Growth responses of *Avicennia germinans* and *Batis maritima* seedlings to weathered light sweet crude oil applied to soil and aboveground tissues

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Abstract

Oil spills are a significant stressor to coastal and maritime environments worldwide. The growth responses of *Batis maritima* and *Avicennia germinans* seedlings to weathered *Deepwater Horizon* oiling were assessed through a mesocosm study using a factorial arrangement of 4 soil oiling levels (0 L m⁻², 1 L m⁻², 2 L m⁻², 4 L m⁻²) × 3 tissue oiling levels (0% of stem height, 50% of stem height, 100% of stem height). Overall, growth metrics of *B. maritima* displayed much greater sensitivity to both tissue and soil oiling than *A. germinans*, which exhibited a relatively high tolerance to both routes of oiling exposure. *Batis maritima* in the 4 L m⁻² soil oiling treatment demonstrated significant reductions in cumulative stem height and leaf number, whereas no significant effects of soil oiling on *A. germinans* were detected. This was reflected in the end of the study biomass partitioning, where total aboveground and live aboveground biomass were significantly reduced for *B. maritima* with 4 L m⁻² soil oiling, but no impacts to *A. germinans* were found. Tissue oiling of 100% did appear to reduce *B. maritima* stem diameter, but no effect of tissue oiling was discerned on biomass partitioning, suggesting that there were no impacts to integrated growth. These findings suggest that *B. maritima* would be more severely affected by moderate soil oiling than *A. germinans*.

Keywords Coastal wetlands · Salt marsh · Mangrove · Oil spills · Petroleum · Contamination

Introduction

Salt marshes are valuable habitats that provide a number of ecosystem services, including coastal erosion mitigation, carbon sequestration, water quality enhancement, and faunal support (Pennings and Bertness 2001; Barbier et al. 2011; Duke 2016; Gorman and Turra 2016; CPRA 2017). Vegetation in these salt marshes is subjected to a number of environmental stressors, including flooding, anoxic soils, and increased salinity (Pennings and Bertness 2001; Alleyman and Hester 2010; Lonard et al. 2017). However, human activities can present additional stressors to salt marsh vegetation, including those associated with oil spills (Lin and Mendelssohn 2012). Thousands of oil spills occur in waters of the United States (US) annually, and although the vast majority of these incidents are small (< 159 L), 44 spills greater than 1.59 million L in volume occurred in US waters from 1969 to 2010 (National Oceanic and Atmospheric Administration 2017). Oil spills in salt marshes are particularly problematic not only because of direct physical and chemical impact to biota, but also because of the persistence of oil in flooded soils and the fragility of these habitats precluding subsequent clean up (Pezeshki et al. 2000; Michel and Rutherford 2013). The prevalence of oil spills in coastal areas underscores the need to understand how oiling impacts the valuable species occurring in these important habitats.

Oil spills are relatively frequent in areas where large volumes of petrochemical products are extracted and refined, such as the northern Gulf of Mexico. Coastal wetlands along the northern Gulf of Mexico experienced extensive oiling following the *Deepwater Horizon* (hereafter, *DWH*) spill on April 20, 2010 (Nixon et al. 2016), which was the largest marine oil spill in the US to date (Mendelssohn et al. 2012; Michel et al. 2013). The *DWH* spill impacted coastal...
Avicennia germinans (L.) L. (black mangrove) and Batis maritima L. (marine saltwort) are common constituents of high marshes of the subtropical Gulf of Mexico, including coastal Louisiana (Alleman and Hester 2010; Lonard et al. 2011; Lonard et al. 2017). Avicennia germinans occurs in the more southern, warmer saline marshes, such that the species has its northernmost boundaries in the Americas along the barrier islands and salt marshes of Louisiana’s Gulf of Mexico coast (Alleman and Hester 2010) and in the Guana Tolomato Matanzas National Estuarine Research Reserve of Florida’s Atlantic coast (Devaney et al. 2017). Batis maritima has a wide distribution that includes high marsh areas and ridges in the coastal areas of the Gulf of Mexico (Lonard et al. 2011). Although Spartina alterniflora (smooth cordgrass) is the dominant macrophyte in salt marshes of Louisiana, A. germinans is often present as a codominant or subdominant species in these areas (Hester et al. 2005). Batis maritima typically occurs at relatively high elevations in salt marshes throughout the Gulf of Mexico coast (Rassar et al. 2013). However, both A. germinans and B. maritima are commonly present in the high marsh of coastal Louisiana (Hester et al. 2005; Lonard et al. 2011; Lonard et al. 2017). Avicennia germinans, B. maritima, and other plant species of mangrove ecosystems in coastal Louisiana and throughout the Gulf of Mexico contribute to important ecosystem services, including protection from erosion, carbon export and sequestration, nursery habitats for fishes and crustaceans, and resources for humans (Katherisan and Bingham 2001; Alongi, 2002; Nagelkerken et al. 2008; Everard et al. 2014; Lee et al. 2014; Gorman and Turra 2016).

Laboratory studies of mangrove oiling have yielded useful information about survival and growth responses, although most experimental research has focused on soil oiling as opposed to tissue oiling. Getter et al. (1983) compared effects of unweathered oil and/or dispersants on A. germinans and R. mangle seedlings and demonstrated that A. germinans is more sensitive to oils, dispersants, and oil-dispersant combinations than R. mangle. They noted that A. germinans osmoregulates by taking up solutes into the roots then excreting solutes through leaf tissue, with oil included in the uptake and becoming deposited on the leaves, whereas R. mangle excludes this root uptake (Getter et al. 1983). In the study, effects varied among groups treated variably with a light crude oil, a heavy distillate oil, and a light distillate oil, with lighter oils showing increased effects (leaf shape and width) overall, though the lower concentrations of No. 2 fuel oil and bunker C fuel oil had greater growth rates and foliage production in A. germinans than untreated controls. Combining dispersant with oil increased effects in some instances. Getter and Baca (1984) provided further data regarding impacts of unweathered oil and/or dispersant on R. mangle, reporting that root-dosing by injection into the soil had lesser effects than tissue dosing, and also that seedlings of A. germinans and R. mangle obtained from areas that have been chronically oiled grew more foliage in response to Light Arabian oil. The authors proposed that previous oil exposure may result in an adaptive response (Getter and Baca 1984).

In another controlled study, none of the A. germinans seedlings exposed to fresh motor oil as a one-time application of 120 mL or 15 mL per week survived beyond a few weeks in a 59-week study, while 75% of R. mangle survived (Proffitt et al. 1995). A one-time oiling treatment under hot and bright outdoor conditions (as opposed to air-conditioned and diffusely lit laboratory conditions) yielded the greatest mortality (Proffitt et al. 1995). Additionally, acute treatment of A. germinans seedlings with 120 mL of Bonny Light crude oil placed on the soil surface of the base of the seedling showed episodic mortality, with 100% survival at 2 weeks, 70% between weeks 3 and 4, 60% between weeks 5 and 10, 50% at week 11, and 30% between weeks 12 and 16 (Chindah et al. 2011). Chronic treatment with 15 mL weekly resulted in reduced survival in weeks 13 and 14, stabilizing in week 15 (Chindah et al. 2011).

Hughes et al. (2018) studied the effects of weathered Louisiana sweet crude oil on mesocosms of A. germinans (1-year-old seedlings), S. alterniflora, and combined A. germinans and S. alterniflora assemblages. Oil treatments of 8 L m⁻² of a weathered crude oil were applied and drained for 5 days, diurnal tide actions were simulated, and response variables were followed for 1 year. Oiling adversely impacted both species, and mixing the species provided no benefit for S. alterniflora. However, the mixed community showed reductions in the negative effects of oiling for A. germinans. Reduction in A. germinans survival and belowground biomass was mitigated to 12% from 21% and to 19% from 71% in the mixed species condition compared to A. germinans alone.

The frequency of oiling in coastal wetland habitats necessitates studies that provide insight into how oil exposure...
impacts the health and subsequent recovery of specific coastal wetland vegetation species. The effects of oil exposure on A. germinans have been addressed in a number of observational and controlled studies (Getter et al. 1983; Prof- it et al. 1995; Chindah et al. 2011; Hughes et al. 2018). However, knowledge gaps exist in regard to the interactive effect of soil and aboveground tissue oiling for A. germi-

nans seedlings. Furthermore, the effect of oil exposure on B. maritima has not been experimentally assessed at the time of this writing. The purpose of this research is to expand the knowledge base of oil impacts on two high marsh vegetation species relevant to the Gulf of Mexico in order to facilitate coastal management.

Materials and methods

Seedlings of A. germinans and B. maritima were collected with intact adjacent soil in April 2018 from the Caminada Moreau Headland, LA. The plants were then transported to the Nicholls State University Farm greenhouse facility and transplanted into 15-cm (diameter) by 17-cm (height) polyethylene pots that were individually placed into 4.73-L polyethylene reservoirs. Reservoir water levels were main-
tained 10 cm below the soil surface of experimental pots for the duration of the study, with salinities maintained at 18 psu using commercial sea salt (Instant Ocean Spectrum Brands, Blacksburg, VA). Salinity levels in reservoirs were checked biweekly using a handheld meter and adjusted to

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Immediately prior to the initiation of the experimen-
tal treatments, cumulative stem height, stem diameter, leaf number, and visual chlorosis were determined for all experimental units. Cumulative stem height typi-
icluded one stem for A. germinans units, but often involved multiple stems for units of B. maritima, with those multiple stem heights summed into one measure-
ment. Stem height was measured from the soil surface to the highest point on each stem and recorded to the nearest mm. Stem diameter was measured to the nearest millimeter using calipers on the main stem 5 cm above the soil surface. Chlorosis was visually estimated using a scale developed by Mendelssohn et al. (1990): no impact (naturally speckled chlorosis), trace impact (intensely speckled chlorosis), light impact (50% or less yellowing), medium impact (more than 50% yellowing), heavy impact (all vegetation dead). Cumulative stem height and stem diameter, mortality, leaf number, and visual chlorosis were determined biweekly for both species.

At the conclusion of the study, all leaves of A. ger-
minans were harvested, rinsed, blotted dry, and scanned into a digital image using a flatbed scanner (Canon LiDE 110, Melville, NY). A small ruler was included in each scanned image for determination of scale. Digital images were analyzed using ImageJ software (Abramoff et al. 2004) to estimate individual leaf area. Following scanning, the leaves were placed into individual, numbered manila coin envelopes, dried to a constant weight at 65 °C, and individual leaf weights determined. Specific leaf area (leaf area/leaf mass) was then calculated on a whole plant basis for A. germinans. Due to morphological differences, specific leaf area was not calculated for B. maritima. For all experimental units, aboveground biomass was clipped at the soil surface using shears, rinsed of debris above a screen, partitioned into live and dead components, and dried to a constant mass before weighing. Thereafter, experimental units were emptied, and belowground material rinsed free of soil and debris over a screen and dried to a constant mass before weighing for a measurement of the total belowground biomass component.

Data were analyzed using an ANOVA framework for each species with a priori contrasts in R 3.6. For metrics meas-
ured at one point in time (e.g., biomass metrics collected at harvest), univariate factorial ANOVAs were executed using the aov command in R. For metrics collected over time (e.g., cumulative stem height), a mixed-model factorial ANOVA approach with time as the random effect was implemented using the lme command within the nlme package.
Results

Only a significant effect of time was detected for *A. germinans* cumulative stem height (Fig. 1 bottom panel; $F = 3.97, P < 0.001$), stem diameter (Fig. 2 bottom panel; $F = 5.76, P < 0.001$), leaf number (Fig. 3 bottom panel; $F = 25.16, P < 0.001$), and chlorotic index (Fig. 4 bottom panel; $F = 168.89, P < 0.0001$), reflecting general growth and tissue maturation over the course of the experiment. In contrast, a significant effect of time (Fig. 1 top panel; $F = 41.07, P < 0.0001$) and significant interaction of time and soiling (Fig. 1 top panel; $F = 2.04, P < 0.01$) was detected for *B. maritima* cumulative stem height, with the interaction resulting from all soil oiling treatments initially having similar stem heights, but the 4 L m$^{-2}$ soil oiling treatment being significantly reduced compared to the 0 L m$^{-2}$ treatment at the conclusion of the study (Fig. 1 top panel; contrast $t = 3.48, P < 0.01$). Similarly, *Batis maritima* stem diameter was significantly lower in the 4 L m$^{-2}$ soil oiling treatment compared to the 0 L m$^{-2}$ soil oiling treatment (Fig. 2 top panel; contrast $t = 2.28, P < 0.05$) at study week 16. Interestingly, a priori contrasts also revealed that *B. maritima* stem diameter in the 100% tissue oiling (mean± standard error: 0.199 ± 0.028 cm) was significantly reduced compared to the 0%
tissue oiling treatment (mean ± standard error: 0.276 ± 0.021 cm) at study week 16 (contrast $t = 2.81$, $P < 0.01$).

*Batis maritima* leaf number significant increased over time (Fig. 3 top panel; $F = 10.34$, $P < 0.0001$), and an a priori contrast revealed significantly lower leaf number of the 4 L m$^{-2}$ soil oiling treatment compared to the 0 L m$^{-2}$ soil oiling treatment (contrast $t = 2.13$, $P < 0.05$) at study week 16. Similarly, the a priori contrast of the 4 L m$^{-2}$ soil oiling treatment versus 0 L m$^{-2}$ soil oiling treatment for *B. maritima* at study week 16 revealed increased chlorosis (Fig. 4 top panel; contrast $t = 3.58$, $P < 0.01$). No significant effect of either tissue or soil oiling, or the interaction thereof, was detected for *Avicennia germinans* total aboveground (Fig. 5 bottom panel), live aboveground (Fig. 6 bottom panel), or belowground biomass. In contrast, for *B. maritima*, the a priori contrast of the 4 L m$^{-2}$ soil oiling treatment demonstrated significant reductions compared to the 0 L m$^{-2}$ soil oiling treatment for total aboveground (Figure 5 top panel; contrast $t = 2.54$, $P < 0.05$) and live aboveground (Figure 6 top panel; contrast $t$
= 2.88, \( P < 0.01 \)) biomass. No significant effect of tissue oiling was detected for *Batis maritima* live aboveground or total aboveground biomass, and no significant effect of either soil or tissue oiling was detected for *Batis maritima* belowground biomass. Interestingly, *A. germinans*-specific leaf area at the time of harvest was significantly greater in 100% tissue oiling treatments compared to 0% tissue oiling treatments (Fig. 7; contrast \( t = 2.16, P = 0.038 \)).

**Discussion**

Oil spills are among the significant threats to coastal marsh regions, as was recently highlighted by the DWH incident, the largest marine oil spill thus far in US waters (Mendelssohn et al. 2012). The research presented herein reveals differential tolerance by two important Gulf of
Mexico marsh plant species, *A. germinans* and *B. maritima*, to weathered DWH oil. Impacts of oiling to short-term, but not integrated, growth responses were discernible for *A. germinans*, whereas both short-term and integrated growth responses in *B. maritima* were clearly impacted by oiling. Importantly, these findings not only confirm the relatively high tolerance of *A. germinans* seedlings to DWH oiling recently documented by Hughes et al. (2018), but also refines the oiling dosages (1, 2, and 4 L m\(^{-2}\)) at which this tolerance can be anticipated. Additionally, this study elucidates hitherto unknown DWH oil exposure growth responses for *Batis maritima*, an important subdominant high marsh species in the Gulf of Mexico. This research also corroborates prior studies (e.g., Meudec et al. 2007; Lin and Mendelssohn 2012) suggesting that when in isolation, soil oiling is often more detrimental to plant growth than tissue oiling. Interestingly, tissue oiling does not seem to synergistically increase injuries due to
soil oiling. These findings enhance the existing knowledge base on which estimates of the likely severity of oil spills to Gulf of Mexico coastal plant community are based.

In a similar study, Hughes et al. (2018) applied 8 L m$^{-2}$ of Louisiana Sweet crude oil weathered with a bubbler aerator for 5 days to outdoor mesocosms containing either \textit{A. germinans}, \textit{S. alterniflora}, or a mixed planting of the two and compared these to untreated mesocosms. The oil application was repeated and drained daily for 5 days, and a diurnal tidal regime was simulated throughout the 1-year experimental duration. Similar to the findings presented herein, Hughes et al. (2018) detected no effect of oiling on \textit{A. germinans} stem height. Furthermore, a consistent negative impact of oiling was not detected for crown volume, a metric representative of \textit{A. germinans} aboveground growth by Hughes et al. (2018), which is consistent with the lack of impacts
Fig. 6 Mean (± SE) live aboveground biomass of *Avicennia germinans* and *Batis maritima* based on experimental soil oiling level.

A. germinans aboveground biomass reported here. Other studies assessing the survival and growth of *A. germinans* when exposed to oils other than weathered *DWH* oil reveal a range of responses. For instance, all *A. germinans* seedlings died within a few weeks of being planted in sediment oiled with 12 L m\(^{-2}\) (120 mL in the experiment) of fresh lubricating oil (Proffitt et al. 1995). Similarly, application of 120 mL of Bonny Light crude oil to the base of *A. germinans* seedlings resulted in lower stem height and stem diameter compared to the control over a 16-week study and impacts with respect to leaf length, leaf width, leaf production, leaf senescence, and seedling survival beginning in the third week (Chindah et al. 2011). Although, such impacts were not detected in this study, it employed a weathered oil that would be expected to exhibit reduced toxicity (Grant et al. 1993; Mendelssohn et al. 2012) at lower soil oiling levels. Getter et al. (1983) found that unweathered Bunker C fuel oil, No. 2 fuel oil and light Arabian crude oil each applied in dosages of 12.5, 25, 250, 2,500, and 25,000 μL to *A. germinans* seedlings demonstrated decreased leaf width with...
each oil type and at each dose, with a threshold effect on new foliage detected at 2500 μL dosing. This experiment used weathered crude oil applications in the amounts of 1800, 3500, and 7,100 μL. Although the amounts applied to soil in this study are comparable to those of Getter et al. (1983), the lower toxicity of weathered oil (Pezeshki et al. 2000) may explain the lack of detection of similar impact.

Oiling impacts to *B. maritima* were detected for multiple growth indicators, indicating that *B. maritima* has a greater sensitivity to weathered *DWH* oiling than *A. germinans* seedlings.

This sensitivity was reflected in a previous oil spill damage assessment in which field surveys conducted for a tanker spill of 75,000 to 150,000 gallons of crude oil-water emulsion in the Florida Keys noted mortality of *Batis* spp. in areas where substrate, stems, or leaves were coated with the contaminant (Irwin et al. 1997). Although the current controlled study did not result in complete mortality of *B. maritima*, significant impacts to growth processes were detected with soil and tissue oiling. Tunnell Jr et al. (1995) examined regrowth of vegetation following oil contamination from a ruptured pipeline in the high marsh at Upper Copano Bay, Texas, and the subsequent burning of oil that remained after oil recovery processes. Secondary succession by climactic perennial species, such as *B. maritima*, in oiled areas showed a trend toward increasing frequency over time.

Results of this research are generally consistent with the range of responses reported from mesocosm studies that assess the impacts of experimental *DWH* oiling on other common coastal vegetation species of the Gulf of Mexico, such as *Spartina alterniflora* (Lin and Mendelssohn 2012), *Juncus roemerianus* (Anderson and Hess 2012; Lin and Mendelssohn 2012), and *Phragmites australis* (Judy et al. 2014). For instance, Lin and Mendelssohn (2012) also detected differential sensitivity of two marsh species: *Juncus roemerianus* and *Spartina alterniflora*. Specifically, *Juncus roemerianus* growth processes were found to generally be susceptible to one-time weathered *DWH* oil application to 70% or more of aboveground tissues, as well as 8 L m⁻² of weathered *DWH* to the soil, whereas *Spartina alterniflora* only demonstrated impacts to growth metrics with repeated oiling of 70% of its aboveground tissues, as well as soil oiling. The sensitivity of *Juncus roemerianus* was corroborated by Anderson and Hess (2012), who observed deleterious effects on *J. roemerianus* survival and photosynthetic processes when Louisiana sweet crude was applied at 6, 12, and 24 L m⁻² to the soil in a simulated tidal system, regardless of the degree of oil weathering. Similarly, applications of weathered oil at rates of 8, 12, and 16 L m⁻² were found to reduce various *Phragmites australis* growth processes in an experiment by Judy et al. (2014), although *Phragmites australis* was found to be relatively resistant to oiling overall. These studies further substantiate the interspecific variation of coastal vegetation species to oil, as well as the generally greater sensitivity of coastal vegetation to soil oiling, which was observed in this study.
Conclusions

The current examination of soil and tissue oiling with weathered MC252 did not detect deleterious impacts to the growth of *A. germinans* seedlings, but did reveal that some growth responses of *B. maritima* were adversely affected at greater levels of exposure. The tolerance of *A. germinans* suggests that it may survive and play an integral role in recovery of coastlines contaminated by crude oil spills. The detection of negative effects on *B. maritima* growth with higher levels of oiling is consistent with field observations of oiling impacts to areas where this species occurs. However, the apparent absence of impacts to *Batis maritima* with lower levels of weathered crude oil contamination implies that this species, also, can contribute to spill recovery at lower levels of pollution. These findings provide novel insights into the likely impacts to Gulf of Mexico high marsh habitats under possible future oiling scenarios.

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Data availability  The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Author contribution  JW conceived the research; WH set up and executed the study and performed data collection; WH and JW equally contributed to statistical analysis and interpretation and the writing of the manuscript.

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Declarations

Ethics approval and consent to participate  Not applicable.

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