

Morphological, Genetic, and Biochemical Traits Variation of *Halodule uninervis* at Different Microhabitats Along Egyptian Red Sea Coast

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ABSTRACT

Halodule uninervis exhibits remarkable adaptability across environmental gradients in the Egyptian Red Sea. This study investigated five microhabitats ranging from the desiccation-prone, silty-sand flats of NIOF (location I: <0.5m depth, 41.35–41.54‰ salinity) to the thermally unstable sands of Wadi El Gemal (location V: $\Delta T = 34.74^{\circ}\text{C}$), integrating morphological, genetic, and biochemical analyses. At the morphological level, high-stress sites (I and V), exposed to intense light and heat, supported shorter shoots and roots (12–18% reduction), narrower leaves, and lower abundance traits that enhance stress tolerance. In contrast, more stable mid-depth NIOF (location II) and Marsa Alam (locations III and IV) showed longer shoots and roots with broader leaves and high abundance optimized for resource acquisition. Genomic fingerprints exposed striking patterns: shallow, high-stress populations (I/V) showed convergent evolution (0.87 genetic similarity) despite 120km separation, while adjacent moderate locations (II/III/IV) exhibited near-clonal profiles (0.94). The southern population (V) emerged as a genetic outlier (0.54 similarity with IV), likely shaped by strong specific microhabitat conditions. Metabolomic profiling further supported adaptive divergence: high-stress populations accumulated elevated levels of defensive phenolics (e.g., sinapinic acid, 2.1× higher) and structural hydrocarbons, while stable sites invested more in osmoprotective sugars (7.36% dry weight) and antioxidant compounds. This tripartite response morphological, genetic, and biochemical highlights the phenotypic plasticity and adaptive potential of *H. uninervis*. The results provide novel insights into how environmental gradients shape seagrass resilience, informing conservation strategies under climate change pressures.

INTRODUCTION

Seagrasses are submerged marine angiosperms that serve as ecological engineers in coastal ecosystems. They are vital components of marine ecosystems, providing essential ecological services such as habitat provision, carbon sequestration, and coastal protection

(Orth *et al.*, 2006). The taxa regarded as seagrasses belong to a very limited number of plant families, all classified within superorder Alismatiflorae (Monocotyledonae) (Dahlgren *et al.*, 1985), also generally known as the Helobiae (Tomlinson, 1982). The subclass Alismatanae (Kubitzki *et al.*, 1998) is with respect to its contents identical with Alismatiflorae. *Halodule uninervis* is a seagrass species classified under the family Cymodoceaceae in the order Alismatales. It belongs to the genus *Halodule*, which comprises slender, fast-growing seagrasses commonly found in tropical and subtropical coastal waters. The species is characterized by its narrow leaves with a single prominent midvein (*uninervis* meaning "one-veined"). Taxonomically, it falls under the kingdom Plantae, clade Tracheophytes, and clade Angiosperms. *H. uninervis* is a widespread species inhabiting tropical and subtropical intertidal zones, exhibiting considerable morphological and physiological plasticity in response to environmental gradients (Duarte, 1991; Short & Neckles, 1999). The various species of seagrass in the Red Sea form vast meadows from the tidal zone to depths of 70m (Head & Edwards, 1987; Lipkin *et al.*, 2003). Due to the soft-bottom sediments found in these regions, they tend to be concentrated in shallow water regions such as lagoons, sharms and mersas (Den Hartog, 1970). Twelve seagrass species were recorded in the Red Sea. In Egypt, Wadi El Gemal National Park alone has seagrass beds spanning over 1,783 hectares, hosting 11 out of the 12 species reported from the Red Sea (El Shaffai, 2011). On the northern islands of Hurghada, three dominant species include *Th. ciliatum* (61%), *H. stipulacea* (43%), and *H. uninervis* (42%) (Mahdy *et al.*, 2021). Seagrasses face numerous direct threats. These include higher CO₂ concentrations in coastal waters (Brierley and Kingsford, 2009), diminished light availability caused by rising sea levels (Grantham *et al.*, 2011), and increased physical disruption elevated water temperatures (Hyndes *et al.*, 2016). These environmental changes provoke physiological reactions in seagrasses, leading to transformations in the composition and function of seagrass ecosystems (Björk *et al.*, 2008), alterations in species distribution (Hyndes *et al.*, 2016), and the emergence of localized invasions or extinctions (Mellin *et al.*, 2016). As policies undergo regular review, it is essential that future legislative frameworks expand beyond mitigation efforts (Nachmany *et al.*, 2014) to incorporate adaptive and responsive strategies that directly address both current and predicted impacts on coastal ecosystems, particularly seagrass meadows (Frost *et al.*, 2016). Heterogeneity drives phenotypic and genetic differentiation, influencing seagrass population structure and function (Reusch, 2006; Pazzaglia *et al.*, 2021). Previous studies have demonstrated that morphological adaptations, such as leaf thickness and root length, enable *H. uninervis* to withstand thermal and desiccation stress in intertidal zones (Zhang *et al.*, 2023). Genetic tools, particularly Start Codon Targeted (SCoT) markers, provide robust means to detect polymorphisms and population divergence linked to habitat specificity (Collard & Mackill, 2009; Rai, 2023). In parallel, biochemical profiling offers insights into the metabolomic adjustments of seagrasses, with phenolic compounds playing crucial roles in

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antioxidant defense and environmental stress mitigation (Rodríguez-Rojas *et al.*, 2024; Botes *et al.*, 2025). Seagrasses display considerable morphological plasticity as a response to environmental stressors, including light availability, substrate composition, and tidal exposure (Duarte, 1991). For example, Short and Neckles (1999) highlighted how leaf morphology and root development vary with desiccation intensity, influencing nutrient uptake and anchorage. Genetic variation and population structure genetic diversity within seagrass populations underpins their capacity to adapt to environmental change (Phair, 2016). Molecular markers such as SCoT have been successfully applied to reveal significant polymorphism and site-specific genetic signatures in plants (Herrera & Bazaga, 2010). Alotaibi *et al.* (2022) demonstrated that seagrasses populations exhibit marked genetic differentiation correlated with habitat conditions. Biochemical adaptations and metabolomics phenolic compounds and primary metabolites serve as biochemical indicators of stress response and ecological fitness in seagrasses (Griffiths *et al.*, 2020). This study integrates morphological measurements, genetic diversity analysis, and biochemical metabolite profiling to comprehensively evaluate the adaptive responses of *Halodule uninervis* populations across five contrasting intertidal locations along the Egyptian Red Sea. Understanding these multi-level variations is critical for predicting resilience and guiding conservation under increasing anthropogenic and climatic pressures. Additionally, understanding the plant's response to such spatial heterogeneity is vital for assessing its resilience under environmental stress and future climate change scenarios.

MATERIALS AND METHODS

Characterization of studied sites

Halodule uninervis samples were collected from five distinct intertidal locations along the Egyptian Red Sea coast. Field surveys were undertaken from April 2020 until August 2020 and samples of vegetative blades of *Halodule uninervis* plants were collected by hand during low tide or by SCUBA diving during high tide. The sites selected were based on different *H. uninervis* morphology characteristics; encompassing two locations at NIOF Hurghada (location I (27°17'3.92"N, 33°46'26.43"E) and location II (27°17'6.48"N, 33°46'23.63"E), two at Marsa Alam beach (location III (25°4'37.20"N, 34°53'43.44"E) and location IV (25°4'31.83"N, 34°53'48.36"E) , and one location (V) at Wadi El-Gemal (24°30'48.38"N, 35°8'23.70"E).

Climate data acquisition

Site-specific climatic parameters were obtained from the NASA Prediction of Worldwide Energy Resources (POWER) database. Data were extracted from the

"NASA/POWER Source Native Resolution Monthly and Annual Dates (month/day/year): 01/01/2020 through 12/31/2020 ([NASA/POWER Data Viewer](#)).

The parameters retrieved included: Precipitation Corrected (PRECTOTCORR) in mm, Surface Pressure (PS) in hPa, Wind Speed at 2m (WS2M) in m/s, Relative Humidity at 2m (RH2M) in %, Air Temperature at 2m (T2M) in °C and Temperature Range (T2M_RANGE) in °C. Data were extracted using the latitude and longitude coordinates of each sampling station to ensure accuracy and site-specific resolution. The long-term averages of these parameters were used to evaluate the potential influence of microclimate on the morphology, genetic and biochemical composition of *H. uninervis* populations.

The soil samples texture analysis were conducted by drying at 65°C for 96 hours in a glass jar. The samples were allowed to pass through a series of sieves (from 2 to 0.02mm) attached to automatic shaker to separate; gravel, coarse sand and fine sand. The samples were shaken vigorously and then the content of each sieve was weighed and its percentage was determined. For determination of clay and silt, the pipette analysis method of **Carver (1971)** was used. Salinity of water samples was determined by the argentometric method as described in **American Public Health Association (1995)**.

Seagrass morphology and abundance

Characteristics that **den Hartog (1964, 1970)** used in the taxonomy of the *H. uninervis* complex, leaf tips and leaf widths, were also compared. Morphometric characters such as shoot length, root length, leaves width, and shoot-to-root ratios were measured from fresh samples using a digital caliper and ruler. Leaves morphology was categorized based on visual check into "thin" or "wide" classes. At each site, three 0.25m² quadrats were randomly using the Global positioning system (GPS) coordinates. Seagrass abundance was defined as percent benthic cover of each seagrass species and was determined using a modified visual assessment scale of seagrass cover within the quadrat, where 1=0-5%, 2= 5-25%, 3=25-50%, 4=50-75%, and 5=75 100% (**Khang, 2021**). At each location, three replicates of *H. uninervis* were randomly collected, including the leaves, shoots, and roots. Samples were gently washed with seawater to remove debris, packed in labeled sterile bags, transported on ice to the laboratory, and then stored at -20°C until further molecular analysis and biochemical examinations.

Molecular analysis (SCoT Markers)

To evaluate the genetic diversity between the *H. uninervis* in the five locations, ten SCoT were utilized. DNA was extracted using the CTAB method from leaf tissues. Start Codon Targeted (SCoT) polymorphism analysis was carried out using ten primers. PCR products were resolved via agarose gel electrophoresis, and banding patterns were scored as present (1) or absent (0). The total number of bands, polymorphic bands, and

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unique bands were recorded to calculate genetic diversity and polymorphism percentage (Williams *et al.*, 1990).

Biochemical constituents and MS Analysis of Phenolic Compounds was performed as composite samples depending on similarity of morphology and genetics indicators. Sample 1 included I and V while sample 2 included II, III, and IV. GC-MS Analysis of Phenolic Compounds was conducted to investigate the phytochemical profiles, phenolic compounds were extracted from composite samples (Sample 1: locations I and V; Sample 2: locations II, III and IV) using methanol. The methanol extracts were derivatized and analyzed using Gas Chromatography-Mass Spectrometry (GC-MS) according to the method of Kovács *et al.* (2008). Compounds were identified based on their retention times and comparison with NIST spectral libraries. The number of compounds, total retention time, peak areas, and major bioactive constituents were recorded for comparison between the two groups. Identifications were made by library searches (Adams, 1995) combining MS and retention data of authentic compounds by comparison of their GC retention indices (RI) with those of the literature or with those of standards available in our laboratories. The retention indices were determined in relation to a homologous series of n-alkanes.

RESULTS AND DISCUSSION

Characterization of sampling locations

The locations are characterized by varying longitudes and latitudes, indicating a diverse geographical setting. For instance, the longitude ranges from 24°30'48.38" to 27°17'6.48", while latitude varies from 33°46'26.43" to 35°8'23.70". This geographical diversity may influence local environmental conditions and the adaptability of *Halodule uninervis*. Location I – NIOF I (27°17'3.92"N, 33°46'26.43"E): Located nearby to aquaculture ponds, this site lies in a low-energy intertidal shoal with silty-sand substrate and very shallow waters (<0.5m) with air-exposed during low tide. The area experiences relatively moderate wind speeds (5.12 m/s) and precipitation (0.03 mm), coupled with a barometric pressure of 100.65 hPa. The air temperature averages 25.13°C, but the daily temperature range is wide (26.57°C), silty-sandy soil and high salinity (41.35–41.54%). Exposure to air leads to high desiccation, heat and light stress, due to high solar irradiance promoting compact growth. High salinity may causes osmotic stress, enhancing metabolite accumulation. Strong wind favors flexibility over elongation. Location NIOF II (27°17'6.48"N, 33°46'23.63"E) is placed near location I. It features a silty-sand intertidal platform at a depth range of 0.5–1.5m (submerged), with similar exposure and environmental parameters, including moderate relative humidity (52.64%) and wind speeds of 5.12 m/s and temperature, with high salinity (41.35–41.54%). However, there isn't air exposure at low tide. Stable submersion allows for better

elongation than location I and salinity stress persists but is mitigated by constant water cover. Locations III – and IV at Marsa Alam Beach (25°4'37.20"N, 34°53'43.44"E and 25°4'31.83"N, 34°53'48.36"E): This site transitions to a sandy intertidal shoal, located further south along the Marsa Alam coastline. The site is characterized by slightly calmer wind conditions (4.65 m/s) and higher relative humidity (63.97%), creating a relatively moist microclimate. It is known for the sandy substrate and moderate intertidal exposure with slightly lower salinity. The air temperature is higher (25.74°C), while the daily temperature range is narrower (17.63°C), indicating more heat stable conditions at central Red Sea. Location V at Wadi El Gemal (24°30'48.38"N, 35°8'23.70"E) is located in a marine protected area; this southernmost site is distinct in its lower wind speed (3.33 m/s) and lowest atmospheric pressure (97.76 hPa) among all sites. Despite having a similar mean air temperature (25.84°C), Site V exhibits the widest diurnal temperature range (34.74°C) and fluctuating salinity levels (38–40 PSU), likely due to the influence of nearby freshwater sources. This site may experience increased thermal stress and UV radiation, along with a high risk of evapotranspiration due to low humidity and high solar irradiance.

Temperature is a critical factor influencing photosynthesis and growth rates in seagrasses (Short *et al.*, 2011). An experimental study by Khalafallah *et al.* (2013) demonstrated that *Halodule uninervis* shows notable salinity tolerance, maintaining physiological integrity at salinity levels up to 45 PSU. Their findings revealed no visible damage or stress-related physiological indicators under these moderately hypersaline conditions. Additionally, *H. uninervis* prefers growing in sandy and silty soils (Al-Bader *et al.*, 2014).

Table 1. Environmental parameters of *Halodule uninervis* locations

Sites	NIOF		Mars Alam beach		Wadi El Gemal
	I	II	III	IV	V
locations					
Long.	27°17'3.92	27°17'6.48	25° 4'37.20	25° 4'31.83	24°30'48.38
Lat.	33°46'26.43	33°46'23.63	34°53'43.44	34°53'48.36	35° 8'23.70
PRECTOTCORR (mm)	0.03	0.03	0.02	0.02	0.03
PS (hPa)	100.65	100.65	100.94	100.94	97.76
WS2M (m/s)	5.12	5.12	4.65	4.65	3.33
RH2M (%)	52.64	52.64	63.97	63.97	43.5
T2M_RANGE (°C)	26.57	26.57	17.63	17.63	34.74
Mean Depth (m)	0.5>	1.5-0.5	1.5-0.5	1.5-0.5	1.5-0.5
Association	pure population				
Exposed to air	Yes	No	No	No	No
	intertidal	intertidal	intertidal	intertidal	intertidal
Salinity %	41.35	41.35	~38.65	~38.65	38 – 40
soil	silty-sand .	silty-sand	Sandy	Sandy	Sandy

Halodule uninervis morphology and abundance

Halodule uninervis is one of the six most commonly found seagrass species along the Egyptian Red Sea coast and shows a significant increase in abundance toward the southern Red Sea (**Geneid, 2009**). Significant variation in both morphological traits and abundance of *H. uninervis* was observed across five microhabitats within three intertidal sites along the Red Sea coast (Table 2 & Fig. 1).

Sites with the highest seagrass coverage—55–60% at NIOF II, Marsa Alam III, and IV—exhibited broader leaves, longer shoots (8.10–8.95 and 8.85cm, respectively), and longer roots (3.85, 5.33, and 5.30cm, respectively), along with lower shoot-to-root ratios (2.55, 1.93, and 1.78, respectively). These morphological characteristics suggest optimal growth conditions, likely resulting from a suitable temperature range, stable salinity, and adequate water depth (0.5 to 1.5m). These factors support healthy belowground biomass allocation, essential for anchorage and nutrient uptake (**Kenworthy & Fonseca, 1996; Terrados & Duarte, 2000**).

In contrast, sites I and V, which showed the lowest *H. uninervis* abundance (16–20%), had thinner leaves, shorter shoots (7.15–7.40 cm), shorter roots (2.40–2.45 cm), and higher shoot-to-root ratios (3.38–3.43). These traits reflect stress adaptations to extreme environmental conditions. Site I experiences high light intensity, thermal stress, and frequent air exposure due to shallow depth (<0.5 m), while Site V is subjected to salinity fluctuations and reduced water movement due to low wind activity. Such conditions likely induce combined thermal, light, and osmotic stress, leading to reduced root development and thinner leaves as a survival strategy (**Short & Neckles, 1999; Touchette & Burkholder, 2000**).

The observed morphological shifts correspond with abundance patterns, indicating that environmental stressors strongly influence the distribution of *H. uninervis*. High-abundance sites (II, III, IV) benefit from stable conditions—moderate temperature fluctuations, consistent salinity, and minimal human disturbance—which promote vegetative growth and meadow persistence. Conversely, low-abundance sites (I, V) face multiple stressors, including heat, desiccation, and salinity variability, which limit seagrass survival and productivity (**Zhang et al., 2023**).

These results are supported by **Bandeira and Paula (2014)**, who reported that *H. uninervis* leaf size increases with water depth, and canopy height is positively correlated with depth. Additionally, **Aiba and Kohyama (1997)** observed that leaf mass ratio (LMR), specific leaf area (SLA), and leaf area ratio (LAR) tend to decrease with increasing shoot height and decreasing light availability. **Kenworthy and Fonseca**

(1996) also noted that deeper rooting and lower shoot-to-root ratios are associated with long-term bed stability and resilience in healthy meadows.

However, short-term heat exposure and high light intensity during low tides can lead to dramatic increases in internal leaf temperature due to the poor heat conductivity of air, causing severe damage to seagrass tissues (Zhang *et al.*, 2023). According to Terrados and Duarte (2000), seagrass root development improves under stable sediment and salinity conditions, enhancing biomass and abundance.

Compared to other tropical seagrasses, *H. uninervis* demonstrates moderate to high heat tolerance (Campbell *et al.*, 2006). Nonetheless, the observed declines in abundance at Sites I and V suggest that even this resilient species has physiological thresholds. When surpassed, these thresholds can result in meadow degradation. Marine heatwaves and prolonged low-tide exposure have been shown to cause rapid biomass loss in other species such as *Amphibolis antarctica* (Fraser *et al.*, 2014) and *Zostera marina* (Jarvis *et al.*, 2014). While *H. uninervis* can acclimate to short-term environmental stressors, repeated or extended extremes may exceed its adaptive capacity, ultimately leading to meadow decline.

Table 2. Morphological traits of *H.uninervis* among the microhabitats studied along the Red Sea coast

	I	II	III	IV	V	F value
Leaves shape	Thin	Wide	Wide	Wide	Thin	-
Shoot length (cm)	7.15 ± 0.58	8.10 ± 1.10	8.95 ± 0.66	8.85 ± 0.31	7.40 ± 0.84	4.8*
Root length (cm)	2.40 ± 0.29	3.85 ± 1.55	5.33 ± 0.45	5.30 ± 0.48	2.45 ± 0.31	13.7***
Shoot/Root ratio	3.43 ± 0.57	2.55 ± 0.87	1.93 ± 0.25	1.78 ± 0.25	3.38 ± 0.51	8.2**

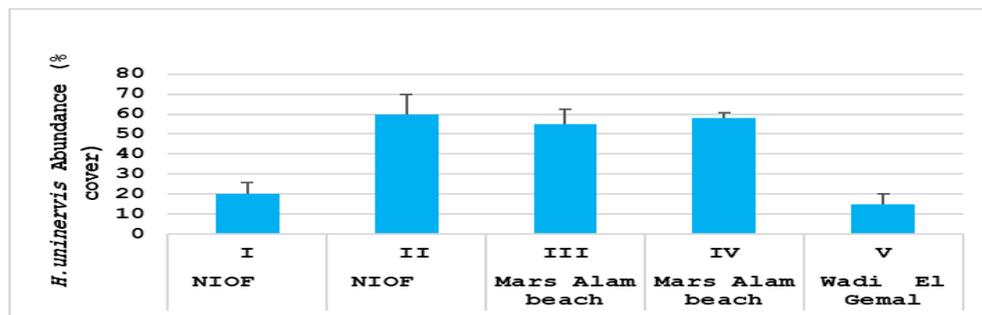


Fig. 1. *H.uninervis* abundance (% cover) in studied locations

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Molecular diversity analysis of *Halodule uninervis* populations at the five studied microhabitats using SCoT markers

Table 3. Primers used for SCoT analysis of *Halodule uninervis* cultivars

Primer Name	Sequences	Total Band	Monomorphic Band	Polymorphic band	Unique Band	Polymorphic %
SCoT 1	ACG ACA TGG CGA CCA CGC	10	3	7	1	70%
SCoT 3	ACG ACA TGG CGA CCC ACA	6	2	4	2	33.33%
SCoT 4	ACC ATG GCT ACC ACC GCA	7	1	6	1	85.71%
SCoT 5	CAA TGG CTA CCA CTA GCG	4	3	1	1	25%
SCoT 6	CAA TGG CTA CCA CTA CAG	4	1	3	0	75%
SCoT 7	ACA ATG GCT ACC ACT GAC	4	3	1	0	25.00%
SCoT 8	ACA ATG GCT ACC ACT GAG	4	3	1	-	25%
SCoT 10	ACA ATG GCT ACC ACC AGC	6	1	5	2	83.33%
SCoT 12	CAA CAA TGG CTA CCA CCG	7	2	5	1	71.43%
SCoT 15	CCA TGG CTA CCA CCG GCT	3	2	1	-	33.33%
Total		55	21	34	8	61.82%

Start Codon Targeted (SCoT) markers have demonstrated high efficiency in seagrass genetic studies due to their gene-targeted nature, which provides valuable functional genomic information (Collard & Mackill, 2009). These markers require no prior genomic knowledge, making them ideal for non-model species (Xiong *et al.*, 2011), and they exhibit higher reproducibility than Random Amplified Polymorphic DNA (RAPD) markers (Luo *et al.*, 2012). Their simplicity and reliability make SCoT markers particularly useful for assessing genetic diversity in non-model plant species such as seagrasses.

In this study, genetic diversity among *Halodule uninervis* individuals collected from five microhabitats was assessed using ten SCoT primers. As shown in Table (3), a total of 55 bands were generated, of which 34 (61.82%) were polymorphic—indicating considerable genetic variation among the sampled populations. This level of polymorphism is notably higher than the 42% reported in *Zostera marina* RAPD studies (Reusch *et al.*, 2000). Furthermore, eight unique bands were detected, suggesting location-specific genetic signatures and potential markers for local adaptation.

The genetic characteristics of conspecific seagrass populations often exhibit significant spatial heterogeneity. The variation observed in *H. uninervis* populations may result from several ecological and evolutionary factors. For example, **Franconi *et al.* (1995)** used eight RAPD primers to assess *Posidonia oceanica* populations in the Tyrrhenian Sea, identifying both species-specific and site-specific polymorphisms. Their study found genetic variation correlated with abiotic variables such as light intensity, photoperiod, and temperature—especially near anthropogenic stressors like coastal power plants. Similarly, microsatellite-based analyses by **Nguyen *et al.* (2014)** revealed strong genetic differentiation in *Halophila* species across the Western Pacific and Eastern Indian Ocean, shaped by ocean current-mediated dispersal barriers and historical isolation during Pleistocene sea-level fluctuations.

Among the primers used, SCoT 4 and SCoT 10 yielded the highest polymorphism levels (85.71% and 83.33%, respectively), indicating their effectiveness in distinguishing genetic differences among individuals. Conversely, SCoT 5, 7, and 8 showed lower polymorphism levels (25%), suggesting limited usefulness in capturing intraspecific variation in this context. SCoT 15 produced minimal variation. Overall, polymorphism percentages ranged from 25% to 85.71%, reflecting varying degrees of marker informativeness.

Pairwise genetic similarity values, based on Jaccard's coefficient, ranged from 0.54 to 1.00. As illustrated in Fig. (2), the dendrogram shows that locations I and V exhibited the highest genetic similarity (0.87), suggesting a strong genetic relationship potentially driven by similar environmental conditions. Both sites are characterized by shallow depths (<0.5m), high light intensity, and frequent air exposure, which may promote parallel adaptation to thermal and UV stress. Additionally, their similarity could be due to recent divergence or ongoing gene flow. Heat shock proteins (Hsps), which function as molecular chaperones, are known to play a crucial role in thermotolerance and the heat stress response in plants (**Guan *et al.*, 2014**).

High genetic similarity was also observed between locations II and IV (0.83), and most notably between III and IV (0.94), implying recent common ancestry or minimal genetic divergence likely due to environmental stability and possible gene flow. In contrast, the greatest genetic differentiation was found between locations IV and V (similarity = 0.54), highlighting the influence of environmental heterogeneity and microhabitat-specific selective pressures.

These findings underscore the pivotal role of environmental stressors and microhabitat variability in shaping adaptive genetic diversity in *H. uninervis*. As **Lorenzana (2019)** noted, such data are essential in population structure analyses, phylogenetic studies, and genetic diversity assessments. High genetic similarity typically

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indicates gene flow or shared habitat conditions, while low similarity suggests adaptive divergence or distinct ecological constraints.

In conclusion, SCoT markers proved highly effective and reproducible in detecting genetic diversity in *H. uninervis*. The high polymorphism levels, especially from SCoT 4 and 10, highlight substantial genetic variation that underpins adaptability to environmental stress. The presence of unique bands suggests site-specific genetic adaptations, likely driven by localized selective pressures. These patterns are consistent with broader evidence that environmental variability can drive genetic divergence in seagrass populations, influencing their resilience and long-term persistence.

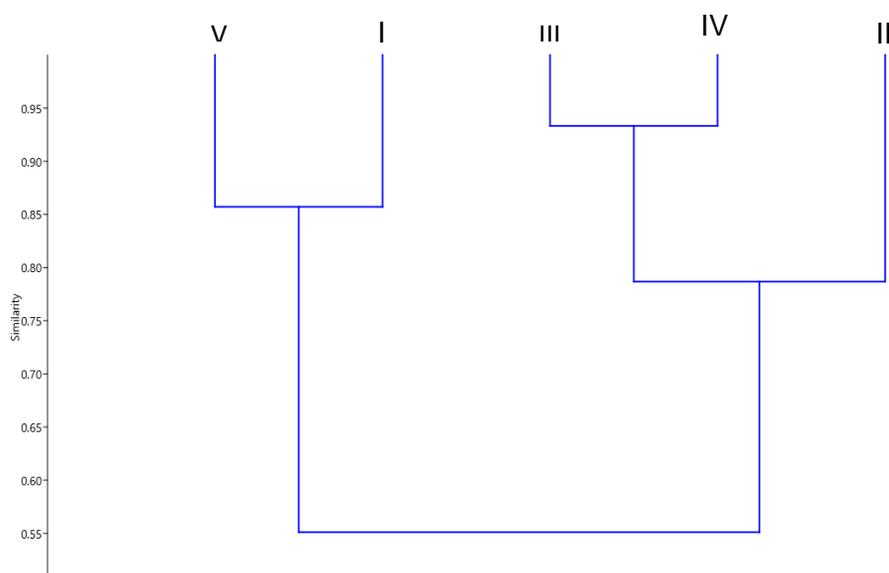


Fig. 2. Dendrogram of *H.uninervis* at the five studied microhabitats depending SCoT

Chemically classified secondary metabolites in both composite sample 1 (location I and V) and sample 2 (Locations II, III and IV) of *Halodule uninervis*

The GC-MS profiling of both *Halodule uninervis* composite samples (I and V) and (II, III, and IV) revealed a diverse array of secondary metabolites. To select the composite samples for GC-MS analysis based on the morphogenetic similarities among the sites, the following criteria were considered. Sample 1 had a greater diversity of phenolic and derivative compounds (26 vs. 18 compounds) and a longer cumulative

retention time (17.5 vs. 15 minutes), indicating higher biochemical complexity. These compounds can be chemically classified into several key groups, each contributing to the plant's physiological and ecological adaptation.

The comparative data between Sample 1 (similar habitat pressures, such as thermal variability and UV radiation exposure as a result of frequent air exposure in low-depth (<0.5 m) habitats; high light intensity at site I; and lower wind with high solar irradiance and air exposure in site V, leading to parallel adaptation) and Sample 2 (moderate-depth sites with stable salinity and temperature) highlight both overlapping and site-specific compounds, reflecting biochemical responses to differing microhabitat stressors.

Sugars and sugar alcohols

Sugars such as sucrose, D-psicofuranose, D-mannopyranose, and ribose serve essential osmoprotectant functions, aiding in osmoregulation and maintaining cellular turgor during environmental stresses (**Singh *et al.*, 2015; Pamuru *et al.*, 2021**). Inositol derivatives (muco-/myo-) and ribitol are key in signal transduction and osmotic adjustment, respectively (**Siracusa *et al.*, 2022**). Glucopyranose and erythritol, detected in Sample 1, suggest energy provisioning and stress mediation under heat stress. Notably, sucrose and D-psicofuranose showed higher abundance in Sample 2, suggesting enhanced carbohydrate accumulation under moderate-depth, possibly more nutrient-rich or stable conditions.

Fatty acids

Fatty acids like palmitic, oleic, stearic, and linolenic acids contribute to membrane integrity and adaptability to thermal fluctuations. Sample 2 shows enrichment in alpha-linolenic acid and palmitic acid, correlating with enhanced antioxidant production and improved membrane fluidity under moderate stress conditions (**Xue *et al.*, 2017; Narayanan, 2021**). Behenic acid, found mainly in Sample 1, reinforces protective wax formation to minimize water loss.

Phenolic acids and antioxidants

Phenolic compounds such as sinapinic acid, caffeic acid, and 3,5-dihydroxybenzoic acid are critical in mitigating oxidative stress via ROS scavenging (**Gong & Zha, 2023; Du *et al.*, 2024**). Their occurrence in both samples reflects a baseline antioxidant defense. Sinapinic acid's higher presence in Sample 1 than Sample 2 implies that Sample 1 has well-documented antioxidant and UV-protective roles under thermal stress (**Nićiforović & Abramović, 2014; Guo *et al.*, 2024**). This phenolic is typically upregulated in response to oxidative stress and is crucial in shallow marine ecosystems.

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Sterols

Sterols like campesterol and β -sitosterol help maintain membrane stability and regulate stress response. Detected only in Sample 1, they could be adaptations to higher temperatures and desiccation stress (Alharbi *et al.*, 2023; Nokhsorov *et al.*, 2024).

Hydrocarbons

Long-chain alkanes such as eicosane and pentacosane act as protective surface waxes, reducing water loss (Wang, 2000; Zuo *et al.*, 2023). Their varied presence across samples suggests environmental modulation of surface lipid biosynthesis (Batsale *et al.*, 2021).

Organic acids and esters

Organic acids like gulonic acid and oxalic acid function as antioxidants or metal chelators. Gulonic acid, a precursor to ascorbate, highlights enhanced oxidative buffering in Sample 2 (Smirnoff & Stewart, 1985). Esters, such as sulfurous acid derivatives, indicate possible unique metabolic pathways or environmental screening functions.

Aromatic/volatile compounds

Volatile organics like substituted benzene and pyridine derivatives may play roles in allelopathy or plant signaling. Sample 1 features these more prominently, aligning with stress-induced secondary metabolism (Bais *et al.*, 2003).

Alkaloids and miscellaneous compounds

Lysergide, an ergot-related alkaloid, was detected in Sample 2. A beta-alanine derivative in Sample 1 likely reflects stress-triggered nitrogen metabolism; this result is supported by Khan *et al.* (2019).

Disaccharides and oligosaccharides

Oligosaccharides such as mannobiose serve structural or signaling roles and were prominent in Sample 2, indicating advanced carbohydrate-based adaptive strategies (Couée *et al.*, 2006).

Ketones/Terpenoids

Compounds like substituted naphthalenones may act in defense signaling (Kumar *et al.*, 2025), with their presence in Sample 2 suggesting niche-specific chemical communication.

This classification reveals clear biochemical distinctions aligned with environmental variability. Sample 1, representing a hotter, shallower microhabitat, shows enrichment in sterols, hydrocarbons, and stress-responsive volatiles. Sample 2 reflects

greater accumulation of osmoprotective sugars, antioxidants, and signaling molecules, implying a more balanced or nutrient-rich environment promoting complex metabolic responses. Such insights reinforce the role of metabolomics in revealing plant ecological adaptation mechanisms, supporting their use in marine conservation and stress physiology.

Table 4. Chemically classified secondary metabolites in both composite samples (I and V) and (II, III and IV) of *Halodule uninervis*

Chemical Class	Compound Name	Sample
Sugars and Sugar Alcohols	Sucrose, 8TMS derivative	Both (1 - 2)
	D-Psicofuranose, pentakis(TMS) ether	Both (1 - 2)
	D-Mannopyranose, 5TMS derivative	2
	D-Ribose, 4TMS derivative	2
	Muco-/Myo-Inositol, 6TMS derivative	2
	Ribitol, 5TMS derivative	1
	Glucopyranose, 5TMS derivative	1
	Erythritol, 4TMS derivative	1
Fatty Acids	Palmitic Acid, TMS derivative	Both (1 - 2)
	Alpha-Linolenic Acid, TMS derivative	2
	Linoelaidic Acid, TMS derivative	Both (1 - 2)
	Oleic Acid, TMS derivative	1
	Stearic Acid, TMS derivative	1
	Behenic Acid, TMS derivative	1
Phenolic Acids and Antioxidants	Sinapinic acid, 2TMS derivative	Both (1 - 2)
	Caffeic acid, 3TMS derivative	2
	3,5-Dihydroxybenzoic acid, 3TBDMS	1
Sterols	Campesterol, TMS derivative	1
	β -Sitosterol, TMS derivative	1
Hydrocarbons	Eicosane / Pentacosane / Heneicosane / Hexacosane, 9-octyl	Both (1 - 2)
Organic Acids and Esters	Gulonic acid, γ -lactone	2
	Oxalic acid, isobutyl hexyl ester	1
	Sulfurous acid, 2-propyl tetradecyl ester	1
Aromatic/Volatile Compounds	Benzene, 4-ethenyl-1,2-dimethyl-	1
	Pyridine, 2-hydroxy-3-chloro-	1
Alkaloids/Other	Lysergide, TMS derivative	2
	N-Substituted β -alanine derivative	1
Disaccharides/Oligosaccharides	3- α -Mannobiose, octakis(TMS), methyloxime	2
Ketones/Terpenoids	7-Isopropenyl-1,4a-dimethyl-4,4a,5,6,7,8-hexahydro-3H-naphthalen-2-one	2

CONCLUSION

This study provides a comprehensive assessment of *Halodule uninervis* adaptive strategies across diverse intertidal microhabitats along the Egyptian Red Sea coast. By integrating morphological, genetic, and biochemical analyses, we demonstrate that this *H.*

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uninervis exhibits distinct but effective responses to environmental stress. Morphologically, populations in high-stress sites (e.g., extreme salinity or temperature) developed shorter shoots and roots with narrow leaves and low abundance, enhancing stress tolerance. In contrast, populations in more stable habitats exhibited longer shoots and roots with broader leaves and high abundance to optimize light capture and resource use. Genomic analyses revealed unexpected genetic convergence between geographically distant, shallow high-stress populations of NIOF (I) and Wadi El Gemal (V), likely driven by parallel selective pressures such as high irradiance, frequent aerial exposure, and thermal variability. These conditions may promote similar adaptive mechanisms, potentially mediated by conserved stress-response pathways like heat shock protein regulation. Notably, population Wadi El Gemal (V), as the southernmost, displayed a dual genetic identity—sharing traits with distant stress-adapted populations while remaining genetically distinct from its neighbor Marsa Alam (IV), indicating localized selection and microhabitat-specific adaptation. In contrast, genetically uniform patterns among adjacent populations of NIOF (II), Marsa Alam (III), and Marsa Alam (IV) reflect environmental stability, limited divergence, or ongoing gene flow. Biochemically, stressed populations invested more in phenolic compounds and hydrocarbons for defense, while stable habitats showed higher levels of osmoregulatory metabolites such as specific carbohydrates and sinapinic acid. These findings emphasize how both geographic distance and microhabitat variation interplay to sculpt morphogenetic and biochemical diversity, underscoring the need to consider fine-scale habitat differences when assessing resilience and conservation value in marine plant populations. These insights are crucial for informing conservation and management strategies in the face of climate change. Future research should: expand to seasonal variations, incorporate transcriptomics to link genetic markers to functional adaptations, test transplant experiments to validate adaptive potential. This work establishes a framework for understanding seagrass resilience, providing critical insights for coastal ecosystem management in warming seas.

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