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Biostimulant potential of Brazilian macroalgae: seasonal variations and effects on early growth and germination of lettuce

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Abstract
A wide variety of commercial seaweed-based biostimulants is available worldwide for improving plant growth and development for agriculture and gardening purposes. Biostimulant properties are influenced by species, seasonality, preparation methods, and harvest site. This study evaluated the biostimulant properties of the methanolic, hot aqueous and aqueous extracts of three Brazilian macroalgae—*Sargassum vulgare* C. Agardh (Ochrophyta, Phaeophyceae), *Palisada flagellifera* (J. Agardh) K. W. Nam (Rhodophyta), and *Ulva fasciata* Delile (Chlorophyta)—in two different periods (dry and wet seasons) on germination and early development of *Lactuca sativa* Linnaeus. All three algae showed biostimulant activities, with the root length being the primary factor that exhibited growth enhancement. The length of the roots increased by an average of 40% when in contact with the extracts, ranging from 28 to 55% for *P. flagellifera*, 37–48% for *S. vulgare*, and 28–79% for *U. fasciata*. The extracts promoted resource allocation for elongation of roots, which can aid the plant survival by improving competition for water and nutrients. In general, the biostimulant properties of seaweed extracts varied between harvesting period, since the activity of methanolic and aqueous extracts were influenced by the seasons. Methanolic extracts from the dry season and aqueous extracts from the wet season showed the most biostimulant effect, although overall, the dry season extracts were the most effective. In conclusion, the studied extracts of three Brazilian macroalgae have significant biostimulant properties, which can vary depending on the harvesting period and extract type.

Keywords Biostimulant · Germination · Lettuce seedlings · Seasonality · Seaweed

1 Introduction

Marine macroalgae or seaweeds have been utilized for centuries to improve soil fertility and enhance crop productivity (Lloret et al. 1999; Craigie 2010). In recent years, a wide variety of seaweed-based biostimulants, including liquid extracts or powdered products, have become available for agriculture and home gardening purpose (Khan et al. 2009). Most of the algal species used in agriculture are the brown seaweeds *Ascophyllum nodosum* (Linnaeus) Le Jolis, *Fucus* Linnaeus spp., *Laminaria* J.V.Lamouroux spp., *Sargassum* C.Agardh spp., and *Turbinaria* J.V.Lamouroux spp., but green and red seaweeds have also been employed for this purpose (Mukherjee and Patel 2019; Ali et al. 2021).

According to Khan et al. (2009), more than 20 seaweed-based products have been utilized as biostimulants for plant growth. These products, available in both liquid and powder forms, can provide nutrients and bioactives that are found exclusively in seaweed. For example, algal polysaccharides, such as ulvans, agarans, and fucoidans, have been documented in the literature as biostimulant (du Jardin 2015; Ali et al. 2021). Besides, growth regulators commonly found in land plants, such as auxin and cytokinins, have also been reported as important bioactive components in seaweed extracts (du Jardin 2015; Ali et al. 2021).

Seaweeds-based biostimulants have been shown to enhance crop productivity, promote the development of healthy root systems, and increase resistance to both biotic and abiotic stresses. For example, Layek et al. (2017) reported that a foliar spray derived from the red algae

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Kappaphycus alvarezii (Doty) L.M.Liao and *Gracilaria edulis* (S.G.Gmelin) P.C.Silva promoted rice (*Oryza sativa* Linnaeus) growth, chlorophyll index, crop growth rate, and yield, while Sharma et al. (2019) showed that sap from *Gracilaria dura* (C.Agardh) J.Agardh enhanced drought tolerance in wheat (*Triticum aestivum* Linnaeus). In a study by Di Filippo-Herrera et al. (2018) that investigated liquid extracts from brown and red seaweeds, the best biostimulant effects were observed for extracts from *Ecklonia arborea* (Areschoug) M.D.Rothman, Mattio & J.J.Bolton and *Gracilaria parvispora* I.A. Abbott, which promoted the length and weight of the mung bean (*Vigna radiata* (L.) Wilczek).

As a natural product and wildly or mariculture harvested material, the biostimulant action of seaweed extracts depends on several factors, such as seaweed species, biofertilizer production, application modes, preparation methods, crop species, environmental conditions, and harvest site (Sujeeth et al. 2022). As photosynthetic marine organisms that inhabit natural environment, seasonality is also crucial to the chemical composition of the algal products, which changes among the seasons (Sujeeth et al. 2022). However, studies on seaweed-based fertilizers do not analyze the seasonal changes in the products and their effects on crop responses (e.g., Frioni et al. 2018). Nevertheless, the seasonal investigations of the biostimulant properties can provide practical significance, aiming for higher extract yields and maximal biostimulant effects on the crop.

The agricultural productivity should increase to guarantee food security for a growing global population. However, synthetic agricultural chemicals are non-sustainable, threating the ecosystem and human health (Shukla et al. 2022). Thus, considering the current trend toward efficiency and sustainability, the demand for biostimulant products in the agriculture might increase. Despite agriculture being one of the mainstays of Brazil's economy, seaweeds are an underexplored agricultural resource. Only calcareous red alga *Lithothamnium* Philippi sp. is commercially exploited from carbonate sedimentary deposits on the Brazilian coast due to the presence of calcium and magnesium carbonates used to correct soil acidity (Amatussi et al. 2020; Mógor et al. 2021). Local small-scale production of algae-based biofertilizer is also related.

In recent years, there has been a growing interest in biostimulant research in Brazil, with more than 80% of the field's research occurring within the last 5 years (2018–2023) (These data were sourced from the 48 references—see the supplementary material). However, the majority of research predominantly use the non-endemic species *A. nodosum* (L.) Le Jolis (Tavares et al. 2020; Langowski et al. 2021; Repke et al. 2022; Villa e Vila et al. 2023). In contrast, only a small number of studies (approximately 30%) have focused on Brazilian algae. The research articles that have explored Brazilian algae have primarily concentrated on aqueous extracts, with a specific emphasis on *Ulva* species found in the south region of the country (e.g., de Borba Marlon et al. 2019; de Borba et al. 2021; de Freitas and Stadnik 2015).

In the present study, we aim to contribute to the growing body of research on the biostimulant potential of Brazilian seaweeds. Our specific aim was to evaluate the biostimulant properties of the methanolic, aqueous and hot aqueous extracts of three Brazilian macroalgae—*Sargassum vulgare* C. Agardh (Ochrophyta, Phaeophyceae), *Palisada flagellifera* (J.Agardh) K.W.Nam (Rhodophyta), and *Ulva fasciata* Delile (Chlorophyta). These macroalgae were collected from the northern region of Brazil in two different season periods (dry and wet). Our focus was on assessing the influence of these seaweed extracts on germination and early development of *Lactuca sativa* Linnaeus (lettuce), an effective plant model used in laboratory assays due to their high reproducibly and germination rates. Through our research endeavor, we aspire not only to uncover the untapped potential of locally sourced Brazilian macroalgae as valuable biostimulant resources but also to advance our understanding of their effectiveness across different seasons.

2 Materials and methods

Collection of seaweed samples – Three seaweed species (Fig. 1), each one representing a different taxonomic group of brown algae (*S. vulgare*), red algae (*P. flagellifera*) and green algae (*U. fasciata*), were harvested from Northeast Brazilian coast at Morro de Pernambuco Beach in Ilhéus city, Bahia State—14°48′21.6″ S, 39°01′25.6″ W) during the dry season in November 2013 and the wet season in May 2014. The harvested algal samples were washed in tap water to remove excess salt and dried at 40 °C for three days. The dried materials were then ground into a fine powder using a knife mill (Fortinox® STAR FT 80) and sieved through a 30-mesh. The species were identified by COI barcode analysis (Saunders 2005), and the sequences were compared with public reference database.

Environmental parameters – The study region has a humid tropical climate with irregular precipitation patterns. However, precipitation is highest from April to August throughout the year. As a result, the region is characterized by the occurrence of two seasons traditionally defined as wet season and dry season. Nevertheless, the UV radiation index better distinguishes between the two periods. The so-called dry season is characterized by the higher UV index, while the wet season has a lower UV index (Fig. 2). Another abiotic factor that could be considered was temperature. However, in the studied area it was very similar between the dry and wet seasons (Fig S1– supplementary material).

Fig. 1 General aspect of **a** *Sargassum vulgare*, **b** *Palisada flagellifera*, and **c** *Ulva fasciata* in the natural environment

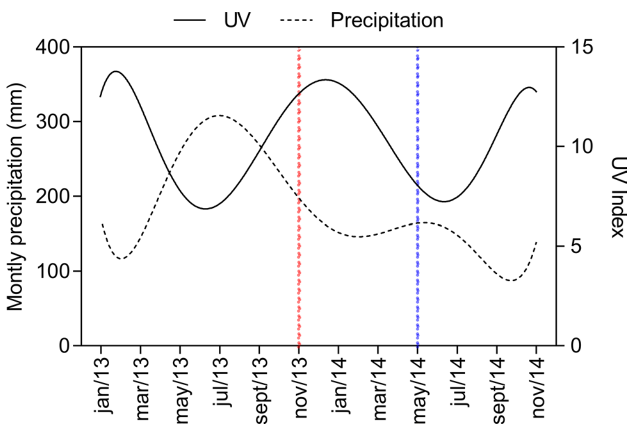

Fig. 2 Precipitation and UV radiation index for the Municipality of Ilhéus (Brazil) from 2013 to 2014. The two harvested periods are highlighted with vertical lines as dry season—November 2013 (red line) and wet season—May 2014 (blue line)

The seaweed samples were harvested in November 2013 (during the dry season) and May 2014 (during the wet season). All environmental parameters were obtained at the Instituto do Meio Ambiente e Recursos Hídricos (INEMA) and Instituto Nacional de Meteorologia (INMET).

Seaweed extract preparation – The algal powder of each species and season was macerated (1:10 w/v) on an orbital shaker at room temperature firstly with methanol and then with ultrapure water for 24 h (three-times). The resulting residues were again macerated with ultrapure water (1:10 w/v) at 70 °C for 1 h (three-times). After filtration, each extract was concentrated on a rotary evaporator at 40 °C and freeze-drying. Three extracts for each species and season were obtained, as following: methanolic extract (M), aqueous extract (Aq), and hot aqueous extract (H-Aq). The extract yield was calculated based on the dry mass of each sample.

Germination and growth assays – Germination and early growth tests of *L. sativa* (lettuce) were performed using six-well plates ($n = 4$) following the protocols established by Novaes et al. (2015) and Torres et al. (2018). Each well was lined with filter paper, and ten lettuce diaspores of the "Grand Rapid" variety (ISLA®) were uniformly distributed in each well. Subsequently, 1 mL of the of the crude extracts at concentration of 1 mg mL^{-1} in 0.5% dimethyl sulfoxide (DMSO) was pipetted to each well. In contrast, a separate set of wells (designated as the negative control) received 1 mL of a 0.5% DMSO solution without any added extract. Four independent replicates were executed for each extract or negative control, yielding a total of four microplates to each extract or negative control. The microplates, sealed with Parafilm M®, were transferred to B.O.D. incubator (FANEM® 347 CDG, Guarulhos, SP, Brazil) at 24 ± 1 °C and photoperiod of 12 h. The growth measurements (root and hypocotyl lengths) were performed after seven days using ImageJ® software. Seeds were considered germinated when radicles were longer than 2 mm.

Statistical analysis – The data analysis and graphing software was GraphPad 8®. The total, root, and hypocotyl lengths and root-shoot (only hypocotyl) ratio (R-S) were normalized with respect to the negative control and the results were expressed in percentage of effect related to the control (mean ± standard deviation). The data were submitted to Bartlett's test for equal variances. The mean of each treatment (extracts independent of season) was compared using Kruskal–Wallis and Dunn's multiple comparison test as a *post-hoc* analysis, with a significance level set at $p < 0.05$ both tests. Comparisons between seasons (extracts of the same solvent) were made with Welch's *t*-test, with a significance level set at $p < 0.05$). Principal Component Analysis (PCA) was used to analyze root, hypocotyl, and total lengths and R-S ratios to discriminate between species, extracts, and seasons. PCA was performed using Statistica software. A Welch's *t*-test for categorical variables comparison was used for summarizing effects and responses.

3 Results

Biostimulant effects of the extracts – Although no significant effect was observed on the germination percentages of lettuce seedlings (Fig. S2—supplementary material), extracts from all three seaweeds exhibited potent biostimulant activities, as evidenced by the increased total lengths of lettuce seedlings (Fig. 3). The red alga *P. flagellifera* exhibited biostimulant activities in the M extract from the dry season (34% increase in the total length), Aq extracts (22% and 48% increases from the dry and wet seasons, respectively), and H-Aq extracts (42% and 39% increases from the dry and wet seasons, respectively). The brown alga *S. vulgare* exhibited biostimulant activities in the M extract from the dry season (42% increase), Aq extract from the wet season (21% increase), and both H-Aq extracts (52% and 30% increases from the dry and wet seasons, respectively). Lastly, the green alga *U. fasciata* exhibited the highest biostimulant activity in the M extract from the dry season (66% increase), while the H-Aq extract from the dry season (25% increase), M extract from the wet season (26% increase), and Aq extract from the wet season (23% increase) showed similar biostimulant activities. The M extracts of brown and red seaweed from wet season did not exhibit stimulant activity, which was observed with M extract of *U. fasciata*.

The R-S ratios increased in the range of 31–104% for active extracts of *P. flagellifer*a, with the highest R-S ratio observed for the H-Aq extract from the dry season. The R-S ratios for *S. vulgare* increased on average by 66%. For *U. fasciata*, the ratio ranged from 23 to 106% for active extracts, with the M extract from the dry season showing the highest ratio. The root lengths for the extracts from the three algae were increased on average by 40%. Significant increases in root lengths ranged from 28 to 55% for *P. flagellifera* extracts, 40–50% for *S. vulgare* extracts, and 30–80% for *U. fasciata* extracts (Fig. 4).

The extracts from *P. flagellifera* (M extracts, Aq extract from the dry season, and H-Aq extract from the dry season) and *S. vulgare* (H-Aq extract from the wet season) were found to inhibit hypocotyl elongation, with an average inhibition of 17% and 18%, respectively (Fig. 4). Only the M extract from *U. fasciata* during the dry season were found to inhibit hypocotyl elongation, with an average inhibition of 13%. However, the Aq extract from *S. vulgare* during the dry season was found to be a hypocotyl biostimulant, with a 15% increase (Fig. 4).

Effects of the harvest period on the biostimulant activities – Principal Component Analysis (PCA) were conducted to visualize the effects of the harvesting period on the biostimulant activities (Fig. 5). The two principal factors account for 99.7% of the total variability (PC1 with 73.88% and PC2 with 25.82%). The variables with the highest contribution for PC1 were total length (L; 29%), root length (R; 30%), and R-S ratio (RS; 32%), while shoot length (S) contributed with 74% for PC2. Total length, root length, and R-S ratio from PC1 influenced the separation of a group (highlighted in Fig. 5) formed by the most active extracts. In general, the extracts from the dry season compose this group. PCA

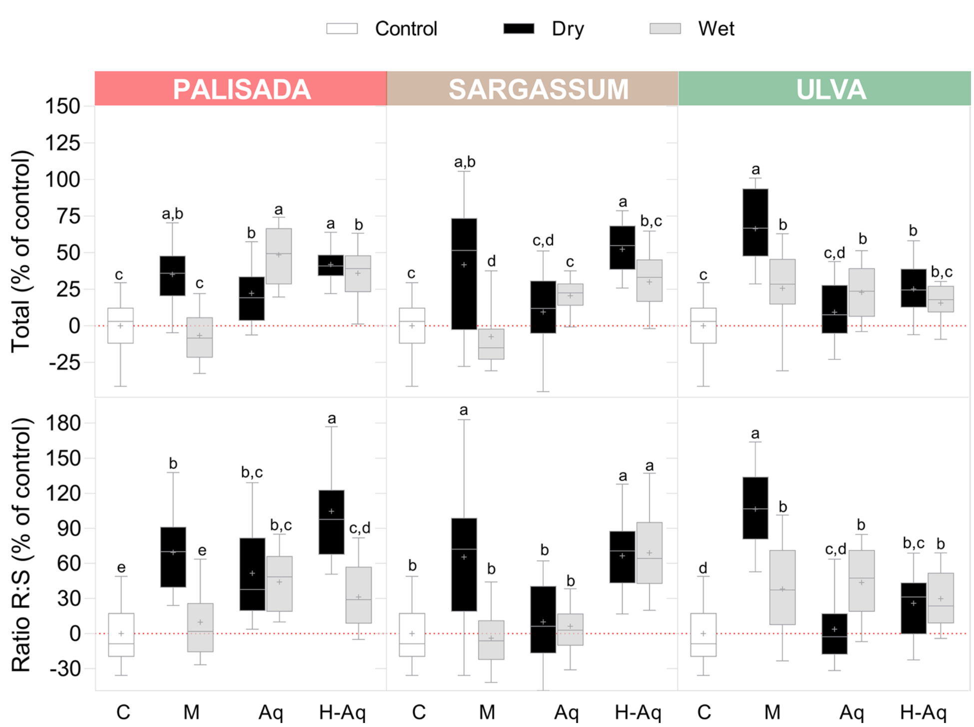

Fig. 3 Effects on the total length and root-shoot ratio (R-S) of lettuce seedlings (% of control) when grown with methanolic (M), aqueous (Aq), or hot aqueous (H-Aq) extracts obtained from three different types of algae (*Palisada flagellifera*, *Sargassum vulgare*, and *Ulva fasciata*) harvested during wet and dry seasons. Each dot represents a value from a seedling, and the mean of the data is represented by a plus symbol (+). Different letters indicate significant differences ($p < 0.05$, Kruskal–Wallis *post-hoc* Dunn's test)

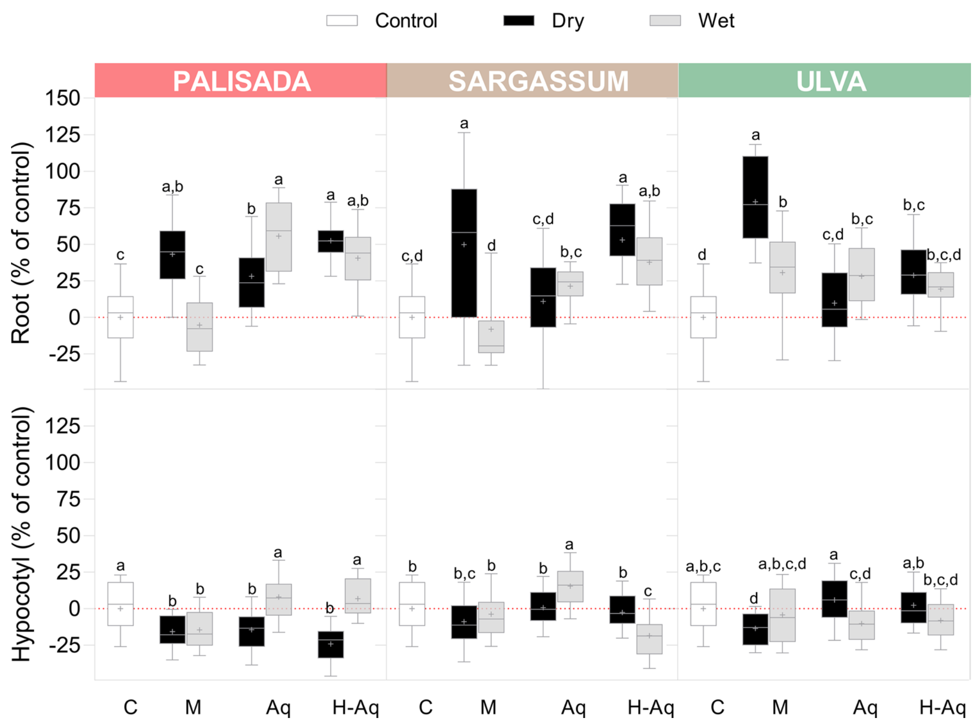

Fig. 4 Effects on the root and hypocotyl lengths of lettuce seedlings (% of control) when grown with methanolic (M), aqueous (Aq), or hot aqueous (H-Aq) extract masses obtained from three different types of algae (*Palisada flagellifera*, *Sargassum vulgare*, and *Ulva fasciata*) harvested during wet and dry seasons. The data are presented as box plots with whiskers indicating minimum and maximum values. Each dot represents a value from a seedling. Each dot represents a value from a seedling, and the mean of the data is represented by a plus symbol (+). Different letters indicate significant differences ($p < 0.05$, Kruskal–Wallis post-hoc Dunn's test). Values (means ± SD) were expressed in the percentage of the negative control

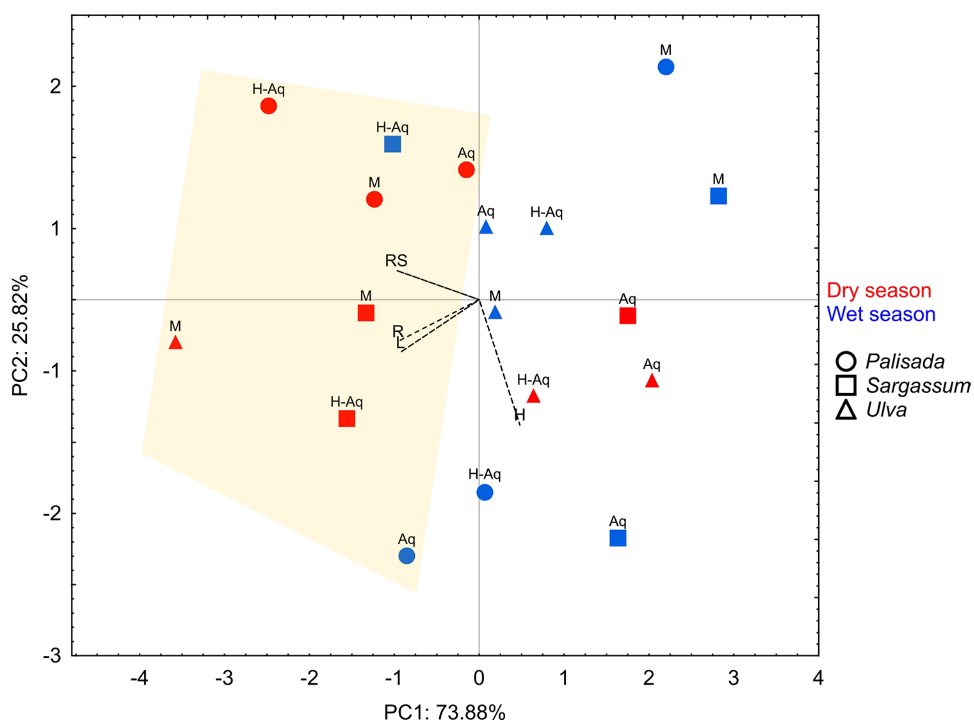

Fig. 5 Score biplot of the first two components of the principal component analysis (PCA) grouped by dry and wet seasons for the macroalgae *Palisada flagellifera, Sargassum vulgare*, and *Ulva fasciata*. M: methanolic extract, A: aqueous extract, H: hot aqueous extract, RS: root-shoot ratio, R: root, L: total length, and S: hypocotyl. Dry and wet seasons were represented by red and blue colors, respectively. The highlighted group represents the most active extracts from three seaweed species

segregates the more active extracts from the less active ones. Nevertheless, when examining individual extracts and contrasting them with their counterparts by season, the seasonal effect is also discernible among the less active extracts (Table 1). The M extracts were the most influenced by season, followed by Aq extracts (Table 1). The M extracts from the dry season were more active than those from wet season (Table 1). In contrast, the Aq extracts from the wet season were more active than those from the dry season (Table 1).

Table 1 Categorical comparison of the biostimulant effect of the extracts obtained from algae harvested during dry and wet seasons ($p < 0.05$; Welch's *t*-test). and (–) No significant differences

Algal species	Growth measures	Methanol extract		Aqueous extract		Hot aqueous extract	
		Dry	Wet	Dry	Wet	Dry	Wet
Palisada flagellifera	Total length	**Higher**	Lower	Lower	**Higher**	–	–
	Root	**Higher**	Lower	Lower	**Higher**	**Higher**	Lower
	Hypocotyl	–	–	lower	**Higher**	Lower	**Higher**
	R-S rate	**Higher**	Lower	–	–	**Higher**	Lower
Sargassum vulgare	Total length	**Higher**	Lower	–	–	**Higher**	Lower
	Root	**Higher**	Lower	–	–	–	–
	Hypocotyl	–	–	Lower	**Higher**	**Higher**	Lower
	R-S rate	**Higher**	lower	–	–	–	–
Ulva fasciata	Total length	**Higher**	Lower	Lower	**Higher**	–	–
	Root	**Higher**	Lower	Lower	**Higher**	–	–
	Hypocotyl	–	–	–	–	–	–
	R-S rate	**Higher**	Lower	Lower	**Higher**	–	–

Bold terms represent phytotoxicity

4 Discussion

We evaluated the effect of the extracts obtained from three marine macroalgae (*P. flagellifera, S. vulgare,* and *U. fasciata*) harvested during dry and wet seasons on the early growth of lettuce. The three algae showed extracts with biostimulant activities, regardless of the seasons and solvent for extraction (Fig. 3), in agreement with Hernández-Herrera et al. (2013) and Ali et al. (2022) for *Sargassum* species, and Godlewska et al. (2016), Castellanos-Barriga et al. (2017), Chanthini et al. (2019), Mzibra et al. (2020) and Ali et al. (2022) for several species of *Ulva*. In agriculture, the most commonly exploited seaweed biomass belongs to the brown algae (Phaeophyceae), including *Sargassum* species in Southeast Asia (Hurtado and Critchley 2020). Several studies in the literature have reported the biostimulant effect of *Sargassum* extracts on various plants. Ali et al. (2022) reported that the foliar application of alkaline extracts from *S. vulgare* promoted several growth improvements on plant height, root length, plant dry weight, flowers per cluster, and fruit per cluster of tomato and sweet pepper, while Hernández-Herrera et al. (2013), studying aqueous extracts from *Sargassum liebmannii*, reported an increase in the root elongation of the tomato seedlings. *Ulva* species include important seaweeds reported with biostimulatory activities (Godlewska et al. 2016; Castellanos-Barriga et al. 2017; Chanthini et al. 2019; Ali et al. 2022). Mzibra et al. (2020) investigated hot aqueous extracts from *U. fasciata*, *Ulva lactuca* Linnaeus, and *Ulva rigida* C.Agardh on the tomato growth parameters. *Ulva lactuca* and *U. rigida* showed a promoting effect on the tomato length. On the other hand, *U. fasciata* was not biostimulant. In our study, the H-Aq extract from *U. fasciata* only was biostimulant when it was obtained from the dry season (Fig. 3A). In contrast to *Ulva* and *Sargassum* species, biostimulant properties from *Palisada* species were not evaluated as far as we know.

Variations in the R-S ratios predict a change in the resource allocation of the seedling. The active extracts for the three algae in the present study showed a high R-S ratio, suggesting a promotion of resource allocation of the seedlings for the roots promoted by extracts from algae (Fig. 3). As expected, the algal biostimulant effect was focused on root elongation (Fig. 4). However, a decrease in the hypocotyl elongation observed for *P. flagellifera* (Fig. 4) also contributed to a higher R-S ratio for the respective extract (Fig. 3). Seedling phase is the most vulnerable stage in the life cycle of a plant, and changes in the resource allocation response can affect the survival (Lloret et al. 1999). Seedlings with a higher proportion of roots can compete more successfully for soil water and nutrients. Root elongation is an ecological advantage for seedlings with smaller seed nutritional reserves, as they must allocate a greater amount of resources in the early development (Souza and Fagundes 2014). Promoting significant root growth is a well-known biostimulant effect of algal extracts (Khan et al. 2009; El Boukhari et al. 2020). For example, Traversari et al. (2022) evaluated the substitution of synthetic auxin in the rooting of rose cuttings and found that a commercial seaweed extract (Kelpak®) improved the rooting parameters and rates. Consequently, Kelpak® was proposed as an alternative to synthetic auxins.

Finally, we asked whether biostimulant effect of seaweed extracts varied between harvest periods. PCA was used to reduce the dimensionality of the data. Extracts with the highest biostimulant activities were mostly derived from the dry season (Fig. 5). Similar to our study, extracts of several species harvested in warm season presented higher bioactivity, such as the cytotoxic activity from *Cystoseira* *tamariscifolia* (Hudson) Papenfuss (Mansur et al. 2020) and *Fucus vesiculosus* Linnaeus (Heavisides et al. 2018), and anti-inflammatory activity from *Bifurcaria bifurcata* R.Ross and *Ericaria selaginoides* (Linnaeus) Molinari & Guiry (Pedro et al. 2022). On the other hand, extracts of *S. vulgare* showed the highest antioxidant and anti-HIV activities during the wet season in our previous study (Santos et al. 2018). Thus, seasonality studies regarding chemical composition and bioactivity of the extracts are important for more effective resource management.

Analyzing the extracts separately, the M and Aq extracts were the most influenced by season, with the M extracts being more biostimulant during the dry season and Aq extracts during the wet season (Table 1). In the literature, water is the most widely used solvent for the extraction process of seaweed-based biostimulants, as aqueous extracts are rich in polysaccharides. The three algae evaluated in our study have their sulfated polysaccharides described in the literature: fucoidans from *Sargassum* sp., ulvans from *Ulva* sp., and galactans from *Palisada* sp. These polysaccharides, especially fucoidans and ulvans, are well-known plant biostimulants (Ali et al. 2021; Munaro et al. 2021). Modifications in the structure of polysaccharides, such as variations in sulfation degree, are responsible for differences in the activities of the same type of polysaccharide. On the other hand, organic extracts can contain hormone and other secondary metabolites that can be improve the growth, development, and defense. For example, both phenolic biostimulants phloroglucinol and eckol were detected in algal liquid biostimulant using methanol (Rengasamy et al. 2016).

In conclusion, the three species of seaweeds studied showed a biostimulant effect on *L. sativa* seedlings, regardless of the type of extract and the harvesting season. The results suggest that the algal extracts promoted the allocation of resources to the root and stimulated the growth of lettuce seedlings by elongation of the roots. As the seedling is a critical stage in the plant life cycle, resource allocation and elongation of the roots can be an advantage for plant survival, aiding in the competition for water and nutrients from the soil.

Overall, our results showed that the biostimulant properties of seaweed extracts varied with harvesting period (dry and wet seasons), once the activity of methanolic and aqueous extracts were influenced by the seasons. The season with the highest biostimulant effect varied depending on the type of the extract: methanolic extracts from the dry season and aqueous extracts from the wet season exhibited more biostimulant activity. However, in general, the dry season extracts showed the highest biostimulant effect. Therefore, the finding of this study can help in suggesting the best time to harvest, aiming to achieve greater biostimulant efficacy of algal products used in crops.

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Author's contributions JPS and FC conceived the study and designed the experiments, while JPS, PT, and AMA were responsible for conducting the experiments and analyzing the data. BNTS identified the algae, and PT performed the statistical analyses. PT, JPS and AMA wrote the initial draft of the manuscript. FC and DYACS performed editing and revisions of the manuscript. FC provided financial support for the study. All authors have read, contributed, and approved the final version of the manuscript.

Availability of data and material All data are included in this article.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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