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The interactive effects of water flow and reproductive strategies on seed and seedling dispersal along the substrate in two sub-tropical seagrass species

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ABSTRACT

We quantified the effects of water flow on secondary seed and seedling dispersal for two seagrass species with different reproductive strategies: turtle grass (*Thalassia testudinum*) whose large seeds (15.1 ± 0.8 mm tall) have the potential for long distance dispersal by current-mediated transport of buoyant fruits, and shoal grass (*Halodule wrightii*), whose small seeds (2.1 ± 0.1 mm tall) are released adjacent to the parent plant and create a persistent seed bank. Results from field dispersal experiments in Texas indicate that under normal flow conditions (mean water velocity < 5 cm s^{-1}), turtle grass seedling movement is greater over bare sand than within seagrass beds and seedlings have the potential to move up to 2.1 m d^{-1}. Fine hairs on the seedling base trap sand grains, which likely leads to final seedling establishment after a few days and a potential secondary dispersal distance along the substrate of <20 m from the point of release. Under normal flow conditions, shoal grass seeds have the potential to move up to 1.1 m d^{-1}, but seed entrapment in sediment ripples likely limits the total secondary dispersal distance to <10 m from the parent plant. Secondary dispersal dynamics are species-specific, related to seed morphology and tightly coupled to each species' reproductive strategy. This phase of seed dispersal has the potential to shape plant population structure and aid in colonization of unvegetated habitats.

1. Introduction

Seed dispersal represents a critical life history stage for many plant species. Dispersal from the parent plant can decrease sibling competition, enable seed escape from mortality near the parent, aid in recolonizing disturbed habitats, and increase the likelihood of the seed finding a suitable substrate in which to grow (Willson and Traveset, 2000). The 'seed shadow', or spatial distribution of dispersed seeds around the parent plant, can be influenced by such factors as plant height (Greene and Johnson, 1996), seed morphology (Bakker et al., 1996), habitat patchiness (Hoppes, 1988), wind speed and direction (Howe and Smallwood, 1982), and biotic dispersal agent behavior (Bakker et al., 1996). The distance a seed disperses from the parent plant is tightly coupled to the species' life history and reproductive strategy (Bakker et al., 1996), and most species are specialized either for efficient seed dispersal or for building a persistent localized seed bank (Bakker et al., 1996). Seed-bank forming species produce seeds that often remain dormant in the sediment until a trigger (genetic or environmental) stimulates germination (Amen, 1968). By having a distinct period of dormancy, these seeds are not only dispersed in space, but also dispersed in time (Bakker et al., 1996).

Seed dispersal can be mediated by abiotic or biotic factors, and seed morphology frequently indicates the general dispersal mechanism. The two phases of seed dispersal, primary and secondary dispersal, encompass all seed movement after release from the parent plant. Primary dispersal includes initial seed deposition to the substrate and secondary dispersal involves all subsequent seed movement until final seed establishment (Watkinson, 1978). Primary dispersal of wind-dispersed seeds, for example, involves the airborne transport of seeds from the parent plant to the ground, and secondary dispersal encompasses all seed movement following initial settlement (Greene and Johnson, 1996). Secondary dispersal has the potential to substantially alter the seed shadow from primary dispersal and consequently can be more important than primary dispersal in shaping plant population structure and demography (Chambers and MacMahon, 1994; Harper, 1977).

Although a large body of work exists on secondary seed dispersal in terrestrial plants, relatively little is known of secondary seed dispersal strategies or the resulting seed shadows in seagrasses. Seagrasses are submerged marine angiosperms capable of both sexual reproduction and asexual clonal growth by subsurface rhizome elongation. Interestingly, the relatively few (~70) species of seagrasses display a remarkably wide variety of reproductive strategies. Species each have unique

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characteristics of reproductive timing and effort, mode (surface or submarine flowering and pollination), and reproductive structure morphology (Ackerman, 2006). For example, whereas some species (e.g., *Thalassia testudinum*, *Zostera marina*) are reproductive in the spring and summer, others (e.g., *Posidonia australis*, *Amphibolis griffithii*) flower in the fall and winter (Ackerman, 2006), and while some species produce many seeds per fruit (e.g., *Halophila decipiens*, 30 seeds fruit^{-1},van Tussenbroek et al., 2010), others produce a single seed within a fruit (e.g., *Syringodium filiforme*, McMillan, 1981).

Because of the variability in life history and reproductive strategies used by seagrasses, it is also likely that these species should exhibit substantial variation in primary and secondary seed dispersal distances (Bakker et al., 1996; Nathan and Muller-Landau, 2000). Historically, research examining seagrass expansion has favored clonal growth, as it was considered the dominant form of propagation for aquatic plants (Arber, 1920). As a result, sexual reproductive dynamics in seagrasses are not fully understood. Recent work has reported that over large spatial scales, genotypic diversity for individual species is high, suggesting that (1) the role of sexual reproduction in seagrasses was historically undervalued and (2) dispersal among seagrass beds likely contributes to observed genetic diversity (Kendrick et al., 2012). Although dispersal can also be achieved through transport of vegetative plant fragments (Hall et al., 2006; Thomson et al., 2015), seeds provide the best opportunity for transport over long distances (McMahon et al., 2014). Therefore, studies focused on seagrass reproductive biology, and particularly seed dispersal, are necessary to fully understand seagrass propagation and life history dynamics.

Seagrass seeds, like their terrestrial counterparts, are dispersed by abiotic and biotic mechanisms. Abiotic transport by water currents is thought to be the dominant mechanism of dispersal (Kendrick et al., 2012), although biotic dispersal by waterfowl, sea turtles, and fish is possible (McMahon et al., 2014; Sumoski and Orth, 2012). The role of hydrodynamics on the movement of seeds depends on the individual species' life history and reproductive strategy and the morphology of the reproductive structures, including seed and seedling size, shape and buoyancy (McMahon et al., 2014; Ruiz-Montoya et al., 2012). Whereas the reproductive structures of some species are transported along the water's surface, structures of other species are transported in the water column, or in/on the sediment surface (McMahon et al., 2014; Orth et al., 2006). Additionally, for some species, dispersal occurs under normal hydrodynamic conditions, although other species require storm conditions to initiate seed transport (Bell et al., 2008; Hammerstrom et al., 2006; McMahon et al., 2014). Several studies have investigated primary dispersal of seeds and seeds encased in propagules (e.g., fruits or rhipidia) and have reported a wide range of dispersal distances (Erftemeijer et al., 2008; Harwell and Orth, 2002; Orth et al., 1994; Ruiz-Montoya et al., 2012; van Dijk et al., 2009). Whereas ephemeral genera such as *Halophila* and *Halodule* tend to have small seed shadows resulting from primary dispersal (on the order of meters), persistent genera such as *Posidonia*, *Enhalus* and *Thalassia* have large seed shadows, with potential primary dispersal distances of hundreds of kilometers from the parent plant (Kendrick et al., 2012). Eleven seagrass genera produce negatively buoyant seeds (McMahon et al., 2014), and for these species, after initial seed settlement to the substrate (primary dispersal), further seed movement can occur through hydrodynamically-mediated transport along the sediment surface (secondary dispersal; Orth et al., 2006; McMahon et al., 2014). At the sediment surface, seed dispersal distance depends on the strength of wave-driven oscillatory flows and topographic features such as sand ripples, sediment mounds, and substrate type (bare or vegetated), as such features can obstruct movement (Koch et al., 2010; McMahon et al., 2014; Orth et al., 2006). Only a few studies exist that examine the dynamics of secondary dispersal (Koch et al., 2010; Lacap et al., 2002; Orth et al., 1994; Ruiz-Montoya et al., 2012), despite the potential for this dispersal phase to shape seagrass population structure and demography.

Turtle grass (*T. testudinum*) and shoal grass (*Halodule wrightii*) are two common subtropical seagrass species with remarkably different life history and reproductive strategies. These species co-occur in mixed beds, but also form separate monospecific meadows. Whereas turtle grass is a climax species, shoal grass is an early colonizing, pioneer species and is able to tolerate sub-optimal conditions and disturbances that turtle grass cannot (Zieman, 1982).

Turtle grass is dominant throughout the Gulf of Mexico and Caribbean Sea. The turtle grass reproductive season generally spans summertime months, but is variable throughout the species range (van Tussenbroek et al., 2006). In Texas where this study was conducted, turtle grass flowers are produced at the base of the shoot in the early summer, with fruit formation, development and maturation occurring June–September. Each fruit contains 1–6 pyriform seeds (10–15 mm in length), but most fruits average only two. Turtle grass seeds have no period of dormancy; seeds germinate within the fruit and are therefore seedlings upon release (Orpurt and Boral, 1964) (Fig. 1A). Fruits often dehisce (open) while still attached to the plant, with up to 90% of seeds settling near or below the parent (van Dijk et al., 2009). However, buoyant fruits can also detach from the parent and be transported by currents up to 360 km before dehiscence and seedling settlement to the substrate (van Dijk et al., 2009). As a result, turtle grass has the potential for long-distance primary dispersal and a large seed shadow. Secondary processes may further increase dispersal distances as seedling cotyledons may act as a sail allowing currents and waves to transport them along the substrate before roots have an opportunity to anchor the young plant.

Shoal grass has a wider geographical range than turtle grass, extending throughout the Caribbean and Gulf of Mexico to the East Coast of the United States and Bermuda (van Tussenbroek et al., 2010). Flower production and fruit and seed development in Texas occur April–July. Generally, two fruits are produced at the base of the female shoot. Each of these fruits contain one black spherical seed about 2 mm in size (Fig. 1B), which is released from the fruit at or below the sediment surface adjacent to the parent plant. Unlike turtle grass, shoal grass does not have a buoyant reproductive phase and therefore has localized primary dispersal and a relatively small primary seed shadow. Shoal grass seeds are surrounded by a hard seed coat and can remain dormant for up to 4 years, forming a seed reserve in the sediment (McMillan, 1981). For shoal grass, the unit of secondary dispersal is a seed.

Turtle grass seedlings are larger and morphologically more complex than shoal grass seeds. Whereas the small, round shape of shoal grass seeds likely restricts them to very low velocity hydrodynamic conditions adjacent to the substrate, the larger size and complex shape of turtle grass seedlings likely exposes them to higher current velocities and oscillatory wave-driven flow in the water column (Koch et al., 2006). The broad leaves characteristic of turtle grass may also provide a wide surface over which the force of water can act; in seedlings, these leaves are often curled (pers. obs.), which may generate lift (Dijkstra, 2012). As

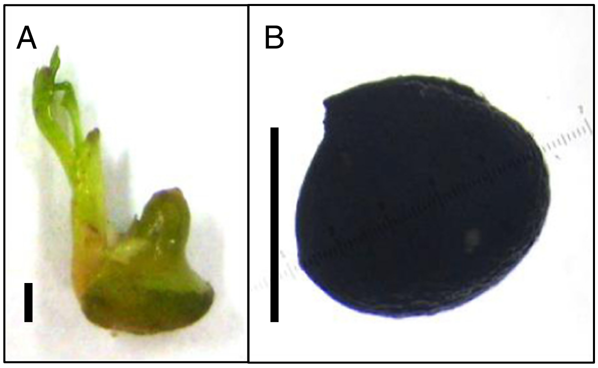

Fig. 1. Examples of a turtle grass (*Thalassia testudinum*) seedling (A) and a shoal grass (*Halodule wrightii*) seed (B). Scale bar = 2 mm.