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Seagrass–Sediment Feedback: An Exploration Using a Non- recursive Structural Equation Model

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ABSTRACT

The reciprocal effects between sediment texture and seagrass density are assumed to play an important role in the dynamics and stability of intertidal–coastal ecosystems. However, this feedback relationship has been difficult to study empirically on an ecosystem scale, so that knowledge is mainly based on theoretical models and small-scale (experimental) studies. In this paper we apply a non-recursive structural equation model (SEM) to empirically investigate, at large spatial scale, the mutual dependence between seagrass (*Zostera noltii*) density and sediment texture, on the pristine, seagrass-dominated, intertidal mudflats of the Banc d'Arguin, Mauritania. The non-recursive SEM allows consistent estimation and testing of a direct feedback between sediment and seagrass whilst statistically controlling for the effects of nutrients and abiotic stress. The resulting model is consistent with the hypothesized negative

feedback: grain size decreases with seagrass density, whereas fine grain size has a negative impact on seagrass density because it decreases pore water exchange which leads to hypoxic sediment conditions. Another finding is that seagrass density increases with sediment organic material content up to a threshold level beyond which it levels off. In combination with decreasing grain size, accumulation of organic matter creates hypoxic sediment conditions which lead to the production of toxic hydrogen sulfide which slows down seagrass growth. The negative feedback loop implies that intertidal *Z. noltii* modifies its own environment, thus controlling its growing conditions. To the best of our knowledge, this study is the first to demonstrate a direct negative feedback relationship in ecosystems by means of a non-recursive SEM.

Key words: abiotic stress; *Zostera noltii*; sedimentation; feedback; simultaneity bias; soft-bottom ecology; remote sensing; intertidal mudflat; Banc d'Arguin; Mauritania.

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Author Contributions: EOF, MvdG, JAvG and TP designed the study. MvdG, JAvG, EJ and EOF carried out field measurements. MvdG organized the dataset. EOF and HO collected and analyzed the remotely sensed data. EOF and TMA analyzed the SEM. EOF wrote the manuscript to which MvdG, JAvG, TMA and TP actively contributed.

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INTRODUCTION

Ecosystem engineers are species that modulate habitats, thus changing their own and/or other species' environments (Hastings and others 2007; Wright and Jones 2006; Jones and others 1994). Based on this definition, seagrasses are ecosystem

engineers because they impact on soft-bottom intertidal ecosystems (Bouma and others 2009; Olf and others 2009; van de Koppel and others 2005) by affecting local hydrodynamics, geomorphology, and sediment properties in intertidal ecosystems.

Seagrasses may influence their own growing conditions by affecting the properties of the water column and the local sediment properties (Koch 2001; de Boer 2007). In a review of experimental and observational field studies on various species of seagrass, de Boer (2007) suggests a positive feedback loop between seagrass density and turbidity of the water column. Due to resistance of the seagrass meadows, water flow velocity is attenuated, which reduces erosion and stimulates deposition of sediment and associated nutrients (Gacia and others 1999; Koch 2001; Bos and others 2007; Widdows and others 2008; van Katwijk and others 2010). In addition, reduced flow velocity and depositions of fine sediments and nutrients facilitate the development of biofilms by benthic microalgae (diatoms) and cyanobacteria (Paterson and Black 1999; Herman and others 2001; Widdows and others 2008). These organisms excrete exopolymeric substances (EPS) which form connective filaments between particles. The filaments build up erosion-resistant biofilms that stabilize the sediment (Grant and others 1986; Miller and others 1996; Paterson and Black 1999; Herman and others 2001; van de Koppel and others 2001). For instance, Widdows and others (2008) found that in the German Wadden Sea the seagrass species *Z. noltii* stabilizes sediments via increased microphytobenthos abundance. The above effects may independently or concomitantly lead to net positive sedimentation, which may decrease the turbidity of the water column. This in turn increases irradiance and thus the rate of photosynthesis as well as the period over which this is possible when seagrass is inundated during high tide.

In addition to reduction of turbidity of the water column, seagrasses may influence local growing conditions in the following ways. First, by decreasing water currents and waves, seagrass meadows reduce the constant movement of sediment and hydrodynamic drag which negatively affect shoots (Fonseca and Bell 1998; Koch 2001; Madsen and others 2001). Second, by retaining receding water, seagrasses may reduce negative effects of desiccation (Powell and Schaffner 1991; Boese and others 2005) which benefits photosynthesis and growth. Third, accumulation of fine sediments, due to reduced water movement, decreases the permeability of the sediment (Koch 1999) which promotes water accumulation at the surface of the mudflat at low tide which further reduces desiccation. Finally,

growth may also be promoted by increased trapping of organic material as a source of nutrients. However, concentrations of organic matter beyond a threshold lead to increased microbial decomposition to the point at which anaerobic conditions and hydrogen sulfide production may begin to negatively affect seagrass density, including *Z. noltii*, as sulfide is a plant toxin which inhibits respiration (Goodman and others 1995; Terrados and others 1999; Koch 2001; Clavier and others 2011; van der Heide and others 2012).

Next to the above positive effects, there is negative feedback related to the fact that seagrasses retain fine sediment which increases sulfide concentrations (being a toxic endproduct of sulfate-reducing bacteria). In a large-scale study in SE Asia, Terrados and others (1998) showed that leaf biomass of seagrass communities declined rapidly when silt and clay content surpassed 15%. Koch (1999) found that low water current velocities are detrimental to seagrass growth due to decreased pore water fluxes which lead to the accumulation of sulfide in the sediment. By contrast, in coarse sediment there is enhanced oxygen transport into the sediment, causing oxidation of the toxic sulfide (Koch 2001).

To get insights into the impact of seagrass on the state of its ecosystem and its own development, it is important to understand the reciprocal relationships between sediment properties and seagrass density. Theoretical and empirical investigations suggest that positive feedback interactions may drive ecosystems into alternative states or regimes (Scheffer and others 2001; van de Koppel and others 2001; Rietkerk and others 2004) and the ecosystems may show qualitative shifts in system dynamics under changing environmental conditions (Levin 1998; Gunderson and Holling 2002; Scheffer and Carpenter 2003; Suding and others 2004). Specifically, when unfavorably disturbed, an ecosystem with extensive seagrass meadows may change from a vegetated to a bare state from which recovery may be difficult, even when the original conditions are restored (van der Heide and others 2007; Carr and others 2010). Hence, insight into potential feedbacks between seagrass density and environmental factors, such as sediment texture, are critical to the understanding of autonomous development of seagrass-dominated ecosystems and their responses to environmental changes.

Knowledge of feedback relationships between seagrass density and sediment texture is mainly based on small-scale field measurements, and localized experiments (de Boer 2007). In this paper we empirically investigate the mutual dependence

between the density of the seagrass species *Zostera noltii* Hornem. and sediment texture across an extensive spatial scale on the pristine, seagrass-dominated intertidal mudflats of the Banc d'Arguin, Mauritania (Wolff and Smit 1990; Honkoop and others 2008; van Gils and others 2012). We analyze the feedback interactions between the seagrass *Z. noltii* and its self-engineered environment by deploying a structural equation model (SEM) based on spatial cross-sectional data. SEM, as a multiple equation model, allows explicit modeling of the non-recursive feedback relationships between seagrass density and grain size, thus controlling for inconsistency and simultaneity bias (Bollen and Long 1993).

Before discussing data collection, methods including SEM and empirical results in detail, we first present the theoretical underpinnings of the seagrass–sediment model, that is, the rationale for the explanatory variables included in the model.

CONCEPTUAL MODEL: DETERMINANTS OF SEAGRASS DENSITY AND SEDIMENT GRAIN SIZE

At the heart of the model is the reciprocal relationship between local, aboveground, seagrass (*Zostera noltii*) density (Z) and local median grain size (MGS) of the sediment (Figure 1) (for

example, Madsen and others 2001; de Boer 2007; Widdows and others 2008), where “local” refers to the sediment of the seagrass plot studied (that is, the sediment in which it grows). In particular, Z depends on the properties of the sediment and, in turn, MGS is affected by the density of seagrass (Z) which captures and stabilizes its “own” sediment. Z further depends on the availability of nutrients (Koch 2001), hydrodynamic stress and temperature. MGS depends on wave exposure and factors that attenuate hydrodynamic stress (Paterson and Black 1999).

Reciprocal Seagrass–Sediment Interaction

The model shown in Figure 1 has two endogenous variables: Z (measured as ash-free dry mass (AFDM) of leaves in g m^{-2}) and MGS which is a measure of coarseness of the sediment. Z and MGS are mutually dependent, that is, Z directly impacts on MGS and vice versa. Z is hypothesized to have a negative impact on MGS because of attenuation of flow velocities which stimulates deposition of fine material from the water column to the sediment surface (Amos and others 2004; Widdows and others 2008; van Katwijk and others 2010). In turn, because of higher pore water flux in coarse sediment, which leads to a reduction of the anoxic conditions, an increase in MGS is expected to have

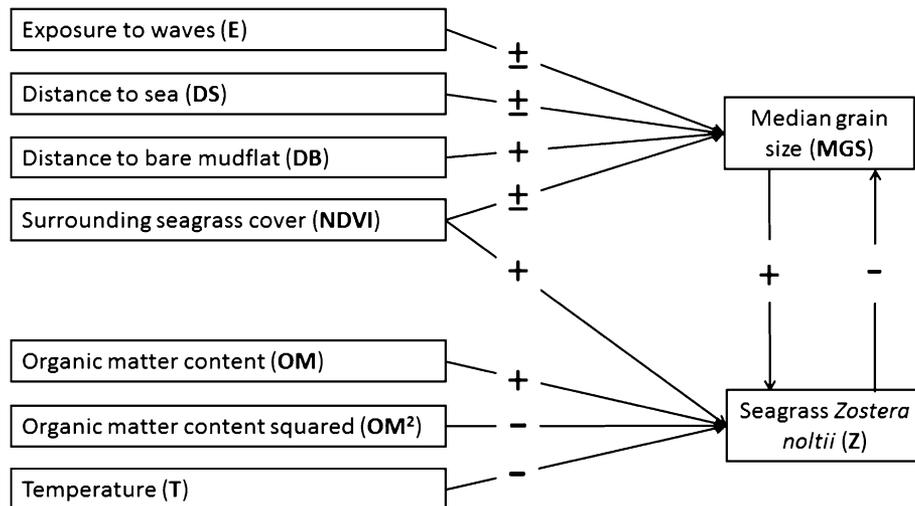


Figure 1. The conceptual seagrass density (Z)—median grain size (MGS) model. MGS decreases with Z and Z increases with MGS rendering a negative feedback loop. Z is furthermore determined by the exogenous variables organic matter content (OM_c), organic matter content squared (OM_c^2), average of the normalized difference vegetation index of the area surrounding the observed location (NDVI) as proxy for hydrodynamic stress and desiccation, and by T as proxy for desiccation. In addition to local Z , MGS furthermore depends on hydrodynamic stress and erodibility measured by wave exposure (E), distance to sea (DS), distance to bare patches (DB), and NDVI. +: positive effect; -: negative effect; ±: ambiguous effect. See text for further details.

a positive effect on Z in already silty sediments (Aller and Aller 1998; Huettel and Rusch 2000). Conversely when the grain-size distribution becomes skewed toward silt and clay, the pore water exchange with the overlying water column decreases (Huettel and Gust 1992; Huettel and Rusch 2000).

Organic Matter

Z is also influenced by the concentration of organic matter (OM) in the sediment which is the major source of organic nitrogen and phosphorous in systems where nutrient concentrations in the water are low (Lee and others 2007). Note that water in the study area is nutrient low (Wolff and others 1993). Hence, OM is expected to promote seagrass density, though up to a threshold. On the basis of a review of several studies, Koch (2001) concludes that the growth of seagrass is constrained in sediments with mass concentrations of organic matter that are higher than 5%. Hence, the effect of OM initially is positive, levels off, reaches a peak and finally decreases. So, we expect Z to be a unimodal function of OM which is accounted for by including both OM and OM^2 in the model. The hypothesized unimodal relationship implies that OM has a positive and OM^2 a negative sign.

In the long run there also may exist an impact of Z on OM in that leaves, roots, and rhizomes ultimately decompose to organic matter (Mateo and others 2006). It may, however, take years for leaves, roots and rhizomes to subside (in the case of leaves) to a depth where it can degrade such that the nutrients become available to seagrass roots (Mateo and others 1997). We therefore did not include a direct impact of Z on OM due to this discrepancy in time scales between the processes.

Hydrodynamic Stress and Desiccation of Seagrass

Hydrodynamic stress, caused by currents and waves, negatively impacts on seagrass density because it inflicts direct damage to the plants or causes uprooting due to erosion of sediment (Fonseca and Bell 1998; Koch 2001). Because we had no information on currents and wave exposure, we used seagrass cover surrounding a particular observation point (irrespective of the density at the sample point) as a proxy. The use of this proxy is based on the fact that seagrass at a given sample location is sheltered by seagrass in its vicinity. That is, hydrodynamic stress is low at locations that are surrounded by areas that are

densely covered with seagrass (Fonseca and others 1982; Ward and others 1984; Madsen and others 2001; Widdows and others 2008). Based on these observations, we take the normalized difference vegetation index (NDVI) surrounding the plot as a proxy for shear stress—that is, the higher NDVI, the lower shear stress (details are given below). On the basis of the above considerations we hypothesize a positive impact of NDVI on Z .

We did not collect information on desiccation damage, water retention, or photo-oxidative stress (due to long exposure to strong light). We proxied these variables by temperature of the mudflat. Specifically, desiccation is affected by several temperature-related factors including the duration of exposure of the mudflat to sunlight at low tide, moisture retention capacity of the sediment, the color (albedo) of the mudflat, and the amount of seagrass in the near-surroundings. Relatively low temperatures prevail at mudflats that are emersed for only short periods during the tidal cycle, or with water tables close to the soil surface (both due to low elevation) and for mudflats with high moisture retention capacity. Because higher temperatures correspond to longer desiccation, and longer exposure to strong light, we hypothesize a negative impact of T on Z . Note that T is an indirect measure for several factors which may affect the sign of its coefficient and its significance.

Powell and Schaffner (1991) show that seagrass meadows prevent desiccation by moisture retention, which is a function of NDVI. Hence, in addition to T which is a proxy with a negative impact on Z , NDVI is a proxy with a positive impact due to mitigation of desiccation.

Hydrodynamic Stress and MGS

In addition to local (micro-level) seagrass density (Z), MGS may be influenced by hydrodynamic conditions at macro-(exposure to waves from the open sea) and meso-levels (at the mudflat), and by erodibility of the sediment. Hydrodynamic conditions at macro-level are included in the MGS equation by means of a dummy variable that distinguishes between sampling stations on mudflats that are directly exposed to waves from the open sea and sampling stations at sheltered locations within the bay behind other mudflats (see Figure 2 and Figure A2 in the supplementary Appendix A for an overview of the geography of the Banc d'Arguin). The level of exposure (E) takes the value 0 for inner sampling stations and 1 for outer stations. This classification is in line with local observations of wave intensity by the authors at

observation towers at the different mudflats during various expeditions in different months over various years. The difference in hydrodynamics between the 0 and 1 group are pronounced whereas the differences within those groups are small. Everything else equal, we expect a positive sign for E because the deposition rate of fine grains will be lower under high wave conditions than under low wave conditions.

The hydrodynamic conditions at the meso-level are a function of distance to sea (DS) and NDVI. The longer the distance waves travel over the shallow mudflats (DS), the more energy they dissipate (Le Hir and others 2000). In addition, the higher the NDVI, the more waves are damped (Koch and others 2006). Hence, everything else equal, DS and NDVI are expected to have negative signs because small sediment particles are only deposited under calm hydrodynamic conditions, that is, at large DS and high NDVI.

A final indicator of hydrodynamic conditions affecting MGS is distance to bare patches (DB). In particular, sampling stations in the vicinity of bare patches (which contain coarse sediment) may receive relatively coarse sediment that is locally translocated. Hence, all else being equal, DB is expected to have a negative impact on MGS.

The above effects of E , DS, and NDVI may be mitigated by erodibility of the sediment and possibly even change the expected signs of the estimated parameters. In particular, sand may erode more easily than clay and silt because (1) it has a rougher surface than clay and thus is more easily moved by flowing water, and (2) small particles are more cohesive and hence more resistant to flowing water (Paterson and Black 1999; Black and others 2002; van Rijn 2007). However, in mixtures of coarse and fine sediment, clay, and silt particles may be washed out together with sand particles. Erodibility thus depends on the texture of the sediment. Another determinant of erodibility is the presence of biotic films of extracellular polymeric substances, formed by microphytobenthos. Biotic films increase the smoothness of the surface which in turn increases hydrodynamic stress thresholds. Biotic films thus have a stabilizing effect, that is, a negative impact on erodibility (Paterson and Black 1999; Widdows and others 2000; Black and others 2002; Widdows and others 2008).

The positive sign of E on MGS is likely to be mitigated and could even turn negative when fine sediment sustains hydrodynamic stress and coarse sediments erode. Under such conditions it is possible that a larger fraction of the coarse particles is deposited at the inner flats. The signs of DS and

NDVI on MGS are also subject to opposing forces. On the one hand, we expect negative signs for DS and NDVI on MGS because both represent reduced hydrodynamic stress. However, erodibility of the sediment may weaken the negative effects of DS and NDVI. For DB we expect a positive effect on MGS because of more hydrodynamic stress in the vicinity of bare patches and the nearby the presence of coarse sediment. Again, erodibility may mitigate this effect. Because of the mitigating and opposing effects of erodibility on E , DS, DB, and NDVI their ultimate signs and significances are uncertain and an empirical matter.

STUDY AREA

Variations in seagrass density and sediment characteristics tend to increase with spatial or temporal scales. It is therefore important to analyze sediment–seagrass interactions over large spatial (or temporal) scales. The near pristine intertidal flats of the Banc d'Arguin, Mauritania, covering a surface of about 500 km² (Wolff and Smit 1990) show pronounced spatial variation in seagrass density and sediment characteristics, which makes them an ideal study system.

The study area is the Iwik region (Figure 2) which is an accessible part of the intertidal area of the Banc d'Arguin (19°60'–19°33'N, 16°33'–16°35'W) off the coast of Mauritania. The study area can roughly be

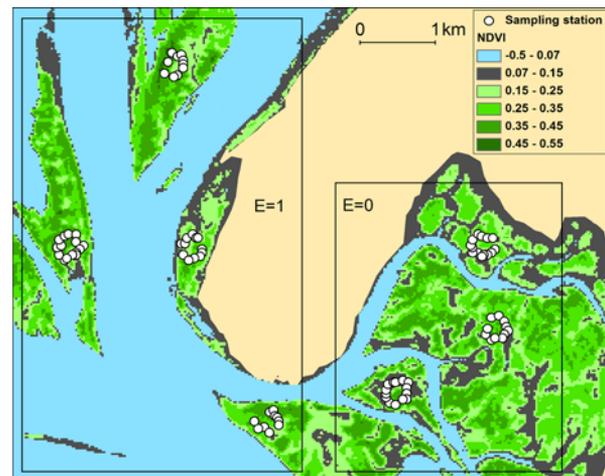


Figure 2. The mudflats of the study area and sampling stations. The colors of the mudflats and sea represent NDVI, as calculated from a LANDSAT 7 ETM+ scene recorded on 22nd January 2003. The rectangles represent subareas that differ in hydrodynamic stress due to the level of wave exposure (E). Waves in the outer subarea ($E = 1$) are larger than in the more sheltered area ($E = 0$).

divided into land, sea, sebkha, and mudflats (Altenburg and others 1982; Wolff and Smit 1990). Sebkhas are sandy, saline flats situated above the mean spring high-tide level and are free of vegetation and infauna. The extremely muddy intertidal mudflats (for our samples: min MGS = 33.6 μm , max = 219.3 μm ; mean = 103.7 μm ; SD = 56.7 μm , see Table 1 in supplementary Appendix B) are dominated by *Z. noltii* (Wolff and Smit 1990; van Lent and others 1991; Honkoop and others 2008). Four of the intertidal mudflats on which data were collected were substantially more exposed to waves than the remaining three, more sheltered mudflats (Figure 2; See Figure A2 in supplementary Appendix A for an overview of the whole intertidal area of the Banc d'Arguin).

DATA COLLECTION

We collected data by field sampling and remote sensing. Because of the strong contrast between vegetated and non-vegetated areas at low tide (Altenburg and others 1982; Mumby and others 1997), remote sensing is considered to be an efficient and accurate method for studying seagrass meadows on intertidal mudflats (Ferguson and Korfmacher 1997).

NDVI and Temperature

NDVI and temperature of the mudflat (T) were obtained from a single scene from the Landsat 7 Enhanced Thematic Mapper plus (ETM+) instrument that covered the whole area of interest (Path 206 and row 046). The image was recorded on 22 January 2003 at 11:20 AM GMT and resampled to a spatial resolution of 25 \times 25 m. It is the latest suitable Landsat7 image recorded at low tide before the Scan Line Corrector (SLC) of the satellite failed. Low tide in Dakar on this date was at 5:37 AM GMT. Low tide in the Iwik region follows on average circa 4 h 50 m after Dakar (Altenburg and others 1982; Wolff and Smit 1990). The image was therefore recorded circa 53 min after the lowest tide ensuring that the mudflats were not inundated during recording of the image. The image was recorded between full and new moon during which period the predicted water levels in Dakar were between 0.30 and 0.32 m. Cloud cover was 0.09%. A false color image is presented in the supplementary Appendix A. Note that the ETM+ was recorded 4 years before the other data were collected. However, during the intermediate period NDVI was stable, as confirmed by comparisons of the 2003 image and 2007 ground truth (see also supplementary Appendix A).

NDVI, surrounding each of our 112 sample plots, was calculated from the Landsat image as $\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})$ where RED and NIR are the digital numbers (DN) corresponding to the spectral values in the red and near-infrared regions, respectively. We estimated seagrass density in the vicinity of a sampling station by the average of the NDVI within an annulus with the sampling station as centroid, radius of the inner circle 25 m and radius of the outer circle 75 m. We took 25 m as the radius of the inner circle to avoid inclusion of the NDVI value of the pixel in which the station is located in the average NDVI value of the surrounding area. The maximum of 75 m was chosen to avoid the possibility that NDVI values of the water column would influence the average NDVI. By choosing a radius of 75 m all the areas surrounding sampling stations were entirely located on exposed mudflats. The use of 100 and 125 m as the outer radius would in some cases have caused the annulus to intersect with the habitat class "water". All pixels of which the centers fell within the annulus were included in the calculation of the average.

Note that the radius of 25 m of the inner circle and the distance of 50 m between the inner and outer circle of the annulus around the sample stations implies a substantial buffer to the sampling stations, so that the risk of compounding Z and NDVI is moderate to small (correlation coefficient = 0.54). At the same time, the distance to the sampling station is not too large to diminish the dampening effects of currents and waves within the annulus.

Temperature of the mudflat (T) was estimated by band 6-2 (high gain) of the ETM+ instrument which measures the emitted radiation in the thermal IR region of the electromagnetic spectrum. Band 6-2 measures spectral radiance at 60 m resolution. To reduce noise and to obtain physically based mudflat temperature, radiation intensity, L_λ , obtained from band 6-2 was converted using NASA's (2009) transformation:

$$T = \frac{K2}{\ln\left(\frac{K1}{L_\lambda} + 1\right)}$$

where T is temperature of the mudflat in Kelvin, $K1 = 666.09$ and $K2 = 1282.71$ are constants. We refer to NASA (2009, p. 117) for conversion from the digital number (DN) to L_λ .

To determine the minimum distance between a sampling point and the sea (DS), the study area was classified into sea, land, sebkha, bare and seagrass covered mudflats by supervised classification

(Supplementary Appendix A). DS was determined by calculating the shortest distance between each sampling station to the class “sea” (as determined by the habitat classification procedure in supplementary Appendix A).

Seagrass and Sediment Sampling Procedures

The survey area was divided into seven sub-regions (Figure 2) which in turn were subdivided into annuli with an outer radius of 200 m and an inner radius of 100 m. Each annulus was split into 16 equally sized and shaped parts. In each part, a sampling station was randomly selected. The sampling procedure thus yielded $7 \times 16 = 112$ observations.

The field work was carried out in March–April 2007. At each station, a seagrass sample was taken with a circular core with a surface area of 0.0038 m² and 10 cm depth into the sediment. The content was sieved over a 500- μ m mesh. The material retained on the sieve was stored in a plastic bag, frozen at -18°C and transported to The Netherlands, where each sample (without detritus) was sorted into either leaves or below-surface components (roots and rhizomes). The ash-free dry masses (AFDM) of the seagrass leaves were determined via the loss-on-ignition method. That is, samples were dried at 60°C for a minimum of 72 h, weighed and then incinerated at 550°C for 4 h after which the remaining ashes were weighed again. The difference between the first and the second measurements gives the AFDM of the leaves in the sample (Z , in g m^{-2}).

At each station a separate sediment sample was taken to a depth of 10 cm by pressing a PVC tube with a diameter of 1 cm into the sediment. The sediment sample was also stored in a plastic bag, frozen at -18°C and transported to The Netherlands where samples were freeze-dried and grain-size distribution of each sample was determined using a particle-size analyzer (Beckman Coulter Model LS 230). From the grain-size distribution the median (MGS) was calculated. Total organic matter content (OM) of the sediment was determined by loss-on-ignition of subsamples of approximately 0.5 g, as described above. For details on particle size and organic content measurement see Honkoop and others (2008).

Of the 112 seagrass samples, 12 were lost during processing. Moreover, eight sediment samples were lost during freeze-drying. After matching the seagrass data set with the sediment data set, data from 98 sampling stations were available for the SEM analysis.

Statistical Analysis

As a first step, we checked the data for possible non-linearities by means of pairwise scatter plots of the dependent variables and their explanatory variables. In the case of a significant squared predictor, the collinearity between the linear and squared term was reduced by mean centering (Kline 2010). This means that the mean value of the linear term was subtracted to obtain a centered variable after which the centered variable was squared to obtain a centered squared term.

We estimated the seagrass density—sediment SEM by maximum likelihood (ML) under the assumption of normally distributed variables on the basis of the covariance matrix of the observed variables. We used the ML procedure in the software package Lisrel 8.80 (Student Edition) (Jöreskog and Sörbom 1996). If the likelihood function is correctly specified, the ML estimator is consistent, asymptotically efficient and asymptotically normally distributed under weak regularity conditions (Bollen and Long 1993). Even in the case of deviation from normality the ML estimator is consistent but the standard errors should be interpreted carefully (Bollen and Long 1993). Note that estimators that do not take the interdependency between dependent and explanatory variables into account, like ordinary least squares (OLS), are inconsistent and subject to simultaneity bias (Bollen and Long 1993). The regression coefficients were standardized (a standardized coefficient represents the standard deviation change in the dependent variable resulting from a standard deviation increase of a predictor variable) so that their magnitudes are independent of the measurement scales. Hence, the explanatory variables can be directly compared and the most important ones can be directly identified by inspection of their coefficients.

When testing the full model (Figure 1), we take into account that variables E , DB , DS , and $NDVI$ strongly overlap which may lead to multicollinearity. In a model with multiple collinear explanatory variables, one or more of them may turn out statistically insignificant, even though they are relevant predictors. We handle this problem by means of stepwise, backward model selection in which variables with regression coefficients with P values greater than 0.05 were eliminated in order of increasing statistical significance (decreasing P values) until all remaining regression coefficients had P values below 0.05. We furthermore consider the models' Bayesian Information Criterion (BIC) in the model selection process. In addition, the full

and subsequent models are evaluated on the basis of overall goodness of fit statistics. In particular, we consider models with χ^2 with P greater than 0.05, normed fit index (NFI) greater than 0.90 (Kline 2010), the root mean squared error of approximation (RMSEA) less than 0.08 (Jöreskog and Sörbom 1996) acceptable. In a SEM, when the observed covariance matrix is in line with the predicted covariance matrix (which is based on the hypothesized model); the χ^2 will be low and the corresponding P value high.

Note that the models estimated below are identified because they meet the necessary and sufficient condition for identification in a simultaneous two-equation model with direct feedback, that is, each equation contains at least one exogenous variable with a nonzero coefficient that is excluded from the other equation (Bollen and Long 1993).

RESULTS

The mass percentage of organic matter in our samples ranges from 0.74 to 11.43% (mean = 4.28 and SD = 3.13). This finding is consistent with our assumption that OM has a unimodal relationship with Z which was based on the review by Koch (2001). The finding implies that the concentrations of organic matter in many of our samples

(Figure 3) would have been detrimental to seagrass growth due to H_2S production.

Except for the relationship between Z and OM, and between MGS and DB, the relationships turned out to be linear (Figure 3). Single equation regression of Z on its exogenous variables showed that OM has a statistically significant positive sign and OM^2 has a statistically significant negative sign which implies that the Z -OM relationship is curvilinear, as hypothesized above. Single equation regression of MGS on DB and DB^2 revealed that DB had a statistically significant negative sign and DB^2 a statistically significant positive sign. As described above, the mean values of OM and DB were subtracted from the OM and DB values to obtain OM_c and DB_c , respectively. OM_c and DB_c were squared to obtain OM_c^2 and DB_c^2 . The correlation between OM_c and OM_c^2 is 0.67. The correlation between DB_c and DB_c^2 is 0.68.

We first consider the initial model. Its $\chi^2 = 10.20$, $df = 6$, $P = 0.12$, and RMSEA = 0.08 (Table 1; Figure 4). The signs of the coefficients of the determinants MGS, OM_c , OM_c^2 , T , and NDVI of Z are as expected and statistically significant except for the coefficient of T which is insignificant (standardized coefficient = -0.03 ; $P = 0.90$). Particularly, the impact of MGS on Z is positive and significant (standardized coefficient = 4.22; $P < 0.05$). The

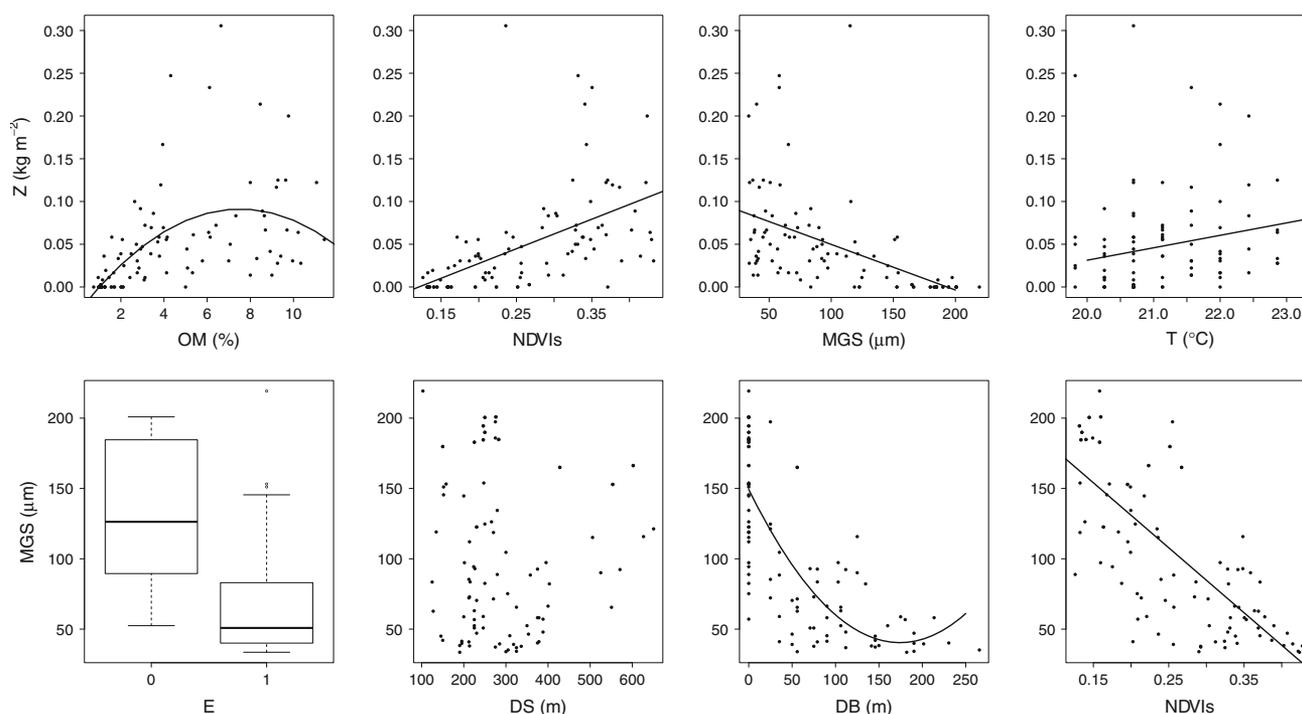


Figure 3. Scatter plots of the univariate relationships between the dependent variables (Z and MGS) and their predictors. In the case of indication of a non-linear relationship a quadratic term was added. See text for further details.

Table 1. Structural Equation Models for Seagrass Density (Z) and Sediment Coarseness (MGS)

	Z	MGS	OM _c	OM _c ²	T	NDVI	E	DS	DB _c	DB _c ²	χ ²	df	P	RMSEA ¹	BIC ²	NFI ³
1	Z	4.22 (1.37)	4.59 (1.37)	-2.14 (0.66)	-0.03 (0.24)	1.21 (0.41)					10.20	6	0.12	0.08	69.81	0.99
	MGS	-1.21 (0.31)				0.25 (0.31)	-0.32 (0.12)	0.07 (0.12)	-0.40 (0.33)	0.29 (0.17)						
2	Z	4.27 (1.40)	4.62 (1.40)	-2.16 (0.68)		1.22 (0.42)					7.33	5	0.19	0.07	62.35	0.99
	MGS	-1.22 (0.31)				0.25 (0.31)	-0.32 (0.12)	0.07 (0.12)	-0.40 (0.33)	0.29 (0.17)						
3	Z	4.18 (1.34)	4.53 (1.35)	-2.12 (0.65)		1.20 (0.41)					5.36	4	0.25	0.06	55.80	0.99
	MGS	-1.19 (0.30)				0.26 (0.30)	-0.34 (0.11)		-0.40 (0.32)	0.28 (0.17)						
4	Z	3.94 (1.19)	4.30 (1.17)	-2.02 (0.58)		1.15 (0.38)					6.27	5	0.28	0.05	52.12	0.99
	MGS	-1.11 (0.25)				1.26 (0.41)	-0.33 (0.11)		-0.17 (0.21)	0.21 (0.14)						
5	Z	4.47 (1.28)	4.81 (1.29)	-2.24 (0.62)		1.26 (0.41)					3.00	4	0.56	0.01	44.27	0.99
	MGS	-1.28 (0.20)				1.23 (0.40)	-0.34 (0.12)		0.14 (0.12)							
6	Z	4.32 (1.20)	4.66 (1.20)	-2.18 (0.58)		1.23 (0.40)					1.59	3	0.66	<0.01	38.27	0.99
	MGS	-1.23 (0.18)					-0.32 (0.11)									

Standard errors in parentheses below (standardized) structural coefficients. 1: initial model; 2-5: intermediate models; 6: final model. The initial model was trimmed by means of stepwise elimination of insignificant predictors. See main text for details on statistical analysis.

¹Root mean squared error of approximation.

²Bayesian information criterion.

³Bentler-Bonnett NFI.

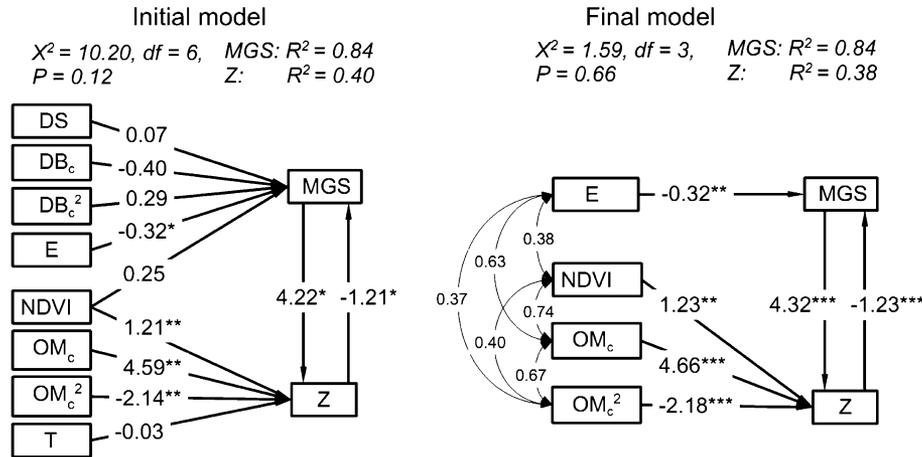


Figure 4. Graphical representations of the initial and final MGS–Z SEM. Arrows represent causal influences. Structural coefficients are standardized. Significance levels are denoted by means of asterisks * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Intermediate models are presented in Table 1. Curved arrows represent statistically significant correlations between the exogenous variables.

impact of Z on MGS is negative and significant (standardized coefficient = -1.21 ; $P < 0.01$), as hypothesized. Of the exogenous predictors of MGS (NDVI, E , DS, DB_c , DB_c^2) only E is significant and negative (-0.32 , $P < 0.05$).

The model was trimmed by first deleting T as a predictor for Z and next DS, NDVI, DB_c , and DB_c^2 as predictors for MGS (Table 1). The final model (6 in Table 1) has a substantially better fit ($\chi^2 = 1.59$, $df = 3$, $P = 0.66$, RMSEA < 0.01) than the initial model (Figure 4). Even though the fits of the intermediate models as measured by NFI were satisfactory, model 6 was selected as the final model on the basis of a superior fit according to BIC, χ^2 , RMSEA, NFI and significance of coefficients.

DISCUSSION

The final SEM strongly supports the hypothesized relationships. Particularly, all coefficients have the expected signs and are significant at 5% levels or less. Consistent with the hypothesized negative feedback, the final model shows a reciprocal relationship in which the impact of MGS on Z is positive and the reverse effect of Z on MGS is negative. The positive impact of MGS on Z , indicates that on the overall silty mudflats of the Banc d'Arguin, seagrass thrives on locations with relatively coarse sediment texture. The negative impact of Z on MGS implies that the median grain size of the sediment decreases with higher seagrass density, which has a negative impact on Z . Note that the main advantage of SEM relative to partial correlation analysis is that it models the reciprocal relationship between

seagrass and sediment, that is, the fact that seagrass modifies its environment by capturing and retaining fine sediment.

The model furthermore confirms that NDVI in the immediate vicinity of a sample location is positively related to Z which suggests that it is an adequate proxy for reduced shear stress and/or desiccation. The final model also supports the curvilinear relationship between OM_c and Z . OM_c has a positive coefficient and OM_c^2 a negative coefficient which implies that seagrass density increases with organic material content up to a point beyond which the density levels off. The model furthermore shows that the level of exposure to waves (E) has a significant, negative impact on MGS. One possible explanation is that fine particles are smooth and cohesive enough to resist being washed away such that at the outer sampling stations small particles dominate. Another possibility, as suggested by NDVI time series analysis (van Gils and others unpublished), is that the outer mudflats have accumulated and retained fine sediment over longer time spells due to more stable seagrass densities.

NDVI, DS, DB_c , and DB_c^2 as predictors for MGS were not retained in the final model. As a last point, temperature (T) turned out to be a poor proxy for desiccation and photo-oxidative stress. This could be due to small variations or because it is an ambiguous measure for desiccation and photo-oxidative stress. Particularly, temperature may increase with the albedo of the mudflat which depends on seagrass cover (seagrass is darker than sand).

The model estimated above shows that *Z. noltii* controls its own habitat by its engineering activities. At the heart of the mechanism is that *Z. noltii* locally decreases sediment grain size by retaining fine particles which slows down its own growth. We have thus revealed and quantified a locally operating micro-scale process (that is, a negative feedback loop). This local process, however, is likely to have substantial effects on the macro-scale properties of the ecosystem. First, the negative feedback regulates seagrass density and sediment dynamics which affect water turbidity with implications for seagrass as well as for other components of the ecosystem. Second, the local impacts of hydrodynamic stress on seagrass are reduced by surrounding seagrass meadows. Third, seagrass controls its own biomass and growth by capturing fine sediment which has implications for the macro-scale properties of the ecosystem. These three processes imply that self-organization of seagrass in the Banc d'Arguin is important for the abiotic and biotic state and development of the ecosystem. Particularly, within the current boundary conditions, the biotic components of the ecosystem and the geomorphology are self-controlled via feedback interactions. The above findings have revealed the driver that keeps the ecosystem in its stable (seagrass) state which is important from a fundamental ecological point of view as well as from a conservation perspective (Levin 2005).

We finally note that analyses of the effects of erratic events, such as storms, require different modeling approaches than the one applied here that operate continuously. However, insight into the regularly operating mechanisms like local seagrass–sediment interaction is a prerequisite for understanding seagrass ecosystem responses to erratic shocks.

DIRECTIONS FOR FURTHER RESEARCH

The above analysis has revealed several topics for further research. First, although the results presented in this paper are in line with theoretical analyses and small-scale experimental studies, for some of the variables remotely sensed proxies had to be used because of lack of appropriate predictors. Therefore, this paper should be seen as a step toward further research in this area. Particularly, it would be useful to further investigate the value of remotely sensed variables as proxies for actual measures of hydrodynamic stress and erodibility.

The analysis has also revealed the need for further research on the interaction between biotic components of the ecosystem on the one hand and

geomorphology on the other. From the literature review it follows that erosion and sedimentation are influenced by the density of seagrasses and by hydrodynamic factors like waves and currents, whose effects are influenced by the distance over which they travel over the shallow intertidal mudflats (Widdows and others 2008). In addition, the literature review has revealed that the impact of hydrodynamic stress on grain size also depends on the erodibility of the sediment (Paterson and Black 1999; Black and others 2002; van Rijn 2007). Surprisingly, we found that grain size was smaller at the outer flats where wave action is stronger than at the inner flats. This outcome contradicts findings in other intertidal areas where the opposite is usually found (Gray and Elliott 2009). However in our study, other variables like erodibility, stability and the local age of the meadow appear to have impacted on the sign of the effect of *E*. Further research, including hydrodynamical modeling, is needed to disentangle the opposing effects of shear stress and erodibility on seagrass-dominated mudflats.

The feedback loop and the process of self organization analyzed in this paper have been studied under the assumptions that the processes have been operating sufficiently long so that the estimated effects are not dependent on any particular time point. Predictions of *Z* thus accommodate the considerable spatial variability in the key drivers (that is, OM, NDVI, and MGS). The system, however, may be subject to gradual development and exogenous perturbations which may in the long-term (longer time scales than the ones implicitly considered in this paper) lead to “shifting mosaics” in seagrass and sediment patterns (Bormann and Likens 1979; Bell and others 2006). For instance, seagrass brings dead organic matter to the sediment (by capturing OM from the water column and by its own root production) which may affect seagrass density in the long-term. Various studies including Smith and others (1984) and Koch (2001), show that too high densities of organic matter may be detrimental to seagrass survival and growth because of the production of toxic hydrogen sulfide by anaerobic sulfate reduction. However, oxygen released from roots during the day oxidizes sulfide and reduces its concentration and thus its toxic impact (Smith and others 1984; Koch 2001; Clavier and others 2011). Hence, also in the long run, seagrasses control the quality of their habitats (import of organic matter) while they alleviate the negative impact in the short term (by oxygen import). Specifically, over time, when the seagrass–OM ratio decreases, the density of seagrass starts to

level off or to decline, which reduces oxygen transport to the sediment, which further reduces seagrass density, and so on. Under such conditions, seagrass may disappear abruptly (Pedersen and others 2004). Further research on these short- and long-term processes and their interaction is needed.

The SEM approach presented in this paper analyzes feedback mechanisms in ecological systems on the basis of cross-sectional spatial data (that is, a snapshot in time) to get insights into system dynamics. As such, it forms a complementary or alternative method to the commonly used time series approach (Scheffer and Carpenter 2003). Because spatial cross-sectional data can usually be more readily obtained than time series data, particularly for slowly changing variables, we expect the SEM approach to be valuable in empirical applications. The results obtained here lend support to further applications of SEM to ecosystem cross-sectional spatial data analysis, particularly with respect to feedback mechanisms which are important in analyzing the impacts of ecosystem engineers in a wide variety of ecosystems.

Whereas SEM—including non-recursive models—is common in other disciplines, such as psychometrics, sociology, and economics (Owens 1994; Jedidi and others 1997; Burns and Spangler 2000), its use has been limited in ecosystem sciences, although it was introduced in this field two decades ago (Johnson and others 1991). Its limited use is surprising as many ecological systems include (direct) feedbacks. Up till now, several studies that have attempted to estimate direct feedbacks by means of non-recursive SEMs in ecosystem sciences have been unsuccessful (for example, Veen and others 2010; Laughlin and others 2010; Anderson and others 2010). To the best of our knowledge, ours is the first successful non-recursive SEM in ecosystem sciences that models a direct feedback. Note that van der Heide and others (2011) reported evidence for positive feedback in seagrass systems. However, their results are based on a SEM with indirect feedbacks. Why many attempts to estimate direct feedbacks have failed is unknown. It could be because of peculiarities of the ecosystems studied or because of the data. This question deserves further investigation because this approach has great potential to contribute to filling the gap between theoretical and empirical ecosystem studies (Grace and others 2010).

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