Effects of Hurricane Wrack on Coastal Pine Savannas

William J. Platt[1,2]

and

Dwayne Joseph[3]

[1]Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803

[2]Corresponding Author: email btplat@lsu.edu

[3]Department of Biology, Grambling State University, Grambling Louisiana 71245

Abstract

Hurricane storm surges deposit wrack (vegetation debris) in coastal habitats. Existing vegetation is buried and killed in patches opened to colonization when wrack decomposes or relocated by another hurricane. We hypothesized that hurricane wrack should influence plant community composition through effects of on survival and recolonization. We explored effects of wrack deposited by Hurricane Katrina in 2005 on groundcover vegetation in pine savannas dominated by slash pine (*Pinus elliottii*) and cordgrass (*Spartina patens*) and located above mean high tide ~5 km inland from the Gulf of Mexico at the Grand Bay National Estuarine Research Reserve, Mississippi. We established paired plots in adjacent areas with and without wrack in three savannas in June, 2008, almost 3 years after deposition. At this time, wrack consisted of wood imbedded in a duff layer not yet incorporated into the soil. Fewer plant species occurred in wrack deposits (1.4 $\pm$ 0.22 per m^2) than nearby areas without wrack (7.9 $\pm$ 0.77 per m^2). We simulated effects of redistribution of wrack during a new storm surge by removing existing wrack from replicated $1m^2$ subplots in each plot and depositing it in similar sized subplots in the paired plot without wrack. Plant species were recorded in treatment and control subplots before manipulations, one month later and one year later. About one-half the plant species present before wrack addition (especially dominant graminoids) grew back through the redistributed wrack by one year after burial. Wrack removal was followed by germination of numerous herbaceous plant species not present in surrounding undisturbed savanna groundcover; after one year species numbers exceeded those in control subplots without wrack. Wrack deposition during hurricanes produces effects ranging from non-catastrophic to catastrophic, and certain life histories convey resistance to burial. Removal of wrack opens space colonized by large numbers of plant species resilient to wrack disturbance, including species that are transported in wrack and that survive intervals between disturbances in the soil. Wrack deposition and subsequent removal generated extreme groundcover heterogeneity, producing patches suitable for transient, resilient species that enhanced above-ground biodiversity.

Key words: localized disturbance catastrophic non-catastrophic Katrina debris plant community composition resistance resilience heterogeneity above-ground below ground biodiversity

Introduction

Tropical cyclones produce storm surges along coasts at the time of landfall. Such storm surges affect large areas along coastlines, especially those with shallow elevation gradients. For example, Hurricane Katrina storm surges extended as much as 20 kilometers inland along the Gulf coast of Mississippi (FEMA 2005, Knabb et al. 2005), and some coastal areas were inundated by >5 meters of ocean water (Fritz et al. 2007, 2008, Raber and Tullis 2007, Powell et al. 2010). Flooding associated with storm surges potentially changes sediments, introduces saline water, and deposits debris, or wrack (Emanuel 2005). Such consequences of storm surges potentially constitute major ecological disruptions of coastal ecosystems (e.g., Davis et al. 2004).

Wrack is often transported inland to elevations above tidal influence by major hurricane storm surges. Along the Gulf coast, wrack mats consist of fragments of herbaceous plants, mostly unattached dead stems of grasses and sedges from coastal marshes, and contain floating wood (Hackney and Bishop 1979). In recent years abundant and diverse items associated with humans (plastic bottles, aluminum cans, household items, etc.) also are pervasive in wrack (personal observations). Deposition occurs inland at distances that depend on height of storm surges, local topography, and obstacles such as vegetation encountered as the storm surge moves inland and retreats (Bush et al. 1996). For example, we noted wrack deposits as much as 1-2 meters thick and 30 meters wide that were deposited 5-6 kilometers inland during Hurricane Katrina (also see FEMA 2005).

Wrack has been noted as an important disturbance in tidal systems. Effects of tide-deposited wrack are variable, varying from no damage to removal of all species (Bertness and Ellison 1987, Valiela and Rietsma 1995). One experimental study (Brewer et al. 1998) examined short-term effects of tide-deposited wrack in marshes at different elevations along a New England coastline. Competitively dominant graminoids were killed by burial beneath wrack; competitively inferior fugitive species increased where wrack was present, benefitting from depressant effects of wrack on the dominant species (also see Bertness and Ellison 1987, Hartman 1988, Pennings and Richards 1998). Wrack thus potentially increases local heterogeneity and biodiversity by opening space in coastal landscapes (Brewer et al. 1998).

Effects of wrack may be dependent on the extent of deposits. Hartman (1988) suggested that most open patches, such as those caused by tidal deposition of wrack, in coastal salt marshes are small enough to be colonized primarily by clonal growth of surrounding dominant graminoids. The consequences of deposition of large amounts of wrack have not often been studied. Wrack deposition has been noted in observations of damage from major storms (e.g., Roman et al. 1994, Guntenspergen et al. 1995, Bush et al. 1996, Guntenspergen and Vairin 1996). These observations indicate three main effects: i) massive carbon deposits are added to the substrate, ii) salinity of the soil is increased because wrack was transported across ocean waters, becoming saturated with salt, and iii) vegetation and soil is buried beneath dense mats of dead vegetation. These observations and studies of wrack deposits suggest that extensive wrack deposited during tropical cyclones may produce large, long-term effects on coastal vegetation.

We studied effects of wrack deposited on "pine islands" containing coastal slash pine savanna surrounded by coastal marshes at the Grand Bay National Estuarine Research Reserve (GBNERR) in southeastern Mississippi, USA. These coastal habitats, about 6 km from the Gulf of Mexico and 15-30 cm above sea level, were inundated by a 5m storm surge during the landfall of Hurricane Katrina (2005). Wrack, often 1-2 m deep, was deposited in slash pine savannas elevated 15-30 cm above surrounding marshes. These wrack deposits were still present in 2008 & 2009. Based on the study of Brewer et al. (1998), we hypothesized that: 1) removal of wrack should facilitate germination and growth of any plants whose seeds survived beneath wrack; 2) deposition of wrack should depress dominant species in the intact groundcover; and 3) responses of species to burial by wrack and to removal of wrack deposits should vary with life form, resulting in differential resistance and resilience to wrack disturbance.

We addressed these hypotheses via field study that involved a combination of empirical and experimental approaches. We located and quantitatively described debris and the groundcover plant communities in areas with and without wrack deposits in coastal slash pine savannas in June 2008. Then we removed wrack to determine if seeds would germinate once the wrack was no longer present. We deposited the wrack that we removed in locations that contained no wrack to determine if that wrack would depress dominant species. In this way we simulated the effects of a new tropical cyclone that might relocate debris, uncovering areas with wrack and burying new areas that formerly did not have wrack. We resampled subplots twice, after one month (July, 2008) and after one year (June, 2009) to collect data on the plant species present aboveground. Thus, our study explored extended effects of wrack deposited above normal tidal influence on pine savanna groundcover and examined potential effects of a hurricane shifting location of wrack deposited by a prior hurricane.

Methods

We conducted our study at the Grand Bay National Estuarine Research Reserve (hereafter, GBNERR), Jackson County, Mississippi. The GBNERR (30^{o} 23’ N; 88^{o} 24’ W) is a 7,284 ha marine protected area located comprised of the Grand Bay National Wildlife Refuge and the Grand Bay Savanna Coastal Preserve (Schmid 2000, Hilbert 2006). Coastal pine savannas at the GBNERR occur on islands of sandy substrate elevated above surrounding marshes that are located about 5-6 km inland from the coastline. *Pinus elliottii* (slash pine) dominates the overstory. The groundcover, dominated by *Spartina patens*, contains a number of species, mostly perennial life forms: grasses (*Panicum virgatum*, *Andropogon virginicus*, *Dichanthelium* sp.), forbs (e.g., *Solidago sempervirens*, *Eupatorium leucolepis*, *Scutellaria integrifolia*, *Polygonum* sp.), shrubs (e.g., *Morella cerifera*, *Baccharis halimifolia*, *Ilex vomitoria*), and lianas (e.g., *Toxicodendron radicans*, *Rubus trivialis*, *Ipomoea sagittata*).

Hurricane Katrina made landfall along the Mississippi coast about 100 km west of the GBNERR on August 29, 2005. The storm surge inundated the entire GBNERR; FEMA estimates of maximum storm surge depths in coastal pine savannas were 5-6m (http://www.fema.gov/hazard/flood/recoverydata/katrina/katrina_ms_jackson.shtm). Bands of wrack several hundred meters long were deposited roughly parallel to the coastline in coastal pine savannas; these deposits were 1-2m deep and 10-40m wide (William J. Platt, personal observations). Most species of groundcover plants did not recover from burial by wrack. Although wrack had become compacted by 2008, few plants had germinated and grown through the wrack. As a result, large patches of wrack with little vegetation present were located among trees that survived the hurricane.

We selected a large pine savanna island for study in June, 2008. This island (30^{o} 24’ N; 88^{o} 24’ W) was located 5.6 km inland from the Gulf of Mexico shoreline and was surrounded by lower swales with fresh and brackish marshes. We designated three spatially separated blocks within the island. Each block contained an area with a large Katrina wrack deposit and an adjacent area without Katrina wrack (a split-block design).

We characterized the vegetation debris comprising wrack deposits and the litter in areas without wrack deposits. We established two transects in each block, one in a roughly north-south direction across the wrack deposit plot and the other in a similar direction and distance in the non-wrack plot. At 2 m intervals along the transect we measured depth of organic debris/litter. In addition, we measured diameters of all wood (logs, branches) along the transect.

We randomly selected eight subplots of $2m^2$ size and with uniform cover in each wrack and each non-wrack plot. A total of 48 subplots thus were used in this study. A $1m^2$ quadrat established in the center of each subplot was marked using rebar, PVC and a metal tag with a unique number. We mapped latitude and longitude of subplots and obtained relative elevations of subplots using a Topcon rotating laser RL-H. We Plants present and their location in each subplot were recorded prior to treatments.

We sampled wrack/litter adjacent to each subplot. Wrack/litter in a 20cm x 20cm area was collected, transported to the lab, dried for three days in a drying oven at 70^oC, and then weighed. The wrack was then separated into 3 sub-divisions: pine needles, wood pieces and duff (decomposing material); each sub-division was weighed and recorded.

We conducted an experiment in which we simulated effects of a subsequent hurricane on wrack deposits and the groundcover vegetation. We removed wrack from four randomly selected subplots within each wrack plot. Within the $2m^2$ subplot (the 1m x 1m quadrant along with the peripheral buffer of 0.5m x 1m) all wrack was removed by clipping along the edges, then carefully picked up using a pitch fork and rake so as not to disturb the underlying soil. This procedure resulted in some wrack particles less than about 2cm in length remaining as a fine layer of debris on undisturbed soil. Wrack removed from the subplot was placed on a tarp placed adjacent to the subplot, and once all wrack from the subplot was on the tarp, it was carefully carried to a randomly selected non-wrack subplot within the same block. This transported wrack was spread evenly over the 1m x 1m subplot. The other eight (8) subplots (4 in the wrack-containing plot and 4 in the non-wrack plot) were left without disturbance to serve as controls.

We sampled subplots for vegetation three times: prior to any treatment (June, 2008), after one month (July, 2008) and after one year (June, 2009). A list of the 76 plant species recorded in subplots during this study and their designated life form is presented in Appendix 1. We recorded total number of plant species and number of plant species of each life form (forbs, shrubs, graminoids & lianas) in treated and non treated plots at each census. These data were used to compare changes in vegetation when wrack had been present (in plots where wrack was removed and where wrack remained) and when wrack had not been present (in plots where wrack was added and wrack was not added).

Results

Wrack Deposits

Substantial wrack deposits were present in pine savannas at the GBNERR in 2008. These deposits, which consisted of herbaceous marsh vegetation intermixed with pieces of wood, had compacted and partially decomposed. Nonetheless, mats of wrack still covered large areas three years following Hurricane Katrina. The depth of wrack varied considerably among and within blocks, but averaged more than 10 cm (Figure 1). In addition, the depth of wrack was much greater than the depth of litter in areas of pine savannas not containing wrack deposits (Figure 1). The density of wood also varied among and within blocks, but on average was about 10 pieces per m^2 in wrack deposits compared to about 5 pieces per m^2 adjacent areas without wrack (Figure 1). Both wrack and non-wrack plots contained a range of sizes of wood, from small braches and stems of shrubs to fallen trees (Figure 1). Non-wrack plots contained larger proportions of wood in the extreme size classes (0-1cm and >5cm), and wrack plots contained larger proportions in intermediate ranges (Figure 1).

Much more dead plant material comprised wrack than comprised litter in adjacent non-wrack areas. The mass of herbaceous plant material, as well as of wood, was much greater in wrack areas than in the litter in non-wrack areas (Figure 2). In contrast, similar amounts of pine needles, which reflected deposition from the overstory pine trees since the hurricane, were present in both areas (Figure 2). As a result, total mass of dead plant material was almost six times as great in wrack areas as in adjacent non-wrack areas. The wrack consisted mainly of densely packed (0.3-0.6 g/cm^3 dry weight, on average) cylindrical culms of dead marsh grasses, almost all of which were oriented in the same direction roughly parallel to the coastline (which reduced air space in the wrack).

Plant species numbers

Wrack burial during Katrina decreased numbers of plant species in coastal pine savanna groundcover. In June, 2008, prior to experimental manipulations, on average there were fewer than 2 plant species per m^2 in wrack subplots, compared to 8 plant species per m^2 in non-wrack subplots (Figure 3). The number of plant species was not related, however, to the mass of wrack or the mass of litter (Figure 4). Localized microsites with little wrack or litter often contained plants, resulting in total species numbers being independent of total wrack or litter in a subplot.

Species in wrack subplots constituted a subset of species that occurred in non-wrack subplots. Of the 9 species recorded in all wrack subplots, only one did not occur in any non-wrack subplot. Nonetheless, on the average only 39.3 ± 1.5 % of the species in wrack subplots also occurred in non-wrack subplots within the same block. More than half the species in wrack deposits thus appeared unlikely to occur within small areas of the surrounding non-wrack groundcover. Over half of these species were shrubs or lianas whose scale of local distribution was such that they were unlikely to be present in $1m^2$ subplots. In contrast, all species of forbs present in wrack subplots also were present in non-wrack subplots in each block.

Removal of wrack and deposition in subplots without wrack resulted in rapid changes in species numbers. Removal of wrack in June 2008 resulted in a fourfold increase in the mean number of species present in subplots over the following month (Figure 5). These increases in species richness resulted from germination of dormant seeds, all of which were graminoids and forbs. In contrast, adding wrack to subplots resulted in an approximately 70% decrease in mean numbers of species present after one month (Figure 5). The decreases in species numbers were most pronounced for graminoids and forbs, especially species with a rosette growth form.

Numbers of species changed even more one year after removal of wrack. One year after initiation of treatments, on average 12.6 ± 3.7 (S.E.) species/m^2 were present in the subplots from which wrack was removed, an almost six fold mean increase following wrack removal. Still, the large standard error indicated considerable variation among subplots in number of species. Examination of the seedlings revealed that the vast majority of germinating seeds had been located beneath the remaining surface layer of debris or in the soil, rather than on the surface, indicating that almost all germinating plants had been present as seeds in the debris. There was a small increase in species numbers in subplots where wrack was present, but not removed; 3.3 ± 0.5 species/m^2 on average were present by June 2009. In the subplots without wrack, but where wrack was added, the mean number of species decreased further, from 7.7 ± 0.9 species/m^2 in June 2008 to 4.8 ± 1.6 species/m^2 in June 2009. In contrast, no large change in species numbers occurred in the no-wrack, wrack not added subplots, which averaged 9.2 ± 0.8 species/m^2 and 10.5 ± 1.5 species/m^2 in June, 2008 and 2009, respectively.

Life forms differed in the magnitude of responses to wrack removal and addition. Mean numbers of species per m^2 for the four experimental treatments (wrack present and either removed/not removed and wrack not present and either added/not added) are presented in Figure 6. Data are presented separately for the four different life forms (graminoids, forbs, shrubs, lianas) for each sampling time (pre-treatment, one month post-treatment, and one year post-treatment). Removal of wrack resulted large increases in the number of species of graminoids and forbs. One year after removal of wrack, as many graminoids and more forbs were present compared to no-wrack, no wrack added subplots. Nonetheless, increases in graminoids and forbs were highly variable among plots, as indicated by the large standard errors in Figure 6. Numbers of species of shrubs and lianas also increased, but only slightly more in wrack removed subplots than in wrack not removed subplots. As with the graminoids and forbs, there was considerable variation in the occurrence of shrubs and lianas among subplots. Addition of wrack to areas that contained no wrack resulted in large declines of graminoids and forbs. Numbers of graminoids and forbs were reduced by >50% one year after wrack was added to plots. In contrast, shrubs and lianas showed almost no declines in numbers of species one year after wrack was placed where there previously had been no wrack. Nonetheless, the two dominant graminoids, *Spartina patens* and *Panicum virgatum*, survived in all plots; some culms of these species extended through wrack we deposited. The density of culms one year after burial was a higher proportion of the original culm density for *P. virgatum* (74 ± 10%) than *S. patens* (31 ± 12%).

Species composition differed in areas with and without wrack. In the initial year (2008), 12.8 ± 2.3(SE) % of the species in surrounding pine savanna were present in plots from which the wrack had been removed. In addition, 49.0 ± 5.0% of the species in plots from which wrack was removed occurred in the surrounding pine savanna. Thus, colonization of areas from which wrack was removed by species in the surrounding pine savanna (either from seeds or clonal growth) was restricted, but about one-half of the species that colonized when wrack was removed did not occur in surrounding pine savanna. When wrack was added to plots, species that survived initially (in 2008) were not those in areas from which wrack was removed. Only 7.6 ± 1.3% of the species in plots to which wrack was added were present in plots from which wrack was removed. Similarly, 41.0 $\pm$ 2.3% of the species in plots from which wrack was removed also occurred in plots to which wrack was added. Thus, many species in plots from which wrack was removed were not species that were capable of surviving burial by wrack.

One year later, species composition was still different in areas with and without wrack. Species from surrounding pine savannas colonized area from which wrack was removed. On the average, 44.0 $\pm$ 16.7% of the species in surrounding pine savanna had colonized plots from which wrack had been removed. Nonetheless, 39.5 $\pm$ 10.0% of the species in plots from which wrack was removed also occurred in the surrounding pine savanna. These data indicated that colonization of areas from which wrack was removed was occurring by species in surrounding pine savanna (either from seeds or clonal growth), but large proportions of the species that colonized when wrack was removed did not occur in surrounding pine savanna. Because numbers of species increased considerably by 2009, this means that the species composition of plots from which wrack had been removed contained large numbers of species that did not occur in the surrounding pine savanna.

When wrack was added to plots, species that were present in 2009 were not those in areas from which wrack was removed. The proportion of the species in plots to which wrack was added that were present in plots from which wrack was removed increased to 26.6 $\pm$ 1.3%. Similarly, 43.6 $\pm$ 2.2% of the species in plots from which wrack was removed also occurred in plots to which wrack was added. Thus, one year later, many species in plots from which wrack was removed were not species that were capable of surviving burial by wrack.

Discussion

Wrack disturbance

Our study indicated that wrack transported inland by storm surges of major hurricanes can produce large negative effects on above-ground coastal plant communities. Discrete patches of wrack 1-2m thick were transported above mean high tide in the Grand Bay National Estuarine Research Reserve in Mississippi by the storm surge of Hurricane Katrina. These deposits, fragments of saltwater-soaked vegetation mixed with wood and human-generated debris, buried and killed groundcover vegetation in localized areas 10-20 meters wide and up to several hundred meters long in coastal pine savannas. Hurricane wrack deposits thus can constitute major disturbances that generate locally catastrophic effects (leave no survivors; Sousa 1984, Platt and Connell 2003) within coastal savannas.

Effects of hurricane wrack may persist over long time intervals. Decomposition of the wrack deposited by Hurricane Katrina has occurred slowly, most likely a result of the large mass of low nutrient and salt-saturated debris located above high tide line. Like some other effects of hurricanes (i.e., saltwater intrusion; Flynn et al. 1995), wrack disturbance may not be ephemeral. Space has opened gradually; after 3-5 years, plants have colonized only edges of wrack deposits and scattered small openings in the interior of wrack deposits. In addition, large hurricane wrack patches seem not to be readily invaded by either guerrilla or phalanx growth forms of dominant graminoids (cf. Bertness and Ellison 1987), at least until secondary events influence wrack or it decomposes. As a result, colonization of sites of hurricane wrack deposits, especially those located above high tide line in major hurricanes may not proceed in ways or at rates resembling those described for some salt marshes (e.g., Bertness and Ellison 1987, Hartman 1988, Bertness and Shumway 1993, Shumway and Bertness 1994, Valiela and Rietsma 1995).

Subsequent events may affect decomposing hurricane wrack, shortening the time it is present on a site. Hurricanes are recurrent disturbances, and some regions like the northern Gulf coast are frequented by hurricanes (Doyle 2009). We experimentally explored one possible secondary event, a second hurricane that redistributes wrack. Movement and re-deposition of wrack several years after an initial hurricane produced effects different from those after Hurricane Katrina. Experimental wrack deposits depressed vegetation initially, but about half the species recovered quickly. These species always were ones capable of producing elongated structures (leaves, stolons, stems) that extended through the wrack to the surface of the deposit. We propose that the severity of disturbance (the extent to which effects of wrack deposition are catastrophic or non-catastrophic; Baldwin and Mendelssohn 1998, Platt & Connell 2003) depends on the mass and depth of wrack deposits (also see Bertness and Ellison 1987). A minimal storm surge (from a low-intensity hurricane or a hurricane some distance from the site) should produce smaller wrack deposits; resistant plant species (sensu Boucher et al. 1994, Bellingham et al. 1995, Batista and Platt 2003) capable of growth through that wrack should survive burial. Pennings and Richards (1998) further suggest regrowth as likely when thin wrack deposits occur in tidal systems. We propose that resistant species should have sufficient underground storage to produce stiff stems, long leaves or culms, or stolons that can penetrate wrack. Nonresistant species, those less likely to survive burial by wrack, should include rosette-forming species; these plants, once buried, are unlikely to grow back to the surface of the wrack.

Spartina patens and *Panicum virgatum*, the most locally abundant graminoids in the coastal pine savannas we studied, were resistant to burial by redistributed wrack. Although these species did not survive burial by wrack in Hurricane Katrina, some culms of these grasses grew through our experimental wrack deposits within a month, and one year later were present at low densities. Since we started our field study, wrack was deposited at GBNERR during storm surges produced by Hurricanes Gustav and Ike in September, 2008. These storm surges were less intense, in large part because the hurricanes did not make landfall in the vicinity of GBNERR; wrack deposits typically were about 50cm deep and located in different areas than the Katrina wrack. Some ramets of these dominant grasses that were buried regrew through wrack deposited in these hurricanes in the spring of 2009. Our experimental data and field observations thus indicate that dominant graminoids are resistant to wrack burial, but also are negatively affected. Effects of wrack appear proportionately greater on phalanx-like growth forms (e.g., *S. patens*). We anticipate that *P. virgatum* may increase in local relative abundance in savanna affected by wrack deposits, like *Distichlis spicata* in more northern salt marshes (Brewer et al. 1998).

We envision that effects of wrack burial in coastal marshes and savannas depend on the mass of wrack deposited locally and the timing of disturbance. At one extreme, catastrophic effects should be likely when large masses of wrack are deposited. At the other extreme at least some species should survive if only small amounts of wrack are deposited or if the wrack is removed soon after deposition. We further suggest that effects may be greatest when wrack is deposited when plants are not actively growing (e.g., late summer, at times of hurricanes) and thus do not regrow through wrack before it compacts and settles. Similar ranges of effects of wrack deposition on plant species have been noted in more northern salt marshes (Valiela and Rietsma 1995, Tolley and Christian 1999). Still, survival appears highly selective at intermediate masses of wrack or decomposing wrack that is redistributed, with resistant species capable of regrowth through the wrack being the ones to persist onsite. Similar patterns of survival have been noted for other large-scale disturbances, such as tephra burial during volcanic eruptions (e.g., del Moral 1983, Tsuyuzaki 1987, 1989, del Moral and Grishin 1999).

Wrack as a disturbance should produce a wide range of localized effects on coastal savanna groundcover. Effects we observed and generated experimentally indicate that models based on transient effects of disturbance (e.g., direct regeneration hypothesis; Boucher 1990, Boucher et al. 1990, Yih et al. 1991, Vandermeer et al. 1995, 2000, Baldwin and Mendelssohn 1998) and models based on catastrophic disturbance (intermediate disturbance hypothesis; Connell 1978, Shumway and Bertness 1994, Baldwin and Mendelssohn 1998) only partly explain effects of wrack disturbances on plant communities. We propose a concept of selective regeneration based on 1) nature of the wrack (e.g., size of patch, amount deposited, and perhaps the structural composition), 2) location (e.g., elevation above sea level and thus tidal influences), 3) environmental conditions associated with both deposition (e.g., salinity, continuousness of cover, seasonal timing) and decomposition (nutrient content, rate of decomposition), as well as 4) potential abilities of species to survive and recover. Such a concept involving interactive relationships among abiotic and biotic conditions (also see Houle 2005) should be applicable to a wide range of coastal herbaceous plant communities that experience wrack disturbance.

Species Responses to Wrack Removal

Removal of Hurricane Katrina wrack resulted in rapid colonization by plants. Within a month after removal of debris, seeds of some plant species buried in/beneath wrack germinated, and seeds of many more species germinated the following spring. Presumably, sufficient time passed between deposition and subsequent removal of wrack that effects of hurricane storm surge flooding and increased salinity (as shown by Middleton 2009) were diminished. Based on observations of plants flowering in the vicinity of plots and locations of germinating seeds in the substrate, colonization after wrack removal resulted from in situ seeds rather than immigration from surrounding areas. Seeds of a number of plant species remained viable through the storm surge and subsequent burial until we generated conditions suitable for germination (exposure to sunlight or warm temperatures). Seedlings grew rapidly, and most flowered within a year.

Some seeds of plants that germinated when intact wrack was removed were associated with a layer of decomposing duff beneath remaining intact debris. At the time of Hurricane Katrina landfall, seeds were carried into pine savanna along with other debris as part of the wrack deposits. Several species transported in wrack typically did not occur in surrounding coastal pine savanna, but apparently emigrated from brackish marshes (e.g., *Echinochloa walteri*, *Hibiscus moscheutos*, *Kosteletzkya virginica*, *Sesbania vesicaria*). Some of these species have been noted as producing buoyant seeds (e.g., Poljakoff-Mayber et al. 1992), which could be dispersed by wrack (Minchinton 2006 and references therein). These seeds often germinated shortly after remaining intact wrack was removed; plants grew rapidly, flowering and dispersing new seeds either the same or subsequent year.

Most species that germinated when wrack was removed were in the soil beneath decomposing wrack. These species appeared to be indigenous to coastal pine savannas and marshes, but were not a random sample of life forms in coastal pine savanna at GBNERR. Seed bank species were much more likely to be graminoids or forbs than shrubs or lianas, consistent with results of many other studies. The seed bank species also were most often annuals or short-lived perennials, also consistent with results of many other studies. Baskin and Baskin (2001) summarize studies indicating that many plant species in saline and non-saline wetland habitats have seeds with physiological dormancy and that these seeds tend to germinate when salinities decrease below some minimal level and water levels are lowered. We noted that exposure to light or warm temperatures following removal of wrack also seemed to be a germination cue for these species. These plants, most of which germinated the spring following removal of wrack, also tended to grow rapidly, flower and disperse seeds either the same or subsequent year.

Some species that germinated when wrack was removed exhibited ephemeral post-disturbance responses. A few species (e.g., *Echinochloa walteri*, *Erechtites hieracifolium*, *Panicum verrucosum*) germinated within weeks after wrack removal, grew rapidly, and flowered/set seed before the next growing season. They then disappeared aboveground, but seeds presumably were present in the substrate. Such species or close relatives have been noted as responding rapidly and ephemerally to large-scale disturbance in a variety of wetland and savanna ecosystems (Dolan 1994, Kirkman and Sharitz 1994, Sparks et al. 1994, Baldwin et al. 1996, Baskin et al. 1999, Slocum and Mendelssohn 2008). Annual species that germinate and grow to maturity following smaller-scale disturbances germinated the spring after wrack was removed, grew to maturity, and set seed. These species then disappeared aboveground from plots, based on field observations in 2010. Some of these were fresh-marsh annuals that might normally germinate under drier than normal conditions (e.g., *Bidens coronata*, *Pluchea rosea*, *Ptilimnium capillaceum*). Others were typical of coastal savannas (e.g., *Sabatia stellaris, Setaria parviflora*). Annual plant species comprised about 15% of the species recorded in the current study, greatly outnumbering similar ephemeral species in more northern coastal wetlands.

Colonists of sites where wrack was removed also included wetland species that persist on sites for more than one year after germination. These species, both graminoids and forbs, commonly were species not present above ground in surrounding coastal savanna without wrack. Genera of graminoids (e.g., *Andropogon*, *Carex*, *Dichanthelium*, *Sacciolepis*, *Schizachyrium)*, as well as forbs (e.g., *Linum*, *Ludwigia*, *Neptunia*, *Polygonum*, *Proserpinaca*, *Ruellia*, *Rumex*, *Samolus*) germinated the spring of the year after wrack was removed, and these plants grew rapidly, often flowering the year of germination. These species were still present when plots were rechecked in 2010. These species collectively comprised 50% of the coastal savanna flora recorded in the current study, resulting in 65% of the total flora recorded consisting of resilient annual and short-lived perennial species not typically found in undisturbed coastal pine savanna.

Assemblages of plants that formed after wrack removal did not resemble assemblages in surrounding coastal pine savanna. Initial colonists were overwhelmingly under-represented in plant assemblages in undisturbed pine savannas. Plant species often have been designated fugitives if they respond to opening of space, but do not persist aboveground in stands during intervals between disturbances. We emphasize that a sizable component of the local coastal savanna species pool actually does persist on site during intervals between disturbances, just belowground (cf. Platt and Connell 2003; also see Baskin and Baskin 2001). We consider these coastal marsh/savanna species as resilient (sensu Boucher et al. 1994, Bellingham et al. 1995, Batista and Platt 2003) to wrack disturbance. Because they do not go extinct locally (the sense of "fugitive" used by Hutchinson 1951, also Platt 1975), post-wrack colonists should be more appropriately considered resilient rather than fugitive species (cf., Bertness et al. 1992, Brewer et al. 1998). Rapid responses to disturbances, followed by rapid return of offspring to a seed bank, have repeatedly been suggested as evolutionary responses to recurrent disturbances that provide transient opportunity for growth and seed production in physically demanding environments, but do not necessitate dispersal to new sites each generation (see reviews in Bazzaz 1979, Sousa 1984, Bertness et al. 1992, Grime and Hillier 2000, Keddy 2010).

Species that colonized plots from which wrack was removed greatly increased aboveground species richness of the local coastal pine savanna. Few species whose seeds germinated in plots were present aboveground in the immediate vicinity of plots from which wrack was removed, and less than half were present aboveground in any plot in coastal pine savanna. Thus, local species pools producing colonists of opened wrack deposits contained more plant species that were not present than were typically present aboveground in undisturbed savanna. Similar life histories (but much smaller components of local species pools) have been noted in other herbaceous-dominated wetland systems (e.g., Hartman 1988, Gerritson and Greening 1989, Kirkman and Sharitz 1994, Baldwin et al. 1996, Van der Valk and Rosburg 1997, Pennings and Richards 1998, Middleton 2009). We suggest that habitats with frequent large-scale disturbances may be characterized by high biodiversity (cf. Connell 1978). Apparent low biodiversity, evidenced by small numbers of species present above ground, may obscure the presence of large numbers of species that are present and capable of post-disturbance responses.

Wrack deposition during major hurricanes introduces local heterogeneity into coastal pine savannas. Relocation or eventual decomposition of wrack opens space in coastal habitats. Species not present (above ground) invade, forming assemblages not present (above ground) in the surrounding undisturbed savanna. Local variation in seed banks in the soil (Baskin and Baskin 2001) and in responsiveness to differences in post-disturbance conditions (e.g., Ungar 1987, Shumway and Bertness 1992, Middleton 2009), coupled with variation in dispersal via tides and wrack (e.g., Huiskes et al. 1995, Chang et al. 2008), results in large variation in aspect dominance and species composition of local post-disturbance assemblages. Such variation in aspect dominance of post-disturbance assemblages contrasts with the similarity of the aspect dominance and magnifies the local variation in species composition of assemblages in the surrounding undisturbed savanna (also see Brown and Peet 2003). In addition, the dynamics of below-ground seed populations, as well as the timing of hurricanes relative to seed production by species capable of being transported by wrack, should result in temporal variation in the immigration-driven biodiversity that results from wrack disturbance. The dynamic relationships between resistance and resilience of species present at the time of disturbance, immigration of new species from elsewhere, as well as the potential influence of local environmental conditions, underscores the potential for disturbance-driven biodiversity in coastal savannas.

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Figure Legends

Fig. 1. Wrack and litter remained in coastal pine savanna at the Grand Bay National Estuarine Research Reserve in 2008, three years after Hurricane Katrina. Lower left: Mean number of pieces of wood along transects across wrack patches and in adjacent non-wrack areas. Lower right: Mean depth of litter along transects across wrack patches and in adjacent non-wrack areas. Upper: Relative size (diameter) distributions of wood along transects in wrack patches and adjacent non-wrack areas. Vertical bars denote standard errors.

Fig. 2. Wrack deposits contained 5-6 as much mass of dead plant material as surrounding areas in coastal pine savanna at the Grand Bay National Estuarine Research Reserve in 2008, three years after Hurricane Katrina. Vertical bars denote standard errors.

Fig. 3. Many fewer plant species per m^2 occur in wrack than surrounding coastal pine savanna at the Grand Bay National Estuarine Research Reserve in 2008, three years after Hurricane Katrina.

Fig. 4. Number of plant species per m^2 is not related to wrack/litter mass in coastal pine savanna at the Grand Bay National Estuarine Research Reserve in 2008, three years after Hurricane Katrina.

Fig. 5. Mean numbers of plant species per m^2 increased one month after wrack was removed from pine savanna groundcover and decreased in surrounding groundcover where wrack was added. Vertical bars indicate standard errors.

Fig. 6. Mean numbers of species per m^2 of life forms (graminoids, forbs, shrubs, lianas) increased over time when wrack was removed and decreased when wrack was added to groundcover without wrack. The three sampling dates are presented in order: prior to (June, 2008), one month after (July, 2008), and one year after (June, 2009) treatment. The two experimental treatments and controls for each are indicated beneath the abscissa. Vertical bars indicate standard errors.

Fig. 1

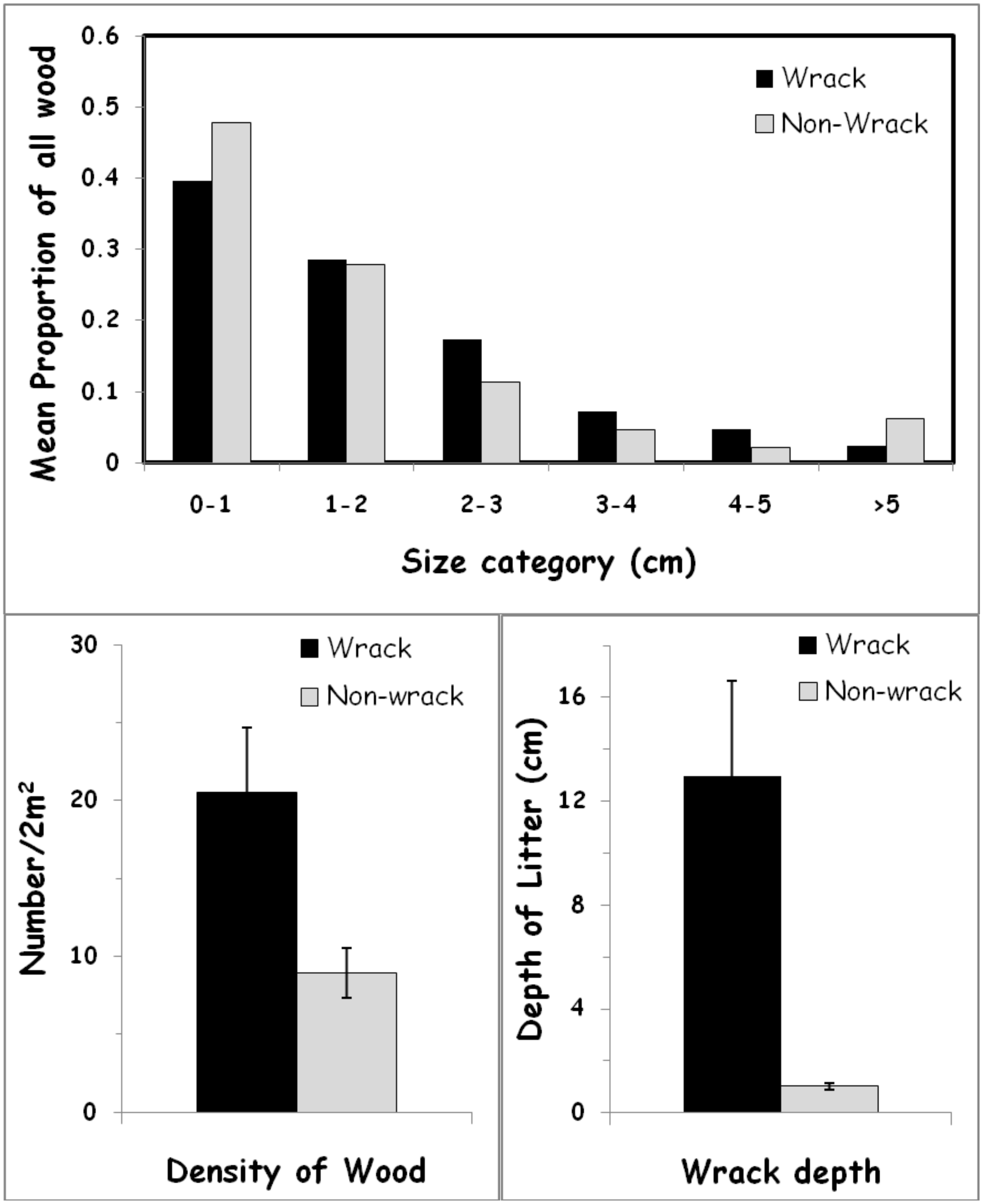
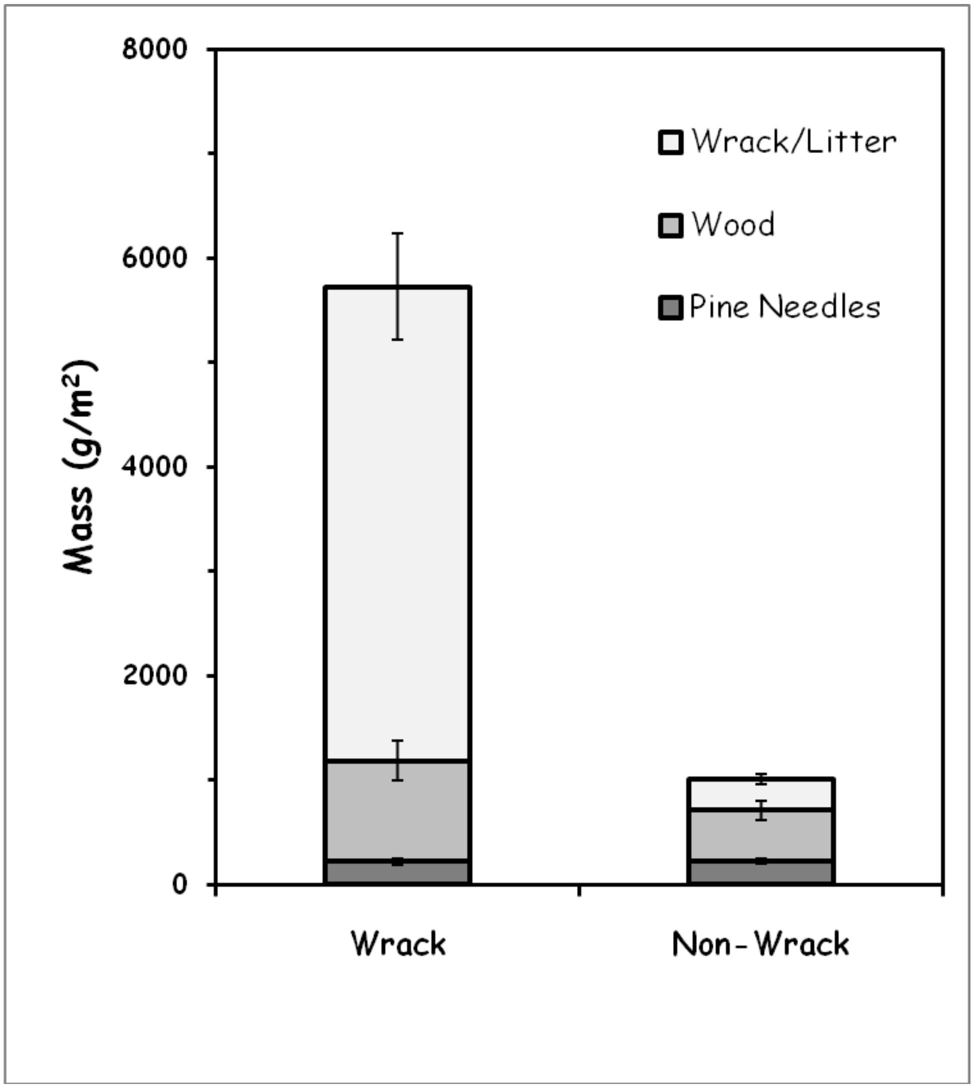

Mean Proportion of all wood
0.6
0.5
0.4
0.3
0.2
0.1
0
Wrack
Non-Wrack
0-1
1-2
2-3
3-4
4-5
>5
Size category (cm)
Number/2m²
30
20
10
0
Wrack
Non-wrack
Density of Wood
Depth of Litter (cm)
16
12
8
4
0
Wrack
Non-wrack
Wrack depth

Fig. 2



8000
6000
4000
2000
0
Mass (g/m²)
Wrack/Litter
Wood
Pine Needles
Wrack
Non-Wrack

Fig.3

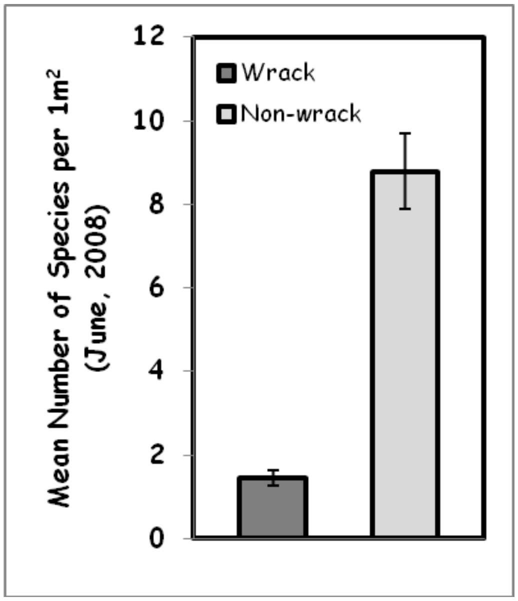

Mean Number of Species per 1m²
(June, 2008)
0
2
4
6
8
10
12
Wrack
Non-wrack

Fig. 4

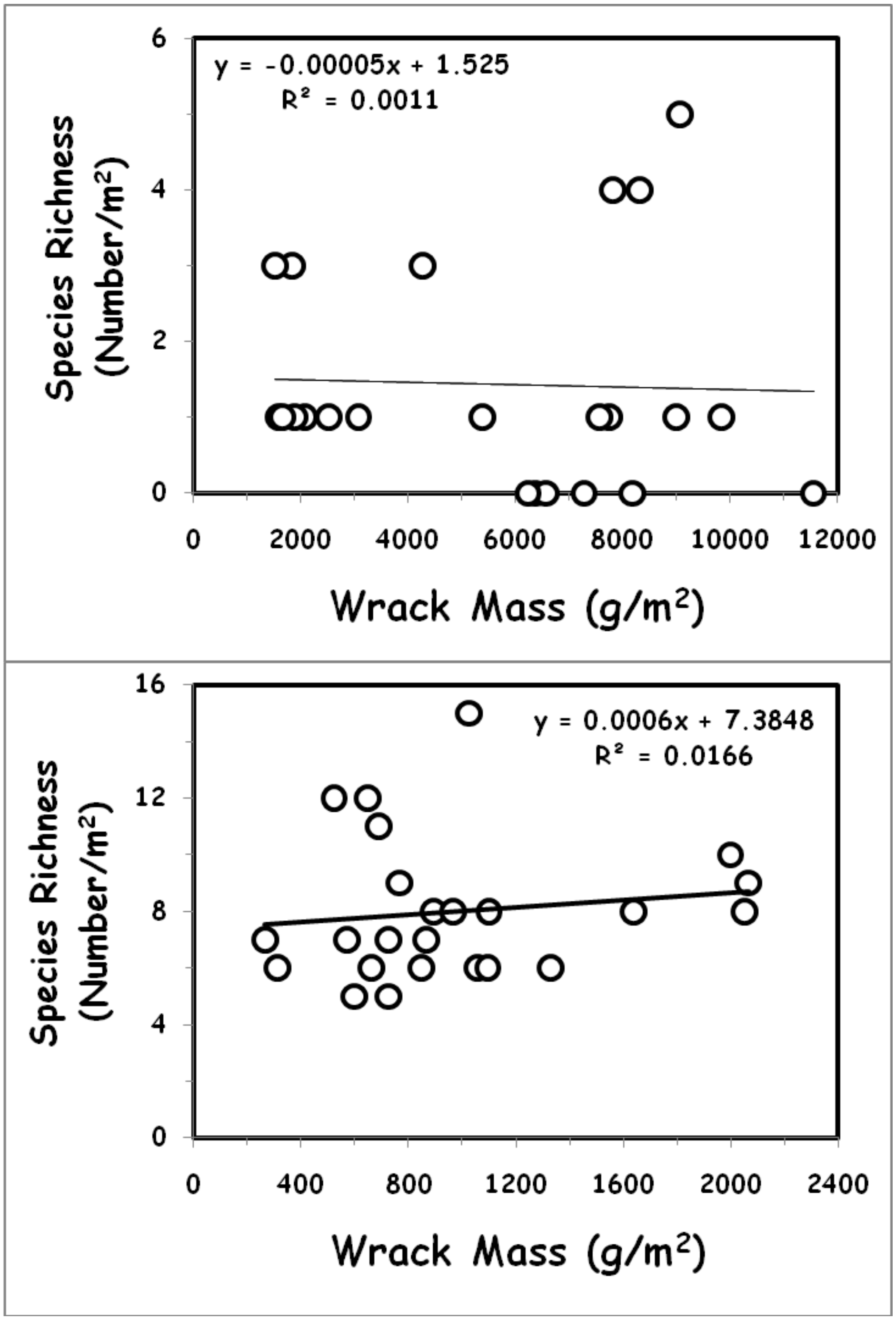
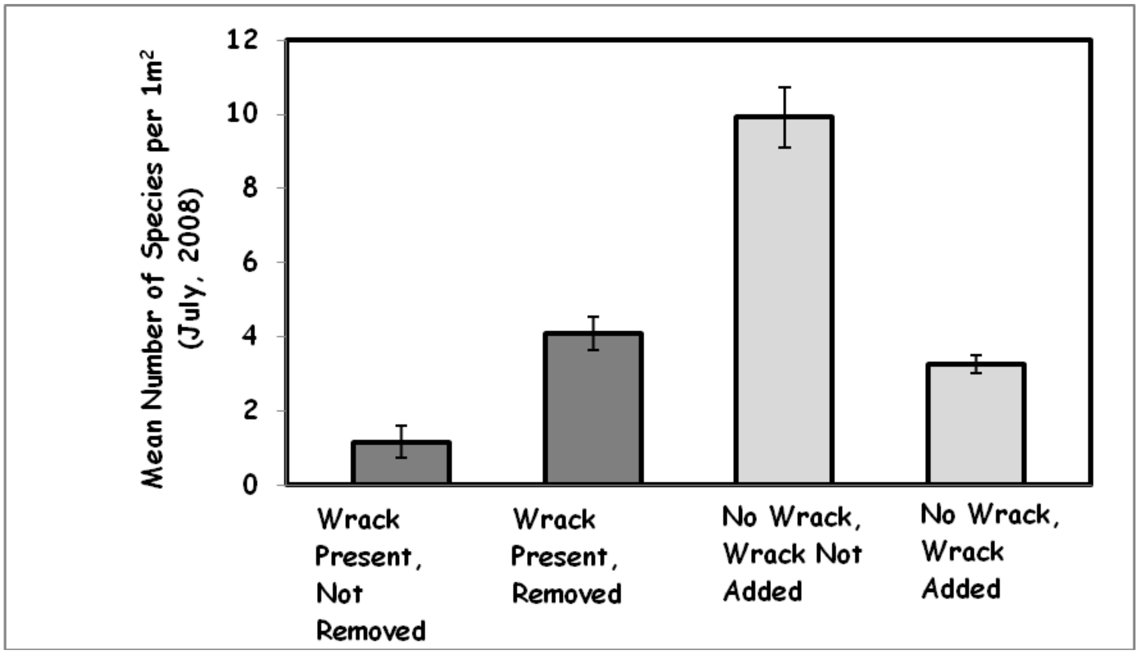
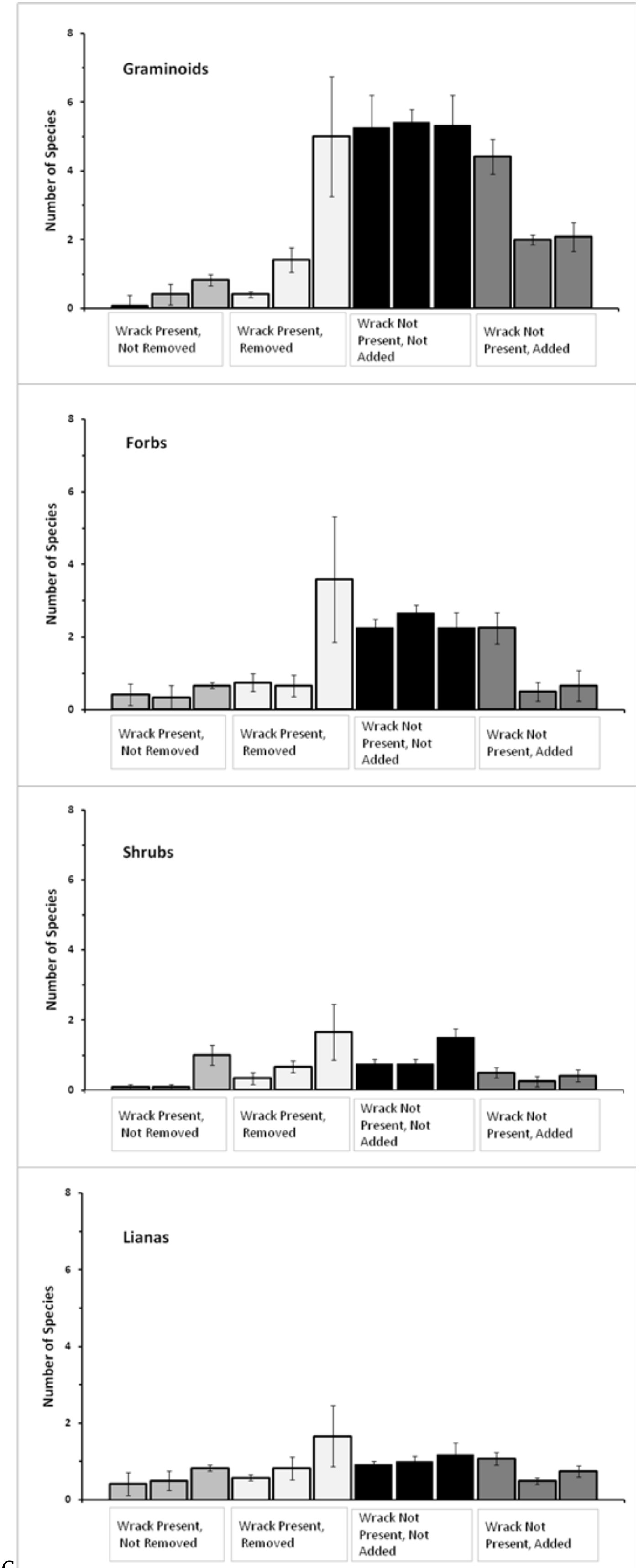

y = -0.00005x + 1.525
R² = 0.0011
Species Richness (Number/m²)
6
4
2
0
0
2000
4000
6000
8000
10000
12000
Wrack Mass (g/m²)
y = 0.0006x + 7.3848
R² = 0.0166
Species Richness (Number/m²)
16
12
8
4
0
0
400
800
1200
1600
2000
2400
Wrack Mass (g/m²)

Fig. 5


Mean Number of Species per 1m²
(July, 2008)
12
10
8
6
4
2
0
Wrack Present, Not Removed
Wrack Present, Removed
No Wrack, Wrack Not Added
No Wrack, Wrack Added

724 Fig. 6


Graminoids
Number of Species
0
2
4
6
8
Wrack Present, Not Removed
Wrack Present, Removed
Wrack Not Present, Not Added
Wrack Not Present, Added
Forbs
Number of Species
0
2
4
6
8
Wrack Present, Not Removed
Wrack Present, Removed
Wrack Not Present, Not Added
Wrack Not Present, Added
Shrubs
Number of Species
0
2
4
6
8
Wrack Present, Not Removed
Wrack Present, Removed
Wrack Not Present, Not Added
Wrack Not Present, Added
Lianas
Number of Species
0
2
4
6
8
Wrack Present, Not Removed
Wrack Present, Removed
Wrack Not Present, Not Added
Wrack Not Present, Added

Appendix 1

	Life Form			
Species	**Graminoid**	**Forb**	**Shrub**	**Liana**
Andropogon capillipes	1			
Andropogon glomeratus var. *glomeratus*	1			
Andropogon gyrans var. *stenophyllus*	1			
Baccharis halimifolia			1	
Bidens coronata		1		
Bigelowia nudata		1		
Carex albolutescens	1			
Carex glaucescens	1			
Centella erecta				1
Cynanchum angustifolium				1
Dichanthelium aciculare var. *angustifolium*	1			
Dichanthelium dichotomum var. *tenue*	1			
Dichanthelium ovale var. *addisonii*	1			
Dichanthelium sabulorum var. *patulum*	1			
Dichanthelium scabriusculum	1			
Dichanthelium sphaerocarpon var. *isophyllum*	1			
Echinochloa walteri	1			
Erechtites hieraciifolia var. hieraciifolia		1		
Eupatorium capillifolium		1		
Eupatorium leucolepis var. *leucolepis*		1		
Eupatorium perfoliatum var. *perfoliatum*		1		
Eupatorium serotinum		1		
Euthamia graminifolia var. graminifolia		1		
Fimbristylis castanea	1			
Hibiscus moscheutos		1		
Hydrocotyle umbellata				1
Hypericum galioides		1		
Ilex glabra			1	
Ilex vomitoria			1	
Ipomoea sagittata				1
Juncus marginatus	1			
Juncus roemerianus	1			
Kosteletzkya virginica		1		
Linum medium var. *texanum*		1		
Ludwigia hirtella		1		

Mikania scandens				1
Morella cerifera			1	
Muhlenbergia capillaris	1			
Neptunia lutea		1		
Osmunda regalis		1		
Panicum anceps	1			
Panicum verrucosum	1			
Panicum virgatum	1			
Photinia pyrifolia			1	
Pinus elliottii			1	
Pluchea rosea		1		
Polygonum punctatum		1		
Proserpinaca pectinata		1		
Ptilimnium capillaceum		1		
Quercus virginiana			1	
Rhynchospora elliottii	1			
Rhynchospora glomerata	1			
Rhynchospora oligantha	1			
Rubus trivialis				1
Ruellia noctiflora		1		
Rumex crispus		1		
Sabatia stellaris		1		
Saccharum brevibarbe var. *brevibarbe*	1			
Sacciolepis striata	1			
Sambucus nigra ssp. *canadensis*			1	
Samolus valerandi var. *parviflorus*		1		
Schizachyrium littorale	1			
Scutellaria integrifolia		1		
Sesbania vesicaria			1	
Setaria parviflora	1			
Smilax bona-nox				1
Solidago fistulosa		1		
Solidago sempervirens var. *mexicana*		1		
Sonchus oleraceus		1		
Spartina patens	1			
Stokesia laevis		1		
Strophostyles leiosperma				1
Symphyotrichum subulatum		1		
Toxicodendron radicans				1

Triadica sebifera			1	
Vaccinium arboreum			1	
Vigna luteola				1
Number of Species	27	29	11	10