

REVIEW

A review of issues in seagrass seed dormancy and germination: implications for conservation and restoration

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ABSTRACT: Seagrasses have received considerable attention over the past 2 decades because of the multiple ecological roles they play in estuarine and coastal ecosystems and concerns over worldwide losses of seagrass habitat due to direct and indirect human impacts. Restoration and conservation efforts are underway in some areas of the world, but progress may be limited by the paucity of information on the role of seeds in bed dynamics. Although flowering occurs in most of the 58 seagrass species, seed germination data exist for only 19 of the 42 species that have some period of dormancy, with only 93 published references to field and/or laboratory studies. This review addresses critical issues in conservation and restoration of seagrasses involving seed dormancy (e.g. environmental vs physiological), existence and type of seed bank (transient or persistent), and factors influencing seed germination (e.g. salinity, temperature, light). Results of many earlier published studies relating seed germination to various environmental factors may need re-examination given more recent published data which show a confounding influence of oxygen level on the germination process. We highlight the importance of conducting ecologically meaningful germination studies, including germination experiments conducted in sediments. We also identify questions for future research that may figure prominently in landscape level questions regarding protected marine or estuarine reserves, habitat fragmentation, and restoration.

KEY WORDS: Seagrasses · Seeds · Dormancy · Seed banks · Germination · Restoration · Conservation

INTRODUCTION

Seagrasses, marine angiosperms comprising 58 species in 11 genera, occur in all coastal waters of the world except the Antarctic (den Hartog 1970). They have been receiving increasing attention worldwide since the 1970s because of recognition of (1) their mul-

tiple ecological functions in estuarine and coastal systems, such as nursery and fish habitat (Coles et al. 1987, Heck et al. 1997) and regions of high primary and secondary production (Larkum et al. 1989, Edgar 1990, Fredette et al. 1990), and (2) losses in many areas of the world due to anthropogenic inputs of nutrients and sediments (Short & Burdick 1996, Short & Wyllie-Echeverria 1996). In addition, considerable seagrass area has been permanently lost to coastal development, primarily from dredge and fill operations (Short et al. 1991) or altered due to commercial/recreational activities such as propeller and anchor scarring

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(Walker et al. 1989, Sargent et al. 1995, Dawes et al. 1997). These issues have led to recent developments in efforts to both restore and conserve these habitats (Fonseca et al. 1998).

Although seagrass restoration has focused on mature or adult plants, discussions over the last decade on biodiversity issues (National Research Council 1995) that entail both conservation biology and restoration ecology suggest that seed ecology should be a critical research topic. Seagrass reproduction and seed output have been largely ignored in questions related to their potential contribution to population structure and genetics, plant demographics, bed maintenance, or in the development of new beds (Kirkman & Kuo 1990, Orth et al. 1994, Williams & Davis 1996, Piazzini et al. 1998, Marba & Walker 1999, Orth 1999). We believe that for conservation and restoration of seagrasses to be effective, more research into their seed germination ecology must be conducted.

Most of the 58 reported species of seagrasses are known to flower and produce fruit, but differ dramatically in seed anatomy and germination strategy (den Hartog 1970). Kuo & Kirkman (1996) characterized the seagrass genera into 3 classes based on seed anatomy, nutrient storage, and germination strategy (Table 1). Seeds from 2 of these classes do not exhibit any type of dormancy, with 1 class, which comprises 4 species in 2 genera, exhibiting viviparous development. The third class, comprising 42 species in 7 genera, produces

Table 2. Seed bank, dormancy, and germination citation counts from the published seagrass literature (from 1938 to 2000)

Genus	Number of citations
<i>Zostera</i> spp.	58
<i>Halophila</i> spp.	13
<i>Cymodocea</i> spp.	8
<i>Halodule</i> spp.	6
<i>Phyllospadix</i> spp.	4
<i>Syringodium</i> sp.	4

seeds with a hard seed coat and some period of dormancy.

Despite more than a century of scientific research and over 2000 yr of recorded observations on factors influencing the dormancy and germination of seeds in terrestrial systems (Baskin & Baskin 1998), there is a dearth of information on seagrass seeds. Searches of the published literature (from 1938 to 2000) revealed seed-based information on only 19 of the 42 seagrass species (Table 2). These studies found some level of seed dormancy, with 93 references to field observations or laboratory/field experiments on seed germination (Appendix 1). This review, which concentrates on the group of 42 species that have some period of dormancy (Kuo & Kirkman 1996), addresses critical issues in conservation and restoration of seagrasses involving seed dormancy, existence and type of seed banks, and

Table 1. Comparison of the type of fruit and seed covering, dormancy, and seed bank characteristics for the 12 genera of seagrasses (modified from Kuo & Kirkman 1996). Definition of dormancy after Fenner (1995), but modified to include seeds that appear to have a highly variable dormancy period. Viviparous = viviparous reproduction

Genus	Fruit/seed covering	Dormancy	Seed bank	Length of dormancy	Source
Class 1					
<i>Enhalus</i>	Membranous	Not distinct	None	None	Kuo & Kirkman (1996)
<i>Posidonia</i>	Membranous	Not distinct	None	None	Kuo & Kirkman (1996)
<i>Thalassia</i>	Membranous	Not distinct	None	None	Kuo & Kirkman (1996)
Class 2					
<i>Amphibolis</i>	Viviparous	Not distinct	None	None	Kuo & Kirkman (1996)
<i>Thalassodendron</i>	Viviparous	Not distinct	None	None	Kuo & Kirkman (1996)
Class 3					
<i>Cymodocea</i>	Hard	Distinct	Transient	Up to 12 mo	Reyes et al. (1995), Pirc et al. (1986)
<i>Halodule</i>	Hard	Distinct	Persistent	46 mo	McMillan (1991)
<i>Halophila</i>	Hard	Distinct	Persistent	Up to 24 mo	McMillan (1991)
<i>Heterozostera</i>	Hard	Distinct	Unknown	Unknown	Kuo & Kirkman (1996)
<i>Phyllospadix</i>	Hard	Distinct	Transient	2 wk–12 mo	Turner (1983), Kuo et al. (1990), Reed et al. (1998)
<i>Syringodium</i>	Hard	Distinct	Persistent	49 mo	McMillan (1991)
<i>Zostera</i>	Hard	Distinct	Transient	Up to 12 mo	Orth & Moore (1983), Moore et al. (1993)

factors influencing seed germination. This review does not include freshwater submersed macrophytes, such as *Ruppia* spp. (for review see Kantrud 1991), which are considered euryhaline and often found co-occurring with seagrasses.

DORMANCY

Species which have some form of dormancy are able to disperse through time as well as space by physical and/or biological vectors (Chambers & MacMahon 1994, Fenner 1995). Terrestrial plants exhibit a suite of dormancy strategies, from willow *Salix* spp., whose seeds germinate in days to weeks, to moth mullein *Verbascum blattaria*, whose seeds can stay dormant for 1000 yr (Fenner 1995, Baskin & Baskin 1998 and references within). As both spatial and temporal disturbances occur in seagrass communities, some form of seed dormancy in seagrasses can be important for long-term population persistence. Many definitions of dormancy have been introduced, based, in part, on the factors that control dormancy (Hilhorst & Karssen 1992, Baskin & Baskin 1998). Classification of dormancy can be assigned according to the residence time in the seed bank (Simpson 1990), the timing of dormancy initiation (Hilhorst & Toorop 1997), or the mechanisms preventing germination (Baskin & Baskin 1998). Classification of plant communities is often founded on the transient or persistent nature of seed banks. From the perspective of the mechanisms controlling dormancy and germination in a given species, the seed developmental stage at which dormancy is imposed is of importance. Dormancy initiated during seed development requires a physiological mechanism, such as embryo maturation, to initiate germination. Dormancy initiated at the time of seed release requires an environmentally mediated factor, such as temperature or oxygen stratification, to initiate germination.

Primary dormancy occurs when dormancy is imposed on the developing seed attached to the parent plant, while secondary dormancy is associated with dormancy regulation factors that occur in the seed bank (Hilhorst & Toorop 1997). The seagrass literature suggests that dormancy is initiated during seed development; however, we are unaware of any studies which test if seeds of those species in the third class (Table 1) will germinate immediately after release from the parent plant.

While dormancy is not a life history strategy for several seagrass genera (notably *Posidonia*, *Thalassia*, and *Amphibolis*), dormancy has been demonstrated in others and ranges from a few weeks (*Phyllospadix torreyi*, Reed et al. 1998) to up to 4 yr (*Syringodium filiforme*, McMillan 1983a). A critical question that has

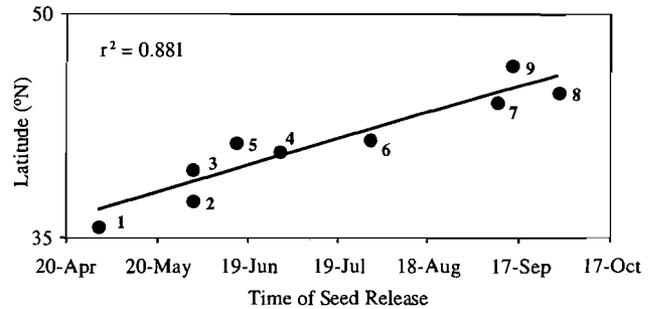


Fig. 1. Correlation between timing of seed release and latitude in 9 populations of *Zostera marina* along the east coast of North America. Notations (in order of increasing latitude): ¹North Carolina, Phillips (1972); ²Virginia, Moore et al. (1993); ³New Jersey, Phillips (1972); ⁴New York, Phillips (1972); ⁵Rhode Island, Churchill (1983); ⁶Massachusetts Addy (1947, Phillips (1972)); ⁷Maine, Phillips (1972); ⁸Nova Scotia, Phillips (1972); ⁹New Brunswick, Keddy & Patriquin (1978)

not been addressed in these studies is whether the environment or some physiological characteristic of the seed is responsible for preventing germination (i.e. environmental vs organic [physiological dormancy], Baskin & Baskin 1998). As in studies on other plant physiology systems, there can be a high degree of interaction between factors (Thomas 1992, Ungar 1995, Hilhorst & Toorop 1997, Khan & Ungar 1997).

Harrison (1991) used seeds collected from parent plants and from the seed bank (1 mo after seed release) to examine dormancy in *Zostera marina*. His experiments, conducted under various temperature and salinity conditions with scarified (i.e. scored) seed coats, concluded that both physiological and physical dormancy exist in this species. Published data (Addy 1947, Phillips 1972, Keddy & Patriquin 1978, Churchill 1983, Moore et al. 1993) from this species' latitudinal range along the North American coast from North Carolina to Canada shows a progressively later period of seed release with increasing latitude (Fig. 1). However, evidence from 3 locations (Virginia, New York, Massachusetts; Fig. 1) suggests that germination occurs in the fall regardless of latitude, suggesting that dormancy may be under environmental rather than inherent physiological control (Baskin & Baskin 1998). Other observational studies have addressed issues of timing of flowering (Jacobs & Pierson 1981) and seed production (Phillips et al. 1983, Silberhorn et al. 1983), and seed release (Fig. 1) along latitudinal gradients; however, seed dormancy has not been tested along a latitudinal gradient under rigorous experimental conditions.

The maintenance of dormancy in terrestrial seeds can be attributed to a variety of factors (Simpson 1990, Hilhorst & Toorop 1997, and references within both), including hormones, secondary plant compounds (i.e.

for allelopathy), light, temperature, salinity, gases (CO₂ and O₂), and nutrients. For seagrasses, studies of these factors have examined their influence on seagrass seed germination rather than dormancy maintenance. Research on maintaining seagrass seed dormancy has been restricted mainly to studies of the retention of seeds for artificial seed reserves (e.g. McMillan 1991, Brenchley & Probert 1998).

SEED BANKS

Seed banks have been studied extensively in many plant ecosystems (Skoglund 1992 and references within) with the notable exception of seagrass meadows. Seed banks are often classified by the type of dormancy present, and they can vary greatly in their characteristics. The seed bank for a given species is population-specific and can be either transient (turn over in less than 1 yr) or persistent (seeds that remain longer than 1 yr) (Simpson 1990). The length of time a seed remains in the seed bank can be critical as long-term population stability is influenced by whether or not the seed reserve exists through the next reproductive cycle (i.e. a 'true' seed bank).

Seed banks are characterized best by a number of generalities. First, distribution of seeds in a seed bank is extremely patchy (Fenner 1995) and temporal variability of seeds in the seed bank can exist in a plant community having either transient or persistent species. This variability makes analyzing seed banks difficult because they require high spatial and temporal sampling resolution (Fenner 1995 and references within). Second, the size of the seed is often directly related to its persistence in the seed bank. This property appears to be a function of per capita expenditure of energy, ability of the seed to percolate into the sediment, and potential to avoid predation (Fenner 1995). Third, abundance of seeds in a seed bank varies by plant community type.

Seed banks in seagrass communities have not been studied extensively. Estimates of seed bank size for seagrasses are comparable to those of most plant community types (Table 3) (Fenner 1995 and references within); however, Inglis (2000) found large heterogeneity in *Halodule uninervis* seed banks at multiple spatial scales. Harrison (1993) documented the dynamics of a *Zostera marina* seed bank in the Netherlands, showing high spatial and temporal variability in a single population. A significant portion of the seeds in the seed bank were lost to autonomous death and a small percentage of the seeds contributed to a persistent seed bank. McMillan (1991) reported seeds of the following seagrass species collected from various sources surviving more than 12 mo under laboratory

conditions: *Syringodium filiforme*, 49 mo; *H. uninervis*, 41 mo; *Halophila engelmannii*, 24 mo; *Halodule wrightii*, up to 46 mo.

Several studies have described the conditions necessary to store seeds, an indirect approach for understanding natural seed banks. Conacher et al. (1994b) reported a maximum of a 50 d storage period for *Zostera capricorni* seeds under conditions of aeration and low temperatures (5 to 10°C). Churchill (1983) found high survival (8 mo) of *Z. marina* seeds stored in water at room temperature. Reed et al. (1998) found that storage of *Phyllospadix torreyi* seeds under cold, dark conditions could delay germination by up to 83 d.

SEED GERMINATION

Successful seed germination following some period of dormancy results from an interaction between physiological and genetic factors (internal) and environmental factors (external), including sediment, light, and temperature (Baskin & Baskin 1998). Both internal and external processes have the potential to create a seed bank for a given population. Critical environmental cues that influence germination can vary over short horizontal and vertical distances as characteristics of the physical environment (e.g. sediment type, pH, organic matter) and biological environment (e.g. abundance and type of sediment-dwelling animals, physical arrangement of plant and animals in space and time) interact to create a mosaic of microclimates (Hamrick & Lee 1987, Woodin et al. 1998).

Termination of dormancy or initiation of germination/seedling growth is influenced by hormones, light (photoperiod), temperature, water (e.g. imbibition, osmotic changes, salinity), nutrients, or mechanical cues (Hilhorst & Karssen 1992, Gutterman 1994). Factors critical to this process can be seed-specific, so the intraspecific range for each factor may span several orders of magnitude (Hilhorst & Toorop 1997). Thus, exact mechanisms are often considered nebulous as

Table 3. Size of seed bank for a variety of plant community types (Fenner 1995) compared to seagrasses

Plant community type	Seed bank size (m ⁻²)
Arable communities	20 000–40 000
Grasslands/moorlands	5 000–20 000
Temperate forests	1000–10 000
Tropical forests	100–1000
Salt marshes	100–1000
Subarctic/alpine forests	10–100
Seagrasses ^a	1–30 000

^aSee references in Appendix 1 for seed bank studies

the existence of multiple factors can preclude identifying the exact mechanism of dormancy termination/germination initiation (Hilhorst & Karssen 1992, Bewley 1997). Additionally there are often interactions between several factors (e.g. salinity and temperature on halophytes, Ungar 1995, Khan & Ungar 1997).

Field and laboratory studies of seagrass germination have focused primarily on salinity, temperature, light, scarification, and, more recently, the sediment where seeds germinate (e.g. oxygen [oxygen-reduction profiles or E_h], Moore et al. 1993, Brenchley & Probert 1998), as critical cues influencing germination processes (Appendix 1). However, no work has been conducted on the precise physiological mechanisms leading to seagrass seed germination. More importantly, it is critical that all seagrass seed germination studies identify a standard 'definition' of germination (e.g. Brenchley & Probert 1998) for comparison to other work, including not just rupture of the seed coat but emergence and growth of the cotyledon (Churchill 1983, Brenchley & Probert 1998).

Most published work on seed germination has been conducted under aerobic, non-sediment conditions, studying temperature and salinity and their interactions (Appendix 1). The majority of studies have demonstrated increased germination at reduced salinities (*Zostera noltii*, Hootsmans et al. 1987, Loques et al. 1990; *Cymodocea nodosa*, Caye & Meinesz 1986). Other studies have shown no effect of salinity on germination (*Syringodium filiforme*, McMillan 1981; *Halodule wrightii*, McMillan 1981; *Z. marina* [perennial form], Hootsmans et al. 1987; *Z. marina* [annual form], McMillan 1983b; *Z. capricorni*, Conacher et al. 1994b). Seeds of *Z. capricorni* (Conacher et al. 1994b) germinated at all tested temperatures (15 to 30°C) at low salinity (1, 5, and 10‰), while seeds held at higher salinities (20, 30, and 40‰) germinated only at lower temperatures. Several studies suggest that temperature stratification may be critical for germination of seeds, but it is not clear whether stratification is a necessary condition for seagrass seed germination, as in many terrestrial species (Baskin & Baskin 1998), because of the potential confounding issues created by germinating seeds without sediment (e.g. different oxygen environment, Moore et al. 1993). Further, seagrass seed germination experiments conducted at low salinities (e.g. 1‰ from Conacher et al. 1994b) may not reflect ambient field conditions.

Both photoperiod and specific wavelengths of light are important for germination in terrestrial systems (Thomas 1992, Gutterman 1994, Fenner 1995, Hilhorst & Toorop 1997). McMillan (1987, 1988b) found light to be an important inducer of germination for both *Halophila engelmannii* and *H. decipiens*, while Birch (1981) reported germination of *H. spinulosa* seeds

under both light and dark conditions. In contrast, light has not been considered important in the germination process for *Zostera japonica* (Bigley 1981) and *Z. marina* (Tutin 1938, Hootsmans et al. 1987, Harrison 1991, Moore et al. 1993).

Scarification of the seed coat resulted in increased germination rates for *Zostera marina* (Harrison 1991), *Z. noltii* (Loques et al. 1990), and *Z. capricorni* (Conacher et al. 1994b), suggesting some form of physical dormancy. These studies also found an interaction between salinity and scarification, with germination increasing at lower salinities. Removal of the seed coat of *Cymodocea nodosa* resulted in increased germination at a lower salinity (20‰) than a higher one (38‰) (Caye et al. 1992). McMillan (1987, 1988b) and Birch (1981) found no effect of seed coat removal for *Halophila engelmannii*, *H. decipiens*, and *H. spinulosa*.

Hormones can influence seed germination in terrestrial plants through either stimulating seed germination (e.g. gibberellic acid, Hilhorst & Toorop 1997; thiourea, Conacher et al. 1994b) or preventing the termination of dormancy (e.g. abscissic acid, Hilhorst & Karssen 1992). While a 1 ppm solution of gibberellin (GA_7 and KNO_3) had no effect on *Zostera noltii* seeds (Loques et al. 1990), more concentrated solutions of gibberellin (50 ppm, GbA_3 and KNO_3) and thiourea (50 ppm) promoted germination of *Z. capricorni* (Conacher et al. 1994b).

One factor common to many of the above studies is that they were conducted in either small aquaria or petri dishes without sediment and did not report oxygen concentrations (Appendix 1). Oxygen levels or some other property of sediments may be the most important factor affecting seed germination (Kawasaki 1993, Moore et al. 1993, Brenchley & Probert 1998). Moore et al. (1993) showed faster germination of *Zostera marina* seeds held in both sediments with no oxygen (as measured by redox potential) and vials with water where oxygen was removed compared to seeds held in similar vials with oxygen. Kawasaki et al. (1988) and Kawasaki (1993) also showed that *Z. marina* seed germination was promoted by either covering seeds with sediment or placing them in water at very low dissolved oxygen levels (below 1 ppm), suggesting a reducing environment was also important for this species. Brenchley & Probert (1998) found similar results for *Z. capricorni* with little apparent difference in seeds held at 2 salinities (15 and 30‰). In contrast, Churchill (1992) found that seeds of *Z. marina* germinated and retained under anaerobic conditions did not develop properly. Hootsmans et al. (1987) also found little survival of *Z. marina* seeds after 30 d under anaerobic conditions. Here, seeds were covered with some form of organic material for 1 mo, which may have resulted in toxic sulfide conditions (not mea-

sured) that may not have reflected natural conditions. The phenomenon of germination in anoxic environments is common for both seeds and tubers in other rooted submersed aquatic plants such as *Potamogeton*, *Hydrilla*, and *Najas* (Sculthorpe 1967, van Vierssen 1982, Spencer & Ksander 1997).

Based on these data, we infer that the variation in timing of seed germination in the field noted in a number of studies results from the interaction between temperature and sediment oxygen levels (i.e. the depth at which a seed is buried). Steep biogeochemical gradients found in the sedimentary environment (Berner 1980, Moriarity & Boon 1989, Woodin et al. 1998) where seagrass seeds are deposited may be a key to understanding forcing functions in the germination history of seagrass species that have some delay between seed release and seed germination. Seeds at different burial depths, at the scale of millimeters, will experience significant changes in these parameters. We also suggest that photoperiod will not influence buried seeds and that salinity, a factor often implicated as a major determinant influencing germination, especially low salinities, may need to be re-examined. Additionally, the lack of extensive information on internal physiological cues (e.g. hormones, enzymes) may limit our understanding of critical germination factors.

SEED GERMINATION RESEARCH: FUTURE DIRECTIONS

Achieving a fundamental understanding of the ecology and population biology of a given seagrass species requires understanding of its seed biology and ecology. Despite some early pioneering work in seagrass seed biology for *Zostera marina* (Taylor 1957a,b), little substantive research has been done for the majority of species. However, in light of the growing concerns about anthropogenic influences on the survival of seagrass populations worldwide (Short & Wyllie-Echeverria 1996), conservation of individual species will demand elucidation of the contribution of seeds to population maintenance and creation of new beds. This work must include basic germination ecology.

Although our review has highlighted the lack of this basic work for many seagrass species (Table 2), it also suggests that previous work be re-examined in light of recent research suggesting that factors intrinsic to sediments, especially sediment oxygen levels (redox potentials), may be the most important ones influencing germination processes for some species (Churchill 1983, Moore et al. 1993, Brenchley & Probert 1998).

Most seagrass seed germination experiments in the literature have incorporated 1 or more of the following

conditions that may have potentially compromised the experimental design: the transfer of seeds from sediments to water (change in redox potential), aerial transport of seeds from distant populations (change in temperature), sterilization, atypical storage conditions, and germination experiments conducted in petri dishes without sediment. Few experiments measure oxygen concentration or include oxygen level as a variable. As environmental stratification (cold) has been found to be important for some terrestrial species (Baskin & Baskin 1998), it is important that there is no experimenter-created environmental stratification (e.g. transporting seeds on ice) in addition to the germination treatments being tested.

Basic work should follow guidelines established in Baskin & Baskin (1998) for 'ecologically meaningful' studies. These guidelines include collecting mature seeds and using intact seeds immediately after harvesting and neither scarifying nor soaking seeds in disinfectants or acid prior to the experiment. Maintaining conditions as close to the natural environment as possible is critical for minimizing experiment-induced biases. Replicated, statistically defensible experiments should be conducted either *in situ* or under conditions that simulate natural conditions, and seeds not used should be stored under natural or simulated conditions (e.g. retained in mesh or burlap bags [Harwell & Orth 1999] under field conditions). Batch seed experiments should be conducted keeping in mind the inherent variability in seed characteristics (e.g. size, coat thickness, color; Arasaki 1950, Fukuda & Yasuie 1981, Takaba 1985, Harrison 1991).

We suggest that future work concentrate on addressing the following questions:

Dormancy

- Does true dormancy exist for seagrass species, and if so, is it environmentally controlled or a property of the seed itself (i.e. organic)?

- If dormancy is organically controlled, is it endogenous (characteristic of the embryo) or exogenous (characteristic of structures such as the seed coat)?

Seed banks

- To what extent do persistent or transient seed banks exist for a given species or between populations of a single species?

- What are the spatial (horizontal and vertical/depth) and temporal characteristics of seed banks?

- What are the relationships between seed bank composition and aboveground community composition in multi-species seagrass ecosystems (e.g. communities in Asia and Australia)?

Seed characteristics

- Are there relationships between size of seed, thickness of seed coat and dormancy, seed bank characteristics, and factors influencing germination?

Germination

•What is a standard definition of 'germination' that future work can be based upon as a common reference?

•Is sediment oxygen level concentration a critical, but often overlooked, factor influencing germination?

•How deep in the sediment can a buried seed germinate and still develop into a viable plant?

•What are the evolutionary relationships in germination requirements to seagrass ancestors?

Keys to the above questions in seagrass research efforts rest not just in the links to the terrestrial and freshwater realm but in the innovative experiments yet to be conducted. Reciprocal transplant experiments of seeds of a species across latitudinal gradients may pro-

vide answers to dormancy and seed bank questions. Most critically, as researchers begin to focus on conservation and restoration, seed work may figure prominently in landscape level issues regarding protected marine or estuarine reserves, patch dynamics, meta-population analyses, and habitat fragmentation as well as basic population biology (Montalvo et al. 1997).

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Appendix 1. Literature summary of factors studied in seed bank, dormancy, and germination experiments in seagrasses. We report whether the study was experimental (E) or observational (O); conducted in a field (F) or laboratory (L) setting; conducted with sediments (S) or water (W); and whether or not the study focused on seed bank characteristics, seed dormancy, or seed germination. Factors tested: a = nothing; b = temperature; c = salinity; d = substrate type; e = time; f = scarification; g = osmotic pressure/dessiccation; h = seedling recruitment; i = seed bank; j = light; k = source; l = nutrients; m = hormone; n = oxygen; o = burial depth; p = color; q = planting treatment; r = disturbance; NA = not available; - = not applicable; Both = study conducted (in part or whole) under both conditions

Taxon	E/O	F/L	S/W	Seed bank	Dormancy	Germination	Source	Factors tested
Cymodoceaceae								
<i>Cymodocea nodosa</i>	O	F	S	Y	N	Y	Caye & Meinesz (1985)	a
<i>Cymodocea nodosa</i>	E	L	W	N	N	Y	Caye & Meinesz (1986)	b,c
<i>Cymodocea nodosa</i>	Both	Both	Both	N	N	Y	Pirc et al. (1986)	b,d
<i>Cymodocea nodosa</i>	E	L	W	N	N	Y	Buia & Mazzella (1991)	e
<i>Cymodocea nodosa</i>	E	L	W	N	Y	Y	Caye et al. (1992)	c,f,g
<i>Cymodocea nodosa</i>	O	F	S	Y	N	Y	Terrados (1993)	h
<i>Cymodocea nodosa</i>	O	F	S	N	N	Y	Reyes et al. (1995)	e
<i>Cymodocea rotundata</i>	Both	Both	S	Y	N	Y	McMillan et al. (1982)	i
<i>Halodule uninervis</i>	E	L	W	N	N	Y	McMillan (1991)	e
<i>Halodule uninervis</i>	O	F	-	Y	N	N	Inglis (2000)	i
<i>Halodule wrightii</i>	E	L	W	Y	Y	Y	McMillan (1981)	c,e
<i>Halodule wrightii</i>	E	L	W	N	N	Y	McMillan (1983a)	e
<i>Halodule wrightii</i>	O	F	-	Y	N	N	McMillan (1985)	i
<i>Halodule wrightii</i>	E	L	W	N	N	Y	McMillan (1991)	e
<i>Syringodium filiforme</i>	E	L	W	Y	Y	Y	McMillan (1981)	b,c,e
<i>Syringodium filiforme</i>	E	L	W	N	N	Y	McMillan (1983a)	e
<i>Syringodium filiforme</i>	O	F	-	Y	N	N	McMillan (1985)	i
<i>Syringodium filiforme</i>	E	L	W	N	N	Y	McMillan (1991)	e
Hydrocharitaceae								
<i>Halophila decipiens</i>	E	L	W	Y	N	Y	McMillan (1988b)	e,k
<i>Halophila decipiens</i>	E	L	Both	N	Y	Y	McMillan (1988c)	d,e
<i>Halophila decipiens</i>	E	L	W	Y	N	Y	McMillan & Soong (1989)	e,j
<i>Halophila decipiens</i>	E	L	W	N	N	Y	McMillan (1991)	e,j
<i>Halophila decipiens</i>	E	L	W	N	N	Y	Kuo & Kirkman (1995)	e
<i>Halophila engelmanni</i>	O	F	-	Y	N	N	McMillan (1986)	i
<i>Halophila engelmanni</i>	E	Both	W	Y	N	Y	McMillan (1988a)	e,j
<i>Halophila engelmanni</i>	E	L	W	N	N	Y	Jewett-Smith & McMillan (1990)	d
<i>Halophila engelmanni</i>	E	L	W	N	N	Y	McMillan (1991)	e,j
<i>Halophila ovalis</i>	E	L	W	Y	N	Y	Kuo & Kirkman (1992)	e
<i>Halophila spinulosa</i>	O	L	Both	N	Y	Y	Birch (1981)	f,j,l
<i>Halophila tricostata</i>	E	L	W	N	N	Y	Kuo et al. (1993)	e
<i>Halophila beccarii</i>	O	F	-	Y	N	N	Zakaria et al. (1999)	i

Appendix 1 (continued)

Taxon	E/O	F/L	S/W	Seed bank	Dormancy	Germination	Source	Factors tested
Zosteraceae								
<i>Phyllospadix iwatensis</i>	E	L	W	N	N	Y	Kuo et al. (1990)	e
<i>Phyllospadix scouleri</i>	E	L	-	N	N	Y	Turner (1983)	h
<i>Phyllospadix scouleri</i>	E	L	-	N	N	Y	Turner (1985)	h
<i>Phyllospadix torreyi</i>	E	L	W	N	Y	Y	Reed et al. (1998)	e,m
<i>Zostera capensis</i>	E	L	W	N	N	Y	Edgecumbe (1980)	b,c,e,j
<i>Zostera capricorni</i>	E	L	-	N	Y	N	Murray & Larkum (1992)	g
<i>Zostera capricorni</i>	O	F	S	Y	N	N	Conacher et al. (1994a)	i
<i>Zostera capricorni</i>	E	L	W	N	N	Y	Conacher et al. (1994b)	b,c,f,l,m
<i>Zostera capricorni</i>	O	F	W	Y	N	Y	Peterken & Conacher (1997)	e
<i>Zostera capricorni</i>	E	L	W	N	N	Y	Brenchley & Probert (1998)	b,c,n
<i>Zostera japonica</i>	Both	Both	Both	Y	Y	Y	Bigley (1981)	b,c,e,j,n,o
<i>Zostera marina</i>	E	L	W	N	N	Y	Tutin (1938)	b,c,e
<i>Zostera marina</i>	O	F	S	N	N	Y	Addy (1947)	e
<i>Zostera marina</i>	E	L	W	N	N	Y	Arasaki (1950)	b,c,p
<i>Zostera marina</i>	O	-	W	N	N	Y	Taylor (1957b)	a
<i>Zostera marina</i>	Both	Both	W	N	N	Y	Phillips (1972)	c,e
<i>Zostera marina</i>	E	L	NA	N	N	Y	Hade et al. (1974)	b,c
<i>Zostera marina</i>	E	Both	Both	N	Y	Y	Hade et al. (1975a)	e,q
<i>Zostera marina</i>	E	F	S	N	N	Y	Hade et al. (1975b)	e,q
<i>Zostera marina</i>	E	F	S	N	N	Y	Hade et al. (1976)	e,q
<i>Zostera marina</i>	E	L	Both	N	N	Y	De Cock (1977)	h
<i>Zostera marina</i>	E	L	W	N	N	Y	Lamounette (1977)	b,c,e,f,g
<i>Zostera marina</i>	E	L	W	N	N	Y	Churchill & Riner (1978)	e
<i>Zostera marina</i>	E	L	S	N	N	Y	Keddy & Patriquin (1978)	b,c,e,f,g
<i>Zostera marina</i>	E	F	S	N	N	Y	Yasuie & Fukuda (1980)	e,q
<i>Zostera marina</i>	E	F	S	N	N	Y	Fukuda & Yasuie (1981)	m,p
<i>Zostera marina</i>	E	F	S	N	N	Y	Yasuie & Fukuda (1981)	i
<i>Zostera marina</i>	E	L	S	N	N	Y	Fukuda & Tsuchiya (1982)	d
<i>Zostera marina</i>	E	F	S	N	N	Y	Churchill (1983)	e
<i>Zostera marina</i>	E	L	W	N	N	Y	McMillan (1983b)	c,g
<i>Zostera marina</i>	E	F	W	N	N	Y	Orth & Moore (1983)	e,k
<i>Zostera marina</i>	E	L	W	N	N	Y	Phillips et al. (1983)	b,c,k
<i>Zostera marina</i>	E	F	S	N	N	Y	Fukuda et al. (1984)	q
<i>Zostera marina</i>	O	F	W	Y	N	N	Gates (1984)	i
<i>Zostera marina</i>	O	F	S	Y	N	Y	Robertson & Mann (1984)	e,g
<i>Zostera marina</i>	O	F	S	Y	N	Y	Bodnar (1985)	e
<i>Zostera marina</i>	E	L	S	N	N	Y	Kawasaki et al. (1985)	b
<i>Zostera marina</i>	E	L	NA	N	N	Y	Takaba (1985)	p
<i>Zostera marina</i>	E	F	S	N	N	Y	Fukuda (1987)	o
<i>Zostera marina</i>	E	F	S	N	N	Y	Fukuda & Sato (1987a)	k,q
<i>Zostera marina</i>	E	F	S	N	N	Y	Fukuda & Sato (1987b)	NA
<i>Zostera marina</i>	E	F	S	N	N	Y	Fukuda & Sato (1987c)	q
<i>Zostera marina</i>	Both	Both	Both	Y	N	Y	Hootsmans et al. (1987)	c,g,j,n
<i>Zostera marina</i>	E	L	NA	N	N	Y	Kawasaki (1987)	b
<i>Zostera marina</i>	E	L	S	N	N	Y	Kawasaki et al. (1988)	e,o
<i>Zostera marina</i>	E	L	W	N	Y	Y	Harrison (1991)	b,c,e,f,p
<i>Zostera marina</i>	E	L	Both	N	N	Y	Churchill (1992)	n
<i>Zostera marina</i>	E	L	-	N	Y	N	Murray & Larkum (1992)	g
<i>Zostera marina</i>	O	F	W	Y	N	Y	Harrison (1993)	h,i
<i>Zostera marina</i>	E	L	Both	N	N	Y	Kawasaki (1993)	b,c,n,o
<i>Zostera marina</i>	E	L	Both	N	N	Y	Moore et al. (1993)	j,n,o
<i>Zostera marina</i>	O	F	S	N	N	N	Olesen & Sand-Jensen (1994)	h
<i>Zostera marina</i>	E	F	S	N	N	Y	Ruckelshaus (1994)	k,q
<i>Zostera marina</i>	E	L	W	N	N	Y	van Lent & Verschuure (1995)	c,e
<i>Zostera marina</i>	E	Both	S	N	N	Y	Harwell & Orth (1999)	o,q
<i>Zostera marina</i>	O	F	-	Y	N	N	Santamaría-Gallegos et al. (1999)	i
<i>Zostera noltii</i>	Both	Both	Both	Y	N	Y	Hootsmans et al. (1987)	c,g,j,n
<i>Zostera noltii</i>	O	F	S	Y	N	N	Loques et al. (1988)	i
<i>Zostera noltii</i>	E	L	W	N	N	Y	Loques et al. (1990)	b,c,f,m
<i>Zostera noltii</i>	O	F	S	N	Y	N	Buia & Mazzella (1991)	e
<i>Zostera noltii</i>	O	F	W	N	N	Y	Goubin & Loques (1991)	e
<i>Zostera noltii</i>	O	F	W	Y	N	Y	Harrison (1993)	i

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