

Article

Evaluation of Substrate and Nutrient Management Effects on Halophyte Cultivation: *Salicornia bigelovii*, *Sesuvium portulacastrum*, and *Batis maritima*

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Highlights

What are the main findings?

- Floating raft substrate produced a greater biomass than clay beads, especially for glasswort and sea purslane.
- Nutrient enrichment was associated with a higher sea purslane yield and with biomass reallocation in glasswort and saltwort, though nutrient and arrangement effects could not be fully separated in this sequential design.

What are the implications of the main findings?

- Cultivation strategies should tailor the substrate and nutrients to each halophyte species.
- Low-cost, effluent-fed raft systems show potential in supporting saline food production in coastal areas, pending validation across multiple sites and systems.

Abstract

Halophyte crops offer a promising solution for food production and nutrient recovery in salt-affected coastal environments where conventional agriculture is increasingly constrained; yet, the cultivation performance of edible halophytes remains strongly influenced by the substrate configuration and nutrient management. This study evaluated, across three sequential experiments, how the substrate type (shallow floating raft versus expanded clay beads) and nutrient regime were associated with biomass production and allocation in three halophyte species, *Salicornia bigelovii* (glasswort), *Sesuvium portulacastrum* (sea purslane), and *Batis maritima* (saltwort), cultivated in a recirculating raceway system at the Naguabo Aquaculture Center, Puerto Rico, across three sequential experiments: no nutrient addition, nutrient-managed mixed culture (N:P = 4:1), and nutrient-managed species-separated culture. Floating raft substrate consistently enhanced the total biomass and productivity over clay, for glasswort and sea purslane in the two experiments where the substrate could be formally tested at the tank level (effect sizes that are large to extremely large), while saltwort showed no significant substrate effect in either; a consistent raft advantage was also observed descriptively under species-separated culture, though the confounded design of that experiment did not permit formal statistical testing. Nutrient management was associated with species-specific effects: sea purslane total and edible biomass were higher under enrichment; glasswort edible fractions remained stable while the total biomass was lower, indicating allocation shifts rather than yield gains; and saltwort biomass was higher under enrichment, though this increase was not statistically significant under species-separated culture. These findings indicate that halophyte productivity was associated with



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the substrate configuration, nutrient context, and species-specific physiology, with floating raft systems showing a consistent biomass advantage over clay within this system and nutrient strategies warranting species-specific tailoring.

Keywords: halophyte crops; saline agriculture; shallow floating raft system; nutrient stoichiometry; edible biomass allocation; hydroponics

1. Introduction

Global food production is increasingly constrained by the soil salinization, freshwater scarcity, and climate-driven degradation of coastal agricultural lands, pressures that already affect more than 800 million hectares worldwide and are expected to intensify in the coming decades [1,2]. These trends challenge the long-term viability of conventional agriculture and underscore the need for alternative cropping systems capable of functioning in saline and marginal environments [3,4].

Halophytes, plants naturally adapted to high salinity, have emerged as promising candidates for sustainable food and bioresource production under these conditions. Beyond their ability to tolerate seawater-level salinities, halophytes can provide multiple ecosystem services, including nutrient recovery from saline effluents, soil rehabilitation, carbon sequestration, and biodiversity support [5–8]. These attributes position halophytes at the intersection of saline agriculture, wastewater management, and integrated aquaculture/aquaponics systems.

Among edible halophytes, glasswort, sea purslane, and saltwort have received increasing attention due to their exceptional salinity tolerance, nutritional value, and functional versatility. Glasswort is among the most salt-tolerant vascular plants, with optimal performance reported between 200 and 400 mM NaCl [9,10], and is valued as a gourmet vegetable rich in minerals and antioxidant and anti-inflammatory properties [11,12].

Sea purslane, a facultative halophyte widely distributed in tropical and subtropical coastal regions, combines rapid biomass accumulation with a strong phytoremediation capacity, and its succulent tissues are nutritionally valuable [8,13,14].

In contrast, saltwort remains less domesticated but exhibits remarkable tolerance to saline and nutrient-poor coastal soils, with seed oils of interest for novel oilseed and coastal land reclamation [15].

Optimizing halophyte cultivation in controlled or semi-controlled systems requires the careful management of both substrate characteristics and nutrient regimes. Unlike glycophytic crops, halophytes often achieve maximum growth under moderate salinity, reflecting the adaptive mechanisms of ion regulation and osmotic balance [16]. Substrate properties such as porosity, water retention, and aeration play a critical role in regulating root development and nutrient exchange, thereby influencing biomass accumulation [17]. Floating raft and expanded-media-bed configurations differ substantially in this regard: raft systems place roots in direct, continuously oxygenated contact with the nutrient solution, whereas granular media can physically constrain root expansion and create localized zones of ion accumulation, with direct implications for nutrient uptake efficiency and biomass accumulation. For example, deep-water hydroponic systems have been shown to outperform nutrient film techniques for glasswort biomass production while enhancing nutrient recovery efficiency [10], and organic amendments can further influence productivity and secondary metabolite accumulation under saline conditions [2,18].

Nutrient management represents an additional layer of complexity in halophyte systems. Salinity alters the nutrient uptake, assimilation, and internal partitioning, often

resulting in species-specific responses to nitrogen and phosphorus availability. Nitrogen form can strongly influence the halophyte growth and tissue composition, with ammonium nutrition sometimes promoting a higher biomass and reduced accumulation of anti-nutritional compounds relative to nitrate, although responses vary among taxa and salinity regimes [19,20].

Phosphorus frequently limits productivity in saline environments, with glasswort requiring relatively high tissue phosphorus concentrations to sustain optimal growth [21]. Micronutrients such as iron, manganese, and molybdenum also play critical roles in maintaining photosynthetic efficiency and enzymatic activity under salt stress [22].

Importantly, halophyte responses to salinity and the nutrient supply often conform to the concept of eustress, whereby moderate environmental stress enhances the accumulation of phenolics, flavonoids, carotenoids, and polyunsaturated fatty acids without severely constraining growth [23,24]. This dual capacity for stress tolerance and improved nutritional quality underscores the potential of halophytes as multipurpose crops in sustainable food and bio-based production systems.

Despite this potential, substantial knowledge gaps remain regarding how the substrate configuration and nutrient management interact to influence biomass production and allocation in edible halophytes, especially when they are grown near or alongside aquaculture facilities. Addressing these gaps is essential for scaling halophyte cultivation in salt-affected regions and for optimizing their integration into nutrient-managed coastal production systems. Specifically, it remains unclear how the substrate configuration and nutrient regime jointly shape not only the total biomass yield but also the allocation of biomass to edible tissue, information needed to translate cultivation-system design into harvestable marketable product.

Glasswort, sea purslane, and saltwort were chosen because, together, they capture meaningful diversity in growth form, salinity tolerance, and functional role within edible halophyte production systems, and all three species have been documented in Caribbean and broader neotropical coastal environments, making them ecologically relevant candidates for regional saline food production systems.

This study evaluated how the substrate type, specifically the shallow floating raft versus expanded clay beads, and nutrient regime shape biomass production and edible tissue allocation across these species in a recirculating raceway system, with the aim of identifying practical cultivation strategies for the integration into saline agriculture and aquaculture-based production systems in salt-affected coastal regions.

2. Materials and Methods

2.1. Study Site and Experimental System

The study was conducted at the Naguabo Aquaculture Center (NAC), located at the Naguabo Fishing Association in Húcares Beach, Puerto Rico from 14 January 2024 to 27 February 2025. A single recirculating cultivation system was used throughout the experiments, consisting of six shallow raceway tanks ($188 \times 66 \times 15$ cm) connected to a circular sump (152 cm diameter $\times$ 22.86 cm depth) with a working system volume of approximately 757 L (Figure 1). The system was initially filled with filtered seawater pumped from Naguabo Bay and operated under full recirculation for the duration of the study with fresh water or saltwater added to maintain salinity. The working water depth in the raceway tanks was maintained at approximately 10 cm using a standpipe, and circulation was provided by a Supreme Aqua-Mag Model 2400 magnetic drive pump operating at 120 V and 237 W with 1-inch inlet and outlet connections.



Figure 1. Experimental layout of recirculating hydroponic system for halophyte cultivation under ambient conditions at the Naguabo Aquaculture Center, Naguabo, Puerto Rico.

Two substrate types were evaluated in the system: shallow floating raft and expanded clay beads. Plant material consisted of vegetative cuttings of sea purslane and saltwort, while glasswort was germinated from seed. Initial planting material consisted of sea purslane and saltwort cuttings with an average wet weight of 2 g per cutting, while glasswort was propagated from seed. Plants were maintained in nursery tanks until established and transferred to the experimental units. Glasswort seedlings were transplanted when the first two leaves and roots were evident, at an approximate wet weight of 1 g.

2.2. Experimental Design

Three sequential experiments were conducted to evaluate substrate and nutrient regime effects under controlled cultivation conditions. A total of six tanks were used, each stocked with 18 plants within the tank. Three tanks were assigned to the shallow floating raft substrate and three tanks to the expanded clay beads substrate.

Experiment 1 (14 January–25 March 2024; 10.3 weeks) evaluated substrate effects in the absence of nutrient supplementation, as nutrient inputs during the experimental period were negligible. All three species were co-cultured within each raceway, and environmental conditions were maintained uniformly across treatments. The three plant species were mixed randomly within each tank with six plants of each species per tank. Salinity averaged 16.17 ± 1.81 ppt throughout the duration of the experiment.

Experiment 2 (3 May–6 August 2024; 13 weeks) evaluated substrate effects under nutrient-enriched conditions. A nutrient solution prepared from the commercial products FloraPro Calcium + Micros (14-0-0) and Liquid KoolBloom (0-10-10) were added weekly to maintain a target nitrogen-to-phosphorus (N:P) ratio of 4:1.

The amount of fertilizer added each week was not fixed; it was calculated from that week's water quality readings for ammonia, nitrite, nitrate, and phosphate, using the difference from the 4:1 N:P target to set the addition. Averaged over the study period, this was 23.8 g FloraPro Calcium + Micros (14-0-0) and 14.5 mL Liquid KoolBloom (0-10-10)

per week, supplying approximately 3.3 g nitrogen and 0.8 g phosphorus per week. The KoolBloom volume is based on an estimated density of 1.32 g/mL derived from the product's listed packaged weight since the manufacturer does not publish a specific gravity. The same was applied throughout Experiment 2 and Experiment 3, totaling approximately 309 g FloraPro Calcium + Micros and 188 mL Liquid KoolBloom per 13-week experiment. Species were co-cultured and randomly assigned to planting positions to minimize positional effects. Each substrate treatment was replicated in three tanks (six tanks total), with 18 plants per tank (108 plants total). Salinity was kept at around 15 ± 3.21 ppt throughout the experimental period.

Experiment 3 (27 November 2024–27 February 2025; 13 weeks) was conducted under the same nutrient regime as Experiment 2, but with each species cultured separately. Each tank contained a single species using both substrate treatments. Plant density remained constant (18 plants per tank), and salinity was maintained at approximately 30 ± 2.01 ppt.

The experiments were conducted sequentially rather than as a fully factorial design; consequently, treatment effects associated with nutrient regime, plant arrangement, salinity and experimental timing are confounded and cannot be fully decoupled from one another. In addition, all six tanks were connected to a single common recirculating system and sump (Section 2.1), so water chemistry and other system-level factors were shared across tanks and are not fully independent even when the tank is used as the experimental unit. Comparisons across experiments should therefore be interpreted as informative system-level responses rather than strictly controlled causal tests, a limitation carried through the interpretation of results and discussion below.

2.3. Water Quality Monitoring and Biomass Measurements

Water quality was monitored throughout the experimental period to ensure comparable growing conditions across treatments. Temperature, pH, and salinity were recorded daily. pH was measured using a YSI EcoSense® pH10A pen-style meter (YSI Inc., Yellow Springs, OH, USA), and salinity was determined using a Vee Gee BTX-1 handheld optical refractometer (Vee Gee Scientific, Kirkland, WA, USA). Oxidation-reduction potential (ORP) was measured weekly with an YSI EcoSense® ORP15A pen-style meter (YSI Inc., OH, USA). Dissolved nutrient concentrations, including ammonia-N, nitrite-N, nitrate-N, phosphate, alkalinity, calcium, and magnesium, were quantified weekly using a YSI EcoSense® 9300 portable photometer (YSI Inc., OH, USA) and a LaMotte WaterLink® Spin Touch® centrifugal fluidics photometer (LaMotte Company, Chestertown, MD, USA). At the end of each experimental period, plants were harvested individually and weighed to determine total fresh biomass.

Edible biomass was quantified by separating and weighing marketable shoot and/or leaf tissue, allowing calculation of total biomass, edible biomass, and edible fraction (edible biomass divided by total biomass). Marketable tissue was defined as succulent leaves and tender shoots for sea purslane and succulent above-ground shoots for saltwort and glasswort. Any stem or shoot tissue that became woody or lignified was considered non-marketable and excluded from total edible biomass. These criteria were applied consistently across substrate and experiment. Biomass productivity was calculated as total or edible harvest biomass divided by the number of cultivation days in the corresponding experiment.

2.4. Statistical Analyses

Water quality data were presented as means $\pm$ standard deviation (SD) to describe how conditions varied over time, while biomass and productivity data were presented as means $\pm$ standard error (SE) to reflect variability among biological replicates within each treatment.

Substrate effects were evaluated separately for each species and experiment using one-way analysis of variance (ANOVA), with substrate treated as a fixed factor. Because substrate was assigned at the tank level (Section 2.2), the tank was treated as the experimental unit for substrate comparison in Experiment 1 and 2, with individual plant measurements aggregated to a mean per tank prior to analysis. In Experiment 3, each species-by-substrate combination was represented by a single tank, so substrate and tank were fully confounded; substrate comparisons for Experiment 3 are therefore reported descriptively and were not subjected to inferential statistical testing. Effect sizes were calculated using Cohen's d and eta squared (η^2) to quantify the magnitude and biological relevance of substrate effects where inferential testing was possible [25].

Because the three experiments differed simultaneously in nutrient regime, plant arrangement, salinity, and time (Section 2.2) between experiments, comparisons cannot isolate a single causal factor. Two planned comparisons were nonetheless examined descriptively, rather than a fully crossed factorial design [26]: Experiment 1 (without intentional nutrient supplementation) versus Experiment 2 (nutrient-enriched conditions), reported as broadly associated with nutrient addition; and Experiment 2 (mixed species) versus Experiment 3 (species separated), reported as broadly associated with plant arrangement. These are reported as associations rather than isolated effects.

For analyses involving nutrient addition or plant arrangement, the tank was likewise treated as the experimental unit to avoid pseudo-replication [27]. Individual plant measurements were aggregated to generate mean per tank for each species and substrate combination.

Total biomass and edible biomass were log-transformed using $\ln(1 + x)$ to improve normality and homoscedasticity. Edible fraction, a proportional variable bounded between 0 and 1, was analyzed using a standard logit transformation appropriate for proportional data [28]. All edible-fraction values reported in the text, tables, and figures are back-transformed and expressed on the original 0–100% scale; the logit transformation was used only internally for significance testing. Model assumptions were evaluated using residual diagnostics. Statistical significance was assessed at $\alpha = 0.05$, and results are reported using F-statistics, p -values, and partial eta squared (η^2). All analyses were conducted in R (version 4.4.2; R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

3. Results

3.1. Water Quality Conditions

Water quality conditions varied among experiments but remained within defined operational ranges throughout the study (Table 1). Across all experiments, pH values were slightly alkaline, and temperature remained within ranges suitable for halophyte growth.

Table 1. Water quality conditions during experimental trials. Mean, standard deviation (SD), minimum, and maximum values of water quality parameters measured during Experiment 1 (no nutrient addition, mixed plant culture), Experiment 2 (nutrient addition, mixed plant culture), and Experiment 3 (nutrient addition, plant species separated). Temperature is reported in °C, salinity in parts per thousand (ppt), oxidation–reduction potential (ORP) in millivolts (mV), nutrient concentrations in parts per million (ppm), and alkalinity in ppm as CaCO_3 .

Experiment 1	pH	Temperature (Celsius)	Salinity (ppt)	ORP (mV)	Ammonia (ppm)	Nitrite (ppm)	Nitrate (ppm)	Phosphate (ppm)	Alkalinity (ppm)
Mean	8.13	25.46	16.17	139.18	0.04	0.03	1.51	1.14	114.95
SD	0.24	1.55	1.81	18.30	0.03	0.03	0.29	0.65	27.69
Max	8.7	29.2	20.0	173.0	0.09	0.09	1.9	1.9	183.0
Min	7.3	21.6	13.0	121.0	0.0	0.0	1.02	0.05	79.3

Table 1. Cont.

Experiment 1	pH	Temperature (Celsius)	Salinity (ppt)	ORP (mV)	Ammonia (ppm)	Nitrite (ppm)	Nitrate (ppm)	Phosphate (ppm)	Alkalinity (ppm)
Experiment 2									
Mean	7.85	29.8	14.3	100.6	0.1	0.0	2.8	0.8	54.0
SD	0.30	1.28	3.21	10.60	0.07	0.05	6.58	0.68	31.72
Max	8.48	33.2	26.0	123.0	0.2	0.2	25.0	2.0	95.0
Min	6.94	25.6	8.0	82.0	0.0	0.0	0.0	0.2	0.0
Experiment 3									
Mean	8.13	25.90	29.72	93.70	0.03	0.04	3.78	0.83	97.22
SD	0.18	1.09	2.01	4.16	0.05	0.07	5.29	0.71	11.54
Max	8.38	27.90	35.00	99.00	0.10	0.20	14.00	2.10	126.00
Min	7.78	24.20	27.00	86.00	0.00	0.00	0.00	0.20	88.00

Experiment 1 was characterized by a moderate temperature and salinity, higher oxidation–reduction potential, and low inorganic nitrogen concentrations. Experiment 2 exhibited higher temperatures, a greater salinity variability, and a lower oxidation–reduction potential, with nitrate showing greater temporal variability. Experiment 3 was conducted under higher salinity conditions, while temperature and pH remained relatively stable. Across experiments, ammonia and nitrite concentrations remained low, and alkalinity varied with the nutrient management regime (Table 1). Notably, the measured water-column phosphate remained modestly higher in the unenriched Experiment 1 (1.14 ppm) than in the nutrient-enriched Experiments 2 and 3 (means of 0.80 and 0.83 ppm, respectively), while nitrate rose from 1.51 ppm in Experiment 1 to 2.80 ppm in Experiment 2 consistently with the added nutrient load. This does not indicate an error in treatment assignment; nutrients were dosed weekly at a fixed N:P ratio (Section 2.2) to the target loading, and the weekly photometer readings in Table 1 capture the standing water-column concentration after the uptake by plants and associated microbial communities, not the applied dose itself; phosphate in particular can be rapidly assimilated or taken up within a small, actively growing recirculating system, so a somewhat lower standing phosphate concentration in the enriched experiments is consistent with efficient uptake rather than a reduced nutrient input.

3.2. Plant Growth Performance

Within each experiment, the raft versus clay substrate comparison is the only comparison in this section that isolates a single factor; the comparison across experiments reflects the combined, non-factorial shift in the nutrient regime, plant arrangement, salinity, and time described in Section 2.2, and is reported descriptively. Values in this section and in Figures 2–4 are treatment totals (summed across $n = 3$ tanks per substrate in Experiments 1–2; single-tank values in Experiment 3). Glasswort exhibited clear substrate-dependent differences in biomass production across all experimental conditions. In Experiment 1, raft-cultivated plants yielded a substantially greater total biomass (641 g) compared with clay-grown plants (326 g), with edible fractions of 81% and 75%, respectively. Following nutrient supplementation under a mixed-species culture (Experiment 2), the total biomass declined for both substrates relative to Experiment 1, reaching approximately 373 g for the raft and 274 g for the clay, while the edible fractions remained high, and similar to Experiment 1, at 80% and 74%, respectively. Under a monoculture with nutrient enrichment (Experiment 3), the total biomass declined further, particularly on clay (105 g), whereas raft-grown plants maintained a moderate production (319 g). Notably, the edible fractions reached their highest values across all treatments in this experiment, exceeding 95% under both substrate types (Figure 2).

Sea purslane yielded the highest total biomass among the three species, with pronounced substrate and treatment effects throughout. In Experiment 1, raft-cultivated plants produced 5820 g total biomass with a 45% edible fraction, while clay-grown plants yielded considerably less (1225 g) but a higher edible proportion (52%). Nutrient supplementation under a mixed-species culture (Experiment 2) drove a marked increase in the total biomass for raft conditions (9162 g), though the edible fraction declined slightly to 37%; clay substrate plants showed a similarly strong biomass response (4766 g) with an edible fraction of 38%. Under a monoculture with nutrient enrichment (Experiment 3), the total biomass declined substantially under both substrates, to approximately 2258 g on raft and 340 g on clay, while edible fractions increased modestly to 51% and 61%, respectively (Figure 3).

Saltwort displayed a distinctly different growth pattern from the other two species, with the total biomass increasing progressively across experiments rather than declining. In Experiment 1, biomass production was low under both raft (143 g) and clay (123 g) substrates, with edible fractions of 69% and 72%, respectively. Following nutrient supplementation under a mixed-species culture (Experiment 2), the total biomass increased moderately for both substrates, reaching approximately 429 g for the raft and 470 g for the clay, with edible fractions of 74% and 72%, respectively. The most substantial growth response was observed under a monoculture with nutrient enrichment (Experiment 3), where raft-cultivated plants reached approximately 993 g total biomass with an 85% edible fraction, while clay-grown plants produced approximately 427 g with an edible fraction of 82% (Figure 4).

3.3. Biomass Productivity

The total harvested biomass productivity and edible biomass productivity differed markedly among species, substrates, and experiments (Table 2).

Table 2. Biomass productivity across substrates and experiments. Total harvested biomass productivity and edible biomass productivity (wet weight, g day^{−1}) of glasswort, sea purslane, and saltwort grown in clay and floating raft substrates across experimental trials. Significance of substrate effect on total harvested biomass tested at the tank level (see Table 3) is indicated by superscript next to the raft value. Total and edible wet biomass productivity were calculated as total and edible wet biomass harvested divided by the number of cultivation days in the corresponding experiment (g day^{−1}).

		Total Wet Harvested Biomass Productivity (Wet wt g/day)		Total Wet Edible Biomass Productivity (Wet wt g/day)	
	Plant	Clay	Raft	Clay	Raft
Experiment 1	Glasswort	4.59	9.03 **	3.42	7.31
	Sea purslane	17.25	81.97 *	9.01	37.25
	Saltwort	1.73	2.01 NS	1.25	1.39
Experiment 2	Glasswort	2.88	3.93 *	2.14	3.13
	Sea purslane	50.17	96.44 *	19.01	35.27
	Saltwort	4.95	4.52 NS	3.58	3.33
Experiment 3	Glasswort	1.14	3.47 NT	1.09	3.34
	Sea purslane	3.70	24.54 NT	2.25	12.58
	Saltwort	4.64	10.79 NT	3.83	9.14

NS = nonsignificant ($p > 0.05$). * Significant at $p \leq 0.05$. ** Significant at $p \leq 0.01$. NT = not tested; Experiment 3 provided only one tank per substrate per species combination, so substrate is confounded with tank, and no valid significance test exist (see Table 3).

Glasswort (*Salicornia bigelovii*)

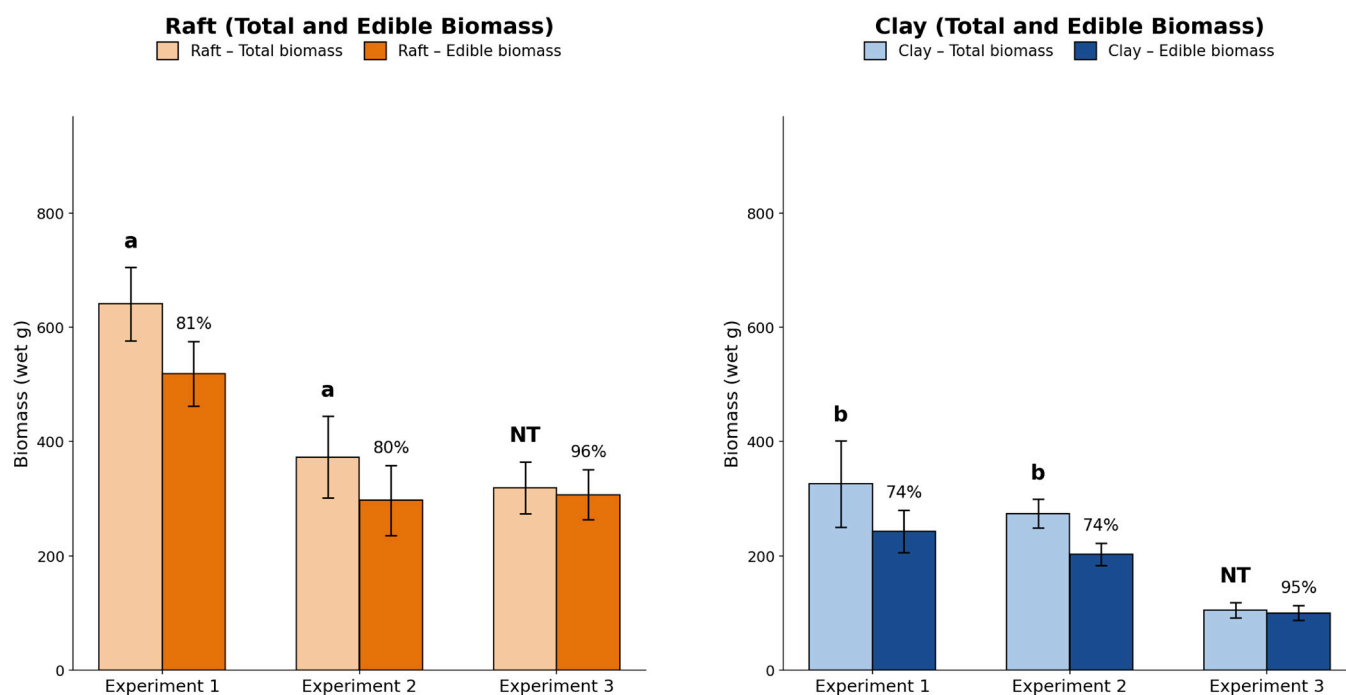


Figure 2. Total and edible wet biomass of glasswort (*Salicornia bigelovii*) grown on raft and clay substrates across three sequential production experiments. Bars show total biomass (light shading) and edible biomass (dark shading) per substrate; error bars represent $\pm$ SE. Values above the edible-biomass bars indicate the percentage of total biomass classified as edible. Lowercase letters above the total-biomass bars denote statistical comparisons between substrates in Experiment 1 and 2 only (one-way ANOVA) using the tank as the experimental unit (see Table 3 for exact n and degrees of freedom); bars sharing the same letter are not significantly different ($p > 0.05$), while differing letters indicate a significant difference ($p < 0.05$). Experiment 3 bars are labeled “NT” (not tested): that experiment provided only one tank per substrate per species combination, so substrate is fully confounded with tank, and no valid statistical test could be performed (Section 2.4); Experiment 3 values are shown for descriptive comparison only.

Across all experiments, raft cultivation resulted in higher productivity relative to the clay bead substrate. Sea purslane consistently exhibited the highest productivity using raft cultivation, reaching peak values in Experiment 2. Saltwort showed a comparatively lower productivity in Experiments 1 and 2, but increased notably using raft cultivation in Experiment 3, suggesting a variable rather than strictly stable performance across conditions. Productivity for glasswort and sea purslane declined in Experiment 3 relative to Experiment 2, coinciding with species-separated growing conditions, although raft cultivation continued to enhance the performance for both species relative to clay.

3.4. Substrate Effects

One-way ANOVA, with the tank as the experimental unit, revealed significant substrate effects on biomass production for several species in Experiments 1 and 2 (Table 3). In Experiment 1, the substrate significantly influenced the biomass production for glasswort and sea purslane, while no significant effect was detected for saltwort. In Experiment 2, a significant substrate effect was detected for both glasswort and sea purslane, while saltwort again showed no significant effect. Because each species by substrate combination in Experiment 3 was represented by a single tank, the substrate and tank were fully confounded

in that experiment and formal significance testing was therefore not possible; Experiment 3 is not included in Table 3.

Table 3. Substrate effects on biomass production assessed by one-way ANOVA with the tank as the experimental unit. Results of one-way ANOVA evaluating the effect of substrate type (raft vs. clay) on total biomass production for each species, using tank means, in Experiments 1 and 2. Effect size is reported as η^2 and Cohen's d (negative values indicate raft > clay).

Experiment	Species	df ^z (Substrate, Error)	F	p-Value	η^2	Cohen's d^x
Experiment 1	Glasswort	1, 4	22.36	0.009114 **	0.85	−3.86 (extremely large)
	Sea purslane	1, 4	12.21	0.025015 *	0.75	−2.86 (extremely large)
	Saltwort	1, 4	0.26	0.638080 NS	0.06	−0.41 (small)
Experiment 2	Glasswort	1, 4	10.86	0.030076 *	0.73	−2.69 (extremely large)
	Sea purslane	1, 4	17.53	0.013836 *	0.81	−3.42 (extremely large)
	Saltwort	1, 4	0.18	0.696280 NS	0.04	0.34 (small)

df^z = degrees of freedom; substrate df = 1, error df = 4 (3 tanks per substrate). η^2 = proportion of total variance in biomass production attributable to substrate type (raft vs. clay). Cohen's d^x effect size thresholds: small ≥ 0.2 , medium ≥ 0.5 , large ≥ 0.8 , very large ≥ 1.2 , and extremely large ≥ 2.0 ; negative values indicate raft > clay. NS = nonsignificant ($p > 0.05$). * Significant at $p \leq 0.05$. ** Significant at $p \leq 0.01$.

Sea Purslane (*Sesuvium portulacastrum*)

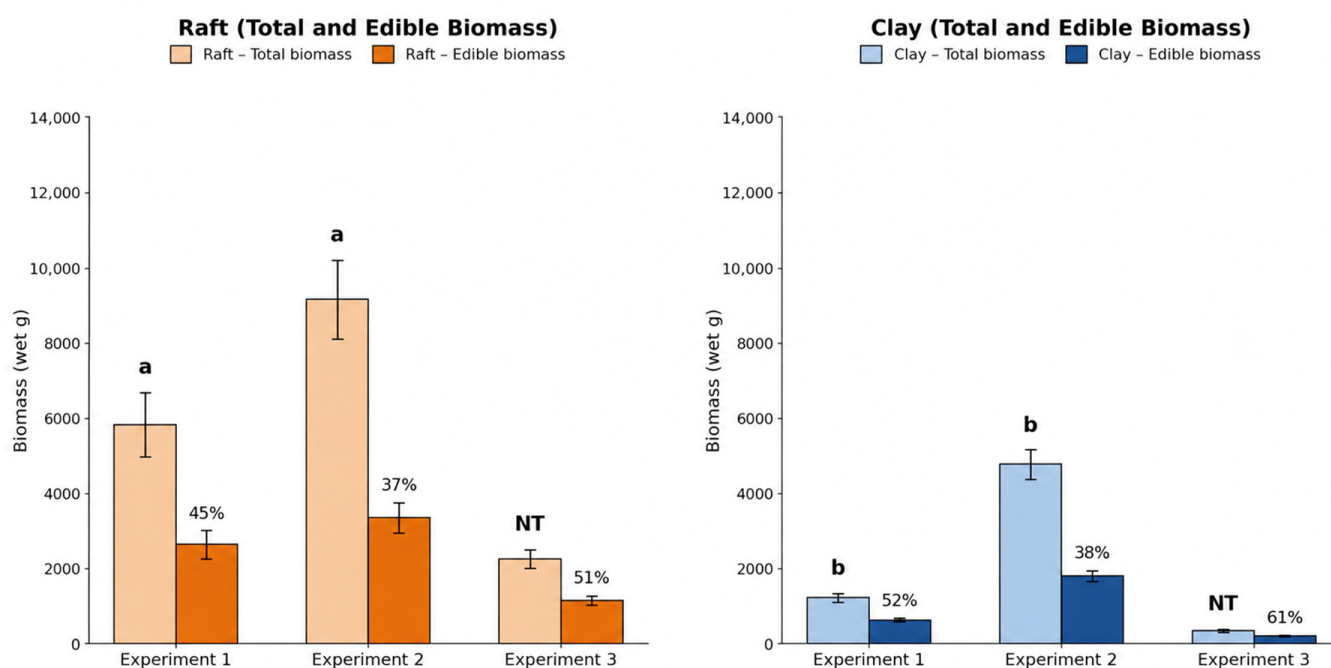


Figure 3. Total and edible wet biomass of sea purslane (*Sesuvium portulacastrum*) grown on raft and clay substrates across three sequential production experiments. Bars show total biomass (light shading) and edible biomass (dark shading) per substrate; error bars represent $\pm$ SE. Values above the edible-biomass bars indicate the percentage of total biomass classified as edible. Lowercase letters above the total-biomass bars denote statistical comparisons between substrates in Experiment 1 and 2 only (one-way ANOVA) using the tank as the experimental unit (see Table 3 for exact n and degrees of freedom); bars sharing the same letter are not significantly different ($p > 0.05$), while differing letters indicate a significant difference ($p < 0.05$). Experiment 3 bars are labeled “NT” (not tested): that experiment provided only one tank per substrate per species combination, so substrate is fully confounded with tank, and no valid statistical test could be performed (Section 2.4); Experiment 3 values are shown for descriptive comparison only.

Saltwort (*Batis maritima*)

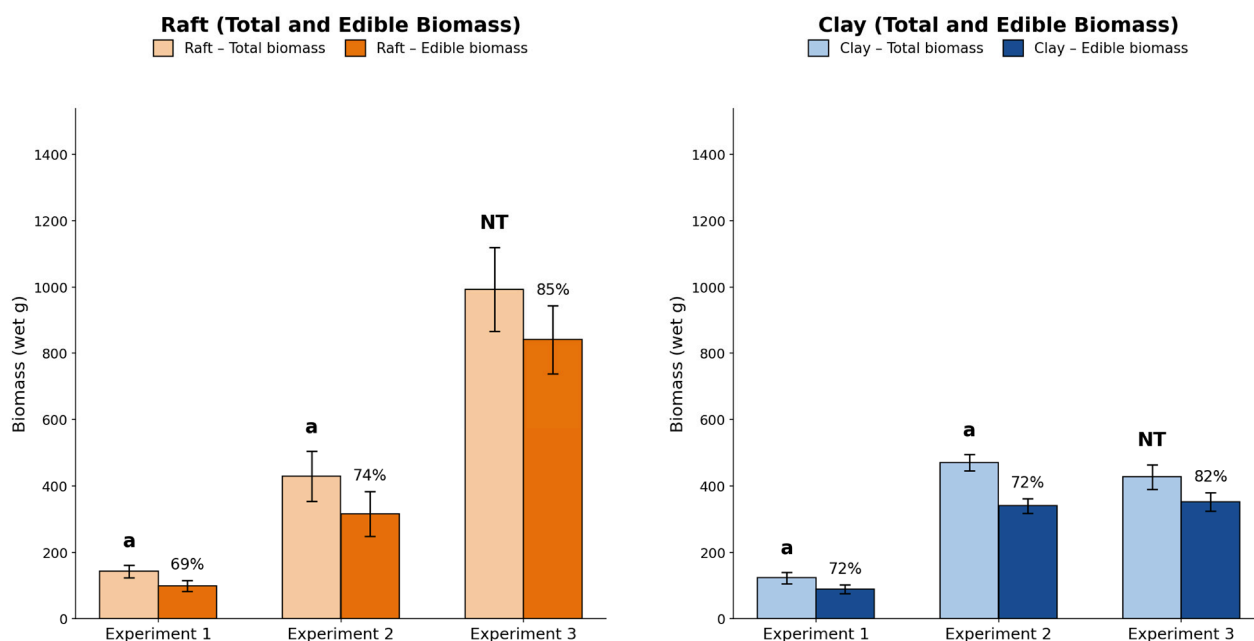


Figure 4. Total and edible wet biomass of saltwort (*Batis maritima*) grown on raft and clay substrates across three sequential production experiments. Bars show total biomass (light shading) and edible biomass (dark shading) per substrate; error bars represent $\pm$ SE. Values above the edible-biomass bars indicate the percentage of total biomass classified as edible. Lowercase letters above the total-biomass bars denote statistical comparisons between substrates in Experiment 1 and 2 only (one-way ANOVA) using the tank as the experimental unit (see Table 3 for exact n and degrees of freedom); bars sharing the same letter are not significantly different ($p > 0.05$), while differing letters indicate a significant difference ($p < 0.05$). Experiment 3 bars are labeled “NT” (not tested): that experiment provided only one tank per substrate per species combination, so substrate is fully confounded with tank, and no valid statistical test could be performed (Section 2.4); Experiment 3 values are shown for descriptive comparison only.

3.5. Effects of Nutrient Management Context on Halophyte Biomass Production and Allocation

The results are presented as the mean per tank ($\pm$ SE). Because Experiments 1 and 2 differ in more than nutrient regime alone (Section 2.2), the Experiment 1 vs. 2 comparison below is reported as associated with the nutrient addition rather than isolated to it; similarly, the Experiment 2 vs. 3 comparison is reported as associated with, rather than isolated to, plant arrangement (Tables 4–6).

With a mixed plant culture, the total and edible biomass for sea purslane and saltwort were significantly higher under the nutrient-enriched Experiment 2 than in the unenriched Experiment 1, consistent with an association with nutrient addition rather than an isolated causal effect (Table 5). For glasswort, the nutrient addition had no significant effect on the total biomass but significantly affected edible biomass allocation ($p = 0.0148$), with the edible fraction remaining stable across experiments. Under nutrient-enriched conditions, the species total and edible biomass for sea purslane were significantly lower under the species-separated Experiment 3 than mixed-culture Experiment 2, consistent with an association with the plant arrangement rather than an isolated causal effect ($p \leq 0.01$), while the effects on glasswort and saltwort were not statistically significant, though moderate-to-large effect sizes were observed for both species ($\eta^2 = 0.41$ – 0.66).

Table 4. Biomass production per tank for Experiment 1 (no nutrient addition, mixed plant culture). Mean per tank ($\pm$ SE) total wet biomass, edible biomass, and edible fraction for glasswort, sea purslane, and saltwort grown on clay and raft substrates under mixed culture without nutrient addition. Statistical significance of the substrate (clay vs. raft) effect within this experiment is presented in Table 3; comparison of these values against another experiment (nutrient or arrangement effects) are presented in Table 7.

Species	Substrate	Mean Total Biomass per Tank (g)	Mean Edible Biomass per Tank (g)	Edible Fraction (%)
Glasswort	Clay	108.67 $\pm$ 31.21	81.00 $\pm$ 16.65	75
	Raft	213.67 $\pm$ 3.28	173.00 $\pm$ 6.51	81
Sea purslane	Clay	408.33 $\pm$ 100.87	213.33 $\pm$ 50.36	52
	Raft	1940.00 $\pm$ 433.86	881.67 $\pm$ 219.30	45
Saltwort	Clay	41.00 $\pm$ 6.93	29.67 $\pm$ 4.91	72
	Raft	47.67 $\pm$ 11.14	33.00 $\pm$ 9.29	69

Table 5. Biomass production per tank for Experiment 2 (nutrient-managed mixed culture). Mean per tank ($\pm$ SE) total wet biomass, edible biomass, and edible fraction for glasswort, sea purslane, and saltwort grown on clay and raft substrates under mixed culture with nutrient addition (N:P = 4:1). Statistical significance of the substrate (clay vs. raft) effect within this experiment is presented in Table 3; comparison of these values against another experiment (nutrient or arrangement effects) are presented in Table 7.

Species	Substrate	Mean Total Biomass per Tank (g)	Mean Edible Biomass per Tank (g)	Edible Fraction (%)
Glasswort	Clay	91.33 $\pm$ 11.72	67.67 $\pm$ 5.84	74
	Raft	124.33 $\pm$ 19.10	99.00 $\pm$ 18.18	80
Sea purslane	Clay	1588.67 $\pm$ 219.40	602.00 $\pm$ 18.23	38
	Raft	3054.67 $\pm$ 219.40	1117.00 $\pm$ 109.23	37
Saltwort	Clay	156.67 $\pm$ 13.35	113.33 $\pm$ 10.85	72
	Raft	143.00 $\pm$ 29.70	105.33 $\pm$ 27.94	74

Table 6. Biomass production per tank for Experiment 3 (nutrient-managed separated culture). Mean per tank total wet biomass, edible biomass, and edible fraction for glasswort, sea purslane, and saltwort grown on clay and raft substrates under species-separated, nutrient-managed conditions. Each species-by-substrate combination in Experiment 3 was represented by a single tank (no replication), so no standard error can be calculated, and no substrate comparison could be statistically tested for this experiment (substrate and tank were fully confounded: Section 2.4); values shown are that single tank's measurement, reported descriptively only. The plant-arrangement contrast comparing these values against Experiment 2 (Table 5) is presented in Table 7.

Species	Substrate	Total Biomass per Tank (g)	Edible Biomass per Tank (g)	Edible Fraction (%)
Glasswort	Clay	105.00	100.00	95
	Raft	319.00	307.00	96
Sea purslane	Clay	340.00	207.00	61
	Raft	2258.00	1157.00	51
Saltwort	Clay	427.00	352.00	82
	Raft	993.00	841.00	85

Values for Experiment 3 are the single tank's total and edible biomass (no $\pm$ SE): each species per substrate combination in that experiment was represented by only one tank, so no tank-to-tank replicate is available (Section 2.2).

Planned ANOVA contrasts were consistent with these species-specific patterns, with large effect sizes associated with the nutrient contrast for sea purslane and saltwort, and a strong association with the arrangement contrast for sea purslane (Table 7). Each contrast

in Table 7 uses the tank means only from the two experiments being compared: the nutrient contrast compares the three Experiment 1 tank means against the three Experiment 2 tank means per substrate ($df = 1,8$, pooling both substrates), and the arrangement contrast compares Experiment 2 against Experiment 3 tank means ($df = 1,4$).

Table 7. Planned ANOVA contrasts examining association between nutrient addition, plant arrangement, and biomass production. Results of planned ANOVA contrasts comparing (i) nutrient addition under mixed plant culture (Experiment 1 vs. Experiment 2) and (ii) plant arrangement under nutrient-enriched conditions (Experiment 2 vs. Experiment 3) for total and edible biomass production. Effect sizes reported as partial η^2 . Each contrast is a two-way ANOVA (Experiment $\times$ Substrate, with interaction) on log transformed per tank means biomass, testing the experiment main effect (Type I sequential sum of squares); the tank mean, not the tank total, is the unit of analysis.

Comparison	Species	Response	Contrast	F (df)	p	η^2
Exp 1 vs. Exp 2	Glasswort	Total biomass	Nutrients	F(1,8) = 4.28	0.0724 NS	0.35
		Edible biomass	Nutrients	F(1,8) = 9.09	0.0167 *	0.53
	Sea purslane	Total biomass	Nutrients	F(1,8) = 29.48	0.0006 ***	0.79
		Edible biomass	Nutrients	F(1,8) = 17.10	0.0033 **	0.68
	Saltwort	Total biomass	Nutrients	F(1,8) = 40.39	0.0002 ***	0.83
		Edible biomass	Nutrients	F(1,8) = 29.05	0.0007 ***	0.78
Exp 2 vs. Exp 3	Glasswort	Total biomass	Arrangement	F(1,4) = 7.64	0.0506 NS	0.66
		Edible biomass	Arrangement	F(1,4) = 2.77	0.1717 NS	0.41
	Sea purslane	Total biomass	Arrangement	F(1,4) = 64.44	0.0013 **	0.94
		Edible biomass	Arrangement	F(1,4) = 74.90	0.0010 **	0.95
	Saltwort	Total biomass	Arrangement	F(1,4) = 3.26	0.1454 NS	0.45
		Edible biomass	Arrangement	F(1,4) = 4.08	0.1136 NS	0.50

η^2 = partial eta squared, representing the proportion of variance attributable to the contrast effect. NS = nonsignificant ($p > 0.05$). * Significant at $p \leq 0.05$. ** Significant at $p \leq 0.01$. *** Significant at $p \leq 0.001$.

3.6. Summary of Biomass Patterns

Across species, glasswort's edible fraction rose to the highest values under species-separated conditions even as the total wet biomass declined (Figure 2); the sea purslane biomass was the highest under the nutrient enrichment mixed culture and significantly lower under species separation (Figure 3, Table 7); and saltwort's biomass increased progressively across experiments under raft cultivation, peaking under species-separated, nutrient-enriched conditions, though without a statistically significant arrangement effect (Figure 4).

4. Discussion

Three patterns emerged from this study: the substrate configuration was consistently associated with a higher productivity for glasswort and sea purslane, with raft cultivation outperforming clay wherever formally tested; the total and edible biomass for sea purslane and saltwort increased with nutrient enrichment, whereas glasswort showed an allocation shift rather than a yield gain; and the sea purslane biomass was lower under species separation than under mixed culture, consistent with, but not proof of, facilitative interactions. Because the underlying experiments were sequential rather than factorial (Section 2.2), these patterns are interpreted below as system-level associations rather than isolated causal effects.

Water quality stayed within ranges suitable for halophyte cultivation throughout, suggesting the biomass responses reflected the substrate and nutrient treatments rather than acute environmental stress, though parameters such as alkalinity, phosphate, and salinity also varied across experiments (Section 2.2) and cannot be fully separated from the treatment effects. Buhmann et al. [29] showed that even moderate shifts in water chemistry can alter the halophyte performance even under stable saline conditions, consistent with

the species-specific responses Doncato and Costa [22] reported in saline aquaponic systems. The progressive decline in phosphate under enrichment conditions suggests active biological assimilation by the plants and microbial communities, consistent with healthy system functioning.

Because Experiment 3 also varied in nutrient history and arrangement (Section 2.2), its response cannot be attributed to elevated salinity alone; nevertheless, it broadly matches known physiological responses to salinity in halophytes. Debez et al. [30] established that saltwort's biomass peaks at a moderate salinity and declines as the salinity rises, accompanied by the competitive displacement of K^+ and Mg^{2+} by excess Na^+ ; Hamed et al. [31] corroborated this, showing that a restricted K^+ and Ca^{2+} uptake under high salinity compounds the osmotic stress and shifts the resource allocation from growth toward regulation. The Experiment 3 response fits this framework, though this remains unconfirmed given the study's confounded design.

Substrate configuration was one of the most consistent correlates of productivity across species, where tested; floating raft systems outperformed expanded clay beads under most conditions, except for saltwort under mixed-culture nutrient enrichment (Experiment 2), where the two substrates produced a comparable biomass. The root-zone geometry and ion transport were not measured directly, but, consistent with Manousaki and Kalogerakis [17], raft systems' direct root exposure to oxygenated, nutrient-rich water likely preserved the Na^+ exclusion and K^+ selectivity better than the more restrictive clay substrate, contributing to the suppressed clay-based yields.

Similar effects appear in marine aquaponics. Boxman et al. [32] found floating raft beds significantly reduced total ammonia nitrogen and phosphorus between the influent and effluent, confirming direct root contact with nutrient-rich water is essential for nutrient removal. The same study found saltwort performed poorly relative to sea purslane, showing the substrate geometry interacts with the species-specific root architecture to shape productivity.

This is supported by Moatabarniya et al. [33], who showed the glasswort root morphology is highly plastic in response to the salinity and nutrient availability, with the unrestricted root expansion under combined nitrogen and saline conditions producing a greater root biomass and length. The granular substrate, by constraining this expansion, would suppress the root responses halophytes rely on for nutrient acquisition under saline conditions, making the cultivation platform a primary, not a secondary, design variable.

The response of glasswort to nutrient enrichment highlights a practically relevant distinction between the total biomass and harvestable yield: the nutrient addition did not proportionally increase the total mass; yet, the harvested fraction held steady and reached near-total values under species-separated conditions. Though not directly tested by tissue-composition data here, glasswort likely redirected resources toward the succulent shoot tissue that defines its commercial value rather than into structural or root tissue, decoupling harvest quality from total biomass accumulation, consistent with known nitrogen dynamics in halophytes, where nutrient enrichment under saline conditions favors shoot succulence over whole-plant growth. Optimizing for the harvestable fraction rather than total biomass may therefore be a more efficient, economically relevant production target.

Because nitrogen and phosphorus were applied jointly at a fixed 4:1 ratio, the present data cannot isolate nitrogen as a driver of the above-ground biomass in glasswort. In terms of nitrogen, Boyer et al. [34] documented nitrogen, not phosphorus, as the driver of *Salicornia virginica* productivity: a sustained nitrogen addition produced two-fold increases in the succulent biomass and branch number, while a phosphorus addition produced no growth response despite altering the tissue nutrient concentration. Howarth and Marino [35] explain this mechanistically: persistently low N:P ratios in saline coastal

ecosystems, combined with the absence of planktonic nitrogen fixation, sustain a structural nitrogen deficit that phosphorus cannot alleviate, making nitrogen the consistent regulator of above-ground productivity while phosphorus shapes the internal nutrient cycling and tissue chemistry. Puccinelli et al. [36] extended this to aquaponic *Salicornia europaea*, which maintained an equivalent biomass across a wide range of nutrient availabilities, with differences appearing only in the tissue antioxidant capacity and secondary metabolites, confirming that, once the nitrogen supply is adequate, additional nutrients shape the product quality rather than the yield.

The decoupling of the biomass and tissue composition raises questions about how well terrestrial nutrient-management frameworks translate to halophytes under saline conditions. Güsewell's [37] conventional terrestrial N:P thresholds (below 10, nitrogen-limited; above 20, phosphorus-limited) are a less reliable guide here, since salinity alters nutrient uptake and cycling through Na^+ competition with K^+ and other cations, and the fixed 4:1 ratio prevents a direct comparison against those thresholds. Agronomic practices such as harvest timing, cutting frequency, and planting density may therefore offer more reliable gains in the edible yield for glasswort than adjusting nutrient inputs alone.

Sea purslane responded strongly to nutrient enrichment, particularly under a mixed culture, suggesting it was operating below its growth potential without added nutrients (Experiment 1), consistent with Messedi et al. [13], who found sea purslane growth stays vigorous under saline conditions as long as the nutrient acquisition and ion balance are maintained, declining mainly when salinity disrupts the nutrient uptake rather than through direct toxicity. The pronounced biomass increase here suggests the added nutrients relieved the physiological limitations, letting the species express the fast-growing, opportunistic strategy typical of coastal pioneer halophytes, as Lokhande et al. [38] also described for facultative halophytes with an enhanced succulence and productivity under moderate salinity and adequate nutrients: an adaptation to rapidly exploit nutrients, not mere salt tolerance.

Although sea purslane's edible fraction remained lower than the other species, the total harvestable biomass was still substantial under raft conditions, consistent with its known role converting nutrient-rich aquaculture effluents into biomass: Boxman et al. [32] linked it to nitrate removal in marine aquaponics, Senff et al. [39] to nitrogen and phosphorus recovery from aquaculture wastewater, and Yuan et al. [8] to the enhanced microbial diversity and stability in wastewater treatment. Pires et al. [14] further described it as rich in minerals, phenolic compounds, and antioxidant activity, with nutritional properties strongly shaped by cultivation conditions, reinforcing its value as a multifunctional species linking saline food production with nutrient recovery and environmental remediation.

A notable finding was the significant decline in sea purslane productivity under species-separated conditions relative to the mixed culture (Table 7), confounded with salinity here (Section 2.2); facilitative interactions among co-cultivated species may sustain growth in mixed systems, though unconfirmed. This is consistent with John et al. [40], who linked the sea purslane rhizosphere's halotolerant, growth-promoting bacteria to an improved nutrient availability and reduced salinity stress, and with facilitative sea purslane–saltwort associations reported separately in coastal mangrove restoration [41,42]. The higher productivity under a mixed culture may reflect a more biologically active root-zone environment; future studies should test whether this reflects microbial interactions, root-zone conditions, or other system-level effects.

Saltwort showed a more variable growth response, though biomass generally increased under raft cultivation. The strongest performance occurred under species-separated, nutrient-enriched conditions (Experiment 3), where both the total and edible biomass peaked, though the arrangement effects were not statistically significant (Table 7), sug-

gesting cultivation conditions mattered more than species separation. The biomass on the clay substrate was less stable, declining slightly from Experiment 2 to Experiment 3; yet, the edible fractions remained consistently high across treatments, underscoring saltwort's broad agronomic potential.

Although saltwort is highly salt-tolerant, its growth can still depend on how well it maintains the mineral balance under salt exposure. Debez et al. [30] documented that saltwort uses sodium compartmentalization to tolerate a high salinity, though excessive salt can still reduce K^+ and Mg^{2+} in plant tissues; the sustained gains observed here under raft cultivation suggest these ionic limitations were not severe enough to restrict growth. The lower, less consistent productivity on the clay substrate reinforces that the cultivation platform remained an important yield factor even for a salt-tolerant species, consistent with the variability Boxman et al. [43] and Schardong et al. [44] observed under different system conditions.

Overall, productivity emerged from the interaction of substrate, nutrient stoichiometry, and species-specific responses rather than any single factor, consistent with the ecological stoichiometric framework of Güsewell [37], and was especially evident under a mixed culture, where sea purslane outproduced species-separated systems. Future work should also evaluate how cultivation strategies affect the nutritional and functional quality, not just biomass: as an indicative (not directly measured) estimate, the weekly fertilizer input (Section 2.2: ~4.4 ppm nitrogen and ~1.1 ppm phosphorus) versus measured water-column concentrations (Table 1) show that the mean nitrogen rose only 1.3 ppm from unenriched (Experiment 1) to enriched (Experiment 2) conditions (~30% of input), while the phosphorus concentrations were actually lower under enrichment (0.80 ppm, Experiment 2) than without it (1.14 ppm, Experiment 1), a net decline of 0.34 ppm despite ~1.1 ppm/week of added phosphorus. This pattern suggests, but does not confirm, that the nitrogen uptake absorbed most of the added input and phosphorus removal exceeded the applied dose. The standing water-column concentrations alone do not constitute a complete mass balance; direct measurements (e.g., the influent–effluent flux, and plant tissue content) are needed to confirm this hypothesis.

These contrasting species responses suggest future studies should jointly examine the substrate type, nutrient balance, and species arrangement, optimizing nitrogen for glasswort and stable water chemistry for saltwort. Rosales-Nieblas et al. [45] demonstrated species-specific physiological and biochemical responses to agronomic management across three halophyte species in a half-strength seawater aquaponics system, reinforcing the case, while Alfheaid et al. [11] highlighted glasswort's nutritional potential as a source of minerals, antioxidants, and bioactive compounds, and Farzana et al. [20] showed salinity and the nitrogen source can trade off biomass against nutritional quality. These findings reinforce that the long-term success of saline agriculture will depend on optimizing the nutritional and functional quality, not just yield.

This echoes a broader principle from protected-cultivation research: management generalized across species can underperform strategies tailored to each species' constraints. Fanourakis et al. [46], reviewing greenhouse vegetable crops, found that physiological differences among crops (e.g., root-zone regulation, and source–sink balance) produce substantially different outcomes from the same management practice. Our results follow this pattern: raft cultivation helped glasswort and sea purslane, not saltwort; and enrichment shifted glasswort's allocation, not its yield. Species-tailored substrate, harvest timing, and nutrient dosing are, therefore, likely to yield the greatest gains going forward.

In the broader context of coastal food security, the increasing soil salinization, freshwater scarcity, and land degradation have intensified the need for saline-tolerant agriculture systems, a challenge highlighted by Rozema and Flowers [3]. This study demonstrated that

meaningful halophyte productivity can be achieved in a low-cost, single-site recirculating system, illustrating its potential for community and small-commercial applications, pending broader validation. At the Naguabo Aquaculture Center in Puerto Rico, the existing coastal infrastructure enabled an integrated approach in which nutrient-rich aquaculture effluents, alongside deliberate fertilization, served as the primary nutrient source for a marketable halophyte crop, supporting the view that saline agriculture, combined with species-tailored substrate and nutrient management, is a practical strategy for coastal regions where salinity and limited freshwater constrain conventional agriculture.

5. Conclusions

Across the three halophyte species tested in this low recirculating, the floating raft system substrate produced a greater biomass than expanded clay beads for glasswort and sea purslane wherever the tank-level comparisons were possible; saltwort showed no substrate effect. Nutrient enrichment was associated with a higher total and edible biomass in sea purslane and saltwort, and with a shifted glasswort allocation toward edible tissue without a corresponding increase in total biomass. The species-separated culture was associated with a lower sea purslane productivity relative to the mixed one, consistent with, though not proof of, a facilitative interaction among co-cultivated species. Because the three experiments were conducted sequentially rather than as a fully factorial design, with the nutrient regime, plant arrangement, salinity, and time varying together, these findings represent system-level patterns rather than isolated causal effects, and the Experiment 3 substrate comparisons are descriptive only. Substrate selection and species-specific nutrient management are both relevant to halophyte production in these low-cost, recirculating systems; the controlled factorial testing of the substrate, nutrient regime, and plant arrangement, together with direct quantifications of nutrient recovery, should guide future work.

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Abbreviations

The following abbreviations are used in this manuscript:

USDA-ARS United States Department of Agriculture, Agricultural Research Service

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