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Effects of seed burial depth on restoration success of wild-sown and nursery-propagated *Thalassia hemprichii* seedlings

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ABSTRACT

Seed-based restoration offers a non-destructive approach to restoring threatened seagrass meadows. Here, we explore the use of *Thalassia hemprichii* seeds and seedlings for restoration by examining the impact of seed burial depths in the aquarium and in the field, and by assessing the benefits of a nursery grow-out period prior to transplantation.

In the aquarium, seeds buried at 0 cm and 1 cm had the highest seedling emergence and survival (100% and 98.7%, respectively), which declined with increased burial depth (2.5 cm: 74%, 4 cm: 23.9%). In the field, seeds buried to 1 cm had the highest survival and seedling emergence (26%), double the seedling survival at 0 cm burial and nine-fold higher than seeds buried to 4 cm. Following a six-month nursery grow-out, 52% of transplanted seedlings survived after 3-months in the field, compared with 11% survival of seeds from the same collection period, but planted directly in the field at the optimum field burial depth (1 cm).

A comparison of effort across the restoration approaches in this study showed sowing seeds directly into the field to a depth of 1 cm provided the best trade-off between planting and propagation effort and subsequent survival at our field site. Nursery propagation and subsequent transplantation required the most effort, cost, and expertise, but produced the highest returns per seed, which may be beneficial when seed stock or the planting window is constrained.

These results demonstrate that small changes in planting technique for *T. hemprichii* can have large impacts on early-stage survival, a key bottleneck in seed-based seagrass restoration, and highlight the need to evaluate trade-offs between yield and effort on a project-by-project basis.

1. Introduction

Seagrass meadows provide a suite of ecosystem services that support ecological, economic, and social well-being around the world (Cullen-Unsworth et al., 2014; Unsworth et al., 2019). Globally, seagrass extent is declining, which has largely been attributed to poor water quality, coastal development, and the impacts of climate change (Buckee et al., 2021; Dunic et al., 2021). Efforts to restore seagrass habitats have accelerated since the 1970's using a variety of approaches that have included passive methods, such as management of degradation sources, as well as active restoration, including sowing of seeds and transplanting mature plants (Uku et al., 2021; Unsworth and Rees, 2025; van Katwijk et al., 2016).

Thalassia hemprichii is a persistent seagrass species occurring across reef tops, lagoons and adjacent to coasts spanning the tropical Indo-Pacific including the Great Barrier Reef (Kilminster et al., 2015). It supports culturally significant megaherbivores such as green sea turtles (*Chelonia mydas*) and dugongs (*Dugong dugon)* (Cullen-Unsworth et al., 2014) and it provides fish habitat and coastal protection (Unsworth et al., 2019). Losses of *T. hemprichii* have been attributed to high grazing pressure from green sea turtles, thermally induced stress from increased temperatures, and physical disturbance from cyclones (Buckee et al., 2021; Saewong et al., 2024). Previous restoration trials of *T. hemprichii* have focused on the movement of adult plants as fragments or sods, which tend to have high survival rates compared to temperate species (Liu et al., 2023; Thangaradjou and Kannan, 2008; Uku et al., 2021).

Thalassia hemprichii produces large fruits at the base of the shoot that

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dehisce to expose 2 – 4 large seeds (<15 mm), which have no hard seed coat or dormancy period (Fig. 2) (Kuo et al., 1991; Sherman et al., 2018). These fruits can be easily collected by hand when sufficient knowledge of the fruiting season is available, and the lack of a dormancy period enables the selection of germinated seeds (Soong et al., 2013; Tongkok et al., 2017). These traits suggest *T. hemprichii* may be a good candidate for seed-based restoration, yet there has been little research on seed ecology or the use of seeds for restoration for *T. hemprichii*.

Seed-based restoration offers several advantages over transplantation of mature plants (Kendrick et al., 2025). Seed collection has less impact on wild donor stock, making it preferable when donor stock is limited or for obtaining collection permits (Van Katwijk et al., 2021). Seeding can be more cost-effective and logistically simpler, allowing practitioners to restore larger areas more efficiently (Unsworth and Rees, 2025). Seeds also enhance genetic diversity within restored meadows, supporting long-term resilience (Van Katwijk et al., 2021). However, success rates can be highly variable due to seed loss from predation or water movement, damage from sediment smothering or abrasion, or germination failure (van Katwijk et al., 2016). The diversity of seagrass life histories means there is no universal approach to seed-based restoration (Kilminster et al., 2015; Sherman et al., 2018).

Seed burial depth has been shown to be critical for seedling survival and establishment in other seagrass species (van Katwijk et al., 2016). *Zostera marina* seeds, which have a hard coat and dormancy, have higher seedling survival and establishment when buried at 2 – 3 cm below the sediment compared to other depths (Jørgensen et al., 2019; Marion et al., 2021; Xu et al., 2021). In contrast, the non-dormant *Posidonia australis* seeds have lower seedling survival when buried at 1.5 cm depth but have greater seedling size compared to unburied seeds (Maulidiyah et al., 2024). For other non-dormant species, *Enhalus acoroides* or *Posidonia sinuosa*, any burial inhibits germination (Dagapioso and Uy, 2011; Liu et al., 2023; Maulidiyah et al., 2024). The response of non-dormant *T. hemprichii* seeds to burial is currently unknown, hindering knowledge of best restoration practice.

Nursery grow-out of seagrass seedlings prior to planting can also improve survival and extend the window of restoration opportunity (Li et al., 2021). Seedling plant outs have been scarcely utilised but have shown some success when the restoration site is suitable and the seedlings have sufficient anchorage (e.g. root depth, deployment technique) (Kendrick et al., 2025; van Katwijk et al., 2016). The characteristics of *T. hemprichii* seeds suggest they may be well suited to utilising nursery grow-out periods prior to restoration. The relatively large nutrient reserves of *T. hemprichii* seeds, combined with the absence of a dormancy period, suggest the seedlings may establish quickly, reducing the required grow-out time (Kuo et al., 1991). The early development of hypocotyl hairs for anchorage and robust seedling morphology, compared to other species such as *Z. marina,* may also reduce the seedlings' vulnerability to handling stress during maintenance and transplanting (Soong et al., 2013). Despite these characteristics, transplanting *T. hemprichii* seedlings has received little attention to date.

Ultimately, the most effective seed and seedling-based restoration method needs to consider the costs and logistics associated with the strategy, weighing up potentially improved survival against the likely considerably increased logistical costs associated with a grow-out facility for seedlings compared with direct seeding methods.

Here, we explore the use of *T. hemprichii* seeds and seedlings for restoration. Firstly, we examined the effects of seed burial depth on *T. hemprichii* emergence and early growth, hypothesising that shallow or no burial would maximise survival. This was conducted both in the aquarium to assess fine-scale responses under controlled conditions and in the field to evaluate survival under restoration conditions. Next, we explored whether a nursery grow-out period for seedlings prior to transplanting to restoration sites could improve early establishment. Finally, we used these results to develop an effort comparison for our study to guide the selection of restoration techniques for *T. hemprichii.*

2. Methods

2.1. Site

The field component of the study was conducted at Green Island (16°45′38.40"S, 145°58′18.41"E), a sandy cay, with a tidal range of 3.1m, approximately 27 km offshore from Cairns, Queensland, Australia (Fig. 1). The island is surrounded by a lagoonal reef platform with 10 seagrass species present, forming dense intertidal and subtidal seagrass meadows, with *T. hemprichii* present throughout (Schrameyer et al., 2018). The sediment composition consists of coralline and foraminiferous carbonate sand, with a paucity of silt and clay particles, which is typical of *T. hemprichii* habitat for this region (Miyajima et al., 1998). Green Island is a low-energy hydrodynamic environment (typical current velocity $< \sim 0.2\ ms^{-1}$), and the planting sites were on the leeward side of the island, sheltered from the southeast trade winds (Hanuise et al., 2025). Regional water temperatures averaged ~25°C in September, increased to ~30°C by January, and decreased to ~29°C by March (AIMS, 2026). The photoperiod ranged from 12 to 13 h per day.

2.2. Seed collection

Mature *T. hemprichii* fruits collected at the Green Island field site were stored until dehiscence (Fig. 2). A three-day period was provided prior to planting to allow for the thin seed coat to break down, ensuring the seeds were negatively buoyant (Kuo et al., 1991; Lacap et al., 2002). Only viable seeds (~75% of collected seeds), those with a cotyledon present, were used for seedling survival experiments.

2.3. Seed burial trial

The aquarium and field trial on seed burial depth ran concurrently, from October to December 2024 (Fig. 2).

2.3.1. Aquarium trial

Seed burial experiments were conducted across three recirculating aquarium systems with artificial seawater (~35 PSU, 26 ± 1.5°C) and a 12-h light: dark cycle (Fig. 2), into Green Island sediment, sieved to 5 mm.

Viable *T. hemprichii* seeds were planted at four depths (0 cm, 1 cm, 2.5 cm, 4 cm). For the 0 cm depth, seeds were placed on the sediment surface with no additional anchorage to reflect natural dispersion. The 1 cm depth ensured seeds were submerged while minimising sediment above. The 2.5 cm burial depth provided an intermediate depth between the 1 cm and the deepest treatment, 4 cm. The deepest treatment was selected based on studies of species with similar seed traits (*E. acoroides, P. australis, P. sinuosa*) (Duarte et al., 1997; Liu et al., 2023; Rollon et al., 2003) and observations of *T. hemprichii* from unpublished pilot studies. A total of 264 seeds were used in the aquaria trial, 66 for each of the 4 burial depths. Seed treatments were distributed randomly across 9 tanks nested within the 3 aquarium systems.

The presence of the cotyledon at the sediment surface was considered the time of emergence. This was assessed daily for two weeks, then every 2-3 days until conclusion at ten weeks (Fig. 2). On conclusion, seedlings that had not emerged were excavated and defined as non-viable when any remaining leaves were pale and stunted, and the seed was soft. All emerged seedlings were measured weekly for maximum leaf height and number of leaves to assess the effect of seed burial depth on seedling development post-emergence.

After ten weeks, twelve seedlings in each treatment were randomly selected to measure growth productivity, leaf elongation, and root biomass (Fig. 2) (Short and Coles, 2001).

2.3.2. Field trial

Field planting occurred in the subtidal seagrass meadow at Green Island, approximately 500 m from the intertidal fruit collection area

Fig. 1. Map of *Thalassia hemprichii* fruit collection sites (green polygons) and the 3 seed planting sites (red points) at Green Island, with an inset of the site location in Queensland, Australia. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

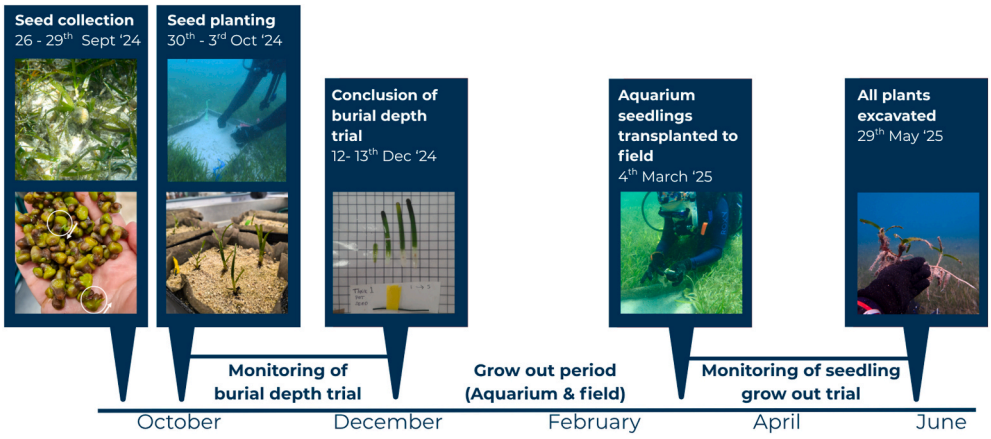

Fig. 2. Experimental timeline with photographs of each stage starting with a mature *T. hemprichii* fruit, seeds with cotyledon present, seedlings planted in the field and aquarium, productivity assessment of aquarium-grown seedlings, planting out aquarium-grown seedlings to the field, and an example seedling at the conclusion of the second trial period.

(Fig. 1). Three sites with similar abiotic conditions were established ~50 m apart at a minimum depth range of 1 – 4m during a spring low tide. Within each site, four plots were cleared of seagrass, and the sediment allowed to re-settle (Fig. 2). A 50 x 50 × 30 cm deep aluminium barrier was inserted in the cleared plots to prevent lateral clonal growth from the surrounding meadow interfering with the seedling trial. The experiment was conducted within an established seagrass meadow to ensure it occurred in an area with suitable growing conditions for *T. hemprichii*.

For the field trial, a total of 432 seeds were planted by SCUBA divers, with 108 seeds for each burial depth. Each plot was subdivided so that each quarter represented one burial depth treatment, with 9 seeds assigned to each depth. Weekly in-water monitoring assessed seedling presence, maximum leaf height and number of leaves (Fig. 2).

2.4. Seedling grow-outs

After the initial 10-week aquarium and field trials, the aquarium seedlings were maintained under constant conditions, and field-reared seedlings were monitored in-situ monthly until March 2025 (Fig. 2). Over this period, one seedling mortality occurred in the aquarium, whilst the overall shoot count across all field seedlings showed a net increase of one shoot. The remaining 140 aquarium-grown seedlings from the 0, 1 and 2.5 cm treatments were then transplanted to the field site to compare survival with the field-grown seedlings. The aquarium-grown seedlings were removed from the sediment and gently buried by scuba divers until the seedling sheaf was flush with the seabed (Fig. 2). Nine seedlings were planted into four additional cleared and bordered plots at each field site. At site 3, there were eight transplant plots, as an additional four plots were planted with eight seedlings each. The aquarium-grown seedlings for the grow-out trial will be referred to as

the transplants from here on.

The transplants were monitored four days after planting for initial survival and then weekly, assessing survival, maximum leaf height, and number of leaves (Fig. 2). Survival was considered the number of shoots per plot, as it was not possible to distinguish between individual plants without disturbing them. Consequently, the transplant analysis reflects shoot persistence from the time of transplanting rather than direct tracking of individual plant survival. On completion, all seedlings were excavated, allowing assessment of individual plant survival and the number of lateral shoots per plant (Fig. 2). The comparison of the field-grown seedlings and transplants evaluates restoration outcomes for the same seed cohort and collection event, over the same trial period (Fig. 2). The nursery treatment represents an alternative restoration technique that intentionally includes a protected grow-out phase prior to field planting.

2.5. Planting effort comparison

Based on the conditions of this study, an estimate of the effort required for the planting techniques with the highest survival rate was calculated to provide a conceptual framework for effort comparisons. The collection rate of 30 fruits per hour was based on three seasons of author observations at Green Island. Seed production was based on an average of 2.5 seeds per fruit (Kuo et al., 1991). A day was defined as one person working 7 h at a typical 2025 Australian university technical staff salary (including overheads). Costs were based on 2025 Australian market prices, including aquarium equipment and electricity at \$0.30 kWh^{-1}, and exclude potential reductions from scaling or volunteer labour. This analysis was not intended to replicate costs for a full-scale restoration effort but instead focus on the relative costs for the trials as conducted in this study.

2.6. Statistical analysis

Due to non-normal data and nested design of the seed burial trial, Generalised Linear Mixed Modelling (GLMM) were fitted in R (McGillycuddy et al., 2025; R Core Team, 2025). Burial depth, trial location (aquarium or field) and assessment week were included as fixed effects. A nested random effect was used to account for the block design, with pots or subplots nested within tanks or plots, which were nested within sites or recirculating systems.

Emergence and survival were modelled with a binomial distribution. Due to overdispersion, canopy height was analysed using a Tweedie function and log link. Due to the absence of variation, the 0 cm aquarium treatment was excluded from the seedling emergence GLMM, as it resulted in complete separation, preventing reliable estimation of standard errors and statistical inference. Consequently, model comparisons focus on treatments with failed emergence only. Leaf count was analysed with a Poisson distribution and a log link. Growth assessments were conducted on emerged seeds only to determine whether seed burial depth affected post-emergence seedling development. The growth models were also fitted with the non-emerged seeds (0 cm canopy height, 0 leaf count) to assess conditioning sensitivity.

Model selection was based on the smallest Akaike Information Criterion value (AIC) and residual diagnostics (Lüdecke et al., 2021). To present the analysis and evaluate interactions, we conducted ANOVA and pairwise analysis using estimated marginal means (Lenth, 2025).

Kruskal–Wallis tests, followed by Dunn's post-hoc comparisons, were used to analyse the effect of burial depth on seedling productivity, canopy height, leaf number and width, sheaf length, and root number, length and width, on excavated aquarium trial samples.

At the commencement of the seedling grow-out trial, the seed burial depth had no significant effect on survival or canopy height and was excluded from subsequent analyses. Net shoot change between transplanting and trial conclusion was used as the primary survival metric. The net changes in shoot count and leaf count were analysed using GLMMs with a Gaussian distribution and log link, and canopy height used a Tweedie distribution with a log link. Grow-out location (aquarium or field) and assessment week were fixed effects, and plot nested within site as a random effect. Morphological analyses were conducted at the shoot level, which was conditional on survival, resulting in varying statistical power across the time points (at conclusion, field-grown shoots $n = 87$, transplant shoots $n = 90$). Due to the small and unbalanced number of seedlings with lateral shoots, lateral shoot production was assessed using means with standard error only.

3. Results

Results from this study showed significant effects of seed planting depth on seedling emergence, survival, and morphology, but the optimum depth varied between controlled aquaria and field-based planting trials (Fig. 3). Additionally, the study found that seedlings grown in aquaria can survive early transplanting stress, resulting in higher returns per seed compared to sowing directly into the field (Fig. 3). The field-sown seeds, however, produced larger plants with more lateral shoot growth (Fig. 3).

3.1. Seed burial trial

3.1.1. Effect of burial depth on emergence

Seedling survival was significantly higher in the aquarium (73%) than the field (13%, $p < 0.001$, Fig. 3, Table 1, Table S1). Emergence was significantly impacted by the seed burial depth, although the response differed between locations ($p < 0.001$, Fig. 3, Table 1, Table S1). In the aquarium, seeds that were not buried (0 cm) exhibited 100% emergence and survival, outperforming all other treatments, and seed emergence decreased progressively with depth, down to 23.9% at 4 cm ($p < 0.001$, Fig. 3). In contrast, slight seed burial improved survival in the field. Field seed emergence was highest for burial at 1 cm (25.9%, $p < 0.001$). There was no significant difference between the 0 cm and 2.5 cm seeds in the field ($p = 0.716$). In both settings, seeds at a depth of 4 cm saw the lowest emergence ($p < 0.001$). At the end of the experiment, all non-emerged seeds across all burial depths in the aquarium were not viable.

3.1.2. Effect of burial depth on canopy height

Overall, seedlings in the aquarium reached significantly greater canopy heights (max 154 mm) than seedlings that were grown in the field (max 95 mm) ($p < 0.001$, Fig. 3, Table 1, Table S1). Seed burial depth only affected the canopy height in the aquarium ($p < 0.001$) and had no effect in the field ($p > 0.05$) (Fig. 3, Table 1, Table S1). In the aquarium, the 0 cm and 1 cm seedlings were significantly taller than for seedlings from seeds buried to 4 cm ($p < 0.05$).

Including non-emerged seeds in the model did not alter the effect of burial depth on canopy height or leaf count compared with the emerged seeds only model. The optimal burial depth for seedling growth was maintained regardless of the likelihood of emergence.

3.1.3. Effect of burial depth on the number of leaves

During early development (<7 weeks), burial depth affected leaf production in the aquarium but not in the field (both $p < 0.001$, Fig. 3, Table 1, Table S1). In the aquarium, the number of leaves was greater in the 0 and 1 cm depths than in the 2.5 cm and 4 cm depths ($p < 0.001$), whereas burial depth had no effect in the field ($p > 0.05$). By week eight, there was no longer a difference between the locations (aquarium or field) ($p = 0.09$) or burial depths.

3.1.4. Effect of burial depth on seedling productivity

At the conclusion of the aquarium burial experiment, seed burial depth had altered seedling morphology, with greater burial depth resulting in increased above-ground biomass and reduced root development (Fig. 4). Despite having the lowest overall seedling emergence success, the surviving seedlings from the deepest treatment (4 cm) had

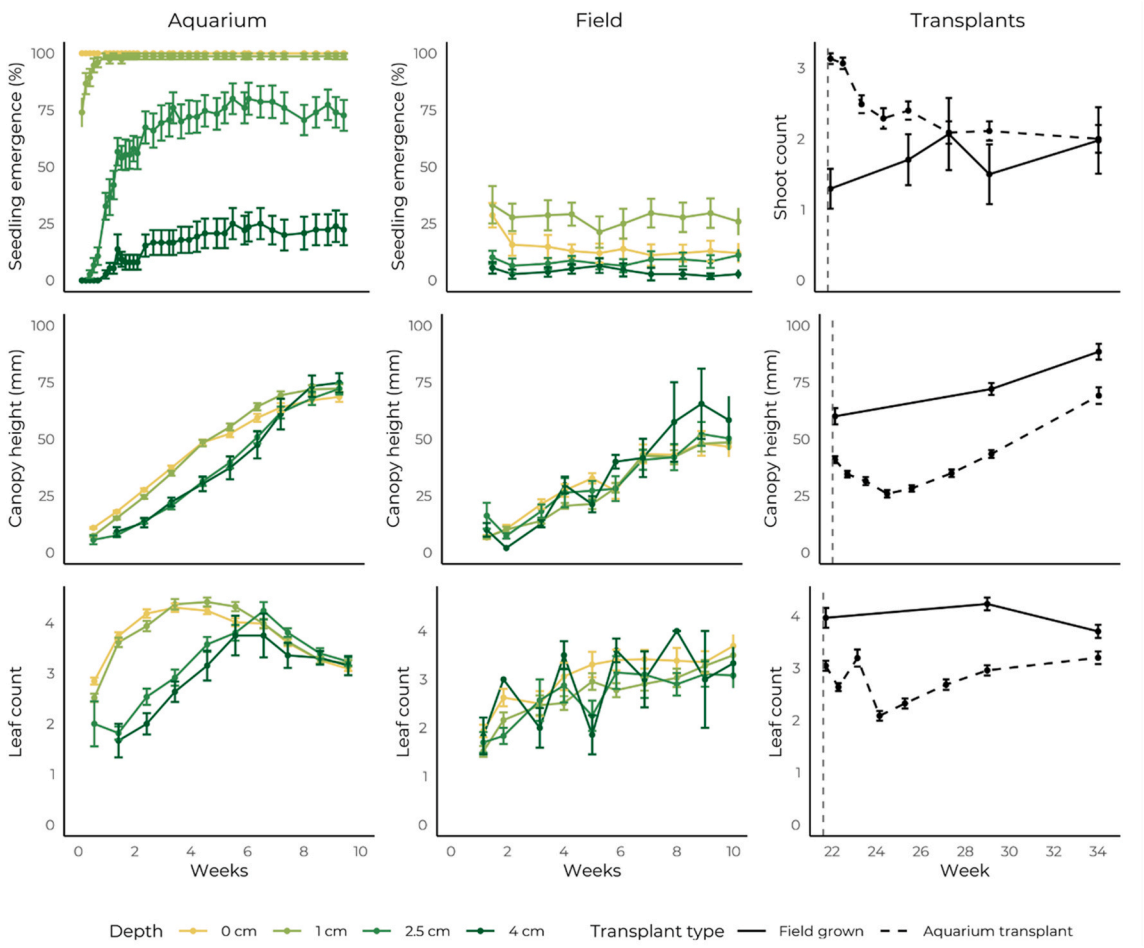

Fig. 3. Mean (±SE) of seedling emergence, canopy height, and leaf count of *Thalassia hemprichii* seeds in the aquaria (left column) and field (middle column). Mean (±SE) of shoot count, canopy height, and leaf count of *Thalassia hemprichii* field-grown seedlings and aquarium-grown transplants (right column). Trial began 21 weeks after seed germination.

Table 1
ANOVA results for GLMMs for *T. hemprichii* seed burial responses. Fixed effects are presented with degrees of freedom, χ^2 statistics, and p-values. The nested random effect is reported using estimated variance and standard deviation only.

Fixed effects	Emergence			Canopy height			Number of leaves		
	df	χ^2	P value	df	χ^2	P value	df	χ^2	P value
Burial depth	3	121.219	<0.001	3	3.276	0.351	3	35.460	<0.001
Location	1	67.947	<0.001	1	11.617	<0.001	1	76.631	<0.001
Burial depth * Location	2	26.307	<0.001	3	10.023	<0.05	3	7.701	0.052
Week	9	397.380	<0.001	9	5974.689	<0.001	9	128.231	<0.001
Random factor	Variance		SD	Variance		SD	Variance		SD
Site: Plot: Subplot	1.587		1.259	0.055		0.235	<0.001		<0.001

significantly higher growth rates than the other depths ($p < 0.001$), producing nearly double the new leaf area per day (45.2 ± 3.98 mm^2) than seedlings from all other depths (Fig. 4). The seedlings from the 4 cm burial treatment also had greater leaf length, leaf width, and sheaf length than the seeds buried at 0 cm or 1 cm (all $p < 0.01$), as well as significantly shorter root lengths and widths (both $p < 0.05$) (Fig. 4).

3.2. Seedling grow-outs

The field-grown seedlings saw a greater increase in shoot counts, taller canopy heights, and greater leaf counts than the aquarium transplants (all $p < 0.001$) (Fig. 3, Table 2, Table 3). Of the 432 seeds initially planted in the field, only 39 plants (9%) survived to the end of the second trial period (34 weeks), collectively producing 87 shoots. Most of the surviving field-grown seedlings (72%) originated from surface placement or 1 cm burial treatments. In comparison, of the 144 aquarium-grown transplants, 76 plants (53%) remained after 3 months in the field, collectively producing 90 shoots. At conclusion, 11% of the seeds directly sown in the field at 1 cm depth survived.

3.2.1. Effect of grow-out location on shoot counts

The field-grown seedlings had a significantly greater increase in shoot count than the transplants over the seedling grow-out trial ($p < 0.001$, Fig. 3, Table 2, Table 3). Field-grown seedlings exhibited a net gain in shoot counts, with a mean increase of 2.73 ± 1.27 shoots per plot, whereas the transplants showed a mean loss of -3.19 ± 0.59 shoots

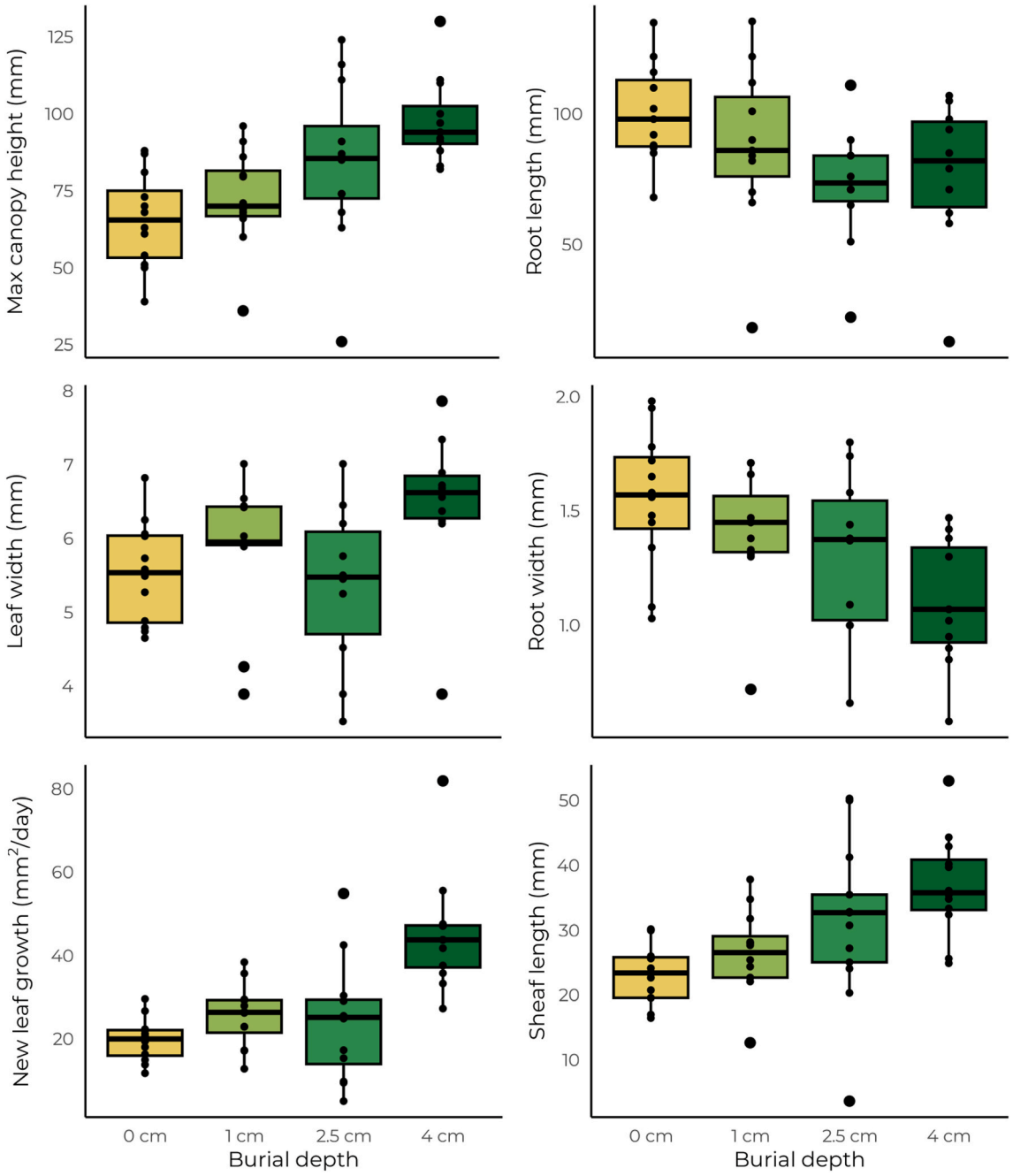

Fig. 4. Box plots of destructively sampled aquarium grown *Thalassia hemprichii* seedlings at each seed burial depth (n = 12).

per plot. The transplants were subject to cropping from herbivory immediately after planting, resulting in an initial drop in the number of shoots over the first 10 days. Transplant shoot count subsequently stabilised but continued to decline to 65.0% ± 6.25 of those initially planted out.

3.2.2. *Effect of grow-out location on lateral shoot growth*

. On excavation at the end of the transplant trial, the field-grown seedlings had more lateral shoots per plant (2.0 ± 0.148, maximum 4) than the transplanted aquarium seedlings (1.2 ± 0.046, maximum 2). Initial seed burial to 2.5 cm saw the most lateral shoots per plant for both the field-grown seeds (2.5 cm - 100%, compared to 0 cm- 62.5%, 1 cm- 61.5%, 4 cm- 40%) and the aquarium transplants (2.5 cm - 30%, compared to 0 cm- 11%, 1 cm- 21.4%).

3.2.3. *Effect of grow-out location on canopy heights*

The shoots of the field-grown seedlings were significantly taller than the transplants throughout the seedling grow-out trial ($p < 0.001$, Fig. 3, Table 2, Table 3). Both field-grown seedlings and the transplants increased in height at a similar rate during the trial, but transplant seedlings were shorter than field seedlings at the start of the trial (Fig. 3, Table 2).

3.2.4. *Effect of grow-out location on number of leaves*

The number of leaves per seedling was greater for the shoots of seedlings grown in the field than for the transplants ($p < 0.001$, Fig. 3, Table 2, Table 3).

Table 2
Mean (±SE) of *T. hemprichii* seedlings from the grow-out trial. Canopy height and leaf count present emerged seedlings only.

Metric	Time period (week)	Field-grown seedling	Transplants
Net shoot change	21 to 34	2.73 ± 1.27	−3.19 ± 0.59
Initial transplant survival	Initial 10 days post transplanting	NA	78.89% ± 4.04
Plant survival across all depths	0 to 34	9.0%	35.2%
Plant survival - 0 cm	0 to 34	9.8%	51.8%
Plant survival - 1 cm	0 to 34	11.1%	51.8%
Plant survival - 2.5 cm	0 to 34	5.6%	37.0%
Plant survival - 4 cm	0 to 34	4.6%	-
Canopy height	21	60 mm ± 3.57	40.9 mm ± 1.50
Canopy height	34	88.4 mm ± 3.47	69.1 mm ± 3.65
Leaf Count	21	3.96 ± 0.19	3.7 ± 0.13
Leaf Count	34	3.05 ± 0.10	3.2 ± 0.12

3.3. Planting effort comparison

When utilising seeds directly in the field, based on the experience and observations of this study, burial to 1 cm resulted in the largest plants with the highest survival rates and the lowest effort and cost (Table 4). The 0 cm burial depth required the least expertise, but a higher upfront seed collection effort to achieve the same number of surviving seedlings and therefore staffing costs than the 1 cm burial depth to achieve similar success. Growing seedlings in aquaria and then transplanting them into the field site required the most effort, cost, and expertise, but yielded the highest seedling survivorship per seed collected, however the resultant seedlings were less well developed than those resulting from direct seed sowing in the field with comparatively smaller and less numerous shoots and less lateral growth and branching.

4. Discussion

The study demonstrates that small adjustments to the seed burial depth of *T. hemprichii* can substantially improve early-stage survival. A shallow 1 cm burial of *T. hemprichii* seeds in the field resulted in the greatest seedling emergence and survival compared with surface placement or deeper burial depths. This differed from the controlled aquarium setting, where surface placement had the highest emergence and seedling survivorship. Furthermore, an initial germination and grow-out period in a nursery setting, before field transplanting, significantly increased the return on successful seedling establishment, although it required much higher cost and effort than direct seed planting.

The seeds of *Thalassia hemprichii* are well adapted for successful germination and seedling establishment at the sediment surface. A high investment in fewer, more advanced seeds with little dormancy, combined with adaptations that encourage correct seed orientation and the early development of hypocotyl hairs, all facilitate establishment at the sediment surface (Kuo et al., 1991; Soong et al., 2013). The high success of surface-placed aquarium seeds in our study reflects this. However, shallow burial of the seeds in the field site conferred a significant advantage over surface-placed seeds, as it likely provides both sufficient protection from hydrodynamic movement displacing seeds and reducing the potential of predation (Marion et al., 2021; Orth et al., 2002). Factors absent in controlled aquarium settings. Shallow burial also likely increased contact between the sediment and the hypocotyl hairs, furthering seed stability and reducing seed loss (Kuo et al., 1991; Soong et al., 2013).

The improved survival of *T. hemprichii* seeds under shallow burial contrasts with some other seagrass species, with a similar lack of seed dormancy, where seedling development is less successful when buried (Dagapioso and Uy, 2011; Liu et al., 2023; Maulidiyah et al., 2024). This includes other tropical species such as *Enhalus acoroides* (Dagapioso and Uy, 2011; Liu et al., 2023), which commonly co-occurs with *T. hemprichii* and they are often grouped together based on life history traits (Kilminster et al., 2015). Such differences emphasise the need for species-specific strategies for seed-based restoration rather than assumptions based on life-history characteristics when empirical data are absent.

Despite the benefits of shallow burial, the substantial in situ early losses in our results reflect a Type III survivorship curve typical of plants and common in seed-based restoration: high initial losses followed by stabilisation of survivors (Kendrick et al., 2025). Although our study was restricted to early establishment, this pattern of high initial losses in the field followed by stabilisation of survivorship also occurred. Despite these losses, achieving a ~30% success of planting in our study likely exceeds natural establishment rates (Statton et al., 2017) and represents a successful return on effort for seagrass restoration.

Seed germination and subsequent survival is strongly influenced by sediment characteristics (Xu et al., 2021). The sand-dominated sediment in our study had relatively high porosity and permeability, likely enabling deep oxygen penetration and lower sulphide toxicity compared with finer grained and muddier sediments. These characteristics likely increased the depth at which seeds could survive (Wang et al., 2016) compared with other sediment types. The sediment at our study site is typical of *T. hemprichii* habitat on the GBR (Carter et al. 202x), but the optimal seed burial depth may vary under different sediment types and conditions and should be a consideration when translating our results to other locations.

Under the aquarium conditions, emergence of new seedlings typically plateaued around two weeks for all burial depths, indicating that this is the window during which seedlings must reach the surface before seed reserves are exhausted (Jørgensen et al., 2019). Emergence of seeds in deeper treatments may have been associated with larger seeds with greater energy reserves, as reported for other species with both dormant and non-dormant seeds (Jørgensen et al., 2019; Liu et al., 2023). However, we did not assess seed size as part of our study.

Seedlings grown in the controlled aquarium conditions showed

Table 3
ANOVA results for GLMMs for the seedling grow-out trial comparing transplanted and field-grown *T. hemprichii* seedlings. Fixed effects are presented with degrees of freedom, χ^2 statistics, and p-values. Random effects are reported using estimated variance and standard deviation only. Seedling type refers to transplants or field-grown seedlings. Shoot count compared the net change in shoots from transplanting to conclusion.

Fixed effects	Shoot count			Canopy height			Leaf count		
	df	χ^2	P value	df	χ^2	P value	df	χ^2	P value
Seedling type	1	30.849	<0.001	1	25.771	<0.001	1	13.241	<0.001
Week	-	-	-	7	365.951	<0.001	7	35.149	<0.001
Random effects	**Variance**	**SD**		**Variance**	**SD**		**Variance**	**SD**	
Site	4.582	2.141		<0.0001	<0.0001		0.004	0.065	
Site:Plot	2.604	1.614		0.029	0.172		0.006	0.079	

strong initial effects of burial depth on plant morphology. In the initial stages, deeper burial reduced emergence success and subsequently affected the canopy height and leaf count of the seedlings that emerged, likely due to the stress of photoinhibition prior to emergence (Cabaço et al., 2008; Duarte et al., 1997). In contrast, canopy height and leaf count remained consistent across seed burial depths for seedlings that emerged in the field. Here, the impact of burial was likely masked by the variability of abiotic and biotic disturbances, such as herbivorous fauna, currents, storms, and nutrient availability (Marion et al., 2021; Maulidiyah et al., 2024; Unsworth et al., 2023). Such differences in results between controlled laboratory studies and field-based trials stresses the importance of conducting both: controlled laboratory/aquarium settings reduce environmental variability to enable identification of fine-scale mechanisms and effects; while field conditions capture the dynamic real-world ecological responses that may modify the outcomes seen in laboratory trials.

Morphological plasticity can represent compensatory responses to burial stress. Increased sheath length of deeper-buried seeds, as seen in *Thalassia testudinum,* and observed here, may benefit the seedling by protecting emerging leaves from sediment abrasion, providing more rigid plant material to act as anchorage and an increased area of nutrient acquisition (Cabaço et al., 2008; Duarte et al., 1997; Zhang et al., 2011). Dislodgement risk may be further reduced by the sheath trapping more sediment around the base of the shoot (Zhang et al., 2011). Seedlings

Table 4
A case study of the effort, cost and training required for a target of 1000 seagrass shoots after 8.5 months based on observations from this study. To aid visual interpretation, each element has been colour-coded: green for no or low effort or cost, amber for medium and red for high.

		Seeds planted at 0 cm in field	Seeds planted at 1 cm in field	Aquarium-grown seedlings (0 cm) transplanted to field
Mean survival after 8.5 months		12%	26%	100% in aquaria, then 65% in the field
Total seeds needed		8,340	3,850	1,550
Total fruits needed	Based on 2.5 seeds / fruit	3,340	1,540	600
Collection time	Worker for 7 hours / day	16	8	3
Collection staff cost	$59 AUD / hour	$6,608	$3,304	$1,239
Collection training		Low	Low	Low
Collection area	1 fruit per m2 (Green Island)	3,340 m^2	1,540 m^2	600 m^2
	6 fruits per m2 (Philippines)	556 m^2	257 m^2	100 m^2
	138 fruits per m2 (Philippines)	24 m^2	11 m^2	4.3 m^2
	161 fruits per m2 (Thailand)	21 m^2	9.5 m^2	3.7 m^2
Fruit and seed separation		3 days	3 days	3 days
Seed separation staff time	1 hr per day per 1500 seeds	$984.12	$454.30	$182.90
Seed separation training		Low	Low	Low
Seed separation facility	Salt water, container, air pump	$90.00	$90.00	$90.00
Separation overheads	Electricity cost ($0.30 / kWH)	$0.28	$0.28	$0.28
Aquarium facility		None	None	Complex
Aquarium set-up cost	Tanks, frame, pipe work, clips, chillers, lights, UV filter, pump, pots, pot lining, sediment, cleaning equipment, water quality testing, aquarium salt	$0.00	$0.00	$36,000.00
Aquarium care time	Averaging 1 day per week for 5 months	0	0	20 days over 5 months
Aquarium training		None	None	High

Aquarium staff cost		$0.00	$0.00	$1,180.00
Facility overheads time		0	0	5 months
Facility overheads cost	Electricity cost ($0.30 / kWH)	0	0	$6,300.00
Transport to restoration site		Simple (Seeds only)	Simple (Seeds only)	Complex (Sediment and seedling)
Planting skill level		Mixed (Skipper and staff)	High (Skipper and SCUBA)	High (Skipper and SCUBA)
Planting technique		Hand broadcasting	SCUBA, Direct injection system	SCUBA
Planting time		1 day of 2 people (Skipper and staff)	2 days of 3 people (Skipper and 2 SCUBA)	3 days of 3 people (Skipper and 2 SCUBA)
Planting staff cost		$826.00	$2,478.00	$3,717.00
Boat cost	JCU research vessel per day	$500.00	$1,000.00	$1,500.00
Training level required		Low	Medium	High
Total effort	Days	**21**	**17**	**35**
Total cost	AUD in 2025	**$9,008.40**	**$7,326.58**	**$43,909.18**

from the deeper-burial treatment also developed longer and wider leaves but shorter roots, and had greater leaf growth, suggesting a shift in resource allocation from below-to above-ground biomass. Such a redirection in response to altered environments (e.g. burial depth, hypoxia, sulfide toxicity, hydrodynamic exposure, microbiome, nutrient concentrations) reflects a recognised functional shift during early seedling establishment (Jørgensen et al., 2019; Pereda-Briones et al., 2018; Statton et al., 2017; Zenone et al., 2025).

Increased investment in leaf growth may represent a compensatory response to hypoxic and higher sulfide sediment conditions by enabling access to the oxygenated water column and initiating photosynthetic onset. In contrast, greater root mass can increase the seedlings' resilience to disturbance: roots reduce the risk of dislodgement and provide reserves if the above-ground biomass is damaged (Duarte et al., 1998, Zenone et al., 2025). Prior to transplanting, seed burial depth no longer had a significant effect on the aboveground morphology of aquarium or field-grown seedlings, suggesting the compensatory growth response may have been temporary and not continued into adult life. This contrasts with the findings of *Z. marina*, which still showed altered seedling biomass resulting from seed burial at 6 months (Jørgensen et al., 2019). In our study, destructive sampling was only done at 10 weeks, so nuances at later stages may not have been detected.

Once transplanted, leaf growth did not appear constrained by the original grow-out environment, similar to the response of *P. oceanica* seedling transplants (Balestri et al., 1998). The initial decline of the aquarium-grown seedlings likely resulted from handling stress and from leaf cropping observed following planting. In addition to providing protection, further fine-tuning of aquarium conditions to optimise seedling growth, and priming seedlings to site conditions prior to transplanting, may reduce the initial post-transplanting decline (Provera et al., 2024). This includes identifying the optimum age for *T. hemprichii* transplanting, as ontogenetic shifts may occur which alter vulnerability to dislodgement, resilience to disturbance or palatability (Jiménez-Ramos et al., 2024).

Like many other seagrass species, mature *T. hemprichii* plants (Duarte et al., 1997) increase rhizome branching frequency as a compensatory response to sedimentation (Balestri and Lardicci, 2014; Cabaço et al., 2008). Investing in lateral shoots may offset the reduced photosynthetic capacity of partially buried primaries. Such processes may also be present with seed and seedling burial. Results of our study suggest a trade-off: 1 cm or no burial maximises initial emergence and survival, while 2.5 cm burial promotes shoot production, yet 4 cm hinders plant survival (Cabaço et al., 2008; Duarte et al., 1997).

The benefits seen in our results of shallow seed burial and a seedling grow out phase before transplantation need to be considered against the relative effort and cost required for the different approaches. Effective restoration balances ecological viability with economic and logistical feasibility and social appropriateness (Unsworth et al., 2025; van Katwijk et al., 2016). Although 1 cm burial had the highest in situ establishment for *T. hemprichii*, hand-planting seeds to a set depth is labour-intensive and costly at large restoration scales, unless automation is possible (Table 4) (Unsworth and Rees, 2025). Hand broadcasting of seeds, i.e. no seed burial, allows a larger area to be covered more quickly and with less effort than utilising a 1 cm burial (Unsworth and Rees, 2025). However, double the seed collection effort would be required to achieve a similar yield based on our study results (Table 4). This may not be an issue at sites where higher fruiting densities occur (Rollon et al., 2001; Tongkok et al., 2017), but at our location, and likely many others in the GBR, this would be difficult to achieve. By bypassing the high mortality of early seed establishment, nursery propagation reduced the seed collection effort required fivefold, but required higher long-term effort and costs to set up and maintain a facility to support the nursery grow out phase (Tanner and Parham, 2010). Restoration practitioners need to consider the equipment, running and maintenance costs of an aquaculture facility, the skilled personnel required, biosecurity risks, and the more complex logistics and permitting involved with the movement of plants rather than seeds (Bell-James et al., 2023; Unsworth et al., 2023; Van Katwijk et al., 2021).

The comparison of effort presented here does not account for all variables associated with a large-scale restoration program and is

limited to the local conditions of this one-off experimental-scale study. A range of factors, such as variation in fruiting effort, collector and planter experience, and plant survival, may influence associated effort and cost. Labour barriers could be offset through community involvement opportunities, such as seed collection, hand-broadcasting, or aquarium maintenance (Unsworth et al., 2025). The high upfront nursery costs presented in this comparison do not account for amortisation or scale. Offsetting infrastructure costs across multiple restoration seasons, combined with improved efficiency and lower per-unit equipment costs associated with larger-scale aquaculture, could substantially reduce the cost difference between propagation and direct seeding. Nevertheless, the relative differences in effort provide useful guidance for designing restoration programs and highlight the need for careful examination of relative costs when designing restoration approaches.

By identifying the optimal seed planting depth (1 cm) for our study site and demonstrating the feasibility of aquarium-based propagation, these findings provide a foundation for developing scalable and cost-effective *T. hemprichii* seed-based restoration. Refinements such as these enable evidence-based decisions to maximise efforts to restore ecosystem function and resilience in degraded coastal habitats.

CRediT authorship contribution statement

Evie Furness: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft. **Timothy M. Smith:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Paul H. York:** Conceptualization, Supervision, Writing – review & editing. **Laura Forte Valiente:** Data curation, Investigation, Writing – review & editing. **Michael A. Rasheed:** Conceptualization, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108310.

Data availability

Data will be made available on request.

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