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Research Article

Environmental influence on intraspecific trait variation in the tropical seagrass *Halodule uninervis*

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Intraspecific trait variation (ITV) enhances the precision of applying functional trait approaches in plant ecology. Despite its benefits, ITV is rarely considered in functional trait-based seagrass research. The goal of our research is to measure ITV in the tropical seagrass species *Halodule uninervis* and assess the environmental factors associated with its variation. We measured eight traits of *H. uninervis* collected along the Queensland coast. Statistical analyses were conducted to identify the range of ITV, determine the relationship between environmental factors and trait variation, and estimate the potential effect of ITV on ecosystem services supported by these meadows. *H. uninervis* exhibits a distinct dimorphic pattern of ITV, particularly evident in leaf width and rhizome diameter, with air exposure and mean sediment grain size associated with variation in these traits. These findings highlight the importance of accounting for ITV in seagrass field surveys and suggest that variation within species may influence their ecological responses and functional roles in meadows.

Keywords: ecosystem service, functional trait, *Halodule uninervis*, intraspecific trait variation, seagrass

Introduction

Functional traits are characteristics of an individual that affect its fitness within its environment (Violle et al. 2007, Nock et al. 2016). The trait-based response-effect framework extends individual functional traits to a community level, linking them to ecosystem services provision (Suding et al. 2008, Díaz et al. 2013). This framework distinguishes between two categories of traits: response traits and effect traits. Response traits determine an individual's performance in its habitat; for example, leaf area can indicate photosynthetic efficiency. Effect traits, on the other hand, reflect an individual's capacity to modify their environment, such as how root density influences soil erosion. By carefully selecting key traits or combinations of traits, the trait-based framework allows response traits to be used to predict species' response to changes in environmental conditions, while effect traits highlight their role in providing ecosystem services (Streit and Bellwood 2022). In seagrass research, this approach has been applied to predict meadow-scale biomass stocks using five morphological traits and two biochemical traits (Gustafsson et al. 2025)

While the trait-based framework aids in predicting species' responses to environmental changes and highlights their ecological roles, incorporating intraspecific trait variation (ITV) is crucial as ecological processes are inferred from trait composition and become more accurately estimated when ITV is included (Albert et al. 2011). Both upper and lower 5% trait values within a population are important when understanding responses to selection pressures as individuals at the tails of the trait distribution may be the only ones able to survive and reproduce under changing conditions. For example, the maximum distance of seed dispersal will influence a species' potential for range expansion more than the average dispersal distance (Katul et al. 2005). In contrast, in community-level performance assessments, such as estimating soil fertility based on community weighted mean (Daou et al. 2021), dominant trait value has stronger influence, and ITV plays a smaller role. Spatial scale also affects the relevance of ITV: in a small-scale study with relatively few species, ITV can exceed interspecific variation (Bolnick et al. 2011), whereas in regional studies with a larger species pool and environmental gradient, ITV might be less influential (Albert et al. 2011). Studies incorporating ITV are becoming more common as they provide critical insights into the adaptive potential of communities to environmental changes and their ecological functions (Crawford et al. 2019, Herrick and Blesh 2021, Luiz et al. 2022).

The application of ITV is still limited in seagrass trait-based research despite increasing recognition of its role in understanding ecological dynamics and ecosystem services. Compared with terrestrial plant communities, seagrass meadows typically have relatively simple species composition, making ITV a key source of trait diversity and niche partitioning. Widely distributed seagrass species that encountered broad environmental gradients often rely on local adaptation and phenotypic plasticity to survive and these are expressed as ITV (Albert et al. 2011). In tropical Queensland, Australia, 13 species of seagrass have been recorded (Waycott et al. 2004), with noticeable leaf morphological ITV observed in three species, *Halodule uninervis*, *Halophila ovalis* and *Zostera muellerei* (Waycott et al. 2004, York and Rasheed 2021, Lin et al. 2024). Both *H. uninervis* and *N. mullerei* exhibit two distinct growth forms (wide and narrow leaf) but no specific environmental condition has been linked to these growth forms. In contrast, *H. ovalis* presents a different expression of ITV than the other two species as its leaf is reported to be larger in deep and clear water (York et al. 2015). Although ITV has been noted in *H. uninervis*, it has not been quantified and its relationship with environmental conditions remains unclear. This gap hinders the application of trait-based framework on seagrass meadows containing *H. uninervis*.

The goal of this study is to assess the role of ITV in *H. uninervis* within a functional trait-based response–effect framework. We investigated ITV for response traits that react to environmental factors, including water depth, average temperature, precipitation, relative exposure, air exposure during low tide, runoff, and sediment grain size. To do so, we collected seagrass samples and environmental data from multiple field sites in Queensland, measuring eight traits, including above- and below-ground morphological characteristics. Using statistical approaches, such as principal component analysis and mixture regression models, we evaluated trait variation in relation to environmental factors. This study underscores the importance of accounting for ITV in trait-based frameworks, particularly for understanding *H. uninervis*' responses to environmental conditions, with broad applications in seagrass conservation and management.

Material and methods

Sample design and sample sites

Seagrass samples were collected at 12 locations in Queensland between 24 September 2022 and 24 January 2023, within the austral summer season (Fig. 1). All sampled meadows are dominated by *Halodule uninervis* and seven were multispecific, with additional species including *Halophila ovalis*, *Cymodocea serrulata*, *Thalassia hemprichii* and *Zostera mullerei* (Supporting information). At each location, three seagrass samples and one sediment sample were collected. Sampling points were spaced at least 300 m apart and visually examined to avoid the margin of a seagrass meadow and abnormal conditions, such as exposed rhizomes. A 15 cm diameter PVC pipe was used as a core to collect *H. uninervis* seagrass samples, including their rhizomatous structures. The samples were gently washed onsite to remove excessive sediments for further processing in the laboratory. The sediment samples were collected separately but adjacent to the seagrass samples. A 5 cm diameter PVC pipe was used, and 10 cm depth of sediment were collected and stored in a zip-locked bag for further sorting in the laboratory.

Seagrass sample processing:

Eight morphological traits of seagrass were measured: leaf width (mm), leaf length (mm), canopy height (mm), root length (mm), internode distance (mm), rhizome diameter (mm), above-ground dry mass per shoot (mg shoot^{-1}), and below-ground dry mass per shoot (mg shoot^{-1}) (Table 1). The selected traits were those previously reported to be related to seagrass resilience (O'Brien et al. 2018) or service provision (Ricart et al. 2020, Jones et al. 2021). Seagrass samples were stored in a minus 20°C freezer before processing. Each leaf and rhizome selected for measurement was visually inspected to ensure leaf tips retained their natural teeth and that rhizome surface were undamaged. Although root tips may have experienced slight damage during freezing, this should not affect our analysis results since all samples were treated consistently. All non-root morphological trait values in this study are comparable with other seagrass trait studies. Root traits are also comparable with studies that also store samples frozen prior

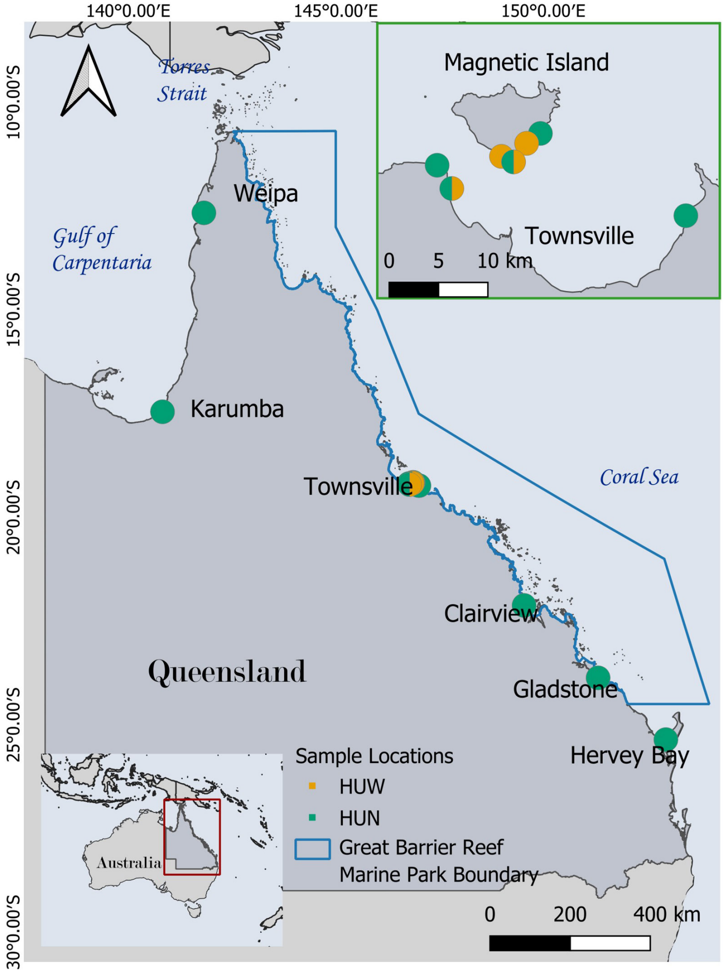

Figure 1. Map of the 12 sample locations of the study and the distribution of two *Halodule uninervis* growth from. The inset map on the upper right shows the locations of sites near Townsville. The species composition of each location is presented in the Supporting information.

to measurement (Pansini et al. 2021, Gustafsson et al. 2025). Once defrosted, *H. uninervis* samples were separated from each core sample and the following procedures were used to measure traits. The total number of shoots was counted for the whole sample, where a shoot was defined as the plant parts arising from a single stem. 10 shoots and 10 rhizomes were randomly selected and carefully spread on 5 mm grid paper. The canopy height, leaf length, leaf width, rhizome diameter, internode distance, and root length were measured by calipers for the selected plants. Photos were taken before measurements as a reference. For the plant parts that were thinner than 0.5 mm (e.g. rhizome diameter and leaf width), the caliper measurements were confirmed with measurements on high resolution photos using ImageJ 1.53t (Schneider et al. 2012). After counts and measurements were completed, the whole sample was separated into above-ground and below-ground parts and weighed. The scale of measurement was up to four decimal points. Once the wet weight was measured, the samples were transferred to an oven at 60°C. The samples were weighed again at 24 and 48 h to make sure all water was completely evaporated to record dry weight. We divided the measurements by the shoot number to obtain above-ground dry mass per shoot and below-ground dry mass per shoot.

Environmental variables and habitat characteristics

The environmental variables and habitat characteristics used in the statistical analyses were sourced from a range of available datasets. These included water depth, average temperature, precipitation, relative exposure (to wind and wave activity), air exposure index, and runoff (Table 2). Additionally, sediment grain size distribution at each sample location was determined. Sediment samples were initially wet sieved with mesh sizes of 4 mm, 2 mm and 1 mm, respectively. The four size categories were dried in a 60°C oven for at least 72 h or until completely dry. The size category were then weighed and the dry weight of the four size categories were recorded. The size category below 1 mm was rehydrated and dispersed using an ultrasonic cleanser (Soniclean). This size category was measured three times using the Mastersizer 3000 (Malvern Panalytical), which provided the grain size distribution from 0.01 μm to 1000 μm by volume proportion using the settings provided in (Bainbridge et al. 2021).

Table 1. List of measured traits of *H. uninervis*, their units, definition, and measurement method applied in this study.

Trait name	Unit	Definition	Measurement method
Leaf width	mm	Width of a leaf at the widest section	Measured with caliper. Measurements thinner than 3 mm were cross-checked with ImageJ 1.53t
Leaf length	mm	Maximum length of a leaf (excluding sheath)	Measured with caliper
Canopy height	mm	Maximum length from rhizome to tip of a shoot	Measured with caliper
Root length	mm	Maximum length of a root	Measured with caliper
Internode distance	mm	Distance between base of two shoots	Measured with caliper
Rhizome diameter	mm	Length of a straight line of a rhizome which cross the center	Measured with caliper. Measurements thinner than 3 mm were cross-checked with ImageJ 1.53t
Above-ground dry mass per shoot	mg $shoot^{-1}$	Dry mass of above-ground parts, which includes leaves and stems divided by shoot number	Samples were dried in 60°C oven for 48 h and measured
Below-ground dry mass per shoot	mg $shoot^{-1}$	Dry mass of below-ground parts, which includes rhizome and roots divided by shoot number	Samples were dried in 60°C oven for 48 h and measured

The sieve data were then merged with the Mastersizer data (i.e. using the mass of the < 1000 μm fraction) to produce a distribution range between 0.01 and 4000 μm. To best represent the variability of sediment grain size, we used size percentage weighted mean for each sediment sample, which range from 119 to 2017 μm.

Statistical analysis

Descriptive statistics were applied to quantify and visualize ITV. After confirming the existence of distinct growth forms, we used a mixture regression model to identify the most distinctive traits and their distribution within each growth form, providing a clear definition of the distinct growth forms present in tropical Queensland. This type of model is applied when there are potentially multiple processes influencing the observed data, but no clear grouping factors, such as treatment groups, or geographical differences are present (Hamel et al. 2017). In this study, the model classified each sample by estimating its probability of belonging to a specific growth form and quantified trait patterns within each growth form. We applied this model to analyse the eight measured traits, identifying traits with multiple correlated processes. The multivariate mixed regression model was implemented using a Bayesian approach. We used R as an interface and performed the non-U-turn sampling in Stan (Stan Development Team 2023) to explore the posterior distributions. The model was run with four Markov chain Monte Carlo (MCMC) chains, each consisting of 6000 warm-up steps and 2000 sampling steps providing 8000 posterior draws.

Additionally, we performed two principal component analysis (PCA) based on both traits and environmental factors using 'pcaMethods' package (Stacklies et al. 2007) to examine the contribution of traits and environmental factors on grouping of samples. The trait-based PCA offered a dimensionally reduced presentation of data separation, highlighting the contribution of each trait to the principal

Table 2. List of environmental factors and habitat characteristics used in the statistical analysis.

Environmental factor	Unit	Description	Method/source
Total relative exposure (REI)	unitless	Monthly dominant wind multiplied by the closest fetch length and summed over a year	Processed from multiple data sources using the method of Mason et al. 2018
Depth	meter	Depth of the seagrass meadow. Interpolated from contour lines	National intertidal digital elevation model (Bishop-Taylor et al. 2019)
Air exposure	unitless	Air exposure index reflects the proportion of the time that seabed is exposed to the air	Intertidal extents model (Bishop-Taylor et al. 2019)
Average temperature	°C	Average temperature across nine years (2015–2023)	ERA5 'hourly data on single levels from 1940 to present' (Hersbach et al. 2023) access from Copernicus Climate Change Service
Runoff	m	Average of monthly surface and sub-surface runoff across nine years (2015–2023)	ERA5 'hourly data on single levels from 1940 to present' (Hersbach et al. 2023) access from Copernicus Climate Change Service
Total precipitation	m	Monthly precipitation across nine years (2015–2023)	ERA5 'hourly data on single levels from 1940 to present' (Hersbach et al. 2023) access from Copernicus Climate Change Service
Mean sediment grain size	μm	Sediment was processed and analysed by wet sieve and Mastersizer	Field sample collection

components, and provided insights into how traits influence the grouping of seagrass samples. The environmental factors based PCA incorporated the sample grouping information and indicated the contribution of each environmental factor to the separation of growth forms.

Generalized linear mixed models (GLMMs) were applied to examine the relationships between environmental and habitat characteristics and four *H. uninervis*' traits, leaf width, rhizome diameter, above-ground dry mass per shoot and below-ground dry mass per shoot. Leaf width and rhizome diameter were tested separated for each growth form, as the mixture model identified two distinct underlying processes. In contrast, above-ground dry mass and below-ground dry mass were tested for the entire set of collected samples. The models use sample locations as a random intercept to account for hierarchical sampling design. These analyses used the same MCMC sampling setting as described above, with the 'rethinking' package (McElreath 2020) used to run the Bayesian regression models. We evaluated a set of models including: 1) the seven environmental variables listed in Table 2, and 2) variables with higher variability across the sites, that includes relative exposure, depth, runoff, air exposure, and weighted mean sediment grain size (see the Supporting information for details of each model). The MCMC diagnostic and residual validation ('bayesplot' package, Gabry et al. 2019, Gabry and Mahr 2024) were applied to all models. Model selection was based on widely applicable information criterion (WAIC).

Results

Visual examination of *Halodule uninervis* samples revealed the presence of two growth forms, and the bimodal distributions of leaf width and rhizome diameter were confirmed using a multivariate mixture regression model (Fig. 2, Table 3, Supporting information). The narrow form (*H. uninenvis* narrow – HUN) comprised 63% of the samples, with smaller estimated mean values for leaf width (0.61 mm) and rhizome diameter (0.65 mm), compared to wide leaf form (*H. uninenvis* wide – HUW) (2.92 and 1.05 mm, respectively). These estimations along with the standard deviation, provide clear definitions and ranges of two growth forms of *H. uninervis* in tropical Queensland. Although the rhizome diameters of HUN and HUW overlapped (Fig. 2a), the model was still able to classify them into two groups, and such differentiation of rhizome diameter has not previously been reported from field observation. No bimodal distribution was found for the other six traits.

The two PCAs suggested the roles of measured functional traits and environmental factors in distinguishing the growth forms. The trait-based PCA separates the samples into two groups (Fig. 3a), with the first two components explaining 70.0% of total variance. The first component (PC1), accounting for 46.9% of variability, is mainly driven by above-ground dry mass per shoot, rhizome diameter, leaf width, and below-ground dry mass per shoot. In general, most HUW samples are positioned on the positive side of PC1, characterized by wider leaves, thicker rhizomes and higher dry mass per shoot. In contrast, the second component (PC2) explained 23.1% of variability and is primarily influenced by root length, leaf length and canopy height. The HUN samples are largely situated on the negative side of PC1, reflecting narrower leaves, thinner rhizomes and lower dry mass per shoot. Additionally, some HUN samples on the negative side of PC2 exhibited longer root length and internode distance than all others. The environmental factor-based PCA suggested that air exposure index (i.e. intertidal meadows) is positively correlated with HUN, while mean sediment grain size and run-off are linked to the HUW. However, the relatively low explained variance (57.9%) and the occurrence of meadows containing both growth forms (Fig. 1) suggest that the assessed environmental factors (Table 2, Supporting information) alone may not fully account for the differences between the forms.

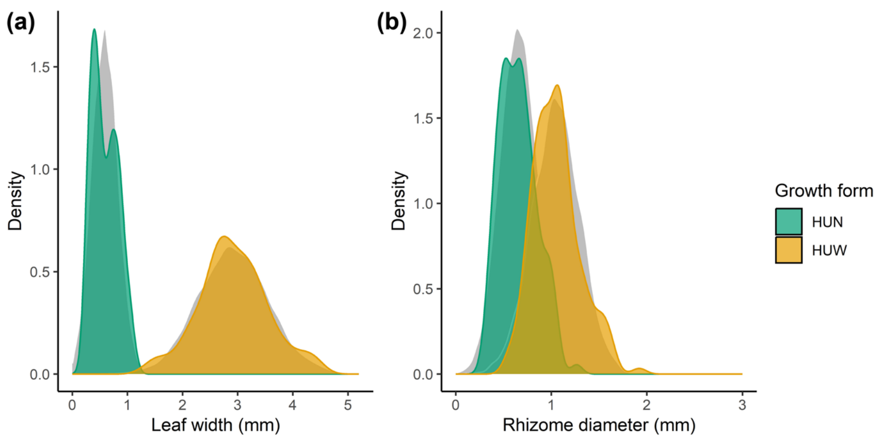

Figure 2. Density plots of the distribution of two *H. uninervis* traits, leaf width (a) and rhizome diameter (b), displaying a bimodal distribution corresponding to the two distinct growth forms: narrow leaf form (HUN, green) and wide leaf form (HUW, yellow). The underlying grey distributions represent the grouping as identified by the mixture regression model, highlighting the trait variation between two growth forms.

Table 3. Model estimates for growth form proportions (narrow leaf form: HUN, wide leaf form: HUW), as well as the mean and standard deviation (SD) for two traits (e.g. leaf width and rhizome diameter) based on a multivariate mixture regression model. For each estimate, the mean, SD, lower 5.5%, upper 94.5%, R-hat statistic (Rhat), and effective sample size (n_eff) are presented.

	Mean	SD	5.50%	94.5%	Rhat	n_eff
HUN proportion	0.63	0.02	0.59	0.67	1	10 410.28
HUW proportion	0.37	0.02	0.33	0.41	1	10 410.28
Mean leaf width of HUN	0.61	0.01	0.59	0.63	1	8101.7
Mean rhizome diameter of HUN	0.65	0.01	0.63	0.66	1	7149.03
Mean leaf width of HUW	2.92	0.05	2.84	3	1	10 939.49
Mean rhizome diameter of HUW	1.05	0.02	1.02	1.08	1	10 604.67
SD of HUN leaf width	0.23	0.01	0.21	0.24	1	9347.19
SD of HUN rhizome diameter	0.19	0.01	0.18	0.2	1	9018.19
SD of HUW leaf width	0.64	0.04	0.58	0.71	1	9970.3
SD of HUW rhizome diameter	0.25	0.01	0.23	0.27	1	9018.19

Percentage weighted mean sediment grain size was identified in GLMMs as a significant factor for leaf width and rhizome diameter in HUW, but not in HUN, with the magnitude of its effect varying between growth forms and traits (Fig. 4, Supporting information). For leaf width, mean sediment size has the opposite relationship with the two growth forms. HUW growing in habitats with larger sediment particles is predicted to have wider leaves compared to those in habitats with smaller sediment particles (Fig. 4a). A similar trend is observed in HUN, but the relationship is weaker. Rhizome diameter is also related to mean sediment size, but it exhibits the same negative correlation with both growth forms (Fig. 4b). The models that do not distinguish between growth forms show that mean sediment size is positively correlated with both above-ground and below-ground dry mass per shoot (Supplemental information).

Discussion

This study addresses a critical knowledge gap associated with intraspecific trait variation (ITV) in the tropical seagrass, *Halodule uninervis*. We confirmed that *H. uninervis* exhibits a dimorphic pattern of ITV using a statistical approach based on samples collected along the Queensland coast of Australia. Principal component analysis of eight measured traits clearly separated the samples into two distinct groups, wide leaf form (HUW) and narrow leaf form (HUN) (Fig. 3a). Additionally, a mixture regression model effectively defined the range of these two growth forms, with leaf width and rhizome diameter as key distinguishing traits (Table 3). Environmental factors, such as air exposure and mean sediment grain size were identified as potential drivers of ITV in *H. uninervis*.

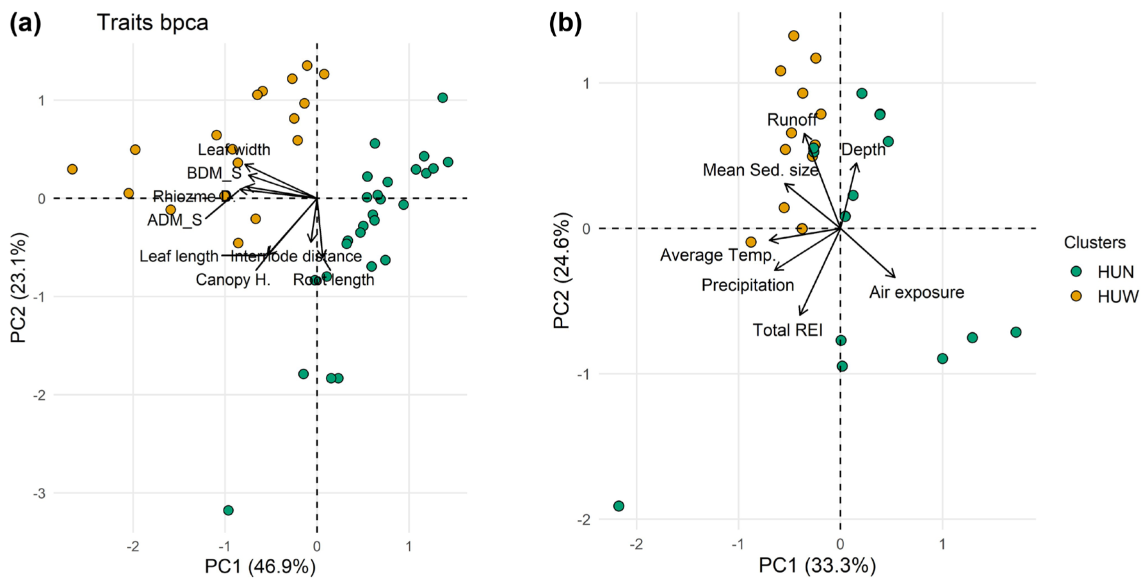

Figure 3. Principal component analysis (PCA) of *H. uninervis* based on traits (a) and environmental factors (b). Samples are colored according to the growth form identified in the laboratory: narrow leaf form (HUN, green) and wide leaf form (HUW, yellow). (a) The trait-based PCA shows a separation of seagrass samples based on their trait values. The first two principal components (PC1 and PC2) explain 70.0 % of the variance. Traits including above-ground dry mass per shoot, rhizome diameter, leaf width, and below ground-dry mass per shoot, strongly correspond to PC1, while root length, leaf length, and canopy height contribute to the separation along PC2. (b) The environmental factor-based PCA suggests higher air exposure is potentially correlated with HUN while larger mean sediment grain size, and higher run-off are linked to HUW. Loadings of both PCA, trait distributions, and environmental factors are provided in the Supporting information.

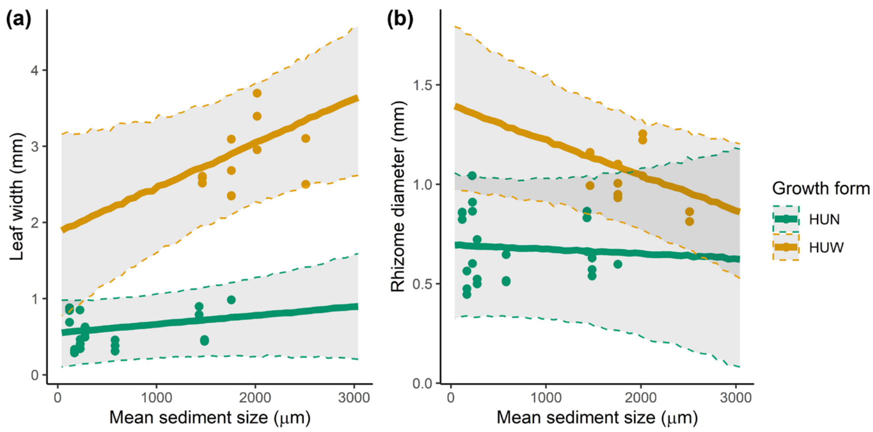

Figure 4. The relationships between percentage weighed mean sediment grain size and leaf width (a), and rhizome diameter (b) on leaf width trait of *H. uninervis*. The solid line is a model simulated trait value with 95% credible intervals in a dash line and the points are the measured traits and mean sediment grain size. The y-axis ranges encompass both the measured and model-estimated leaf width and rhizome diameter.

Patterns of ITV in *H. uninervis* reported in Southeast Asia align with our findings. In Singapore, three growth forms of *H. uninervis* have been recorded (Kwan et al. 2023), with two being more common: one with leaf widths at 0.4–1.0 mm and the other one at 1.1–2.2 mm. The rhizome diameter of these two growth forms were reported as 0.4–0.7 and 0.5–1.3 mm, respectively. In Malaysia, a dimorphic pattern of *H. uninervis* has been reported, with a HUN ranging from 0.5 to 1.5 mm and HUW between 1.5 and 4.0 mm (Japar Sidik et al. 1999). Based on their reported sample size, average, and standard deviation of leaf width, our mixture regression model supports this pattern, with average leaf widths at 1.02 mm (27 %), and 2.31 mm (73%). Findings in India vary: two distinct growth forms were observed in the intertidal seagrass meadow of Pokkadera in North Andaman Island of India (Elrika D'Souza, Nature Conservation Foundation, India, pers. comm.), but no separation was noted in Chilika lagoon, northeastern India (Mishra et al. 2021). The leaf width measurements of our study in Queensland most closely align with the dimorphic pattern reported in Malaysia, with comparable categories for the two growth forms. The rhizome diameter measurements correspond closely with two common growth forms described in Singapore.

Air exposure was identified as a key environmental factor correlated to the separation between growth forms, as indicated by environmental factors-based PCA. Higher air exposure during low tide was positively correlated with HUN, meaning that leaf width tends to decrease with an increase in the duration of seagrass exposure to air at low tides regardless the growth forms. Similar effects of air exposure on seagrass morphology have been reported in other species, such as in *Zostera japonica* (Kim et al. 2016), *Z. muelleri* (Kohlmeier et al. 2014) and *Halophila ovalis* (Kaewsrikhaw et al. 2016). Seagrass meadows experiencing high air exposure are often located in the upper intertidal zone, where they are exposed to air and direct sunlight more frequently than other habitats. For species adapted to submerged conditions, prolonged exposure to direct sunlight and air can lead to desiccation and negatively impact photosynthesis efficiency (Unsworth et al. 2012, Petrou et al. 2013). Reducing leaf surface area helps mitigate these effects, which explains the decrease leaf width with increased air exposure observed in our study. Additionally, no HUW was found in upper intertidal zone in sample locations. The large ITV in leaf width observed in *H. uninervis* may provide an advantage, allowing the species to adapt locally to both high and low/no air-exposed habitats.

According to the GLMM analyses for each growth form, larger sediment grain size was linked to wider leaves in the HUW (Fig. 4a), while this factor had minimal effect on the HUN. A culture study (McMillan 1983) found that HUW individuals had their leaf widths reduced from 3–5 to 1.8–2.6 mm after 5.5 months in fine sandy loam, a substrate containing a range of sand particle sizes (760–1630 μm). This corresponds to the lower end of the mean sediment grain size used in our simulation (750–3000 μm), so reduction in leaf width is consistent with our model prediction. In the same study, the leaf widths of the HUN and intermediate leaf form individuals, which ranged from 1.0 to 1.9 mm, did not change during the culture period aligning with our finding that narrow leaf growth form is minimally affected by sediment grain size. However, the positive correlation between leaf width and grain size in HUW is unexpected, as coarser grain sizes are typically associated with higher-energy environments characterized by stronger wave or current velocities, which would likely cause damage to leaves. Additional environmental factors may contribute to this relationship; for example, individuals in subtidal habitats, where light availability is limited, tend to produce short and thin leaves (Collier et al. 2007, 2012). However, due to the limited resolution of available environmental factor data in our study, the extent of these influences and interaction remains unclear.

An important implication of our research is the implications for estimating services provided by tropical seagrass ecosystems. For example, fish biomass supported by seagrass meadows and carbon sequestration potential are two important functions provided by seagrass meadows and both can be estimated through effective traits. In an additional analysis (Supporting information), we estimated relative carbon storage and fish biomass supported by hypothetical *H. uninervis* meadows with different growth form compositions to understand what the implications could be in a simulated scenario. Results indicated that both services increased with the proportion of HUW, consistent with previous findings that larger seagrass species provide greater ecosystem services (Nordlund et al. 2016, 2018, do Amaral Camara Lima et al. 2023). However, because smaller species and forms often recover more rapidly following disturbance (Kendrick et al. 2012, O'Brien et al. 2018), this suggests a potential tradeoff between ecosystem service provision and resilience in meadows with substantial ITV. While potentially informative, this simulation was based on several assumptions (e.g. constant shoot density and homogeneous landscape), and did not include additional factors such as growth rate, meadow history and belowground carbon accumulation (Macreadie et al. 2012, 2014, Zou et al. 2021, Johannessen 2022). These results suggest both the value and limitations of incorporating ITV into service estimates, emphasizing the need for more comprehensive inclusion of ITV in field-based monitoring.

Our study is limited by the lack of temporal information on the *H. uninervis*' ITV and relatively low HUW sample size. Obtaining long-term trait data is challenging due to the ephemeral nature of tropical seagrass meadows. Common garden experiments, which involve culturing individuals from different populations under identical environmental conditions, can address some of the challenges related to temporal aspects of ITV (Pazzaglia et al. 2021). Previous research has demonstrated significant changes in leaf morphology in *H. uninervis* during experiments (McMillan 1983). Recent common garden approaches not only assess the morphological responses but also incorporate genomic tools to study local adaptation (De Villemereuil et al. 2015). These studies provide evidence that common garden experiments with controlled environmental factors can provide insight into ITV patterns and their causes. The limited geographic range of HUW samples, primarily collected in Townsville, restricts the environmental factors considered and may bias the analyses. Future research should aim to include a broader range of habitats and conduct global meta-analyses to improve our understanding of the role of ITV in seagrass species and enhance ecosystem service assessments.

Conclusion

This study outlines the pattern of intraspecific trait variation (ITV) in *Halodule uninervis* in Queensland and explores its implications for conservation and management within a trait-based response–effect framework. We identified a distinct dimorphic pattern in ITV, most notably in leaf width and rhizome diameter, while the remaining six traits, though not dimorphic pattern, exhibit substantial variation that may enhance the species' adaptive potential under selection pressures. Air exposure is a key environmental factor driving the differentiation between growth forms, while mean sediment grain size also influences trait variation specifically in the HUW. Overall, our results suggest that ITV is essential for understanding *H. uninervis*' response to environmental pressures and should be incorporated into monitoring programs intended to inform management, such as the assessment of ecosystem service provision.

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Author contributions

Chieh Lin: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (lead); Writing – review and editing (equal). **Michael A. Rasheed**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Robert G. Coles**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Paul H. York**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (equal). **Stephen Lewis**: Conceptualization (supporting); Formal analysis (supporting); Methodology (equal); Supervision (supporting); Writing – review and editing (equal). **Alana Grech**: Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Project administration (equal); Resources (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Trait data collected in this study are avaialbe in the Seagrass TraitDB (https://seagrasses.ccmar.ualg.pt/). The porcessed input data for analyses are archived on Figshare https://doi.org/10.6084/m9.figshare.30740582, (Lin et al. 2026). All analysis scripts are available in a GitHub repository (https://github.com/orcachieh/Trait_variation_analysis).

Supporting information

The Supporting information associated with this article is available with the online version.

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