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Review

United States Gulf of Mexico Coastal Marsh Vegetation Responses and Sensitivities to Oil Spill: A Review

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Abstract: The present review summarizes the literature on the effects of oil spill on the U.S. Gulf of Mexico coastal vegetation including freshwater-, brackish-, and salt-marshes. When in contact with plant tissues, oil may have adverse impacts via physical and chemical effects. Oil may also become detrimental to plants by covering soil surfaces, leading to root oxygen stress and/or penetrate into the soil where it becomes in contact with the roots. The affected vegetation may survive the impact by producing new leaves, however, an episode of oil spill may impose severe stress. Oil spills may lead to partial or complete plant death but in many situations plants recover by regenerating new shoots. Plant sensitivity to oil varies among species; plants from salt marshes appear to be more sensitive than freshwater species. In addition, sensitivity appears to be dependent on the oil characteristics and the quantity of oil being spilled, repeated oiling events, season of spill, greenhouse *vs.* field conditions, and plant age are among the many factors that interact simultaneously. Many aspects of coastal plant responses to oiling remain in need of additional research, including the possibility that differences in oil sensitivity may interact with changes in the environment, and contribution to additional wetland losses through coastal erosion. Environmental stressors such as drought and salinity may also interact with oil, leading to the observed changes in plant species community composition following an oil spill.

Keywords: coastal marshes; plant responses to oil spill; environmental pollution; plant stress

1. Introduction

In U.S. Gulf Coast wetlands, coastal marshes are diverse habitats encompassing vast and productive systems. The maintenance of these ecosystems is critical to shoreline protection, sustainability of fish and wildlife habitats, and water quality [1–4]. However, these systems are subject to significant petroleum exploration, refining, and transportation, thus to occasional oil spill events. In fact, each year numerous oil spills occur across this vast region, though most spills are relatively small [5]. Nonetheless, occasionally a major oil spill does occur, impacting coastal marshes. For example, in 2010 the Deepwater Horizon oil spill released approximately five M barrels of oil into the Gulf of Mexico during the 87 day episode [6]. Post-spill studies that followed this event confirmed the adverse impact on vegetation. Seven months after the spill event, oil persisted in marshes and concentrations in the surface two cm of the heavily oiled marsh soils were reported as high as 510 $mg \cdot g^{-1}$ [7]. Approximately 18 months after the event, the adverse ecological effects of the spill on salt marsh habitats along the southeastern Louisiana coast persisted and were evident [8]. The concerns and uncertainties regarding the short- and long-term impacts of the event on wetland ecosystems' health still exist [3,7,9].

Generally, the reported effects of oil spill on coastal ecosystems, the biota responses, and the short- and long-term impact varies in the literature (for reviews see Pezeshki [2]; Mishra *et al.* [8]; Lin *et al.* [10,11]; Mendelssohn *et al.* [3]; Silliman *et al.* [12]; Biber *et al.* [13]; Michel and Rutherford [14]; Nyman and Green [15]). As far as oil spill effects on plants are concerned, the reported impacts range from reductions in transpiration and carbon fixation to partial or complete mortality of plant aboveground components over the short-term (Tables 1 and 2; [2,8,16]). For example, low levels of crude oil had little effects on *Spartina alterniflora* [16] while high levels accumulated in the soil or persisted in the marsh for extended time led to death of this species [7,17–22]. Numerous other field and laboratory studies investigated the effects of oil spills on coastal vegetation and the data suggest a rather complex set of interactive factors involved in marsh plant responses to oiling. A partial list of these plant and environmental factors include the oil characteristics and amounts being spilled, the season of spill, the tidal/wave events during and post-spill, the soil/sediment characteristics, whether oil covered the soil surface or penetrated into the soil, oil coverage of the aboveground plant components (partially or completely), and the plant age and species [2,3,7,8,15,23,24].

Although the present review focuses on emergent marsh species, many other macrophytes, including submerged and floating species are present and persist in U.S. Gulf coast marshes and the associated water bodies. These species may have various level of sensitivity to oiling [25–27]. For instance, Lopes *et al.* [25] reported that floating *Eichhornia crassipes,* an invasive plant also common to Louisiana salt marshes, was sensitive to high concentrations of crude oil. Root and leaf growth were inhibited and anatomical modifications in leaves were noted under high oil concentrations. While mortality of floating species was reported to be low, it may increase over time due to the alterations in plant morphological and anatomical features that are critical for plant functioning. Data on other aquatic species presented by Lopes *et al.* [25] and Lopes and Piedade [26] showed that oil spills led to substantial changes in the mixture of aquatic species as well as the dynamics of vegetation in the floodplain. In addition, Martin *et al.* [27] reported that *Ruppia maritima*, a common inhabitant of salt marsh ponds and protected embayments in Louisiana salt marshes, was sensitive to oiling. *R. maritima* plants showed significant changes to reproductive output and root morphology in response to oiling in the laboratory. Clearly, oil can spread throughout the marsh and the associated water bodies, thus exacerbating the contamination problem for aquatic plants [26]. Much data is needed in this important research area that has so far been overlooked in the literature. Future research efforts in this area will allow assessment of oil impacts on aquatic macrophytes in addition to the emergent marsh species.

Given the complexity of the various interactive factors, uncertainty persists concerning the extent of oil spill impact on coastal marsh vegetation and how other environmental factors and plant response mechanisms interact in response to such events. Previous laboratory and greenhouse studies have covered some factors representing a relatively narrow range of conditions, but have limited application to field situations. In contrast, field data obtained from the actual oil spills lack the pre-spill data on site characteristics and suffer from inability to establish post-spill "control" reference sites for comparison [2,28,29]. The objective of this review is to summarize the current literature on the effects of oil spill on physiological ecology, growth, and recovery responses of coastal emergent marsh plants in view of the aforementioned limitations and to update the previous review by Pezeshki *et al.* [2]. The aim is to help understand how oil affects plants in coastal systems, particularly the United States Gulf of Mexico coastal marshes, where substantial petroleum exploration, refining, and transportation activities subject these marshes to occasional oil spills.

2. Oil Characteristics and Plant Response Outcome

The impact of spilled oil on coastal vegetation is partially dependent on the type of oil spilled. Several parameters associated with the oil may influence the extent of plant responses, including oil persistence and toxicity. In general, designations categorize oils from very light to very heavy or weathered [14,23]. This classification is not precise, but can be used to assess the potential effects of different oil types [2,23]. Light refined products such as No.2 fuel oil, diesel, kerosene, and jet fuels do have high toxicity on marsh vegetation that appear to be dose related. For instance, *Spartina alterniflora* plants subjected to oiling with Bunker C oil did not produce any new leaves and the plants died [30].

Crude oils can lead to toxicity if the oil coats plant tissue, particularly if oil covers most of the aboveground plant surfaces, but recovery can occur in a relatively short time of weeks to months [2,14]; however, there are also contrasting reports indicating field recovery of macrophytes may be slower than previously thought. McClenachan *et al.* [31] reported that it could take at least two years to evaluate the effects of heavy oiling on a marsh shoreline. Furthermore, the presence of vegetation alone may not be an adequate indicator of complete recovery. Other reports on monitoring of marshes in the Gulf of Mexico after oil spill events suggest that marshes are relatively resilient to oil spills when evaluated over two years or longer, and some field studies suggest complete recovery in four years [12,28]. The contrasting data confirm the complicated nature of the interacting biotic and abiotic factors and the need for additional comprehensive long-term studies of marsh response to oiling.

3. Physical and Chemical Effects of Oil on Plants

The overall adverse effects of oil on plants may be categorized into physical effects and chemical toxicity. Oil may affect plants by physical impact through coating of the plant foliage. The resulting impact can be dramatic due to a number of critical plant functions that are disrupted. For example, the importance of oxygen transport from the leaves to roots via aerenchyma tissue for wetland plant functioning is well documented [32–36]. It is a critical mechanism that prevents or reduces oxygen stress in plant roots growing in saturated soils where soil oxygen is severely limited or absent. Therefore, if oil covers leaf surfaces, it can easily block the stomatal pores. Blocking oxygen diffusion to the roots leads to initiation of root oxygen stress, which is a primary factor limiting plant growth, survival, and functioning in wetlands [3,35–38]. In addition, oil that covers plant leaves causes temperature stress due to blocking the leaf transpiration mechanism [2,7,39]. The impact can be dramatic, leading to leaf death as noted in a number of studies summarized by Pezeshki *et al.* [2]. Even if leaf death does not occur, leaf critical functioning, including photosynthesis, is adversely affected because of the blockage of stomatal pores, leading to a restricted entry of CO_2 [2,3,7,13,30,38–40].

The adverse effect of oiling on photosynthesis by physical blockage of stomatal pores is dependent on the extent of plant surfaces covered by oil (Tables 1 and 2; also see Pezeshki *et al.* [2]; Mishra *et al.* [8]; Lin and Mendelssohn [7]; Mendelssohn *et al.* [3]; Biber *et al.* [13]). The impact also depends on the amount of oil spilled, the hydrologic conditions (tides, winds), and the dispersion of oil that is primarily dependent on oil type. However, the stomatal blockage and temperature-induced mortality is often followed by recovery and regrowth of new shoots, as has been reported for some dominant marsh species such as *Spartina alterniflora* [39,40] and *Juncus roemerianus* [2,39,41]. Vigorous regeneration of new shoots were reported after oil spills under greenhouse and field conditions for several marsh species, perhaps a result of extensive underground rhizomes that is a common feature among these species [2,39,41,42]. However, the impact of oil spills on health, persistence, and extent of the underground rhizome systems is unknown and thus provides an intriguing piece of the puzzle regarding marsh plant responses to oiling.

During high tides or storm events, plant leaves may become subject to oiling because of the currents. As mentioned above, there is a wide range of the potential adverse effects of oil on coastal plants, from reductions in photosynthesis to plant mortality over the short- or long-term [2,3,8,13]. High levels of crude oils accumulated or persisted in the marsh for an extended time led to death of *S. alterniflora* [7,17–22]. Other studies [16,21,41,52] have found that biomass production of *S. alterniflora* recovered within one year following an oil spill. Lin and Mendelssohn [21] and DeLaune *et al.* [41] reported that oiling reduced aboveground biomass production of *S. patens* approximately four months after oil application. Hester and Mendelssohn [42] noted that *S. patens* recovered within four years after an oil spill in a Louisiana brackish marsh.

Table 1. Effects of oil on US Gulf coastal brackish and saltmarsh species.

Oil Type	Exposure Rate	Species/Marsh System	Physiological Effects	Growth and Survival	Reference
Louisiana crude oil	0.25 $L\cdot m^{-2}$ spill in marsh	*Spartina alterniflora*	Not reported	Little damage to existing stocks and new colonizers	de la Cruz *et al.* [43]
Louisiana crude oil	0.28 $L\cdot m^{-2}$ spill in marsh	*S. alterniflora*, *S. patens*	Not reported	64% decrease in cover in mixed species assemblage	Mendelssohn *et al.* [44]
Louisiana crude oil	1 $L\cdot m^{-2}$ exp. marsh	*S. alterniflora*	Not reported	No significant difference in above-ground biomass	DeLaune *et al.* [16]
Louisiana crude oil	2 $L\cdot m^{-2}$ oil in marsh	*S. alterniflora*	CO_2 fixation decreased at 6 days and recovered at 13 days	No significant difference in above-ground biomass	Smith *et al.* [45]
Mexico Sour crude	2 $L\cdot m^{-2}$ on foliage, 5-week study	*S. alterniflora*	100% oil cover: no photosynthesis Partial oil: photosynthesis decreased 50%–80%	Not reported	Pezeshki and DeLaune [39]
Louisiana crude oil	8 $L\cdot m^{-2}$	*S. alterniflora*	Not reported	No significant difference in above-ground biomass	Crow *et al.* [46]
Oil (undetermined)	Not reported	*S. alterniflora*	Not reported	Decreased production early, but no long-term effects	Lytle [47]
Louisiana crude oil	32 $L\cdot m^{-2}$ greenhouse	*S. alterniflora*	Not reported	No significant difference in above-ground biomass	DeLaune *et al.* [16]
Louisiana crude oil	8 $L\cdot m^{-2}$ and higher in a greenhouse	*S. alterniflora*	Not reported	No regrowth in the year following oil application	Lin and Mendelssohn [21]
Chronic exposure to mixed oil	3.3–33.3 $g\cdot C\cdot m^{-2}\cdot day^{-1}$	*S. alterniflora*	Not reported	Non-linear response; stimulated plant growth and microbial activity at low level, but inhibited at higher levels	Li *et al.* [48]
Louisiana crude oil	8 $L\cdot m^{-2}$ to sediment only	*S. alterniflora*	Substantial variation in photosynthetic responses	Substantial variation in growth responses	Hester *et al.* [49]
Louisiana crude oil	2 $L\cdot m^{-2}$ oil in marsh	*S. alterniflora*	Photosynthesis decreased in 6 and recovered in 13 days	No significant difference in above-ground biomass	Smith *et al.* [45]

Table 1. *Cont.*

Oil Type	Exposure Rate	Species/Marsh System	Physiological Effects	Growth and Survival	Reference
Louisiana crude oil	2 L·m^{-2} field study	*S. alterniflora*	No significant difference in CO_2 fixation rates	No significant difference in biomass	DeLaune *et al.* [50]
Deep Water Horizon Oil Spill	Field study following oil spill	*S. alterniflora*, *J. roemerianus*, *S. patens*, *Distichlis spicata*	Not reported	Biomass not reported, visible plant stress symptoms, lack of recovery over the 2 year study	Zengel *et al.*, [24]
Macondo Oil, a Louisiana Crude oil	Field study-Oil in the surface 2 cm was as high as 510 mg·g^{-1}	*Spartina alterniflora*, *Juncus roemerianus*	Not reported	Complete death of both species in heavily oiled sites. Moderate oiling impacted *S. alterniflora* less severely than *J. roemerianus*. Significantly reduced aboveground biomass and stem density of *J. roemerianus*.	Lin and Mendelssohn [7]
Macondo Oil, a Louisiana Crude oil	Applied to plant and/or soil at various rates in a greenhouse	*Spartina alterniflora*, *Juncus roemerianus*	Following initial oil exposure, both species were equally affected by the oil. Photosynthesis was inhibited after 3 weeks if 100% of shoot were covered by oil. After 7 months photosynthesis of S. alterniflora recovered to the level of the control but slower recovery was noted for *J. roemerianus*	After 7 months live stem density and shoot height in S. alterniflora recovered to the level of the control. However, J. roemerianus growth parameters did not recover completely except in the 30% oil coverage treatment.	Lin and Mendelssohn [7]

Table 1. *Cont.*

Oil Type	Exposure Rate	Species/Marsh System	Physiological Effects	Growth and Survival	Reference
Louisiana crude oil	5 $L \cdot m^{-2}$ to sediment only	*S. patens*	Significant reduction in photosynthesis	Partial death of above-ground tissue, followed by regrowth	Hester *et al.* [49]
Louisiana crude oil	8 $L \cdot m^{-2}$ and higher in a greenhouse	*S. patens*	Significant reduction in photosynthetic rates	Significant reductions in above-ground biomass and no regrowth in the year following oil application. Significant increase in biomass and stem density	Lin and Mendelssohn [21]
Macondo 252 oil from the Deepwater Horizon oil spill	Field study following DWH oil spill	*S. alterniflora*	Not reported	Biomass not reported. Percent plant cover slightly lower in oiled plots, marsh erosion	McClenachan *et al.* [31]
N/A	N/A Oil spill in the field	*S. patens*	Plant photosynthetic measurements revealed no significant differences between control and plots heavily impacted by oil 4 years after oil spill	Recovered within 4 years after oil spill	Hester and Mendelssohn [42]

Table 1. *Cont.*

Oil Type	Exposure Rate	Species/Marsh System	Physiological Effects	Growth and Survival	Reference
South Louisiana Crude & Arabic Medium Crude	2 L·m^{-2} Field and greenhouse conditions	*S. alterniflora*, *S. patens*	Significant reduction in photosynthesis in *S. alterniflora* one week following exposure to either oil types. After eight weeks photosynthetic rates recovered. *S. patens* also showed substantial reductions in CO_2 fixation. Some recovery was noted after 8 weeks for newly regenerated shoots.	Biomass reduction in both species 3 months after exposure in the greenhouse. *S. patens* was more sensitive to South Louisiana Crude as compared to Arabic Medium Crude oil. Differences between field and greenhouse responses. Under greenhouse, *S. patens* died following exposure to SLC. *S. alterniflora* was also adversely affected. However, in the field both species recovered following oiling without long-term impact on growth.	DeLaune *et al.* [41]
N/A	N/A Oil spill in the field	*S. alterniflora*	Significant reduction in photosynthesis was recorded one year after the spill event.	Plant stress was detectable one year after the spill event.	Biber *et al.* [13]
Light motor oil	6 L·m^{-2} applied to soil in a greenhouse	*Phragmites australis*, *Spartina alterniflora*, *Spartina patens* (and others)	Reduction in photosynthetic rates shortly after oil exposure	Not reported	Caudle and Maricle [38]
South Louisiana Crude	2 L·m^{-2} Field study	*S. alterniflora*	Not reported	Application of oil had short-term detrimental effects. However, one year later, many of the plant measured growth parameters approached or exceeded control plots.	Lindau *et al.* [22]

Table 2. Effects of oil on US Gulf coastal freshwater marsh species.

Oil Type	Exposure Rate	Species	Physiological Effects	Growth and Survival	Reference
Louisiana crude oil	Up to 24 $L \cdot m^{-2}$	*Sagittaria lancifolia*	Not reported	Significant increase in biomass and stem density	Lin and Mendelssohn, [21]
South Louisiana Crude/Arabic Medium Crude	2 $L \cdot m^{-2}$ Field and greenhouse	*Panicum hemotomom*	Significant reduction in photosynthesis one week following exposure to oil. After eight weeks photosynthetic rates recovered.	Biomass not affected by oiling in *P. hemitomon* 3 months after exposure in a greenhouse.	DeLaune *et al.* [41]
South Louisiana Crude/Arabic Medium Crude	2 $L \cdot m^{-2}$ Field and greenhouse	*Sagittaria lancifolia*	Oil did not have a significant effect on photosynthesis 1 and 8 weeks after oil exposure.	Biomass not affected by oiling in *S. lancifolia* 3 months after exposure in a greenhouse.	DeLaune *et al.* [41]
South Louisiana Crude /Arabic Medium Crude	2 $L \cdot m^{-2}$ Field and greenhouse	*Scirpus olneyi*	Oil did not have a significant effect on photosynthesis 1 and 8 weeks after oil exposure.	Biomass not affected by oiling in *S. olneyi* 3 months after exposure in a greenhouse.	DeLaune *et al.* [41]
South Louisiana Crude/ Arabic Medium Crude	2 $L \cdot m^{-2}$ Field and greenhouse	*Typha latifolia*	Oil did not have a significant effect on photosynthesis 1 and 8 weeks after oil exposure.	Biomass not affected by oiling in *T. latifolia* 3 months after exposure in a greenhouse.	DeLaune *et al.* [41]
South Louisiana Crude	2 $L \cdot m^{-2}$ Field study	*Sagittaria lancifolia*	Not reported	Oil had short-term detrimental effects. However, one year later, many of the measured plant growth parameters approached or exceeded control plots.	Lindau *et al.* [22]
South Louisiana Crude	2 $L \cdot m^{-2}$ Field plots	*Sagittaria lancifolia*	Carbon fixation in oiled plots measured periodically over the 52-week monitoring period did not show any reduction in carbon fixation due to oiling compared to control.	Growth parameters in oiled plots not significantly different from control 5 to 6 weeks after treatment	Lindau and DeLaune [51]

Shortly after exposure to oiling, *S. alterniflora* plants displayed reduced stomatal conductance and no detectable photosynthetic activity, which suggested non-stomatal photosynthetic dysfunction in addition to the stomatal limitations in leaves subjected to oil application [30]. Such breakdowns of leaf structure and/or chlorophyll system may occur because of leaf temperature increases and/or direct adverse effects of oil penetrating into the leaf tissue destroying cellular integrity [2,30]. Generally, photosynthesis may be reduced even if the spilled oil is contained to the sediment and does not come in contact with the foliage [2,21,38]. However, there are contrasting reports showing less sensitivity of photosynthetic rates to oiling for some species [42,51]. Caudle and Maricle [38] reported that photosynthetic rates in leaves were sensitive to oiling in the soil and varied across the six species studied, indicating metabolic dysfunction due to non-stomatal inhibition of photosynthesis. Such inhibitions are found in response to environmental stressors including flooding and drought, and generally a result of decreased activity of photosynthetic enzymes, chlorophyll breakdown, and reduced light-harvesting complexes [36,38,53–56]. Caudle and Maricle [38] further reported that certain chlorophyll fluorescence parameters (including F_V/F_M) did not change in response to oiling. This finding indicated the observed non-stomatal inhibition of photosynthesis did not result from damage to light-harvesting machinery but was likely due to the toxic effects of oil penetrating into cells leading to biochemical changes [57–59]. It appears that the question of mechanism(s) allowing some species to be more “oil tolerant” than others remains as an open question for future investigation.

The initial short-term adverse effects of oil on leaves are dramatic. Nevertheless, in many reported cases, plants subsequently recovered from the impact. In *S. alterniflora*, leaf mortality following oiling was noticeable up to 40 days post oiling event [30]. Pezeshki *et al.* [30] reported that complete coverage of *Spartina alterniflora* plants with South Louisiana crude oil initially led to rapid death of all leaves. However, new leaf production began within two weeks, and the new leaves showed similar photosynthetic rates to those of control plants within two months. Similar results were reported from other studies on *S. alterniflora* and *J. roemerianus* [16,39,45]. DeLaune *et al.* [41] reported that in field experimental plots, *S. alterniflora* plants showed rapid recovery following application of South Louisiana crude oil. Plants that were coated with oil died but the marsh vegetation recovered rapidly by regeneration of new shoots. Photosynthetic measurements also showed substantial recovery in the oiled plots following the regeneration and development of new leaves. Thus, the initial short-term adverse effects of oil on plants were apparent; however, plants did recover subsequently.

The chemical effects of oil on vegetation differ among oil types. For example, certain crude oils such as Arabian Crude, Mexican Crude, and No. 6 fuel appeared to have some short-term adverse effects on *S. alterniflora* (Table 1). In contrast, refined, light oils and Bunker C oil appeared to have penetrated into the plant tissues, leading to leaf death and prevention of leaf and shoot regeneration [2,7,30,40,41,60]. Chemical effects can also be further classified on the basis of the effects via penetrating foliage tissue *versus* effects through oil penetrating into the soil’s root zone (described below). Oil penetrating into the leaf tissue destroys cellular integrity [2,38]. Similarly, oil penetrated into the soil and its subsequent contact with the root tissue can damage rhizome and root cellular integrity. In some salt-tolerant plants, oiling apparently interfered with root membrane functioning, leading to plant ionic imbalance and subsequently the plant’s ability to tolerate salinity [61].

4. Oil Coverage of Plant Leaves *versus* Coverage and Penetration into the Soil

The initial adverse effects of oil coverage of leaves are dramatic, however, in many reported cases, plants recovered. Reports from studies of oil coverage of leaves of *S. alterniflora* and *J. roemerianus* by South Louisiana crude oil showed that oil initially led to rapid leaf death; however, new leaf production began rapidly [16,30,39,45]. DeLaune *et al.* [41] reported that in field experimental plots, *S. alterniflora* plants showed rapid recovery following application of South Louisiana crude oil. Plants that were coated with oil died but new shoots appeared rapidly. The photosynthetic measurements also showed substantial recovery following the regeneration and development of new leaves. Refined oils have a different effect on leaves than crude oils. For instance, *S. alterniflora* plants subjected to oiling with Bunker C oil did not produce any new leaves and the plants died [30].

In addition to oil coverage of aboveground plant tissue, soil can be fouled where oil is left on the soil surface by falling waters. Oil covering of the soil hampers soil oxygen exchange with the atmosphere. Such restriction can lead to anoxic soil conditions, thereby imposing root oxygen stress [2,13,15,62,63]. While coating of plant tissue such as leaves by oil appears to have a more noticeable initial effect on plant than oil coverage of the soil surface, the soil coverage may lead to persistent exposure of new shoots, and thus can be harmful over a longer period [21,28,40,44]. In fact, the reported cases where oil penetrated the soil show that significant initial mortality occurred and the recovery was prolonged. Longer recovery of more than two to four years has been reported in the literature [3,9,24,31,42,64,65].

Chronic oil spills may lead to accumulation of oil and penetration in the sediment. Soil texture (sand, loam, clay) and soil organic matter (OM) appear to be important to the persistence of oil in soil, thus to the extent of damage to marsh vegetation [2,15]. In general, oil impact appears to be most dramatic in highly organic soils. Soil OM apparently slows biodegradation because it can replace oil as a substrate for oil-consuming bacteria. Consumption of soil OM can also lower nutrient availability, particularly in nutrient-poor conditions. Due to these factors, soil OM is expected to increase the time that plants are exposed to toxins. On the other hand, soil OM may adsorb toxins, thus reducing their bioavailability to plants. Most petroleum components associate more readily with organic than with mineral particles in soil [66]. Lin and Mendelssohn [21] reported that oil concentrations in the soil were strongly associated with the soil OM content. In the range of 4–24 $L \cdot m^{-2}$ of oil dosages, *S. patens* grown in marsh sods with higher soil OM consistently had higher oil concentration in the soil, while the low oil concentration was found in the *S. alterniflora* sods, which had lower soil OM.

Lin and Mendelssohn [21] noted that in marsh soil with high organic matter content (42%), oil concentration was much higher compared to soil with the same mineral compositions but OM removed. Because the quantity and quality of the OM varies with dominant species, it is likely that the influence of OM on plant response to oil also varies with dominant vegetation type. Results from a mesocosm study [67] showed that after 18 months, significantly lower amount of oil persisted in commercial topsoil (mineral soil) than in a mix of topsoil with 50% peat (by volume). When oiled, *Panicum hemitomon*, *Sagittaria lancifolia*, and *Phragmites australis* displayed greater rates of photosynthesis and biomass production when grown in topsoil medium. The topsoil sediment planted with either *P. hemitomon* or *S. lancifolia* showed the best plant performance and the least oil amounts persisting in the sediment. Additional research is needed to determine how soil OM influences plant responses to oiling.

Some studies indicated that size fraction of soil mineral matter (*i.e.*, sand, silt, clay) may influence degradation rates such that clays slow degradation [68]. Slower degradation rates may lengthen the time that plants are exposed to oil. However, saline marshes have more mineral matter (primarily clays) and more oil-sensitive vegetation than fresh marshes [21,69,70]. In addition to soil OM, soil texture could also affect the residual oil concentration in the soil and marsh vegetation. Ferrell *et al.* [71] reported that *S. alterniflora* grown in oiled fine-textured sediments performed better than those growing in coarse sand. The differential response reported was probably due to the difference in pore space size. Large pore spaces in sandy soils allow deeper and more rapid oil penetration, whereas smaller pore spaces in fine-textured soils present impediment to oil penetration. It appears that sensitivity varies primarily among plant species, and that size fraction of soil mineral matter may be a secondary factor in moderating sensitivity [2]. Clearly, additional research on the relationship between size fraction of soil mineral matter and marsh vegetation response to oil is needed.

The effect of oil-contaminated soils on plants also varies with the plant age. Mendelssohn *et al.* [72] reported that under greenhouse conditions, exposure to 8 $L \cdot m^{-2}$ of South Louisiana Crude oil in soil significantly reduced photosynthesis of established shoots in *S. alterniflora*, whereas only 4 $L \cdot m^{-2}$ was required to significantly reduce production of the new shoots. Preventing new shoot production clearly hampers regeneration and may contribute the substantial mortality of *S. alterniflora* stands that has been reported when high levels of crude oils accumulated in the soil or remained in the marsh for extended periods [17,18,20]. Such adverse long-term effects may impact the overall system productivity because marsh vegetation contributes to the detritus-based food web of estuarine ecosystems [4].

Oil may also affect soil microbial communities [3,73] that control nutrient mineralization and therefore regulate vegetative productivity and energy flow through food webs [74]. If toxic components of oil inhibited bacterial decomposition of soil OM and the associated nutrient re-mineralization, then plant growth may be slowed. Burns and Teal [75] reported that oil persisted in soil for as long as 7 years after a spill event raising additional concerns over the possibility of long lasting adverse effects of an oil spill. However, Li *et al.* [48] noted that low doses of an artificial mixture of 10 hydrocarbons stimulated microbial activity. Nyman [76] found that Louisiana and Arabian crude oils accelerated, rather than slowed, microbial activity in fresh marsh soils. Accelerated organic matter mineralization suggests increased nutrient re-mineralization rates and may help explain the reported observations of enhanced plant growth following exposure of *S. alterniflora* [20,48,77]) and *S. lancifolia* [21] to oil. However, additional data on the effects of other oils and the responses of marsh plants is needed before definitive cause and effect relationships can be established [2].

A major trend emerging since the April 2010 Deepwater Horizon oil spill accident in the U.S. Gulf coast is that coastal marshes affected by oiling are more susceptible to erosion. This has been shown in both field studies [12,31,78] and through laboratory manipulative experimentation [27]. Nonetheless, currently data quantifying the relationship between oil spill in coastal areas and marsh erosion are limited. Khanna *et al.* [78] reported that several indexes of plant stress were consistently higher in areas of oiled marsh next to the shoreline and decreased with increasing distance from the shoreline. McClenachan *et al.* [31] reported there appears to be a threshold where soil condition changes substantially with a small increase in oil concentration. Such conditions weaken the soil, create a deeper undercut of the upper layer of the marsh edge, and cause accelerated rates of sediment erosion along the shoreline. Other studies also indicated that heavily oiled marsh sites are eroding faster than control marshes over the 18 months following an oil spill event [12]. McClenachan *et al.* [31] suggest that it could take at least two years to properly evaluate the effects of heavy oiling on a marsh shoreline. Furthermore, the presence of aboveground vegetation alone may not be an adequate indicator of a complete recovery. Clearly, this area of research needs additional enquiries to allow assessment of the numerous interactive and complicated factors involved in marsh response to oiling events that focus on vegetation persistence and recovery over five years or longer.

5. Species Differences in Sensitivity to Oil

In the U.S. Gulf coastal region, tidal marshes include salt-, brackish-, and freshwater marsh habitats. Plant species and hydrologic regimes differ among these systems. Tidal freshwater marshes support a diverse plant community while salt marshes are composed of limited plant species. Numerous oil impact studies have been conducted on species that represent plant communities across the region [2,3,7,12,15,16,18,21,24,28,44,48,72,79,80]. Lin and Mendelssohn [21] reported that *S. patens*, a species predominantly found in brackish marshes, was more sensitive than *S. alterniflora* to South Louisiana crude oil but both species displayed complete mortality at oil dosages of 8 $L·m^{-2}$ and higher. Pezeshki and DeLaune [39] found that *Juncus roemerianus*, a species found in both brackish and salt marshes was initially less sensitive to oiling than *S. alterniflora*, although both species showed rapid recovery [39].

Tidal, freshwater marshes in this region are also subject to oil spills. Lin and Mendelssohn [21] studied four fresh marsh species, *S. lancifolia*, *Eleocharis quadrangulata*, *Cyperus ordoratus*, and *Ammania teres*. *C. ordoratus* and *A. teres* had complete mortality in response to oiling. *E. quadrangulata* survived oil levels up to 8 $L·m^{-2}$. In contrast, *S. lancifolia* survived all oil dosages, including higher oil dosages of 16 $L·m^{-2}$ and 24 $L·m^{-2}$, exhibiting a high relative oil tolerance. In addition, *S. lancifolia* showed enhanced growth in response to higher oil dosages. DeLaune *et al.* [41] noted remarkably low sensitivity to oiling for several freshwater marsh species. Although biomass production was not affected by oiling in *Panicum hemitomon, Sagittaria lancifolia, Typha latifolia*, and *Scirpus olneyi*, there was clearly a wide range of sensitivity shortly after exposure to oiling among these species. The results demonstrated the apparent differences in responses of freshwater species to oil spills.

Plant community composition changes may also become evident during the post spill. The change has been attributed to variations in species' sensitivities to oil and the disturbance that follows during the clean-up operation. Burk [81] reported that an oil spill in a freshwater marsh led to reduction in relative abundance of 14 species, increased or did not affect the relative abundance of 23 species, and eliminated 18 species. Following a spill of South Louisiana crude oil in a brackish-saline marsh in a Southern Louisiana marsh dominated by a mixture of *S. patens*, *Distichlis spicata*, and *S. alterniflora*, Mendelssohn *et al.* [28,44] noted that *S. patens* had slower recovery than either *D. spicata* or *S. alterniflora*. *S. alterniflora* had the fastest recovery and rapid growth following the spill, probably due to less sensitivity to oil than *S. patens* [21,44]. *D. spicata* showed some increases in cover relative to *S. patens* [28,44]. Therefore, differences in oil sensitivity may interact with certain environment factors leading to the observed changes in plant species community composition following an oil spill [15]. Additional research is needed to test this hypothesis using a range of environmental conditions in coastal wetlands.

In addition to the observed differences across species in response to oiling mentioned previously, there are indications of intraspecific differences in oil sensitivity. Hester *et al.* [49] investigated variation in response to oiling in *S. patens* and *S. alterniflora*. Ecotypes from several U.S. Gulf coast populations of each species displayed significant intraspecific variation in photosynthesis, vegetative regrowth through the oiled sediment, and other indicators of plant recovery parameters when South Louisiana crude oil was applied. Therefore, the apparent inconsistencies in the reported responses of certain marsh species to oiling may be partially explained in light of this finding though clearly additional research is needed to further explore the possibility of intraspecific difference in oil sensitivity across other marsh species and the various mechanisms that may be involved in such a variable response. Overall, Louisiana Coastal Marsh plants when exposed to similar greenhouse conditions have been shown to vary in their sensitivity [10,15,21,27,41,82]. Based on the data obtained from these experiments, the following species can be ranked from least to most sensitive as shown in Figure 1.

Figure 1. Ranking of relative sensitivity to oiling for selected Louisiana Coastal Marsh plants.

Even though under greenhouse conditions, differences in sensitivity to oiling among wetland plant species have been documented, some studies conducted under field conditions showed that marsh vegetation recovered rapidly following heavy oiling of above ground components of vegetation [16,41]. In a study that compared oil impacts on photosynthetic of two species, *Spartina alterniflora* and *Juncus roemerianus*, *S. alterniflora* was more sensitive to partial oil coating than *J. roemerianus* [39]. In contrast, moderate oiling had no significant effect on *S. alterniflora*, but significantly reduced aboveground biomass of *J. roemerianus* [7]. Table 3 shows the reported recovery time under field conditions for dominant Louisiana coastal wetland plant species.

Table 3. Reported field studies of vegetation response and recovery following oiling for selected Louisiana coastal marsh plants.

	Species	Oiling Rate	Recovery Time	Reference
1	*Spartina alterniflora*	2 L·m^{-2}	Months to <year.	Lindau and DeLaune [51] DeLaune *et al.* [41]
2	*Spartina patens*	2 L·m^{-2}	Months to <year.	DeLaune *et al.* 2003 [41]
3	*Spartina alterniflora*	Field oil spill	>1 year with marsh erosion at heavily oiled sites	Silliman *et al.* [12]
4	*Spartina alterniflora*	Field oil spill	>2 years with marsh erosion at heavily oiled sites	McClenachan *et al.* [31]
5	*Sagittaria lancifolia*	2 L·m^{-2}	2–4 months	Lindau and DeLaune [51]

6. The Effects of Season of Spill

The occurrence of an oil spill during a given season influences the potential impact on vegetation [40,83–85]. In general, oil spill during senescence did not cause significant mortality in salt marsh vegetation [83]. In contrast, plants were more sensitive to oil during the active growing season. For example, *S. alterniflora* showed higher sensitivity to oiling during active growing season (spring and summer) as compared to the dormant seasons (late fall and winter) [2,8,13]. In another study, the adverse effects of oil on *S. alterniflora* were more severe during the spring than the fall season [40]. Similarly, Alexander and Webb [80] reported that No.2 fuel oil applied to the soil and the entire *S. alterniflora* shoot at a rate of 2 L·m^{-2} led to a greater reduction in live biomass in May (during the growing season) than in November (at the end of the growing season). Lin [86] reported that exposure of S. *alterniflora* and *S. lancifolia* to South Louisiana crude oil applied to soil led to reduction of photosynthesis, aboveground biomass, and regeneration of both species. The effects were more profound when oil was applied in June than when applied in late October. Based on these and other studies [27], it is apparent that in general, plant sensitivity to oiling increases over the active growth periods as compared to pre-dormancy and dormancy. However, reports on monitoring of marshes in the Gulf of Mexico after an oil spill show that marshes are relatively resilient to oil spills when evaluated over two years or longer, and some field studies noted complete recovery in four years [12,28]. In situations where oil penetrates into the sediments, recovery may take even longer [3,42,64,65], or may not occur because of sediment erosion that follows vegetation mortality [3]. For example, following a crude oil spill, oil concentrations in the sediment ranged between 5 mg·g^{-1} and 51 mg·g^{-1}, led to reduced growth of *S. alterniflora* for 18 months. The observed plant stress led to erosion that was evident 32 months after the spill event [18]. In a recent study [12], plant mortality was reported in heavily oiled wetlands, leading to increased rates of coastline erosion over 18 months compared to a control marsh that remained vegetated. Oil-impacted sediments and plants could be lost to open coastal waters within one to three years. Other recent studies also showed rapid recovery in marshes in Louisiana, especially in high-energy coastlines where oil contamination was rapidly diluted and removed [12,23,87]. The results of these studies suggest that salt marshes can be very resilient to even heavy oil contamination and that photosynthesis and growth can recover quickly, in some cases within less than one year, if oil contamination is rapidly reduced by tidal and wave flushing. The many interacting factors affecting plant-sediment processes requires detailed assessment to evaluate the impacts of oil spills on salt marshes and to determine long-term resilience of a marsh [10,13,15].

During the growing season plants are active; thus, any interruption of plant physiological functions or damage to plant tissue can lead to various stress symptoms [2,13,38]. Much of this sensitivity is due to the interruption of physiological functions that result from oiling. As stated previously, oil coverage of leaf stomatal pores blocks the transpiration pathway imposing leaf temperature rise and high temperature stress [2,3,30,38,41]. Oil may also penetrate into the leaf tissue, resulting in tissue damage. Baker [84] noted reduction of flowering after above-ground tissues were oiled while the flower buds were being developed. In addition, flowers exposed to oil rarely produced viable seeds and oiling of seeds reduced germination. In a recent study, Martin *et al.* [27] reported that oiled *Ruppia maritima* plants exhibited changes in reproductive output and root morphology. Furthermore, roots growing in the high oil treatment were shorter and wider and required less force to uproot. Clearly, more research is needed to address the physical and chemical effects of oil on plant functioning, including the various stages of reproductive process during the growing season. Such research must consider many biotic and abiotic interacting factors involved, including soil conditions, variation in sensitivity of plants to oiling, as well as variations in chemical composition of oils.

7. Conclusions

The effects of oil spills on marshes are complex but it is known that in general, lighter weight oils are more toxic to plants than heavier oils. The reported immediate plant responses for the most part may be due to the effects related to the coverage of the gas-exchange surfaces of the plant by oil. Such impact tends to be most severe on above-ground tissue and often acts through direct tissue toxicity or blockage of plant gas-exchange (transpiration and photosynthesis). The effects of oil on soil can lead to oxygen stress in rhizomes and roots as well, due to reduced gas exchange between the soil and the atmosphere, thereby disrupting root membrane ion selectivity. Anoxic conditions may also adversely affect underground rhizomes and roots as well as the vegetative regrowth of new, sensitive emerging shoots as these plant components come in contact with the oil. For these types of effects, heavier weight oils can be as detrimental to plants as lighter oils that are known to disrupt plant metabolic processes and membrane functioning.

In the U.S. Gulf coastal area, differences in the sensitivity to oiling are evident at the plant community as well as the species level. Certain freshwater marsh species may display little sensitivity to oiling and may even show enhanced growth while some brackish- and salt-marsh species appear to be highly sensitive. Furthermore, ecotypes of some predominant US Gulf coast marsh species display intraspecific variation in response to oiling, some being less sensitive than others, though data thus far are limited. It appears the question of mechanism/s allowing some species to be more “oil tolerant” than others remains an open question of importance for future investigation.

Reports of monitoring marshes in the Gulf of Mexico after an oil spill show that marshes are relatively resilient to oil spill when evaluated over two years or longer, and recovery is possible in four years. However, in situations where oil penetrates into the sediments, recovery may take even longer or may not occur because of sediment erosion that follows vegetation mortality. Oil-impacted sediments and plants could be lost to open coastal waters. The many interacting factors affecting plant-sediment relationship and processes that control erosion rates require detailed assessment to evaluate the impacts of oil spills on salt marshes and to determine long-term resilience of a marsh.

Additional research is needed to address the specific effects of oils on coastal plants, including submerged and floating plants, that may be due to oil and other biotic interacting factors discussed throughout this manuscript. The potential interaction between oiling and other environmental stressors that are present in these systems such as flooding, drought, nutrient deficiency or excess, and salinity require additional research. Such investigations may explore the interaction between oiling and predominant environmental factors as well as mechanisms underlying differences among various marsh species in susceptibility to oil exposure.

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Author Contributions

Both co-authors contributed to the planning, literature review, analyses, and writing of this paper.

Conflicts of Interest

The authors declare no conflict of interest.

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