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A Synthesis of *Ruppia maritima* (Wigeongrass) Seed Ecology with Implications for Seed-based Seagrass Restoration

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ABSTRACT

Seagrasses are declining globally, increasing interest in scalable seed-based restoration. *Ruppia maritima* (wigeongrass) is a pioneer submerged aquatic plant species that occupies variable-salinity estuaries and often expands following disturbance. This review synthesizes published literature describing relevant field and laboratory observations and research to evaluate seed production, seed-bank dynamics, storage, viability, germination, and early recruitment in *R. maritima*. Studies were drawn primarily from eastern United States estuaries, with some comparisons from South America, Australia, and Asia. *Ruppia maritima* in the eastern United States, like other global *Ruppia* species, produces abundant but episodic seeds, but its seed-bank longevity, viability, and recruitment vary with habitat stability and local hydrologic regime. Germination is commonly inhibited by elevated salinity while viability is retained, and often increases, after salinity reduction, indicating osmotic control and salinity-history effects. Temperature and drying further regulate germination in population- and habitat-specific ways. For restoration, seed collection, storage, and deployment should be matched to local salinity, temperature, and hydrologic conditions, while protecting donor/source beds and recognizing that short-lived seed banks and seedling establishment may constrain recruitment.

Key words: *Ruppia*, *Ruppia maritima*, seed bank, seed germination, seed production

INTRODUCTION

Seagrasses are marine angiosperms that play a central role in coastal ecosystems (Sogin et al. 2022), providing essential services that support ecosystems of high ecological and economic importance. These include supporting fisheries and coastal communities by providing habitat and nursery areas for juveniles of commercially important species (Beck et al. 2001; Heck et al. 2003; Nordlund et al. 2016; Lefcheck et al. 2019), protecting shorelines through seabed stabilization with their root-rhizome systems (Potouroglou et al. 2017) and slowing water movement (Infantes et al. 2022), and improving water quality by trapping suspended particles (Infantes et al. 2022) and taking up excess nutrients (Burkholder et al. 2007). Seagrasses also play a central role in key biogeochemical processes by storing carbon in their biomass and releasing dissolved organic carbon that supports microbial life (Sogin et al. 2022).

Despite their importance, coastal meadows dominated by seagrasses are experiencing accelerating global decline (Orth et al. 2006; Waycott et al. 2009; Dunic et al. 2021; Unsworth et al. 2023). This decline is driven largely by human coastal pressures such as storm- and wastewater management practices (LaPointe and Matzie 1996), coastal development and channel dredging (Holon et al. 2015; Benham et al. 2016), and ecosystem shifts due to increased CO2 (Tang and Hadibarata 2022).

Although seagrasses typically dominate coastal meadows, seagrasses often grow in mixed beds of submerged aquatic vegetation (SAV) that includes diverse marine and estuarine angiosperms

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(Moore 2009). In shallow lagoons and estuaries of the eastern United States, *Ruppia* can co-occur with seagrasses in the genera *Zostera*, *Halodule*, and/or *Thalassia* as well as other types of SAV associated with low-salinity brackish conditions. Within these communities, *Ruppia* species are especially important in variable-salinity environments, as they can withstand salinities ranging from fresh to hypersaline, often inhabiting areas too saline, fresh, or unstable for other marine macrophytes (Verhoeven 1980), and providing a natural bridge between marine seagrass meadows and other coastal plant communities.

Ruppia maritima

Ruppia, the only genus within the family Ruppiaceae, occupies habitats that range from freshwater to hypersaline conditions and often persists in environments unsuitable for other submerged aquatic vegetation (Verhoeven 1979, 1980; Les et al. 1997; Mannino et al. 2015; Rasmusson et al. 2021). Members of the genus share many ecological characteristics, including flexible life-history strategies, and an ability to colonize dynamic or ephemeral habitats. However, recent molecular studies have shown that *Ruppia* is considerably more diverse than previously recognized. In the mid-20th century, the genus was treated largely as the *R. maritima* complex. Approximately 12 species are now broadly accepted, with additional taxa continuing to be proposed (den Hartog et al. 2016; Triest et al. 2018; Zou et al. 2023; POWO 2026; Table 1). Because morphology is highly plastic and hybridization is common, species boundaries remain difficult to distinguish using morphology alone (den Hartog and Kuo 2006; Mannino et al. 2015). As a result, ecological studies across the genus provide valuable context for understanding shared adaptations to dynamic coastal habitats.

Ruppia maritima L. (wigeongrass) functions as an important pioneer species for its ability to thrive in disturbed or early successional habitats (Cho et al. 2009). In estuaries, which are characterized by frequent disturbances associated with natural fluctuations in freshwater and temperature and increasing human pressures, *R. maritima* has been observed to increase relative to traditionally dominant seagrass species. Across North America, these estuaries include those associated with the Chesapeake Bay (Maryland and Virginia), Lake Pontchartrain (Louisiana), Grand Bay National Estuarine Research Reserve (Mississippi), and San Diego Bay (California; Johnson et al. 2003; Cho and Poirrier 2005a; Cho et al. 2009; Hensel et al. 2023).

Ruppia maritima can reproduce both asexually through rhizomes and sexually. It produces a high number of seeds, up to 20-40,000 seeds/m^2 (Cho and Biber 2010), making it a strong candidate for low-cost, scalable restoration in dynamic estuarine environments. Because *R. maritima* occupies habitats and latitudes that vary widely, there are notable differences in morphology and life-history timing. For instance, *R. maritima* inhabiting temperate climates reproduces annually in the summer (Bigley and Harrison 1986), while some populations found in subtropical climates, like those of the southeastern United States, flower twice annually in the spring and fall (Dunton 1990; Cho and Poirrier 2005b). Beds of *R. maritima* are known to be more ephemeral than other seagrasses. Although there is limited research on seed dispersal and colonization, this is thought to take place via accumulated seed banks, endozoochory, and hydrochory, with successful establishment being highly influenced by environmental variables (Kantrud 1991; Charalambidou et al. 2003; Strazisar et al. 2016). This makes seed-bank ecology especially important for understanding persistence and restoration potential in this species.

Importance of *Ruppia maritima* to Seagrass Restoration

As seagrass meadows are declining, active restoration is now a crucial part of coastal management and climate adaptation work (Waycott et al. 2009; van Katwijk et al. 2016). Most restoration projects take one of two basic approaches: transfer of adult shoots or sods from a healthy meadow into a damaged area, or planting seeds to initiate a new meadow (van Katwijk et al. 2016; Tan et al. 2023). Shoot- or sod-based transplanting can give reasonably quick aboveground cover and often seems successful in short-term assessments, but it also depends on having donor meadows that are healthy enough from which to harvest. It is also labor-intensive and expensive at larger scales (Tan et al. 2023; Watson et al. 2023). In contrast, seed-based methods are attractive because they can, in

Table 1. Currently accepted *Ruppia* species and their geographic distribution, according to the Royal Botanic Gardens (POWO 2026).

Species	N. America	Caribbean	C. America	S. America	Europe	Asia	Africa	Australia	New Zealand
R. maritima L.	X	X	X	X	X	X	X	X	
R. cirrhosa (Petagna) Grande (*R. spiralis* L.)	X			X	X	X	X		
R. bicarpa Yu Ito & Muasya							X		
R. brevipedunculata Shuo Yu & den Hartog						X			
R. didyma Sw. ex Wikstr.	X	X	X						
R. drepanensis Tineo					X		X		
R. filifolia (Phil.) Skottsb.				X					
R. megacarpa R. Mason						X		X	X
R. mongolica Y. Zou & X.W. Xu						X			
R. polycarpa R.Mason								X	X
R. sinensis Shuo Yu & den Hartog						X			
R. tuberosa J.S.Davis & Toml.								X	

principle, be done at much larger spatial scales. Seed-based work also has the potential to transfer much more genetic diversity into a restored site, rather than cloning a small number of genotypes from a donor patch through shoot transfer. However, restoration using seeds is not straightforward: many seeds never reach the sediment, are washed away, or are consumed before they can successfully establish (Unsworth et al. 2023). Additionally, seed germination is often low, and seedlings can be buried by mobile sediment or torn out by waves (Tan et al. 2023; Unsworth et al. 2023).

During the past few decades, attention has focused on improving protocols for the use of *Ruppia maritima* seeds in restoration (Cho and Sanders 2009; Ailstock et al. 2010a; Gersten et al. 2026; Hensel et al. 2024) given its high ecological importance. Seed collection from mature *Ruppia* beds has proven highly effective, with fresh seeds showing germination rates exceeding 95% under controlled conditions (Cho and Sanders 2009). However, long-term storage and delayed germination present more complex challenges. While *R. maritima* does not appear to exhibit organic dormancy (Cho and Sanders 2009), many seeds display delayed germination following winter (Cho et al. 2024b), suggesting the influence of environmentally induced dormancy or osmotic-inhibition mechanisms.

Various studies have tested combinations of cold stratification, dry storage, wet storage, scarification, and salinity treatments to overcome delayed germination or environmentally induced inhibition (Cho and Sanders 2009; White 2014; Cho et al. 2024a, b). For example, dry stratification has been shown to accelerate germination, but it may reduce overall seed viability (Cho and Sanders 2009). These tradeoffs underscore the need for habitat-specific protocols that balance rapid germination, seed longevity, and successful field establishment. The purpose of this synthesis paper is to document life cycles and restoration-relevant seed ecology of *Ruppia maritima* across habitat types (ephemeral, permanent, impounded, open estuaries, rivers, and manmade ponds), including reproductive seasonality, seed production, seed-bank persistence, viability, and germination, with a special focus on eastern United States populations.

METHODS

We reviewed 58 available publications to identify knowledge in both the *Ruppia* genus and *R. maritima* of seed production, seed bank dynamics, viability, and germination across a range of habitat types and regions. Studies of other *Ruppia* species were included when they provided insight into ecological or life-history traits shared across the genus. Searches were conducted initially through Google Scholar, using distinct and combined searches of the keywords: *Ruppia*, *Ruppia maritima*, seed storage, seed bank, germination, viability, salinity, and temperature. Ultimately, 16 peer-reviewed journal articles and three published datasets were compiled for synthesis of findings.

The review focused primarily on papers and datasets published between 2000 and 2026, to focus on the most up-to-date species classifications; however, one study from 1988 was included because it provided unique insight into the differences of two *Ruppia maritima* populations that are geographically proximate but occupy distinct habitat types. Older studies were included for the provision of important background on the life history, seed production, or taxonomy of *Ruppia*. Because the objective of this paper was to identify broad trends and recurring patterns in the literature rather than quantitatively evaluate response metrics, the review did not follow a formal systematic review protocol. Studies were retained when they reported primary data on *Ruppia* seed production, seed bank density, seed viability, germination, storage, or seedling establishment. Studies that tested the effects of temperature, salinity, and seed storage were also included since these factors have been known to affect seed behavior in *Ruppia* species. Primary literature, reports, and reviews that reported general seagrass background, taxonomy, or restoration context were cited for framing but were not counted as primary seed-ecology records.

Studies from a wide range of geographic locations were included in our review. These locations included numerous temperate and subtropical open estuaries, shallow bays, lagoons, rivers, salt marsh ponds, impounded wetlands, and man-made canals, including numerous large estuaries in the southeastern United States [Florida Bay (Florida), Indian River Lagoon (Florida), Lake Pontchartrain (Louisiana), Grand Bay National Estuarine Research Reserve (Mississippi), and Chesapeake Bay

(Maryland and Virginia)], as well as systems in South America, Australia, and Asia (Table 2). The hydrology of these habitats represent differences in salinity, water depth, and the stability of environmental conditions through time. Studies were grouped by habitat type to examine how differences in habitat types affected seed ecology, including seed-bank density, viability, and germination rates. We also considered if *Ruppia* occurred alone or as part of a mixed SAV community in our synthesis. Collectively, these considerations allowed for comparisons of reproductive strategies and seed bank importance across different abiotic and biotic environmental conditions.

In addition to peer-reviewed publications, publicly available datasets published in Zenodo (**https://zenodo.org**; see Cho 2020; 2025a, b, c) that are associated with published studies were consulted where they provided information on reproductive timing, biomass, seed production, seed-bank density, seed viability, or germination. These datasets were used as published sources of ecological information and were not reanalyzed or treated as new experimental data (Cho 2020, 2025a, b, c; Cho et al. 2024a).

RESULTS AND DISCUSSION

Reproductive Output of North American *Ruppia maritima*

In situ studies on *Ruppia maritima* revealed that this species exhibits a high reproductive output across its range, though the size, viability, and persistence of the seed bank vary widely by geographical region and habitat type. While the timing and magnitude of reproduction differ geographically, populations in U.S. Atlantic and Gulf Coast estuaries are characterized by relatively large seed densities (Table 3). Seed banks are also present in all populations reviewed here, but their size, viability, and persistence differ between habitat types (Table 3).

Reproductive timing and output generally exhibit a broad spring to summer pattern, which varies between site and year. In Lake Pontchartrain (Louisiana), *Ruppia maritima* flowered and produced copious seeds from May to October, with two distinct peaks and germination occurring the following winter (Cho and Poirrier 2005b; Cho 2025c; Table 3). In contrast, sites at GBNERR (Mississippi), located about 160 km east of Lake Pontchartrain, reproduced over a shorter period (April–August), maintained smaller seed banks, and lacked a second reproductive cycle later in the year (Cho et al. 2017; Cho 2025a, b; Table 3). This difference is likely due to the competition with other SAVs, as the early spring growth of *R. maritima* was followed by the later growth of co-occurring seagrass *Halodule wrightii* Asch. in the fall (Cho et al. 2017). Similarly, in water-level controlled mosquito control impoundments in eastern Florida, *R. maritima* appears to complete its annual life cycle by early spring, before seasonal increases in water depth, temperature, and turbidity limited growth (Cho et al. 2024b). Overall, the timing and magnitude of seed production varied even among survey sites within each estuary, indicating that while an established *R. maritima* population may follow a predictable seasonal cycle, local biotic and abiotic conditions influence exact timing and persistence.

Field evidence from Florida Bay further emphasizes that, in variable estuarine environments, population persistence could rely heavily on large annual reproductive events. Strazisar et al. (2016) found that in a fully formed meadow during the reproductive season, only ~20% of seeds within the meadow were intact, and of those intact seeds, <25% were viable. Despite the low proportional seed presence and viability at peak biomass, total seed densities still produced thousands of viable seeds to replenish the seedbank, after the meadow had senesced, further supporting the fact that *Ruppia maritima* relies on high annual output to compensate for low viability rates and periods of stressful environmental conditions. Comparable patterns were observed in other *Ruppia* species. For example, Gu et al. (2021) reported that an annual *R. sinensis* population in an ephemeral habitat in China maintained a significantly larger seed bank than a nearby perennial population in a more stable habitat (Table 3), consistent with greater allocation to sexual reproduction under stressful conditions. During an unexpected drought, the permanent waterbody containing the perennial population dried up; when water returned, the annual population germinated immediately, whereas the perennial population failed to recover. While this contrast may reflect differences in historical exposure to drought cycles, the ephemeral site also had higher total nitrogen in the soil than the perennial site, a key nutrient for seagrass growth (Gu et al. 2021).

Table 2. Summary of habitat conditions by latitude for *Ruppia* studies included in this review. CBP = Chesapeake Bay Program

Species	Location	Approx. Latitude	Salinity Range (ppt)	Temperature Range (°C)	Habitat Type
R. maritima	Chesapeake Bay Maryland, USA	37°N	<0.5-30 (CBP n.d.)	1.1-28.8 (CBP n.d.)	Open Estuary
R. sinensis	Yellow River Delta North China	37°N	<0.5-30 (Yu et al. 2023)	11.7–12.6 (annual average) (Tian et al. 2016)	Delta
R. maritima	Lake Pontchartrain Louisiana, USA	30°N	<1-8 (Cho and Sanders 2009)	12–28 (USGS 2002)	Restricted Estuary
R. maritima	Grand Bay Mississippi, USA	30°N	0-30+ (GBNERR 2023)	1.8-36.7 (GBNERR 2023)	Open Estuary
R. maritima	Indian River Lagoon Florida, USA	28°N	1.7–33.7 (Cho et al. 2024b)	13.3–32.4 (Cho et al. 2024b)	Lagoonal Estuary Impoundment System
R. maritima	Florida Bay Florida, USA	25°N	<10–40 (Kelble et al. 2007)	23–31.5 (Glibert et al. 2009)	Open Estuary
R. maritima	Patos Lagoon Brazil	32°S	0-35 (Haraguchi et al. 2015)	8–30 (Haraguchi et al. 2015)	Lagoonal estuary
R. tuberosam *R. megacarpa*	The Coorong South Australia	35°S	0–190 (Leterme et al. 2015)	12–32 (Leterme et al. 2015)	Lagoonal estuary

Table 3. Published reports of *in situ* reproductive timing and population metrics for *Ruppia* species across geographic locations.

Publication	Species	Location Reproduction	Timing of	Shoot Density	Seed Density	Seed Bank Density	Viability (No Stratification)
Ailstock et al. (2010a)	*Ruppia maritima*	Chesapeake Bay Maryland, USA	July–August	–	16,751–17,230 seeds/kg	–	–
Cho and Poirrier (2005b)	*Ruppia maritima*	Lake Pontchartrain Louisiana, USA	May–June September–October	48,355 m^2	–	–	–
Cho and Sanders (2009)	*Ruppia maritima*	Lake Pontchartrain Louisiana, USA	June–September	–	–	–	immature (94.7%) mature seeds (91.7%)
Cho et al. (2017)	*Ruppia maritima*	GBNERR Mississippi, USA	May–July			0–4160 seeds per m^2	–
Cho et al. (2024)	*Ruppia maritima*	Indian River Lagoon, Florida, USA (impoundments)	April–May		1,526 seeds/L	346 seeds/L	66% (Shoot) 56% (Seed Bank)
Gu et al. (2021)	*Ruppia sinensis*	Yellow River Delta China (annual site)	October	220–439 g/m^2 (biomass)	39,278–13,470 m2	–	–
Gu et al. (2021)	*Ruppia sinensis*	Yellow River Delta China (perennial site)	October	151-282 g/m^2 (biomass)	4,836–26,362 m^{-2}	–	–
Strasizar et al. (2016)	*Ruppia maritima*	Florida Bay (Long Lake) Florida, USA	March–August	2650 m^{-2}	–	2800 m^{-2}	85%

Seedling Survival and Early Life History

Nutrient availability also seems important to early life history of *Ruppia maritima*. In Florida Bay, a phosphorus-limited system with relatively high nitrogen availability, phosphorus-inoculated plots exhibited significantly higher seedling survival compared to natural sediments across multiple plot comparisons (Fourqurean et al. 1992; Strazisar et al. 2021). In variable systems, seedling establishment may be rapid yet still yield limited recruitment, suggesting a narrow window of favorable conditions for both germination and establishment (Strazisar et al. 2016). Consistent with reproductive demands, the molar N:P ratio was significantly lower in reproductive than in short shoots, indicating higher phosphorus requirements for reproductive shoot production (Strazisar et al. 2021).

Growth to Maturity and Adult Survival

Across estuaries of the southeastern U.S. Gulf Coast, *Ruppia maritima* typically shows rapid spring growth, peak biomass in summer, and dieback in late fall and winter. In Lake Pontchartrain, biomass began increasing in March and May, with two distinct peaks in summer and fall, and then senesced between December and February (Cho and Poirrier 2005b; Cho 2025c; Table 3). A similar seasonal pattern was observed at GBNERR, where *R. maritima* was absent from November to February, followed by rapid growth in March–April and peak density in June–July (Cho and Poirrier 2005a, b; Cho et al. 2017, Cho 2025a, b; Table 3).

In Florida Bay, adult survival did not differ significantly between natural and phosphorus-enriched sediments (Strazisar et al. 2021). However, adult growth and shoot production were strongly dependent on salinity stability and light availability. Specifically, the highest shoot densities occurred during the dry season under stable salinities and high light (~14,000 lumens m^{-2}; Strazisar et al. 2021). Sites with stable salinity and high light exposure experienced ~90% genet survival and vegetative shoot densities approximately twice those at other sites. In contrast, shoot production was minimal or absent under hypersaline conditions (>35 psu) and during the wet season when light availability declined (to ~7,000 lumens m^{-2}). Competition with co-occurring macrophytes also constrained performance; the presence of the macroalga *Chara hornemannii* Wallman reduced *Ruppia maritima* vegetative shoot production by 24–75% across sites, regardless of its density (Strazisar et al. 2021). Consistent with these results, Strazisar et al. (2014) reported that moderate salinity fluctuations (e.g., <5 in <72 h, <10 in 96 h) were positively correlated with the ability to transition from seed to reproductive adults, suggesting that while extreme salinity variability can hinder survival and transitions, moderate fluctuations may not inhibit life history progression and may contribute to dominance in transitional habitats

Effects of Salinity on Seed Germination

Salinity appears to be a primary determinant of germination in *Ruppia maritima*, with germination generally suppressed at high salinities and enhanced under low-salinity conditions. Across eastern U.S. populations, germination most frequently occurs in the salinity range 0–10 ppt, although seeds can remain viable across broader salinity ranges (Kahn and Durako 2005; Ailstock et al. 2010a; Strazisar et al. 2013). Similarly to seedling survival, several studies indicate that elevated salinity may function as a temporary inhibitor of germination rather than a lethal stressor, with germination increasing rapidly when salinity subsequently declines, highlighting the role of both absolute salinity and salinity history (Ailstock et al. 2010a; Strazisar et al. 2013).

Multiple studies conducted in the eastern United States suggest that prior habitat salinity could enhance germination of *Ruppia maritima* after a subsequent salinity reduction (i.e., a priming effect). In Florida Bay, seeds incubated at salinities greater than 25 psu exhibited the greatest germination rates when later transferred to freshwater (Strazisar et al. 2013; Table 4). Similarly, seeds from Chesapeake Bay exhibited the greatest germination when seeds experienced saline priming, with germination rates approximately twice as great when warmer induction was paired with transfer to freshwater than when salinity was maintained (Ailstock et al. 2010a; Table 4). However, habitat context is an important consideration, as studies from both populations also demonstrated

Table 4. Published reports of *ex situ* seed response to storage, temperature, and salinity for *Ruppia maritima*.

Location	Study	Storage/Pretreatment	Experimental Factors	Germination Response	Key Interpretation
Florida Bay, USA	Kahn & Durako 2005	Cold stratification (2 weeks at 6–10 °C) required	Salinity 0–28	Germination only at low salinity (0–10); none >28	Low salinity and cold exposure required for germination
Florida Bay, USA	Strazisar et al. 2013	14 days cold stratification at 6°C	Salinity 0–45; temperatures 25 vs 30°C; sediment	77% of germinated seeds at salinity <5; higher germination at 30°C; ~1% germination in sediment	Salinity was dominant filter; temperature accelerated germination under favorable salinity
		Transfer from high salinity to freshwater	>25 to 0 salinity transfer	Germination reached ~80% after transfer	High salinity may induce reversible dormancy rather than mortality
Chesapeake Bay, USA	Ailstock et al. 2010a	9 months storage at 4°C	Salinity 0–30; induction temperatures 5–27°C	Germination nearly doubled from 5 to 15°C; 30 → 0 treatment highest (65%)	Temperature regulated germination speed; salinity reduction stimulated emergence
Chesapeake Bay, USA	Ailstock et al. 2010b	Burial depth experiment	Sediment depth	Germination declined with depth (45% surface → 5% at 2 cm)	Sediment burial suppresses germination
Indian River Lagoon, USA	White 2014; Cho et al. 2024a,b	Control, cold storage, or dry stratification	Drying vs cold storage (1.5–3°C)	Dry-stratified seeds had highest germination (44%) despite lower viability	Drying may act as dormancy-breaking cue in variable habitats
Lake Pontchartrain, USA	Cho & Sanders 2009	10 months dry storage	Salinity treatments after drying	Viability reduced to 35.7%; germination 18–30%	Drying reduced viability but not germination capacity
Patos Lagoon, Brazil	Koch & Seeliger 1988	Dry, moist, or cold storage	Temperatures 15–30°C crossed with salinity 0–40	Warm temperatures and low salinity increased germination; dry stratification doubled germination in ephemeral population	Responses varied ` with habitat hydrology
Virginia, USA	Gersten et al. 2026	Cold storage over 2 years	Storage duration	Peak emergence after 5–7 months; decline after prolonged storage	Cold stratification alleviates dormancy, but prolonged storage may induce secondary dormancy

sediment burial decreased germination rates, regardless of salinity treatment (Ailstock et al. 2010b; Strazisar et al. 2013).

Evidence from a South American *Ruppia maritima* population suggests these responses are not restricted to North American populations. Specifically, Koch and Seeliger (1988) demonstrated habitat-linked variation in germination ecology for *R. maritima* in southern Brazil's Patos Lagoon where source habitats spanned environments with varying hydrological cycles (Table 2). Although germination responses varied between habitats and pretreatment regimes, seeds from both populations germinated most successfully under reduced salinities. The ephemeral saltmarsh population also exhibited approximately twice as much germination following dry stratification compared with untreated controls, suggesting that local habitat conditions can modify dormancy-breaking requirements while maintaining the general response to reduced salinity, reinforcing the consistent association between reduced salinity and increased germination (Koch and Seeliger 1988).

Germination responses of other *Ruppia* species in response to salinity and temperature were assessed by studies in the Coorong in Australia (*R. tuberosa*, *R. megacarpa*) and the Yellow River Delta in China (*R. sinensis*; Kim et al. 2013; Gu et al. 2018; Table 2). Although these habitats differ substantially from one another, as well as from the habitats in the America's reviewed for *R. maritima,* a similar trend in salinity requirements was observed. In the Australian study, salinity history altered germination outcomes. Seeds pre-incubated under hypersaline conditions (105–180 g/L) subsequently germinated at rates of 94% when transferred to a salinity of 30 g/L, compared to 22% for seeds placed directly into salinity 30 g/L within saline priming (Kim et al. 2013). Comparable salinity-history effects were observed in the Chinese population, where seeds exposed to higher salinities (40–50 psu) exhibited enhanced germination after transfer to optimal conditions (5 psu, 30°C; Gu et al. 2018). These studies suggest that salinity functions less as a direct constraint on seed viability and more as an environmental cue to regulate the timing of germination to be synchronized with more favorable periods for seedling establishment.

Collectively, these studies demonstrate a consistent pattern in which elevated salinity suppresses germination while maintaining seed viability, followed by rapid or enhanced germination upon salinity reduction. This response, often expressed as osmotic inhibition or environmentally induced (secondary) dormancy, has been observed in subtropical southeastern U.S. estuaries, temperate systems in the eastern United States, and additional regions and species within the genus (Strazisar et al. 2013; Kahn and Durako 2005; Ailstock et al. 2010a; Koch and Seeliger 1988; Kim et al. 2013; Gu et al. 2018). Together, these studies suggest that high saline conditions act as a temporary inhibitor to germination that allows seeds to remain viable and germinate rapidly under favorable (lower salinity) conditions.

Effects of Temperature on Germination

Temperature plays an important role in regulating germination timing and success in *Ruppia maritima*, often interacting with salinity to determine if germination occurs rapidly, is delayed, or is suppressed. Across laboratory and field studies, germination generally increases under warmer temperatures, although seeds remain viable across a wide thermal range and may require or benefit from prior cold exposure depending on population and habitat context (Kahn and Durako 2005; Ailstock et al. 2010a; Strazisar et al. 2013).

Among eastern U.S. populations of *Ruppia maritima*, germination generally increases with warming from low to moderate temperatures, with temperature strongly influencing both germination magnitude and speed. In Florida Bay, cold-stratified seeds exhibited greater germination at 30°C than at 25°C (Strazisar et al. 2013; Table 4). Similarly, in Chesapeake Bay experiments, germination nearly doubled as temperatures rose from 5 to 15°C, and warmer treatments (21–27°C) produced rapid germination within the first week of incubation (Ailstock et al. 2010a; Table 4).

While warmer temperatures generally promote germination, multiple studies also indicate that low-temperature stratification can increase germination potential rather than suppress it, underscoring population-specific dormancy dynamics. In Florida Bay, seeds required an initial period of cold

stratification, indicating that cold exposure may be necessary for germination in this population (Kahn and Durako 2005; Table 4). Likewise, seeds from a Virginia population exhibited significantly greater germination after at least two months of cold storage, with maximum emergence occurring after five to seven months while viability remained high throughout two years of storage (Gersten et al. 2026; Table 4). This study further suggested that prolonged storage may induce secondary dormancy, as older seed cohorts remained viable but exhibited reduced emergence.

In contrast, results from the Indian River Lagoon system in Florida suggest cold exposure is not universally influential to *Ruppia maritima* germination. In this study, seeds that were cold stratified did not differ significantly from a control group of non-stratified seeds, although storage did reduce seed viability, suggesting that preconditioning may remain important for long-term storage (White 2014; Cho et al. 2024a, b; Table 4). These contrasting responses indicate that while cold stratification commonly promotes germination, dormancy-breaking requirements vary among populations and other local habitat characteristics and adaptations should be considered.

The previously discussed studies from Australia and China also examined the influence of temperature on *Ruppia* seed germination across three species (*R. sinensis, R. megacarpa, R. tuberosa;* Kim et al. 2013; Gu et al. 2018). A similar trend emerged in which temperature appeared to regulate germination timing alongside salinity, light, and sediment treatments, rather than act as a sole driver of germination. For *R. megacarpa* and *R. tuberosa*, day–night thermal cycling (18°C light/10°C dark) was applied across multiple salinity regimes, and germination timing varied with both salinity and sediment conditions. Similarly, in *R. sinensis*, Gu et al. (2018) documented two temperature-related germination peaks: one at warm temperatures (30°C) under low salinity (5 psu), and a second at low temperature (5°C) under high salinity (>20 psu). Together, these findings illustrate how temperature may regulate the timing of germination, while salinity determines whether germination is expressed or deferred (Gu et al. 2018).

Across regions and species, these results demonstrate that temperature does not function as a strict barrier to germination in *Ruppia*. Instead, it regulates the timing and magnitude of germination events. Seeds can remain viable under prolonged cold exposure and exhibit enhanced germination when temperatures increase, particularly when combined with favorable salinity conditions (e.g., Kahn and Durako 2005; Ailstock et al. 2010a; Strazisar et al. 2013 Gu et al. 2018). This temperature-mediated control of germination has been observed in subtropical southeastern U.S. estuaries, temperate systems of the eastern United States, and northern China, indicating that flexible thermal responses are a fundamental component of *Ruppia* seed ecology (Kahn and Durako 2005; Ailstock et al. 2010a; Strazisar et al. 2013; Gu et al. 2018; Gersten et al. 2026).

Effects of Dry Storage on Germination

Dry storage is a cost- and space-efficient method of long-term seed storage for large-scale restoration, but evidence for the role of drying in *Ruppia* varies across regions and habitat types. In some systems, drying delays germination but does not prevent germination once seeds are returned to water, although it may reduce viability and/or depress germination rates depending on the population and drying duration. Overall, the direction and magnitude of drying effects appear closely linked to local hydrologic regime, particularly whether habitats are persistently submerged versus periodically exposed.

Evidence from U.S. Gulf Coast systems indicate that prolonged drying can reduce seed viability of *Ruppia maritima*, but that germination may still occur after rehydration. For example, in Lake Pontchartrain populations, Cho and Sanders (2009) reported that seeds dried for 10 months retained the ability to germinate but viability substantially decreased in comparison to the fresh seeds (Table 4). In contrast, populations from more hydrologically variable environments show patterns consistent with drying acting as a germination cue, even when some viability is lost. In the backwater mosquito impoundments of the Indian River Lagoon, Florida, dry-stratified seeds had lower viability than the control but displayed higher germination overall when compared to cold-stratified or non-stratified groups (White 2014; Cho et al. 2024b).

Similarly, Koch and Seeliger (1988) found that dry stratification approximately doubled germination in *Ruppia maritima* from an ephemeral saltmarsh in southern Brazil, whereas seeds from a nearby permanent estuary showed little response to drying. These studies suggest that, in systems with periodic drawdowns or sediment exposure, drying may function as a dormancy-breaking or germination-triggering signal, trading reduced viability for increased germination expression among surviving seeds (White 2014; Cho et al. 2024b).

In summary, the studies included in this review indicate that seed responses to drying are linked to local hydrologic regimes. However, the evidence base for drying responses is smaller than that for salinity and temperature, so these patterns should be interpreted as population-specific and hypothesis-generating rather than universal. Populations from permanently submerged environments tend to show reduced viability and/or germination following desiccation, whereas populations from ephemeral or drawdown-prone systems may exhibit enhanced germination after dry stratification (Koch and Seeliger 1988; Cho and Sanders 2009; White 2014; Cho et al. 2024b). This pattern suggests that tolerance to drying stress and environmentally mediated dormancy in *Ruppia* seeds may be locally adapted to the environmental conditions experienced by parent plants and their seed banks.

CONCLUSION AND IMPLEMENTATION

Collectively, our literature synthesis and field and laboratory observations indicate that seed-based persistence and restoration potential in *Ruppia maritima* are governed by a tightly coupled set of life-history processes: prolific but episodic seed production sustains seed banks that buffer seasonal senescence and disturbance, while recruitment success is frequently constrained after germination by seedling establishment under fluctuating estuarine conditions. Across systems, salinity emerges as the dominant regulator of germination expression. In particular, high salinity commonly suppresses or delays germination while maintaining viability, and germination often increases rapidly following salinity reduction, consistent with osmotic inhibition or secondary dormancy rather than irreversible loss of viability.

Temperature primarily modulates the timing and rate of germination and can interact with salinity to shift when germination is expressed. Cold exposure may be necessary or beneficial in some populations but is not universally required, suggesting strong population- and habitat-specific dormancy dynamics. Drying further shows context-dependent effects. While prolonged desiccation can reduce viability in persistently submerged systems, dry stratification may act as a germination cue in drawdown-prone or ephemeral habitats, suggesting local adaptation of stress tolerance and dormancy regulation to hydrologic regime.

Results from a recent study of *Ruppia maritima* seed-based restoration further highlight the need to understand place-based hydrodynamic cycles and local population requirements. Specifically, Hensel et al. (2024) experienced the greatest seed-based restoration success when untreated seeds were deployed in the fall to undergo their natural freeze-thaw cycle. These findings are consistent with previous research showing that cold exposure or other seasonal preconditioning can release dormancy in some populations. However, as reflected across the studies reviewed here, environmentally induced dormancy is not consistent across habitat types and populations. Environmentally mediated dormancy in *Ruppia* therefore functions not simply as delayed germination, but as a habitat-linked mechanism that can preserve viability during unfavorable periods and promote emergence when local salinity, temperature, and hydrologic conditions become favorable.

Given the global decline in seagrass coverage, *Ruppia* is a recommended SAV for restoration due to its ability to colonize disturbed coastal habitats. Its functionality as an early-successional species that stabilizes bare areas and supports the recovery of coastal ecosystems is invaluable during this period of anthropogenic driven stress and climate uncertainty. From a restoration perspective, these findings support the view that *R. maritima* seeds can function as a "playing-it-safe" propagule pool in variable estuaries, with salinity history and salinity stability shaping both germination pulses and subsequent survival.

Our findings emphasize effective seed-based restoration strategies should be matched to local habitat regimes by (i) leveraging low-salinity windows and/or controlled salinity reductions to induce germination while preserving viability, (ii) using temperature and preconditioning (cold exposure and/or drying, where appropriate) in a population-specific manner, (iii) harvesting seeds in ways that do not impair local donor/source beds that may themselves depend on recurrent seed production, and (iv) recognizing that recruitment bottlenecks may occur at the seedling stage under rapid salinity pulses, low light, or nutrient limitation despite high seed production and germination potential. Overall, the evidence suggests that germination cues in *Ruppia* operate both as a locally tuned environmental filter and as a dormancy mechanism that preserves viability during stressful periods, enabling rapid population re-establishment and enhancing ecosystem resilience when salinity, temperature, and hydrologic conditions become favorable. This dual role aligns with broader ecological theory in which dormancy buffers populations against environmental unpredictability while maintaining rapid colonization capacity following disturbance.

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