Contribution of Seed Banks to Freshwater Wetland Vegetation Recovery

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Abstract

Recovery of freshwater wetlands after oil spills depends on removal or degradation of the oil and regeneration of the plant community. To quantify the importance of seed banks to re-establishment of vegetation, soil cores (N = 210) were extracted from a freshwater wetland near Dulac, LA and exposed to sweet or sour crude oil, diesel fuel, or tap water. Oils were applied to cores at 2 or 8 L m^{-2}. The seed bank contained a relatively high density of seeds (*ca*. 4000 seedlings m^{-2}) encompassing 24 different species. The application of 2 L m^{-2} of oil, regardless of type, did not affect seedling emergence. Diesel fuel and sour crude oil applied at 8 L m^{-2} reduced seedling emergence by 50%. Of the most abundant species, *Eleocharis* spp. and *Cyperus erythrorhizos* appeared to be insensitive to the application of oil, while *Bacopa monnieri* and *Rotala ramosior* were sensitive to oil. Regeneration of wetland vegetation from a seed bank will be slowed by exposure to oil. Nevertheless, the seed bank potentially contributes a substantial number of seedlings (*ca*. 2000 seedlings m^{-2} in this case) and species. This suggests that seed banks are an essential component of freshwater wetland recovery after a spill.

Introduction

Recovery of wetlands after exposure to an oil spill relies on removal and degradation of oil, and revegetation. Revegetation may occur naturally via vegetative growth and seedling emergence or through restoration efforts (e.g., planting of nursery stock) (Burke, 1997). While many studies have focused on the direct impacts of oil on plant surfaces and on regrowth from rhizomes and roots (e.g., DeLaune *et al.* 1979; Webb *et al.* 1985; Mendelssohn *et al.* 1990; Lin

and Mendelssohn, 1996), few studies have examined the effect of oil on seedling emergence from the seed bank. Yet, emergence from the seed bank may provide the most rapid recovery of vegetation in terms of cover, diversity and community structure because wetland soils contain an abundance of seeds. In non-tidal, fresh and salt water marshes, for example, seed densities range from 696 to 255,000 seeds m^{-2} encompassing as many as 50 species (van der Valk and Davis, 1976, 1978, 1979; Ungar and Riehl, 1980; Kadlec and Smith, 1984). The rapid colonization from the seed bank after disturbance also promotes productivity and nutrient retention and controls erosion (Kinako, 1981). In contrast, a plant community formed by vegetative growth or immigration of seeds lacks the species richness and physiognomic complexity of the original community. Planted nursery stock also results in low species diversity and poor vegetative structure. Outplanting is also expensive (Good, 1989) and may further disturb soil structure and hydrology. Thus, seed banks may represent a superior restoration technique after an oil spill.

Little is known, however, about the impact of oil on seed banks. Only one study has explicitly examined seedling emergence from a seed bank after an application of oil (Leck and Simpson, 1992). In that experiment, the soils of a tidal freshwater marsh in New Jersey were exposed to crude oil, resulting in a 30% reduction in germination. Thus, oil may affect recovering vegetation, derived from a seed bank, by reducing the number of emerging seedlings. Oil can be detrimental to germination via several mechanisms including direct toxicity to the embryo (Amakiri and Onofeghara, 1984), and the formation of anaerobic (McCown *et al*. 1972; Udo and Fayemi, 1975) and hydrophobic (McCown *et al*. 1972; Amakiri and Onofeghara, 1984) soil conditions. Oil may also affect the composition of the recovering vegetation, if differential sensitivity to oil by species occurs. Amakiri and Onofeghara (1984), for example, tested germination of seeds of two varieties of *Zea mays* (F7 and F27) and of *Capsicum frutescens* after soaking for one hour to 32 weeks in crude oil. Seeds of *Z. mays* F7 exhibited no germination

after exposure to oil for longer than seven days. Seeds of *Z. mays* F27 maintained 10 to 15% viability after soaking for 32 weeks. *C. frutescens* exhibited 100% viability after 32 weeks in oil. Thus, the effects of oil on germination may not be consistent between species nor among genotypes of the same species. If oil does not affect germination from the seed bank or if the effects are moderate, natural recovery of vegetation may occur without active restoration efforts. Further, establishment of vegetation from the seed bank may contribute to the long-term success of the recovering plant community. Long-term persistence is, in part, a function of the quantity (and quality) of the genetic diversity present within communities and populations. This is because diversity provides individual differences that may confer a greater probability of survival and reproduction after environmental change. Colonization from the seed bank augments genetic diversity because it contains a record of historical species and genotypes (van der Valk and Davis, 1979). This reintroduction increases genetic diversity.

This project assessed the impact of oil on regeneration from seed banks by quantifying germination from undisturbed wetland soil cores and cores that received an application of oil. The soil cores were extracted from a freshwater wetland near the coast of Louisiana. The project had three specific objectives: 1) To quantify seedling emergence from undisturbed wetland soils and soils exposed to oil; 2) To quantify species richness and diversity of emerging seedlings from these cores; and 3) To identify plant species particularly sensitive or resistant to oil in terms of abundance of seeds present and percent reduction in germination.

Methods

Sampling Procedures - A freshwater wetland near Dulac, Louisiana (lat. 29°23', long. 90°43'), potentially subject to damage from an oil spill, was selected for study. Plant cover was *ca.* 70%. The remaining area was covered with water. The general area was dominated by *Spartina patens*, *Sagittaria lancifolia*, and *Eleocharis* spp. and is typical of many of the

freshwater marshes in the Louisiana coastal system. At the time of the study, May 1997, measurements (mean $\pm$ SE; n = 4) were recorded for water pH (7.25 $\pm$ 0.14), salinity (12.25 ppt) and temperature (33 $\pm$ 3.3 °C). Salinity is generally near 0 ppt for this area except from September to November when it increases to 5 to 15 ppt (Paille, 1997).

Fifteen randomly located, 1 m^2 quadrats were delineated within the wetland. Fourteen soil cores (15 cm diameter x 20 cm deep) were removed from random positions within each of the quadrats. Each core, with vegetation and the litter layer intact, was deposited into a length of 15 cm diameter PVC pipe lined with a plastic bag. The cores were deposited without disturbing the soil profile. Cores were placed in a greenhouse, arranged randomly into blocks as collected, and allowed to acclimate to greenhouse conditions for four weeks (mean minimum and maximum temperatures throughout the experiment = 21.0 and 35.7 °C).

Germination Studies - After the acclimation period, oil treatments were applied to the soil surface of the cores and the lower portions of plants. Treatments consisted of an application of sweet crude (total sulfur content = 0.18%; ASTMD 3177, EarthNet Laboratories, Inc, Ruston, LA), sour crude (total sulfur content = 0.25%; ASTMD 3177), or No. 2 diesel fuel (Conoco, Ruston, LA), at the rates of 2 l m^{-2} or 8 l m^{-2} (n=30). The crude oils were obtained from offshore rigs (Murphy Exploration and Production Company; South Pelto, block 19) near Cocodrie, LA. These oils were chosen because they may potentially contaminate Louisiana's coastal wetlands. In addition, diesel fuel was selected because it is a light oil that may penetrate wetland sediments more readily than crude oils (Breuel 1981). Soil cores serving as controls (n=30) received only tap water. Thus, two randomly selected cores within each quadrat received one of each of seven possible treatment combinations (3 oil types x 2 application rates, and control) resulting in 210 total soil cores (7 treatments x 2 cores per quadrat x 15 quadrats).

After four weeks of exposure to oil, a germination assay was begun. Each soil core was divided in two at a depth of 10 cm. Each half (upper or lower 10 cm) was placed separately in one half of a greenhouse flat. The half flats possessed drainage holes and were inserted into full flats lacking drainage. The remaining oil and water from the cores was also transferred into the flats. Soil was spread to a depth of about 2 cm. Trays, arranged in the blocks as collected in the field, were maintained in the greenhouse until no further germination occurred (*ca*. 15 weeks). Four greenhouse flats of sterile potting mix were also placed in the greenhouse to test whether wind-borne seeds contributed to seedling emergence during the germination assay. Only one seedling (*Oxalis corniculata* L.) appeared in these flats. *O. corniculata* was not found in the flats of wetland soil. During this period, the soils were given tap water as required to maintain a water level at about 1 cm below the soil surface. The total number of seedlings and relative proportion of each species were recorded to examine germination quantity and rate, species diversity (Shannon diversity index = H'; Magurran, 1988), and species composition. Seedlings were removed after being counted.

Data Analysis - Data were analyzed on a per surface area basis. A test of soil dry weight after the assay showed no differences in mean soil weight among oil types and controls ($p = 0.42$; mean dry soil weight = 534 g core^{-1}). Seedling survival was not quantified, but was monitored to ensure that all emerging seedlings were counted. Survival appeared to be *ca*. 100% across all treatments throughout the study. Analysis of variance (ANOVA) and Dunnett's test (JMP, v. 3.1.6; SAS, 1995) were used to test for differences in germination between seed banks exposed to oil and those exposed only to water. Tests for effects of oil on germination rate were performed separately by application rate using multivariate analysis of variance (MANOVA) with block and treatment as main effects. Germination rate was examined using two separate censuses: five and 15 weeks after soils were placed into greenhouse flats. The differences in oil

penetration depth were analyzed biologically by comparing seedling emergence from the upper and lower halves of the soil cores. For this, an ANOVA was used with data pooled across application rates. Treatment (control or type of oil) and core half were fixed main effects, and quadrat was a random effect. Quadrat, treatment (at 8 l m^{-2} only), species and the species x treatment interaction were used as effects in a test (ANOVA) for differential species response to oil using the species representing 90% of all seedlings.

Results

The seed bank of the freshwater wetland contained a relatively high density of seeds (mean $\pm$ SE: 3976 $\pm$ 629 seedlings m^{-2} in controls with a range of 496 to 16,888 seedlings m^{-2}). This is a conservative estimate of seed density because germination requirements may not have been met for all seeds (Simpson *et al.* 1989). The large range in seedling density reflected, in part, differences in germination between quadrats, which represented a significant effect in all analyses. Emerging seedlings encompassed 24 different species (Table 1) with a Shannon diversity index ($\pm$ SE) of 1.9 $\pm$ 0.04 (pooled across quadrats).

The number of seedlings was not affected by exposure to 2 l m^{-2} of oil, regardless of oil type ($p = 0.76$; Figure 1). Species richness (mean across oil types: $S = 24$) and diversity ($H' =$ 1.85 $\pm$ 0.04, 1.84 $\pm$ 0.16, and 1.84 $\pm$ 0.04, for diesel, sour crude and sweet crude respectively) were also unaffected. Oil applied at 8 l m^{-2}, however, reduced seedling emergence by approximately 50% relative to controls. Differences between oil types were small (three-way analysis of variance with oil type, application rate, and quadrats as main effects detected no differences among oil types; $p = 0.72$), but were found using one-way analysis of variance and Dunnett's method to test for differences between controls and each of the different oil types ($p =$ 0.004).

Diesel fuel and sour crude oil reduced seedling emergence relative to controls when applied at 8 l m^{-2} ($p < 0.05$; Figure 2). Diesel fuel also reduced species richness ($S = 19$). Seedling emergence did not differ between sweet crude oil and controls ($p > 0.05$). However, the application of sweet crude oil delayed germination (MANOVA, significant treatment effect, Pillai's Trace: $p = 0.003$; Figure 3).

Fewer seedlings emerged from the lower half of the soil cores (10 to 20 cm below the surface; $p < 0.0001$). No differences in germination were detected at that depth as a function of oil contamination. Differences in seedling emergence from the upper and lower half of the cores among the oil types reflected only the greater seedling emergence from control cores at shallow depths ($p = 0.034$; Figure 4).

Four species represented *ca*. 90% of all seedlings, *Eleocharis* spp. (*ca*. 37%), *Bacopa monnieri* (*ca*. 35%), *Rotala ramosior* (*ca*. 12.5%), and *Cyperus erythrorhizos* (*ca*. 5%). Any change in seedling emergence by these species or in the relative proportions of seedlings among the species will result in a difference between the recovering community and a community not experiencing a spill. Differences in seedling emergence among these four species depended on the particular treatment (species x treatment interaction: $p = 0.0003$; Figure 5). *C. erythrorhizos* and *Eleocharis* spp. appeared to be resistant to the effects of oil on germination. *B. monnieri* was sensitive to oil as was *R. ramosior*, but to a lesser extent.

Discussion

The wetland soil near Dulac, LA contained an abundance of seeds (*ca*. 4000 seedlings m^{-2}) typical of tidal and nontidal freshwater marshes (e.g., Leck and Graveline, 1979; van der Valk and Davis, 1976). These data were collected in May before many species dispersed seeds in the 1997-growing season. Seed density was thus representative of the persistent seed bank. Persistent seed banks are common in systems with unpredictable frequencies of disturbance

(Grime and Hillier, 1992). Because data are based on the persistent seed bank rather than a short-term seasonal seed pool, the results apply to the effects of spills on regeneration regardless of the time of year. In contrast, the direct effects of oil on vegetation have been shown to be a function, in part, of the season of the spill (e.g., Webb *et al.* 1985).

Tidal salt marshes tend to possess fewer dormant seeds relative to freshwater marshes (e.g., 63 to 1375 seeds m^{-2}; Engel 1983; Hopkins and Parker, 1984). The lower seed densities may be the result of salinity (e.g., Lesko and Walker, 1969; Wijte and Gallagher, 1996) or vegetation that is dominated by perennial graminoid and woody species. These species rely primarily on vegetative reproduction (Milton, 1939; Pederson and Smith, 1988; Leck, 1989). Thus, the generality of these results, in terms of the importance of the seed bank for regeneration, may not apply equally to salt marshes.

The density of seeds varied across space (significant quadrat effect in all analyses). This is typical for most seed banks and may be caused by tidal movement (Hopkins and Parker, 1984), seed source distribution (Hopkins and Parker, 1984; Bigwood and Inouye, 1988), spatial environmental heterogeneity (Bigwood and Inouye, 1988), or water flow linked with physical obstructions (Huenneke and Sharitz, 1986; Schneider and Sharitz, 1988). The spatial pattern in the seed bank may contribute to complexity in vegetation structure. Generally, more complex vegetative structure maintains greater animal diversity. Zedler and Powell (1993) demonstrated that proper species composition in created wetlands was necessary, but not sufficient to attract the light-footed clapper rail (*Rallus longirostris levipes*). The proper vegetation structure was also required.

Thus, the natural seed bank of a freshwater wetland will contribute to rapid restoration of the vascular plant community, including a high density of recruits, and high species richness and diversity. Regeneration occurred equally at no or low rates of exposure to oil (0 - 2 l m^{-2}),

regardless of whether the oil spilled was a sweet crude, sour crude or No. 2 diesel fuel. The rapid regeneration of the vegetation will restore the natural functions and structure of the community. The vascular plant species composition of the recovering community will be different, however, from the original community because several of the dominant perennial species present in the extant vegetation may not be represented in the seed bank (e.g., *Spartina patens*).

At higher rates of exposure to sour crude oil and diesel fuel (8 l m^{-2}), recovery of vegetation will be slowed because fewer seedlings will germinate. Species richness may also be affected by sweet crude oil and diesel fuel at this application rate. The causes for the difference in germination between oil types are not known, although differences were minor. The only documented difference in the composition of the two crude oils was the higher sulfur content of the sour crude oil. Sulfur, however, has been shown to enhance germination of cocklebur seeds (*Xanthium pennsylvanicum*; Maruyama *et al*. 1996). Thus, differences in oil composition other than sulfur may be important. Diesel fuel differs from crude oils in that it possesses a higher distillation temperature and carbon number (C_{12} and higher; Morrison and Boyd, 1973). Diesel fuel was shown to have toxic effects on plants when applied to the soil, although no mutagenic effects were detected on *Tradescantia* (Green *et al.* 1996). The lack of mutagenicity may be important for seeds exposed to diesel fuel because a mutation of embryonic cells would affect all the cells in the mature plant derived from the altered cell. Wang and Bartha (1990) also found diesel fuel-containing soil to be toxic to *Secale cereale* and *Glycine max* seeds sown four weeks after the application of the fuel. The toxicity declined over time, however, as a result of microbial degradation of the oil.

The application of Louisiana sweet crude oil at 8 l m^{-2} did not affect the number of emerging seedlings. Germination was delayed, however. A delay in germination may have

consequences for the recovering plant community. Delayed germination may place those species at a competitive disadvantage (e.g., Sagar, 1959; Stockey and Hunt, 1994) if weedy species immigrate into the spill site and become established first. The recovering plant community, therefore, may possess a different species composition and diversity from the original community. The impacts of the delay in germination with sweet crude oil may not be so severe since initial germination (after five weeks) resulted in a mean number of seedlings of 1052 m^{-2}. An additional 1574 seedlings m^{-2} emerged after an additional ten weeks. These numbers may be sufficient to prevent establishment of weedy species.

Thus, an oil spill will impact regeneration of the community when exposure rates are greater than 2 l m^{-2}. However, a relatively large number of seedlings emerged even at the higher application rate and may contribute to recovery, regardless of oil type. If severe spills occur, direct toxicity to the seed may eliminate seeds from the seed bank. Under these conditions, donor seed banks (seed-containing soil from neighboring, undisturbed communities) may significantly contribute to restoration after removal or degradation of oil occurs. The notion of using a donor seed bank for rehabilitation is not new. Federal surface mine regulations require the replacement of top soil after mining in order to ameliorate and revegetate the site (Farmer *et al*. 1982). In addition to seeds, the donor seed bank may add nutrients, and contribute to soil structure and chemistry (van der Valk and Pederson, 1989). Soils possessing seed banks have been effectively used in restoration of perturbed wetlands and in creating mitigation wetlands (Dunn and Best, 1983; Erwin and Best, 1985). Donor seed banks have not been applied, however, to oil spill sites.

No differences were detected in penetration of soil by the oils as indicated by the germination results. Germination from the 10 to 20 cm depth below the soil surface was relatively low for all oil types (444 seeds m^{-2}), but was equivalent to the control cores. The

lighter diesel fuel was expected to penetrate more deeply into the soil relative to the crude oils. Either this did not occur at a level that allowed us to detect a difference in seedling emergence or the differences in penetration occurred within the 10 cm immediately below the soil surface.

Germination response to the application of oil was species specific. *Eleocharis* spp. and *Cyperus erythrorhizos* were found to be resistant to the effects of oil. Rapid recovery of these species is important for wildlife. Ducks, nutria, muskrats, and geese eat parts of *Eleocharis* (Chabreck and Condrey, 1979). In addition, these species may be valuable in restoration efforts, e.g., via seeding. Hydroseeding may be a potential technique to sow seeds into wetlands (Good, 1989). Two species, *Bacopa monnieri* and *Rotala ramosior* were shown to be sensitive to exposure to oil. *R. ramosior*, in particular, is not only sensitive to oil, but poorly represented in the seed bank, and thus may require active restoration.

In conclusion, restoration via seed banks offers an economical alternative to planting nursery stock or sowing commercially available seeds. Seed banks serve as an *in situ* source of colonizers. These colonizers are abundant, diverse, and will promote onset of ecological functions within the system. Colonization may also speed degradation of residual oil by enhancing microbial activity via oxygenation of soil and discharge of exudates from roots.

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Table 1. Vascular plant species emerging from a freshwater wetland seed bank originating from Dulac, Louisiana.

Ambrosia artemisiifolia L.	*Hibiscus* sp.
Aster subulatus Michaux.	*Hydrocotyle verticillata* Thunb.
Bacopa monnieri (L.) Pennell	*Leptochloa* sp.
Carex hyalinolepis Steud.	*Ludwigia leptocarpa* (Nutt.) Hara
Cyperus erythrorhizos Muhl.	*Panicum* sp.
Echinochloa crus-galli (L.) Beauv.	*Polygonum punctatum* Ell.
Echinochloa colona (L.) Link	*Pluchea odorata* (L.) Cass.
Eclipta alba (L.) Hasskarl.	*Ranunculus* sp.
Eleocharis parvula (R. & S.) Link	*Rotala ramosior* (L.) Koehne
Eleocharis spp.	*Sagittaria lancifolia* L.
Galium obtusum Bigelow	*Typha latifolia* L.
Galium tinctorium L.	*Vigna luteola* (Facq.) Benth.

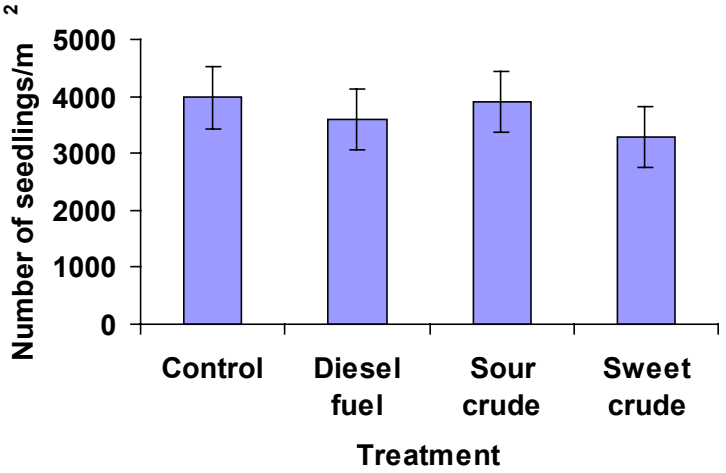

Figure 1. Mean number of seedlings emerging per m^2 from soil cores treated with oil applied at 2 l m^{-2}. Soil cores were extracted from a freshwater wetland near Dulac, LA. Controls received tap water only. Bars indicate $\pm$ SE.

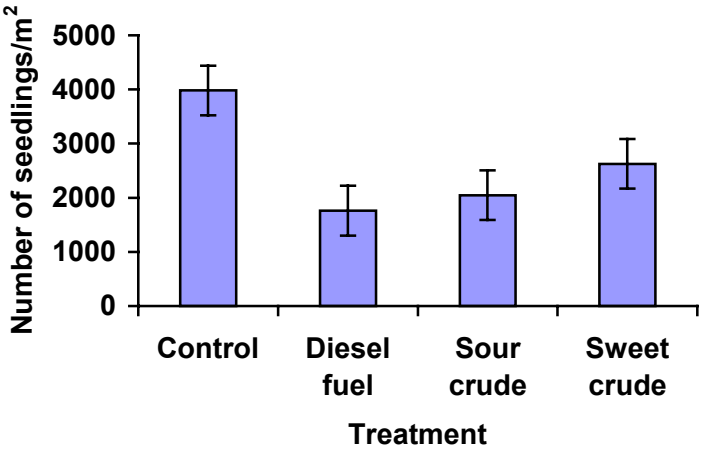

Figure 2. Mean number of seedlings emerging per m^2 from soil cores treated with 8 l m^{-2} of oil. Cores originated from a Louisiana coastal freshwater wetland. Controls received tap water only. Bars indicate $\pm$ SE.

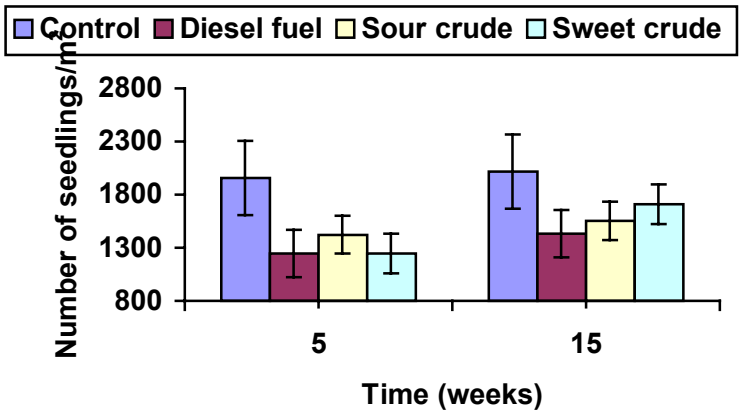

Figure 3. Mean number of seedlings emerging per m^2 five and 15 weeks after a germination assay was begun. Soils, from a Louisiana freshwater wetland had been previously exposed to oil at 8 l m^{-2}. Controls received tap water only. Bars indicate $\pm$ SE.

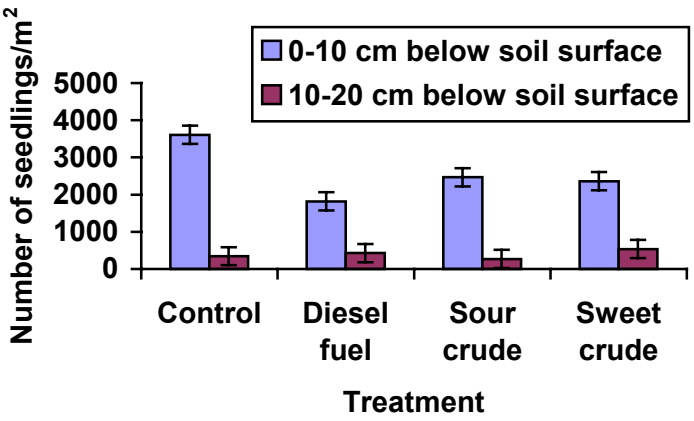

Figure 4. Mean number of seedlings emerging per m^2 in the intervals 0 to 10 and 10 to 20 cm below the soil surface. Soils were extracted from a freshwater wetland near Dulac, LA. Controls received tap water only. Bars indicate $\pm$ SE.

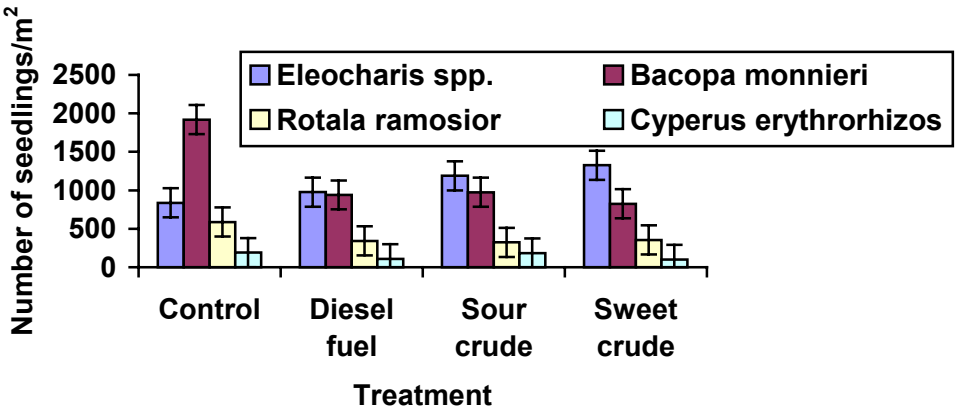

Figure 5. Species-specific germination responses to 8 l m^{-2} of oil. The species represent 90% of the total number of seedlings emerging from a Louisiana freshwater wetland seed bank. Controls received tap water only. Bars indicate $\pm$ SE.