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RESEARCH ARTICLE OPEN ACCESS

Interaction Between Plants Through Litter Input in Mangrove Succession in the Red River Delta

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Keywords: allelopathy | *Avicennia marina* | *Kandelia obovata* | litter decomposition | mangrove | plant-plant interaction | soil metabolomics | specialized metabolites | succession

ABSTRACT

Aims: Dominant or pioneer species litter decomposition was found to be involved in the recruitment of following species during succession in terrestrial plant communities, while knowledge remains scarce in wetland forests such as mangroves. Our study evaluated the influence of pioneer species leaf litter decomposition on (i) the settlement success of species following them or not in the natural succession and (ii) on soil characteristics.

Location: Red River Delta, Vietnam.

Methods: We set up an in situ experiment in mesocosms that followed the survival and growth of three species (*Kandelia obovata*, *Aegiceras corniculatum*, and *Rhizophora stylosa*) planted in soils of *Avicennia marina* or *Sonneratia caseolaris*, with or without leaf litter addition for 203 days. Soil nutrient contents were determined at the beginning and end of the experiment, and their metabolic fingerprints were compared using an untargeted metabolomic approach to highlight potential allelochemicals when a phytotoxic effect was observed.

Results: Seedling response to litter addition was species-specific, which can be linked to their successional status. *K. obovata* was most affected by litter addition, showing better growth with both litter types. Meanwhile, *A. marina* litter substantially decreased survival rates by 50% for *K. obovata* and 33% for *R. stylosa*, suggesting a strategy to delay its replacement by these species through the release of phytotoxic decomposition by-products. Metabolic fingerprints of *A. marina* soils planted with *K. obovata* showed no shift in global chemical composition, but 12 features were found significantly more abundant in the presence of litter. Putative annotations revealed sulfur-containing metabolites, which are probable products of organic matter sulfurization, a frequently occurring process in mangrove sediments. These unusual compounds may act as allelochemicals and should be further assessed.

Conclusions: Our findings suggest that allelopathic processes through litter decomposition may be at play in mangrove community assembly and could be a tool for restoration purposes.

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1 | Introduction

The diversity and composition of plant communities is the result of a complex network of interactions with their environment. Competition for resources, facilitation, and allelopathy are among these structuring interactions (Callaway and Walker 1997; Reigosa et al. 2006). Allelopathy can act as a process in forest renewal and species composition (Mallik 2003; Hashoum et al. 2017), particularly during succession, when plant species are replaced (Gallet and Pellissier 2002; Reigosa et al. 2006; Fernandez et al. 2006), with effects that can either interfere or facilitate the establishment of species from the next successional stage (Fernandez et al. 2013; Meiners 2014).

Litter decomposition is a key element in ecosystem productivity, but its by-products also showed various allelopathic effects on neighboring plants according to litter chemistry and stage of decomposition (Sarker et al. 2020; Bonanomi et al. 2021). Through leaching and microbial degradation, this fundamental process causes the progressive release of essential mineral nutrients (Vitousek and Sanford 1986) as well as low and high molecular weight soluble organic compounds in the soil, which can be beneficial for plant growth (Chomel et al. 2016). Meanwhile, through physicochemical and biological transformations, these chemicals can either increase or decrease their allelopathic effects, ultimately altering neighboring plant growth and functioning, directly or indirectly (An, Pratley, and Haig 2000; Bonanomi et al. 2006; Delory et al. 2021).

In the context of plant succession, litter accumulation and decomposition from pioneer or dominant species is one of the leading mechanisms at play in the recruitment of following species, along with light and nutrient availability, or soil characteristics (Facelli and Pickett 1991; Janišová et al. 2007; Koorem, Price, and Moora 2011). Previous studies addressed the implication of allelopathic processes in this phenomenon mainly in terrestrial ecosystems (Kaligarič et al. 2011; Mudrák and Frouz 2012; Meiners 2014), while knowledge remains scarce in wetland forests such as mangroves (Lang et al. 2021). A wide variety of mangrove communities exist as a result of various geomorphological, ecological, and climatic conditions (Feller et al. 2009). *Avicennia*, *Aegiceras*, and *Sonneratia* are among the main pioneer genera that colonize newly formed mudbanks in the Indo-West Pacific region of mangroves (Duke, Ball, and Ellison 1998; Tomlinson 2016).

In the Red River Delta (RRD) in North Vietnam, *Avicennia marina*, *Rhizophora stylosa*, *Bruguiera gymnorrhiza*, *Aegiceras corniculatum*, *Kandelia obovata*, and *Sonneratia caseolaris* are naturally occurring true mangrove species. Two main pioneer stages co-exist, mainly according to distance to the shore and water salinity. *A. marina* colonizes newly formed mudbanks in more saline waters whereas *S. caseolaris* establishes more inland where waters are brackish (Hong and San 1993). This allows two different succession dynamics to occur: in the mixed stage, *A. corniculatum*, *R. stylosa*, *B. gymnorrhiza*, and *K. obovata* establish under *A. marina* canopy while *A. corniculatum* and three semi-mangrove species (*Acanthus ilicifolius*, *Acrostichum aureum*, *Cyperus malaccensis*) establish under *S. caseolaris* canopy (Hong and San 1993).

Few studies addressed the implications of mangrove allelopathic effects in their successional dynamics. Chen et al. (2009) monitored the development of *Kandelia obovata* (previously identified as *K. candel* (Sheue, Liu, and Yong 2003)) watered with aqueous extracts from leaves of *A. marina*, *A. corniculatum*, *B. gymnorrhiza*, and *R. stylosa* and showed contrasted species-specific responses. Extracts from *A. corniculatum* were the least limiting to *K. obovata* development, which may partly explain the frequent colonization of *A. corniculatum* stands by *K. obovata* in the Guangdong province in southern China from which the plants originated. Recent attention was given to the effects of allelochemicals from litterfall in mangrove natural regeneration in the same province, where Lang et al. (2021) showed that leaf litter leachates from *K. obovata* significantly inhibited the germination and growth of its associated species *A. corniculatum* in a microcosm experiment. Their results highlighted condensed tannins as the main allelochemical compounds, but also suggested that other bioactive materials from leaf litter could be at play. To our knowledge, Chapman and Feller (2011) is the only study that addressed the direct effect of mangrove leaf litter addition on mangrove community composition, showing an influence of litter identity on seedling growth of dominant species in the Atlantic East Pacific. No study evaluated the influence of leaf litter decomposition in the settlement success of species from later successional stages in mangroves in the Indo West Pacific.

Here, we evaluated the influence of two pioneer species leaf litter decomposition on (i) the settlement success of species following them or not in the natural succession to test if pioneer species facilitate their following species specifically and (ii) on soil chemical composition. For this purpose, we set-up an in situ experiment in mesocosms that followed survival and growth of three target species seedlings of the RRD (*K. obovata*, *A. corniculatum*, and *R. stylosa*) planted in soils derived from monospecific communities of dominant *A. marina* or *S. caseolaris* pioneer species, with or without leaf litter addition. We analyzed the chemical composition of tested soils, namely their nutrient contents for all tested interactions. For the most marked target response, we compared the global metabolic fingerprints of soils with or without litter by an untargeted metabolomic approach using liquid chromatography coupled with mass spectrometry, to highlight potential allelochemicals that could explain the effect. We hypothesize a species-specific response where pioneer species litter will (i) specifically facilitate the settlement of species following them in the mixed stage through the release of allelochemicals in soils during decomposition, and therefore (ii) induce a shift in soil chemical fingerprints.

2 | Material and Methods

2.1 | Study Site and Mangrove Species

To evaluate the effect of the pioneer species leaf litter decomposition (*Avicennia marina* and *Sonneratia caseolaris*) on the following species in the succession (i.e., the target species, *Kandelia obovata*, *Aegiceras corniculatum*, and *Rhizophora stylosa*), we performed an in situ mesocosm experiment at the

Mangrove Ecosystem Research Station (MERS, Appendix S1) in a mangrove plantation in the Giao Lac Commune, Giao Thuy District, Nam Dinh Province (20°14'27.1"N 106°30'51.6" E). The major soil type in this area is fluvisol (Nguyen Van et al. 2016). With an average humidity of 84.5% throughout the year, the region has a tropical wet climate with two monsoon seasons. The rainy season between June and October receives 85% of the annual precipitation (1660 mm in 2006) with July being the rainiest month (Minh et al. 2014). The mean seasonal temperature during summertime (May to September) varies between 27°C and 29°C, the highest temperature recorded exceeds 40°C. The Ba Lat estuary is subject to a diurnal, neap tide-spring tide cycle of 14 days, with an average tidal amplitude of 1.92 m during the 1972–1990 period. The tidal waves travel from South to North along the shorelines, and salinity intrusion can be observed up to 20 km inland from the Ba Lat mouth (Minh et al. 2014). However, during the flood season of the Red River (June–October), due to the high fresh-water discharge, the tidal variation and its influences are restricted.

2.2 | Soil and Plant Collection for Mesocosms Preparation

Soils from *A. marina* and *S. caseolaris* (40 cm depth), and their green leaves (5 individuals) were collected from monospecific mangroves stands in the Giao Lac commune (Appendix S1) 1 day before the experiment. Initial soil characteristics are shown in Table 1. After soil homogenization, macroscopic plant parts were manually removed to focus on the effect of leaf litter addition. Homogenized initial soil subsamples, as well as mixed leaves subsamples were kept at –18°C for nutrient content (soils only) and metabolomic analysis.

All the target seedlings were collected from multiple parent trees in the Giao Lac site and kept in separated soil bags in nursery outdoor (MERS) for 6 months before the beginning of the experiment. Healthy seedlings (approximately 5 cm in height and 2 leaves for *A. corniculatum* and 25 cm in height and usually 4–6 leaves for *K. obovata* and *R. stylosa*) were selected for this study and were kept under the same conditions. All mangrove species were identified according to the plant morphology description (Spalding 2011; Tomlinson 2016).

2.3 | Experimental Setup

A graphical representation of the experimental design is shown in Figure 1. In January 2020, 1 day after soils and leaves collection, 60 plastic pots (40 cm × 40 cm × 45 cm) were filled with 17 kg of soil for mesocosm settlement. To study the effect of pioneer species litter on growth and survival of nursed target species, 30 mesocosms were amended with 170 g of leaves (1% of total FW) of one of the two pioneer species that were mixed with the soil. Thirty mesocosms for each pioneer species did not receive leaves and thus constitute control treatment (no litter). This experimental design leads to the following four treatments: *A. marina* soil with no litter (A-NL), *A. marina* soil with *A. marina* litter (A-L), *S. caseolaris* soil with no litter (S-NL), *S. caseolaris* soil with *S. caseolaris* litter (S-L). For each treatment, the five replicate mesocosms were planted with either four seedling of *K. obovata* and *R. stylosa* or five seedlings for *A. corniculatum*. In the field, the five mesocosms of each treatment were disposed randomly in five independent blocks, leading to a total of sixty mesocosms (two sources species (*A. marina* and *S. caseolaris*) × 2 modalities (with or without leaf litter addition) × 3 target species (*A. corniculatum*, *K. obovata*, and *R. stylosa*)). Each block was protected by nets set up underneath and around at 1.5 m high to protect seedlings from predators. Mesocosms were submerged once a day by tide during our assay.

2.4 | Plant Growth and Survival

Regular follow-up measurements were carried monthly from the beginning (t_0) of the experiment 20th of January 2020, until the end of the experiment on the 10th of August 2020 (t_f) where the height and the number of leaves were recorded on each of the seedlings of each of the mesocosms in all five plots (six measurements in total). For survival rates, the numbers of living and dead seedlings were recorded seven times in total.

The seedlings survival rates were determined in each of the mesocosms by considering the number of seedlings in the current and initial time steps:

$$\text{Survival rate at } t_i (\%) = 100 \times \left(\frac{\text{Nb of seedlings at } t_i}{\text{Initial Nb of seedlings at } t_0} \right)$$

TABLE 1 | Pioneer species initial soil characteristics (t_0). Mean ± SE.

Pioneer species	<i>Avicennia marina</i>	<i>Sonneratia caseolaris</i>
Location	20°13'17.0"N 106°29'40.7"E	20°14'34.8"N 106°34'15.7"E
TOC (%)	0.39 ± 0.04	0.84 ± 0.05
N (%)	0.08 ± 0.00	0.11 ± 0.01
CN ratio	5.19 ± 0.09	8.05 ± 0.19
Available N (mg/100g)	1.96 ± 0.09	2.91 ± 0.19
Available P ₂ O ₅ (mg/100g)	0.46 ± 1.15	0.51 ± 1.21
Cl (%)	0.46 ± 0.01	0.51 ± 0.01

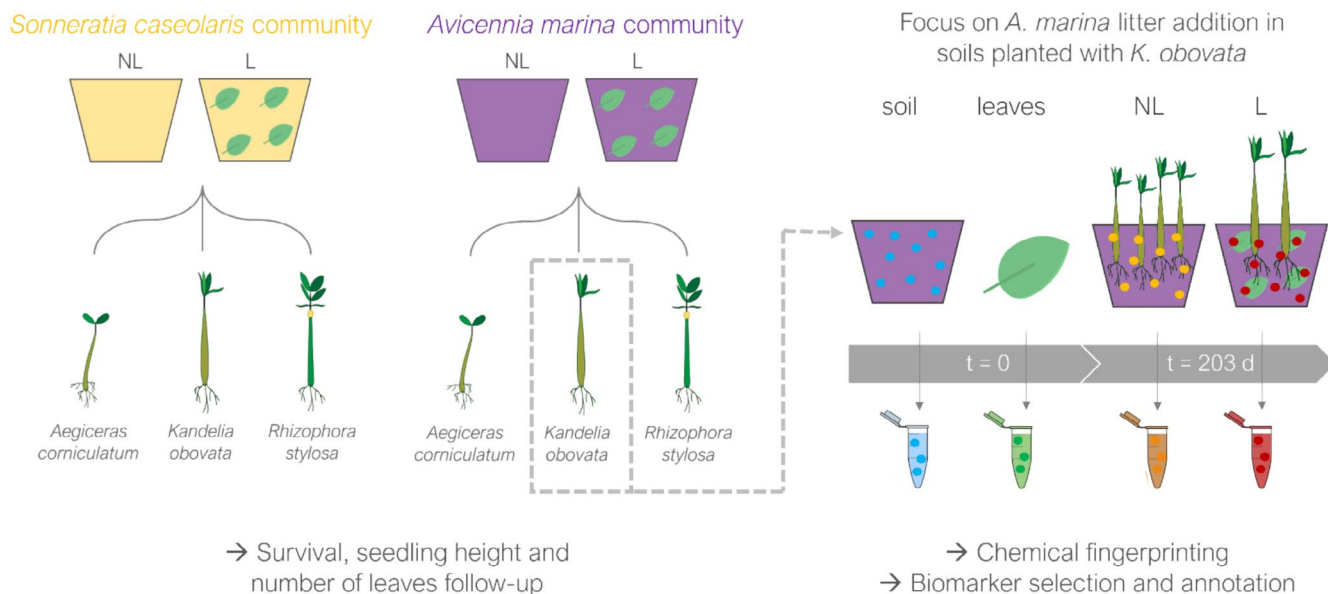


FIGURE 1 | Schematic representation of the experimental design showing the two main steps: (i) assessing three mangrove species growth and survival responses to litter addition in soils collected in *S. caseolaris* or *A. marina* communities (left) and (ii) evaluating the effect of leaf litter addition on the soil chemical fingerprints, and individual metabolite variation after 203 days of experiment, with a focus on *A. marina* soils planted with *K. obovata* (right). At t_0 , soils were collected from two pioneer species monospecific communities and transferred in mesocosms with (L) or without (NL) leaf litter from respective pioneer species and planted with each of the three target species.

with Nb of seedlings at t_i the number of seedlings alive at t_i .

2.5 | Chemical Analysis

2.5.1 | Soil Nutrients

Nutrient content analysis was carried out on initial soil subsamples (t_0) (see section Soil and plant collection for mesocosms preparation) and soils at the end of the experiment ($t_f = 203$ days). At t_f , soils from each mesocosms (five replicates per treatment) were collected and stored at -18°C prior to their analysis. The National Institute of Agricultural Planning and Projection (NIAPP, Hanoi) performed the quantification of the following parameters: chloride concentrations were determined with Mohr's method using silver nitrate titration with chromate indicator (Rajković, Sredović, and Miloradović 2010); total organic carbon (TOC) was determined using the Walkley Black Method (Meersmans, van Wesemael, and van Molle 2009); total nitrogen content (N) was determined with a modified Kjeldahl method using TiO_2 catalyst (Singh, Singh, and Sharma 2021); available nitrogen was determined with a nitrogen distillation and titration method using sodium hydroxide solution (Singh, Singh, and Sharma 2021); available phosphorus was determined using molybdenum blue spectrophotometry, with soil samples extracted by Olsen method (Lin et al. 2021).

2.5.2 | Metabolomic Analysis, Data Pre-Processing and Annotation of Metabolites

For chemical profile determination, we chose to focus on *A. marina* soils planted with *K. obovata*, as this target species showed the most marked decrease in survival in response to litter addition at the end of the experiment. *A. marina* initial leaves added to the mesocosms at the beginning of the assay (A-leaves- t_0)

were analyzed to serve as analytical references for the dereplication of litter decomposition by-products, which could be allelochemicals. Our objectives were (i) to evaluate the differences between *A. marina* initial soils (A- t_0) and soils planted with *K. obovata* with (AL-tf) and without (ANL-tf) *A. marina* leaf litter 203 days after their addition and (ii) to assess the similarities between AL-tf and A-leaves- t_0 .

2.5.2.1 | Initial Leaves Extraction. After freeze-drying (Lyovac GT2) and powdering (MM400, Retsch GmbH.D, Hann Germany), a dry mass of 10 mg of each sample was weighed in 1.5 mL Eppendorf tubes and suspended in 400 μL of methanol (LC-MS grade, Carlo Erba, France) before ultra-sonication at room temperature for 5 min for metabolite extraction. Subsequent sample preparation is shown in Appendix S2.

2.5.2.2 | Soil Extraction. For soil extraction, the microwave-assisted extraction (MAE, CEM MARS 230/60 Microwave Accelerated Reaction System, CEM Corporation, USA) modified from Montesdeoca-Esponda et al. (2013) was used. After freeze-drying (Lyovac GT2) and powdering (MM400, Retsch GmbH.D, Hann Germany), 5 g of dry soil samples were transferred to microwave tubes and suspended in 10 mL of MeOH/Water (70:30 v:v). Subsequent sample preparation is shown in Appendix S2.

2.5.2.3 | UHPLC-ESI-qToF Analysis. The samples were analyzed by Ultra-High Performance Liquid Chromatography instrument, including UHPLC system (Dionex Ultimate 3000, Thermo Electron, France) coupled to a qToF mass spectrometer (Impact II, Bruker Daltonics, Germany). Separation was conducted on a Kinetex XB-C18 column (150 mm \times 2.1 mm, 1.7 μm , Phenomenex, France). More details are shown in Appendix S2.

The raw data obtained from UHPLC-MS/MS were calibrated and converted into Computable Document Format (.cdf) files

using Compass DataAnalysis (Bruker Daltonics version 5.0). These files were then preprocessed (via chromatographic peak detection, integration, alignment, and grouping) using the open-source XCMS package (version 3.6.2 (Smith et al. 2006)) in R 3.6.0 version. To ensure data quality and remove redundant signals, three successive filtering steps were applied as described in Favre et al. (2017). After statistical analysis, the biomarkers specific to *tf*-Am-L soils were selected for putative annotation. The process of metabolite annotations were based on a dereplication strategy as described in Dhaou et al. (2022) with an additional public database interrogation using MetFrag (Ruttkies et al. 2016).

2.6 | Data Analysis

2.6.1 | Growth and Survival Responses of Target Species

Growth and survival responses according to leaf litter addition (NL, L), planted target species (*A. corniculatum*, *K. obovata*, and *R. stylosa*) and their interaction were tested for each pioneer species (*A. marina* and *S. caseolaris*). To take into account repeated measures of seedlings over the days of measurements and over experimental plots (time and spatial dependencies), we used linear mixed-effect models (LMMs) and generalized linear mixed-effect models (GLMMs) (R package *lme4*) that include both fixed (litter addition and target species) and random factors (time and plots). GLMMs with binomial distribution were used for survival rates (proportion data), LMMs for height (continuous data) and GLMMs with Poisson distribution for the number of leaves (count data). When a significant effect was observed, we used a post hoc Tukey test for pairwise comparison.

2.6.2 | Soil Nutrient Contents

The soil nutrient contents according to litter addition, planted target species and their interaction were also tested for each pioneer species. For this analysis, time and spatial dependencies were not considered since soil samples were collected only at *tf* with one sample per experimental plot for each treatment. We therefore used two-way ANOVAs followed by a post hoc Tukey test for pairwise comparison.

When necessary, data were transformed using the *bestNormalize* package to meet the assumptions of normality and homoscedasticity of variances (arcsinh transformation for *A. marina* soils TOC and available N). All the tests were carried out using the R software (version 3.6.0, The R Foundation for Statistical Computing, Vienna, Austria) and plots were created using *ggplot2* package. The map of the experimental site was created using the Free and Open Source QGIS.

2.6.3 | Metabolomics Data

For metabolomic analysis, figures, multivariate (Principal Component Analysis (PCA)), univariate analyses (ANOVA) and boxplots plots were realized using MetaboAnalyst 6.0 online resource (<https://www.metaboanalyst.ca/>, accessed in April

2024). PERMANOVA permutation test (*RVAideMemoire* package on log-transformed data) was performed (10,000 permutations) to test global differences between leaf and soil extract groups and pairwise differences using R software.

3 | Results

3.1 | Survival and Growth Response to Litter Decomposition

The three planted species responded differently to pioneer species leaf litter decomposition. *Aegiceras corniculatum* did not show any significant response to litter decomposition for all variables measured here, whereas *Kandelia obovata* and *Rhizophora stylosa*'s response depended on parameters and pioneer species (Figure 2, Table 2).

Considering seedling mortality, *Sonneratia caseolaris* litter addition and planted target species did not affect seedling survival (Table 2), while a significant interaction of these two factors was observed for *Avicennia marina* (Table 2), where *K. obovata* and *R. stylosa* survival significantly decreased by 46% and 33% in L soils compared with their NL control respectively, after 203 days of decomposition (Figure 2). *K. obovata* showed the most rapid and marked mortality in *A. marina* soils with litter (L) where approximately 31% more seedling died after 81 days of decomposition compared to soils without litter (no litter: NL), when this mortality level was reached by *R. stylosa* seedlings in L soils compared to NL after 203 days of decomposition (Figure 2). Considering seedling growth, litter addition, and target species interacted in their effects for height response for both pioneer species (Table 2), while this interaction was found significant for the number of leaves response for *S. caseolaris* only (Table 2). *R. stylosa* height significantly decreased in *A. marina* L soils compared to NL (−8.3% at the end of the experiment, Figure 2). However, *K. obovata* height was found substantially higher in *A. marina* and *S. caseolaris* L soils compared to NL with a 36% and 24% increase after 203 days of decomposition respectively, while its number of leaves only increased in *S. caseolaris* L soils compared to NL (+50% at the end of the experiment, Figure 2).

3.2 | Soil Nutrient Content Response to Litter Decomposition

At the end of the experiment (203 days), soil nutrient compositions were not equally affected by litter addition or target species, depending on the considered pioneer species (Table 3). Globally, no effect of these two factors or their interaction was observed in *S. caseolaris* soils for all assessed parameters: TOC, N, available N, available P contents, or CN ratios (Appendix S3). For *A. marina* however, no interaction effects were found for all parameters, but we observed significant effects of litter addition on TOC ($F=7.71$, $p<0.05$), N ($F=8.09$, $p<0.01$), available N ($F=6.97$, $p<0.05$) contents and CN ratios ($F=5.16$, $p<0.05$), while no effect of target species was highlighted ($F=0.29$, $p>0.05$ for TOC; $F=0.22$, $p>0.05$ for N, $F=0.07$, $p>0.05$ for available N, and $F=0.45$, $p>0.05$ for CN). For all target species combined, litter decomposition

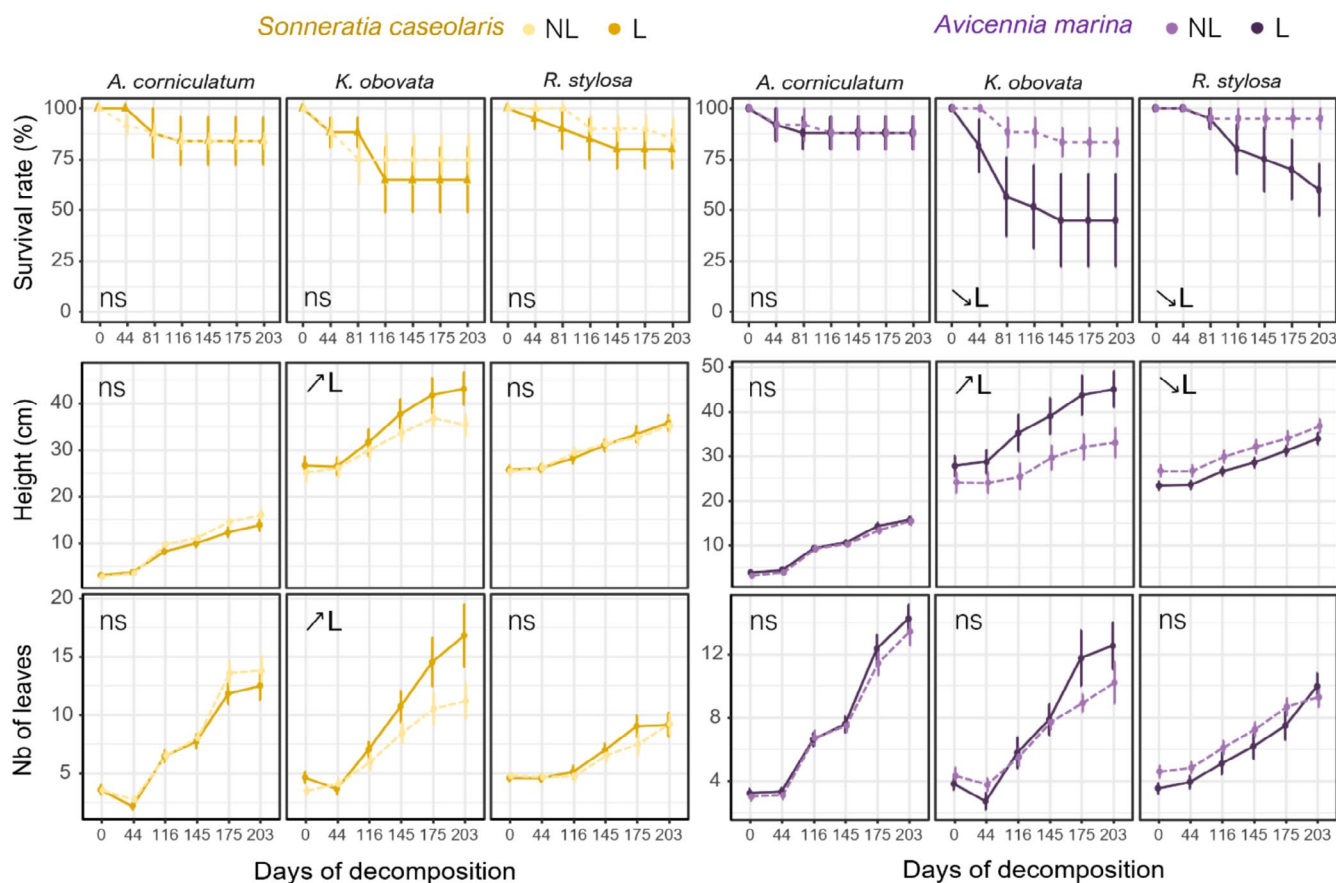


FIGURE 2 | Survival and growth response of planted target species (*A. corniculatum*, *K. obovata* and *R. stylosa*) to leaf litter addition from two pioneer species communities (*S. caseolaris*, left and *A. marina*, right; plain line in dark color: Litter addition (L); dashed line in light: No litter (NL)) during 203 days of decomposition. Mean \pm SE, ↗L and ↘L indicate a significant increase or decrease when litter is added for each target species (post hoc pairwise comparison $p < 0.05$).

TABLE 2 | Results of linear (LMs) and generalized linear mixed models (GLMMs) testing the effects of litter addition, planted target species and their interaction on seedling survival, height and number of leaves for each tested pioneer species during the experiment.

	Survival			Height			Number of leaves		
	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>	χ^2	df	<i>p</i>
<i>Avicennia marina</i>									
Litter addition	0.045	1		0.3899	1		0.8748	1	
Planted species	8.469	2	*	324.0785	2	***	10.8047	2	**
L × T	13.2113	2	**	48.4623	2	***	4.6038	2	
<i>Sonneratia caseolaris</i>									
Litter addition	0.1301	1		2.356	1		4.4684	1	*
Planted species	0.3367	2		406.5496	2	***	7.4497	2	*
L × T	3.4478	2		9.6864	2	**	22.9507	2	***

Note: Significant *p* values are shaded in gray.

substantially increased *A. marina* L soil contents in TOC (1.8-fold), N (1.5-fold), available N (1.8-fold), and CN ratios (1.13-fold) compared to NL (Table 3). Only available P contents were not affected by the tested factors or their interaction in the case of *A. marina* soils and remained similar between NL and L soils (Table 3).

3.3 | Focus on *A. marina* Soils Planted With *K. obovata* for Chemical Investigation

To further investigate soil chemical compositions and highlight potential allelochemicals that could be released during litter decomposition through an untargeted metabolomic approach, we

chose to focus on the most marked survival and growth response to litter addition of the assessed target species. Among the species that were significantly affected by litter addition, *K. obovata* seedlings showed the most rapid and important decrease in survival rates and the most important increase in height in *A. marina* L soils compared to NL (Figure 2). For these reasons, these soils were selected for analysis at the end of the experiment (AL-tf and ANL-tf for *A. marina* soils planted with *K. obovata*, with and without litter addition respectively, after 203 days of decomposition), along with *A. marina* initial soil (A-t0) and leaves that were added to the mesocosms at the beginning of the assay (A-leaves-t0) (Figure 1). Our objectives were (i) to evaluate the differences between A-t0, AL-tf, and ANL-tf extracts and (ii) to assess the similarities between AL-tf and A-leaves-t0.

3.4 | Soil Chemical Fingerprints

After soil extract analysis by an untargeted UHPLC-MS-based metabolomics approach, data preprocessing and filtering allowed to obtain 1232 m/z features dataset (766 features detected in negative mode combined to 466 features detected in positive mode). The resulting PCA score plot (Figure 3a) revealed significant differences between tested soil chemical fingerprints (PERMANOVA, $p < 0.01$). *A. marina* initial soils (A-t0) separated from A-NL-tf and A-L-tf soils fingerprints on the first component (46.9% of total variance), while the latter two clusters overlapped on components 1 and 2 (13.7% of total variance), indicating fingerprint similarity.

TABLE 3 | Nutrient contents of soils collected from assessed mesocosms at the end of the experiment ($t_f = 203$ days) for each pioneer species.

Pioneer species	<i>Avicennia marina</i>		<i>Sonneratia caseolaris</i>	
	NL	L	NL	L
Litter addition				
TOC (%)	0.40 ± 0.04 a	0.72 ± 0.12 b	0.68 ± 0.08	0.8 ± 0.11
N (%)	0.06 ± 0.00 a	0.09 ± 0.01 b	0.08 ± 0.01	0.09 ± 0.01 b
Available N (mg/100g)	1.12 ± 0.08 a	2.02 ± 0.33 b	2.05 ± 0.27	2.12 ± 0.26
Available P ₂ O ₅ (mg/100g)	67.72 ± 1.04	66.43 ± 0.69	71.41 ± 0.76	69.88 ± 0.55
CN ratio	6.69 ± 0.2 a	7.56 ± 0.4 b	7.98 ± 0.24	7.68 ± 0.25

Note: NL and L indicate the absence or presence of leaf litter (added at t_0), respectively. Mean ± SE of data pooled for all planted target species, different letters indicate statistical difference between NL and L with a < b for each tested pioneer species, significant differences are shaded in gray (post hoc pairwise comparison $p < 0.05$).

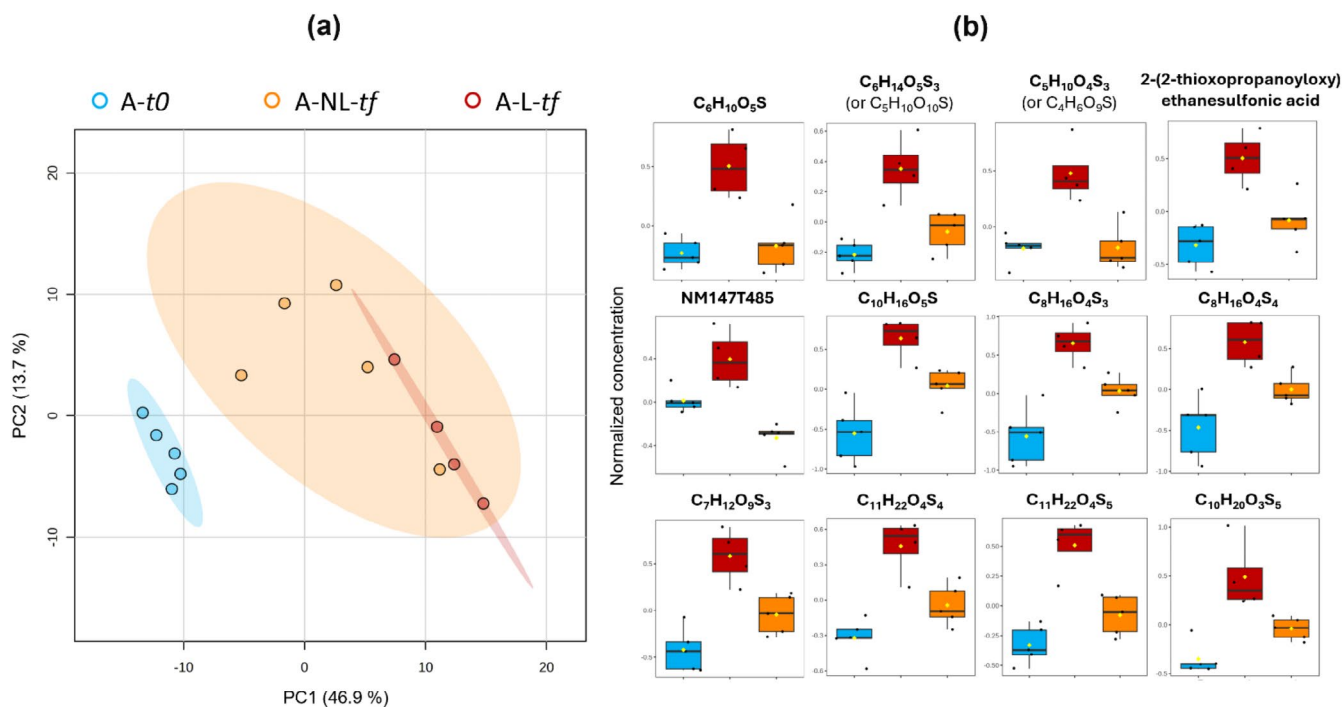


FIGURE 3 | (a) Principal component analysis showing chemical fingerprints of extracts from *A. marina* initial soils (A-t0) and soils collected from mesocosms planted with *K. obovata* with (A-L-tf) or without (A-NL-tf) *A. marina* litter addition, 203 days after decomposition (t_f); (b) Soil type variation in relative concentrations of 12 selected and putatively annotated biomarkers specific to A-L-tf condition (post hoc pairwise comparison $p < 0.05$). The dataset obtained by UHPLC-HRMS (1232 detected features in total) was log-transformed and mean-centered.

3.5 | *A. marina* Litter Decomposition Biomarkers Selection and Annotation

Univariate analysis of each detected m/z feature allowed to highlight 13 biomarkers significantly more abundant in A-L-tf than A-t0 and A-NL-tf (ANOVA, $p < 0.01$). We focused on these 13 features (all detected in negative mode) for putative annotations with MS-based dereplication. When observed, in-source fragments of the same molecule were combined to avoid chemical redundancy and keep metabolites with their monoisotopic molecular ion $[M-H]^-$, which resulted in 12 biomarkers (Figure 3b). Except for the feature NM147T485, all biomarkers molecular formulas could be deduced (Appendix S4). Isotopic patterns and the presence of a MS/MS fragment at m/z 79.956 $[O_3S]^-$ indicated the presence of one or more sulfur atoms in all biomarkers. The only feature that could be putatively identified is NM211T380, suggested as 2-(2-thioxopropanoyloxy) ethane-sulfonic acid, with seven MS/MS fragments out of eight matching with MetFrag database (final match score = 1.0), its MS/MS spectrum and fragmentation pattern is shown in Appendix S5. When available, MS/MS spectra for each biomarker are shown in Appendixes S5–S12.

4 | Discussion

In this study, we investigated whether leaf litter decomposition of pioneer mangrove species in the Red River Delta could (i) influence species recruitment during succession and (ii) modify the chemical composition of soils with decomposition by-products potentially acting as allelochemicals.

Our mesocosm experiment revealed contrasted effects of pioneer mangrove litter decomposition on target seedling growth and survival, with a species-specific response. Indeed, in the case of *Avicennia marina* litter, *Rhizophora stylosa* and *Kandelia obovata* were the only species affected by its decomposition, with heights either slightly inhibited or substantially stimulated respectively, and most of all, an important mortality for both species after 203 days of decomposition. In the case of *Sonneratia caseolaris*, the only species affected by its litter decomposition was *K. obovata*, with a significant increase in height and number of leaves at the end of our experiment, but overall, seedling survival rates remained unchanged. This in accordance with the findings of Sarker et al. (2020), who observed facilitating and inhibitory effects of litter addition on seedling growth in relation to target species identity and litter type in tropical rainforests. Other studies showed litter beneficial effects linked to nutrient enrichment (Ganade and Brown 2002; Brearley, Press, and Scholes 2003) or inhibitory effects linked to allelopathic processes (Fernandez et al. 2006; Meiners 2014; de Heras et al. 2020; Bonanomi et al. 2021).

The more rapid growth of *K. obovata* seedlings in the presence of *A. marina* litter may have occurred in response to its important decrease in survival throughout the experiment, as previous studies showed that low density populations can support tree settlement success with less resource competition and concentration for specific pathogen (Chesson 2000; Liu et al. 2015). Moreover, the two-fold increase in available nitrogen in *A. marina* soils with litter addition compared to no litter

addition at the end of our experiment may have favored *K. obovata* growth, as several field studies showed that nutrient enrichment, and especially nitrogen, favors mangrove tree growth (Feller et al. 2003; Lovelock et al. 2004; Krauss et al. 2008; Reef, Feller, and Lovelock 2010). In the presence of *S. caseolaris* litter however, seedling height and number of leaves were also found higher than seedlings grown in *S. caseolaris* soils without litter despite the absence of soil nutrient enrichment. This is in accordance with Chapman and Feller (2011) findings, who also observed a more rapid mangrove seedling growth in the presence of conspecific litter, irrespective of litter chemical quality and nitrogen release in a mesocosm study conducted in Florida. Still, these studies were conducted in the Atlantic East Pacific regions while knowledge remains very scarce about the specific response of species from the Indo West Pacific regions (Krauss et al. 2008), it is therefore difficult to explain the species-specific growth responses observed in our study through this framework exclusively, which only partially validates our first hypothesis of a better growth through nutrient enrichment.

Within our findings, two other observations further suggest that other factors are involved. First, litter addition effect was not found to be dependent on target species for soil nutrient contents, as opposed to growth responses. Secondly, only *A. marina* soils with litter addition showed higher nutrient contents compared to soils without litter, with almost doubled amounts of total carbon and available nitrogen, and amounts of total nitrogen increased by half, while no significant enrichment was highlighted for *S. caseolaris* soils with litter addition compared to soils without litter. Yet, *K. obovata* grew better in soils amended with litter from both pioneer species in our assay. These results reinforced our second hypothesis of allelopathic processes potentially at play here, further supported by the substantially higher mortality of *K. obovata* and *R. stylosa* that could be due to phytotoxic by-products from *A. marina* leaf litter decomposition.

A strong allelopathic potential of *A. marina* leaves was previously shown on agricultural species (Chen et al. 2009; Dhaou et al. 2022). To our knowledge, Chen et al. (2009) study is the only assessment of *A. marina*'s allelopathic potential on mangrove seedlings. Contrary to our findings, they found that leachates from green leaves of *A. marina* significantly inhibited shoot length of *K. obovata* (previously identified as *K. candel*) in a mesocosm experiment. The variable chemical composition between *A. marina* green leaves and its decomposed litter (Zhou et al. 2010, 2023) may explain our observations. Moreover, although seedling mortality was not assessed, a significant reduction in root length was observed in their study. We may therefore suggest that belowground parts may have been negatively affected by the end of our experiment. Overall, by showing the allelopathic effect of *A. marina* green leaves macerates, Chen et al. (2009) findings suggest a possible phytotoxicity of its litter through the liberation of its decomposition by-products in the soil, to which *K. obovata* could be sensitive. This could have led to the important mortality found in our study for this target species.

For these reasons, we investigated the assessed soil chemical compositions, with a focus on the most affected target seedling, namely *K. obovata* and the most impacting pioneer species, namely *A. marina*. Using an untargeted metabolomic

approach, we compared the chemical composition of initial *A. marina* soils (A-t0) with soils from mesocosms planted with *K. obovata* where *A. marina* leaf litter was initially added (A-L-tf) or not (A-NL-tf), after 203 days of decomposition (i.e., end of our experiment). Contrary to our third hypothesis, leaf litter decomposition did not modify A-L-tf soils' global chemical fingerprints compared to A-NL-tf, and no proximity was observed with our initial leaves analytical reference. Previous studies showed contrasted average times of decomposition of *A. marina* leaf litter according to mangrove types and regions, time to lose half of the initial mass (t_{50}) ranged from 96 to 78 days according to dry and wet season respectively in urban dwarf mangroves and 171–48 days in a rural well-developed mangrove in South Mozambique (Fernando and Bandeira 2009). In South Vietnam, t_{50} ranged from 36.5 days in the dry season to 12.2 days in the wet season (Vinh et al. 2020), while in South China, t_{50} was reached after 19 days of decomposition (Zhou et al. 2010). Mangrove litter decomposition is characterized by an initial leaching of soluble organic (which can occur rapidly for *A. marina* within the first 14 days (Zhou et al. 2010)) and inorganic compounds, followed by microorganism colonization, which initiates physical and biological transformation (Hossain and Hoque 2008). With a maximum t_{50} reaching 171 days for *A. marina* leaf litter decomposition according to previous assessments, *A. marina* litter probably already underwent substantial biological and physical transformations after 203 days in the present study, which could explain the absence of chemical fingerprints proximity between *A. marina* initial litter and A-L-tf soils. This was confirmed by the MS-based annotation of biomarkers specific to A-L-tf soils that did not highlight any tannin or phenolic compound.

Instead, A-L-tf soil biomarkers putative annotations revealed 12 sulfur-containing organic compounds that suggest possible by-products of litter decomposition through a sulfur (S) reducing process. Mangrove sediments are frequently anoxic and rich in sulfates mainly of seawater origin (Balk, Keuskamp, and Laanbroek 2016), with generally high salinity, which favors organic matter (OM) sulfurization that can contribute to up to 50% of carbon burial (Chambers, Osborne, and Reddy 2013). The redox gradients around O_2 -releasing mangrove roots can facilitate the formation of several OM-S complexes by reacting with free polysulfides in porewaters (Raven et al. 2019). Nevertheless, sulfated ellagic acid derivatives were recently described for the first time in roots and leaves of the mangrove genus *Lumnitzera* spp. (Manurung et al. 2021) and *Sonneratia apetala* (Dhaou et al. 2022) respectively, suggesting that some annotated biomarkers could also have been sulfurized prior to their physicochemical or biological transformation in the sediments here.

The leaves of *A. marina* contain abundant and diverse specialized metabolites (Liebezeit 2012; Thatoi, Samantaray, and Das 2016), among them, phenolics were suggested to be responsible for allelopathic effect of this species (Chen and Peng 2008; Chen et al. 2009). No allelopathic assessment of its leaf litter was investigated to our knowledge. Lang et al. (2021) is the only investigation of litter allelopathy conducted on mangrove species, namely *K. obovata* on *Aegiceras corniculatum*. Their results showed the allelopathic potential of its leaf litter leachates, with condensed tannins as the main responsible compounds for *A. corniculatum* germination and growth reduction, while suggesting that

other phytotoxic by-products of decomposition could be at play. Similarly, in other plant models, de Heras et al. (2020) also observed the predominance of phytotoxic effects over positive effects when assessing leaf litter from exotic and native riverine trees on the germination and growth of herbaceous species. They characterized the chemical composition of tested litter samples over time of decomposition and found that among nine species, only *Ailanthus altissima* litter inhibitory effect on growth could be linked to higher phenolic acids and flavonoids contents, suggesting that other compound classes acted as allelochemicals in their study. Quan et al. (2022) assessed the allelopathic potential of aqueous extracts of *Salix caprea* litter and soil layers. After highlighting a significant germination inhibition of three target species, a total of 26 allelochemicals were identified, with mainly organic acids in the soil and humus layers, and phenolic acids in the litter layer. The organic acid annotated as 2-(2-thioxopropanoyloxy)ethanesulfonic acid may therefore be involved in the phytotoxicity observed in A-L-tf soils. The isolated compounds' effects need to be further assessed and other types of specialized metabolites may be involved in the present study. As previously mentioned, the main bioactive compounds may have already been degraded after 203 days of decomposition (i.e., the time after which soils amended with *A. marina* leaf litter and planted with *K. obovata* were analyzed, A-L-tf), considering that the maximum reduction of *K. obovata* survival rates was reached after 116 days, and the relatively fast decomposition rate of *A. marina* leaf litter (Fernando and Bandeira 2009; Vinh et al. 2020).

The allelopathic effect suggested here may have occurred directly or indirectly (i) through chemical modifications of litter by microorganisms during their decay, allowing a phytotoxic effect to occur in the soil (Jilani et al. 2008), or (ii) through the modification of microbial communities exposed to allelochemicals or by-products that caused unfavorable conditions for plant growth or survival in the soil, by limiting nutrient absorption for example (Inderjit 2003; Scavo, Abbate, and Mauromicale 2019). Moreover, allelochemicals can influence not only their plant neighbors but also fungi and bacteria (Schandry and Becker 2020), which can ultimately affect competition for resources between these organisms (mainly saprophytic microbes) and plants in the context of litter decomposition. In the case of mangroves, Lang et al. (2024) showed that leaf litter of *K. obovata*, *A. marina* and *S. apetala* boosts sediment microbial activities and diversities. Their results revealed that the release of mangrove tannins during leaf litter decomposition is one of the key factors driving N cycling, and microbial activities and diversities in mangrove wetlands. Overall, other processes may be at play in combination with resources competition and allelopathy in the present work, this complexity makes the study of litter-plant interactions quite challenging in situ.

Despite the difficulty of describing the mechanisms behind the contrasted seedling responses here (i.e., distinguishing allelopathic effects from competition for nutrients (Weidenhamer, Hartnett, and Romeo 1989)), our results can be interpreted in the framework of mangrove species composition and successional dynamics. Seedling establishment success is critical for mangrove regeneration and community replacement, as vegetative reproduction is rarely employed by these species (Tomlinson 2016). During this process, stem elongation is one of the most important parameter, allowing better access to light and avoidance of tidal immersion. Here, *K. obovata* is the only

target species that showed more rapid growth in the presence of *S. caseolaris* and *A. marina* litter. This suggests a facilitation of *K. obovata* settlement by both pioneer species, which could participate to its dominant status in the studied area. Still, survival of *K. obovata* and *R. stylosa* seedlings was substantially reduced where *A. marina* litter decomposed. In the RRD, these two target species specifically follow *A. marina* in the mixed stage, where they gradually surpass the latter to become dominant, ultimately replacing *A. marina* in the dominant stage by forming dense canopies (Hong and San 1993). We hypothesize that the release of decomposition by-products of *A. marina* litter, specifically phytotoxic to *K. obovata* and *R. stylosa*, may allow the delay of its replacement during succession, as suggested in previous studies in other plant communities (Fernandez et al. 2006; Meiners 2014). On a longer term, the reduction of seedling survival may have indirect beneficial consequences for species settlement by reducing competition for resources (Liu et al. 2015), this could ultimately facilitate the progressive replacement of *A. marina* by *K. obovata* and *R. stylosa*. Overall, *A. corniculatum* did not show any response to the decomposition of both pioneers. Its position in successional dynamics of the RRD might be a reason for this specificity. Indeed, this shrub is the only assessed species that co-exists with both pioneers in the mixed stage as understory, without replacing them in the dominant stage (Hong and San 1993).

5 | Conclusions

The present study shows a species-specific response of mangrove seedlings settlement success to pioneer species leaf litter decomposition, with contrasted beneficial effects on growth and detrimental effects on seedling survival. *Kandelia obovata* is the only species that grew faster with both types of litter, which could participate to its dominant status in the studied area. Meanwhile, contrary to our first hypothesis of pioneer species specifically facilitating the settlement of the species following them in succession, we found a substantial decrease in *K. obovata* and *Rhizophora stylosa* survival rates in the presence of *Avicennia marina*, indicating a potential strategy to delay the pioneer's replacement through the release of phytotoxic by-products of litter decomposition which could act as allelochemicals. Nevertheless, we may hypothesize an indirect beneficial effect for the settlement of these species in the long run through the reduction of intra-specific competition for resources. Finally, we focused on the most marked phytotoxic effect observed in our study to compare soil chemical fingerprints and highlight potential allelochemicals using an untargeted metabolomic approach, namely in *A. marina* soils planted with *K. obovata* amended or not with leaf litter. Contrary to our second hypothesis, we did not observe a shift in global chemical fingerprints in soils where *A. marina* litter decomposed for 203 days, yet our analysis revealed 12 sulfur-containing specific biomarkers, among which the organic acid 2-(2-thioxopropanoyloxy)ethanesulfonic acid. These annotated compounds are probable by-products of litter decomposition through a sulfur reducing process, suggesting that mangrove litter allelochemicals may exhibit previously undescribed original structures. Further studies are necessary to unravel the identity and role of mangrove allelochemicals. Plant succession is an important process during ecosystem development, especially in forests that are recovering from disturbances such as Vietnamese mangroves. Further studies are needed to

better understand the successional process in mangroves and the importance of allelopathy to support restoration projects.

Author Contributions

D.D., C.F., T.D.V., and A.B.-M. conceived the research idea; D.D., A.B.-M., C.F., T.D.V., D.S., H.K.T., S.G., and C.L. collected data; D.D., C.F., D.S., S.G., H.K.T., and R.G. performed statistical analyses; D.D., D.S., H.K.T., and A.B.-M. wrote the paper; all authors discussed the results and commented on the manuscript; A.B.-M., and D.D. acquired the fundings.

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Conflicts of Interest

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

Data Availability Statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4qrfj6qjw>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.