

Rhizome starch as indicator for temperate seagrass winter survival



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ABSTRACT

Key-ecosystems such as seagrass beds are disappearing on a global scale. In order to counter-act local loss of seagrass beds, seagrass restoration projects have been carried out with varying degrees of success. As seagrass biomass peaks in summer, most restoration projects are monitored during this period, while wintering processes are largely ignored. We here attempted to elucidate some important bottlenecks for wintering survival in temperate areas of the intertidal model species *Zostera noltii*, using a three-year transplant-monitoring dataset and a field experiment. We found that next year's transplant success could not be predicted based on the preceding year's growth success, emphasizing the winter as a crucial period for survival of seagrass transplants. In addition, transplant success was neither determined by abiotic site characteristics. Low autumn rhizome starch concentrations in unsuccessful transplants, compared to successful transplants and natural beds, hinted at the importance of starch for winter survival. Hence, we tested the importance of starch, accumulated in autumn, versus the importance of the presence of sparse aboveground photosynthetic winter biomass for winter survival of seagrass transplants in a field experiment. We clipped the overwintering-leaves of three natural beds that naturally varied in their autumn rhizome starch concentrations. Decreased leaf densities in winter did not affect seagrass biomass in June, nor did this treatment affect rhizome starch concentration in June. Autumn rhizome starch reserves did however provide a good indication of next year's growth success, confirming the importance of starch reserves for winter survival. We thus conclude that autumn rhizome starch can be a good predictor of next year's growth success, whereas the preceding growing season shoot density and the presence of leaves during the winter were bad indicators of next year's growth success.

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1. Introduction

Seagrass beds are important coastal ecosystems, as they are highly productive, sequester carbon, support high biodiversity, and can play a role in coastal protection by reducing wave energy and through sediment stabilization (Christianen et al., 2013; Duarte, 2002; Fourqurean et al., 2012; Hendriks et al., 2008). However, seagrass beds are currently disappearing on a global scale, mainly due to anthropogenic disturbances (Orth et al., 2006; Waycott et al., 2009). Therefore, many restoration projects have been carried out, with varying degrees of success (Fonseca et al., 2001), which cannot always be attributed to prevailing abiotic conditions (Orth et al., 2009; Suykerbuyk et al., 2015; Van Katwijk et al., 2009).

As seagrass restoration projects are often costly, it is important to select suitable sites and to predict or identify bottlenecks that may affect these restoration attempts (Short et al., 2000, 2002).

We expect winter processes to be important bottlenecks for transplant winter survival, based on the observation that transplant survival in winter is limited. Temperate and subtropical seagrasses typically display a seasonal biomass peak of high biomass during the growing season (summer), and a strongly decreased biomass during the winter (Duarte, 1989). Seagrass restoration sites are therefore typically monitored during the growing season, whereas wintering processes, which may also affect restoration success, are only occasionally studied (e.g., Marion and Orth, 2012; Vermaat and Verhagen, 1996). However, to date there are no quantitative analyses on the generality of this phenomenon or on what factors affect winter survival. So our overall objective is to identify parameters that have an indicative value for the winter survival of transplants.

Important processes that affect wintering seagrasses in temperate areas are the low temperatures and low light levels, which greatly

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decrease seagrass productivity. As photosynthesis is reduced, the carbon balance of seagrasses, which is determined by the carbon gain (photosynthesis) and carbon demand (respiration and growth), can become negative (Alcoverro et al., 2001, 1999). During this stressful period, seagrasses become dependent on their carbohydrate reserves (Alcoverro et al., 1999; Brun et al., 2008; Zimmerman et al., 1995), which are thus important to seagrass winter survival.

For seagrasses, the most important non-soluble carbohydrate for long-term storage is starch (Pirc, 1989). Starch is mainly stored in the rhizomes, and produced in periods with a positive carbon balance (Olive et al., 2007; Zimmerman and Alberte, 1996). Wintering seagrasses are thus dependent on the production of starch reserves in the preceding growing season. The amount of starch needed for winter survival depends on both internal and external factors; respiration can be affected by temperature and light, but also by biomass and photosynthetic activity (Alcoverro et al., 1999; Fourqurean and Zieman, 1991; Marsh et al., 1986; Vermaat and Verhagen, 1996). In addition, environmental stressors such as ammonium toxicity and sediment anoxia can increase carbon demand (Brun et al., 2008). Growth is another important process that contributes to carbon demand (Alcoverro et al., 1999). Although growth is marginal during the winter months ($0.015 \text{ cm}^2 \text{ cm}^{-2} \text{ day}^{-1}$ versus loss rates of $-0.110 \text{ cm}^2 \text{ cm}^{-2} \text{ day}^{-1}$ in *Zostera noltii*) (Vermaat and Verhagen, 1996), carbon demand for growth in early spring can deplete carbohydrate reserves.

In this study, we aimed to further elucidate mechanisms of seagrass winter survival with regard to seagrass transplants and to look for indicators of winter survival, as we noticed that many restoration efforts fail over winter, whereas other sites have been successful, without having a clear indication of distinctive abiotic differences among sites. Our goals were therefore: to test if and how next year's growth success depends on (1) shoot densities in the preceding growth season, (2) the presence of leaves in winter, and (3) the level of the starch reserves. To answer these questions, we combined monitoring data from large-scale transplants (Fig. 1) with a winter leaf removal field experiment, using *Z. noltii* as a model species.

2. Materials and methods

2.1. Location

We studied the winter survival of the natural *Z. noltii* beds and transplanted *Z. noltii* beds in the Oosterschelde Delta, The

Netherlands (Fig. 1a, $51^{\circ}39' \text{ N}$, $4^{\circ}01' \text{ E}$). The Oosterschelde has a surface area of 351 km^2 , a tidal amplitude of 2.5–3 m (Troost et al., 2009) and freshwater input is highly limited, resulting in a salinity of 30 PSU (Nienhuis and Smaal, 1994). Intertidal *Z. noltii* meadows cover around 75 ha of the mudflats in the Oosterschelde and are located on relatively stable sediments such as clay banks, saltmarsh remnants and natural shell layers (Suykerbuyk et al., 2012). Intertidal *Z. noltii* in the Oosterschelde, which is sometimes referred to as *Zostera noltei*, are generally not nutrient limited (Govers et al., 2014a) and light availability (when submersed) is around 3–4.5 m Secchi disc visibility in summer (Wetsteyn and Kromkamp, 1994).

2.2. Monitoring transplants and natural seagrass beds

As a part of a large-scale seagrass transplantation project, aiming to mitigate seagrass damage caused by dike reinforcements, seagrass sods were mechanically transplanted to $10 \times 10 \text{ m}$ or $15 \times 15 \text{ m}$ plots on several mudflats in the Oosterschelde (for details, see Suykerbuyk et al. (2012)) (Fig. 1). Plots were monitored in spring and summer from spring 2009 to autumn 2011; we counted shoot densities and determined seagrass surface area plot^{-1} with a Real Time Kinematic differential GPS (RTK-dGPS, Trimble, USA). Samples for starch analysis were taken each spring (end of April/start of May) and each autumn (end of October, start of November). Simultaneously, samples for starch analysis were taken from a number of natural seagrass beds in the Oosterschelde. In addition several abiotic characteristics (sediment grain size, sediment organic C, leaf %C, leaf %N, porewater NH_4 , NO_3 , PO_4 , and H_2S) were determined every summer (Table 1). For detailed methodological details on these measurements, please see Govers et al. (2014b).

To distinguish between successful and unsuccessful transplant sites, we compared shoot densities plot^{-1} in September with shoot densities plot^{-1} in the preceding September (year-1). If shoot numbers were $<15\%$ of the shoot numbers in the preceding year, plots were marked as unsuccessful. For transplanted plots in the year of transplanting, we compared shoot densities plot^{-1} in June and September. If shoot numbers had decreased in this period (shoot numbers September $<$ June), we marked those plots as unsuccessful. We classified a transplant site as successful if there were more successful than unsuccessful plots and vice versa. A single transplant site could thus be classified as successful in one year and unsuccessful in the next.

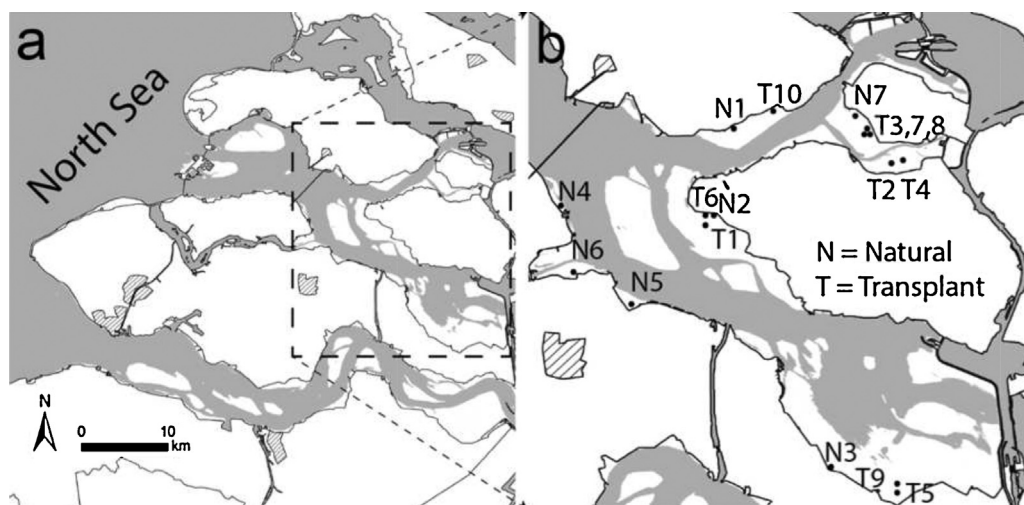


Fig. 1. Maps of (a) the Dutch Delta, and (b) the locations of the transplant sites (T1–T10) and natural seagrass beds (N1–N7) in the Oosterschelde.

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