoxification of the sediment by oxygen release; cf. Greve et al. 2003). This may also be related to the occurrence of other natural stressors for *Z. marina* at our site, such as desiccation (Boese et al. 2003). This combination of low stress resistance and low recovery thus makes them very vulnerable to stress and disturbance.

The capacity of the fast-growing species in our study for stress resistance (by detoxification of sulphide in the rhizosphere) and recovery from an additional disturbance seems to result from the construction of cheap, leaky roots and being capable of fast growth. This demonstrates how growth strategy (Grime 1977) and ecosystem engineering can be used together to explain both resistance and fast recovery (Fig. 5). This strategy is advantageous in highly stressful environments, where a strong ecosystem engineer can successfully resist stress and maintain its habitat (Crain and Bertness 2006; van Wesenbeeck et al. 2007) at low cost in terms of investment in tissues. This strategy might also be more widely applied to other aquatic or wetland plants present in marine or freshwater habitats, for example, *Ruppia maritima* (Jovanovic et al. 2015; Pedersen and Kristensen

2015), bog plants (Armstrong 1971), the submerged macrophyte *Vallisneria spiralis* (Soana and Bartoli 2014) and the common reed *Phragmites australis* (Armstrong et al. 1992). These plants are generally defined as fast-growing and effective in releasing oxygen to detoxify a larger area around the roots; thus, they have the capacity to ameliorate potential sulphide stress. Such low-cost ecosystem engineering strategies (i.e. low investment in tissue but strong ecosystem engineering capacity) might perhaps be considered as an example of extended phenotype engineering, as suggested by Jones et al. (1994) following the extended phenotype theory of Dawkins (1982).

Do we know which types of ecosystem engineering are 'high cost' versus 'low cost'?

Ecosystem engineers can be divided into organisms that modify their environment by their presence (autogenic ecosystem engineering) versus their action/activity (allogenic) (Jones et al. 1994). To our knowledge, the link between ecosystem engineering capacity and high cost (i.e. strong tissue) vs. low cost (i.e. weak tissue) has not been clearly described. In line with Grime, we define high cost as high investment in strong tissues and high biomass, and low cost as a low investment in weak tissues and low biomass. It thus represents a trade-off between tissue/biomass strength and cost for the organisms. A fast-growing species would make cheap tissues at a high rate and a slow-growing species would make more expensive tissues at a low rate. We speculate that ecosystem engineering capacities that act through physical or structural processes (i.e. related to the plant's biomechanical traits and not only morphological) are associated with slow growth. As slow-growing plants tend to invest more in their tissues (Grime 1977), they may become physically stronger (Bouma et al. 2010), which can be a requirement for autogenic ecosystem engineering processes such as wave attenuation (Bouma et al. 2005). Such an ecosystem engineering strategy is then, according to our definition, high cost, as it requires relatively high investment in long-lived and strong tissues. The same may apply to tree or bush species that can enhance their drought resistance through ecosystem engineering, i.e. enhance water infiltration into the soil (Jones et al. 1997; Hille Ris Lambers et al. 2001) (Fig. 5)

In our study, the type of ecosystem engineering investigated was related to oxygenation of the rhizosphere, which is primarily related to physiological activity. In general terms, we speculate that ecosystem engineering depending on physiological activity may be specifically related to fast growth, with cheaper tissues but high activity. The combination of low-cost investment in tissue strength with an ecosystem engineering capacity that alleviates stress, thus, creates a new path in the resilience trade-off for species that are being

both quick to recover (high growth rate) and more resistant (ecosystem engineering) (Fig. 5).

An important question is whether our study represents a rare exception to the rule or may be generally applicable to other vegetation types. We expect the latter because many examples of low-cost strategies for ecosystem engineering may exist. For example, leaf litter created by falling tree leaves represents a low investment from the ecosystem engineer perspective while it can lead to strong self-sustaining feedbacks that also affect other organisms (Facelli and Pickett 1991; Crain and Bertness 2006). Indeed, the subsequently reduced soil temperature, change in pH or shading barrier created by the leaf litter (Facelli and Pickett 1991) can favour seed development or growth in optimal conditions at low cost. Leaf litter and the presence of the fast-growing shrub species *Lupinus chamissonis* also favour nitrate mineralization in the soil beneath its canopy, hence, facilitating the development of other species (Hall Cushman et al. 2010). As another example, flexible plants displaying biomechanically weak leaves [i.e. low stiffness (Bouma et al. 2005)] may be more efficient at protecting soils from erosion due to leaves bending when currents/wind increase (Bouma et al. 2005; Peralta et al. 2008; Ganthy et al. 2015). We speculate that this new path in Grime's trade-off could also apply to high-cost ecosystem engineering strategies when they result in enhanced growth rates (e.g. through nutrient capture; McGlathery et al. 2012), thus enhancing the recovery potential after disturbances (Fig. 5).

We do not think that the current state of knowledge is advanced enough to fully understand how the nature of ecosystem engineering is linked to plant growth rate. However, the conceptual framework presented here might provide a stepping stone to advance our progress in this direction.

Conclusion

Ecosystem engineers provide many ecosystem services due to their presence (autogenic engineers) or their activity (allogenic engineers) (Bertness and Callaway 1994; Jones et al. 1994, 1997; Bruno et al. 2003). Engineering efficiency and the services provided have already been related to physiology and growth strategies (Bouma et al. 2005, 2009, 2010). This study experimentally demonstrates that growth rates and ecosystem engineering capacity form two essential strategies at the organism level that allow some species to develop in environments with both high levels of stress (here sulphide stress) and disturbance (here above-ground removal). Thus, both growth strategies and ecosystem engineering need to be accounted for when evaluating a species' resistance to stress as well as its capacity to recover and to maintain its habitat. As ecologists, we should challenge

ourselves to aim for better integration of these highly important ecological concepts.

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