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Effects of shrub encroachment and removal on South Texas coastal prairie flora

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EFFECTS OF SHRUB ENCROACHMENT AND REMOVAL ON SOUTH TEXAS COASTAL PRAIRIE FLORA

A Thesis

by

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ABSTRACT

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Mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*) are aggressively encroaching onto South Texas coastal prairies, outcompeting Gulf cordgrass (*Spartina spartinae*) with potential legacy effects on the landscape. To measure shrub impacts on understory microclimate and grass cover, light, soil and air temperatures were recorded every 4 hr for 16 mo and grass cover surveyed across a gradient of shrub encroachment. To determine prairie recovery as a consequence of degree of shrub encroachment and shrub removal via mechanical, prescribed fire and herbicide treatments used singly or in combination, vegetation cover and soil conditions were quantified at 4-mo intervals for 2 yr. Air and soil temperatures tended to be lower under large shrub patches compared to open grass areas, but only during summer. Grass cover was generally lower with higher shrub canopy cover. All three removal treatments combined were most effective for reducing shrub resiliency and amount of time needed for natural prairie revegetation.

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CHAPTER I

INTRODUCTION

Shrub encroachment into grasslands is a worldwide phenomenon that has increased substantially during the last century with no signs of abating (Archer et al., 1988; Grover and Musick, 1990). Shrub encroachment is the synergistic effect of myriad factors, including climate change (D'Odorico et al., 2010), overgrazing (Scholes and Archer, 1997; Coetzee et al., 2008) and modifications to natural disturbance regimes, especially wildfire (Box and White, 1969; Lehmann, 1965). Climate warming allows C_3 shrubs to thrive in areas previously dominated by C_4 grasses (Archer et al., 1995), because the C_3 carbon fixation process used by shrubs is more efficient at higher levels of atmospheric CO_2 (Van Auken, 2000). Cattle grazing often allows shrub species like mesquite (*Prosopis glandulosa* Torr.) to proliferate because seeds within palatable seed pods are scarified when passed through the animal's digestive tract; the seed's subsequent deposition in a pile of moist, nutrient-rich dung then promotes germination and initial seedling establishment (Buffington and Herbel, 1965; Archer et al., 1995; Archer et al., 2009). In addition, cattle selectively graze grasses that would otherwise serve as fuel for wildfire (Scholes and Archer, 1997; Briggs et al., 2002), a primary disturbance in most grasslands that keeps shrub encroachment in check by: (1) promoting grass germination and growth by removing leaf litter and woody debris that would otherwise impede these processes (Schramm, 1990; Van Auken, 2000; Briggs et al., 2005), and (2) killing the apical bud of woody shrubs, eventually killing the shrub itself (Van Auken, 2000).

Once shrubs encroach into grasslands, they foster a positive feedback cycle to their own survival and growth. Shrub canopies often create bare patches within their understory, potentially through changes in understory microclimate, light availability, or soil conditions that limit grass growth (Tiedemann and Klemmedson, 1977; Barnes and Archer, 1996; Lett and Knapp, 2005). Furthermore, shrub leaf litter and woody debris can impede the ability of grass seeds to germinate and grow beneath shrubs (Knapp and Seastedt, 1986). The reduced grass cover creates a zone of low fuel abundance around the shrub's base (Buffington and Herbel, 1965), effectively reducing the shrub's susceptibility to damage or mortality caused by fire (Buffington and Herbel, 1965; Schlesinger et al., 1990; Archer et al., 1995). Thus, the combination of anthropogenic alteration of disturbance regime and the shrub's ability to inhibit natural competitors and disturbances leads to a shift in ecosystem structure and function. Without intervention, the ecosystem becomes entrenched in this cycle where woody shrubs increase and grasses decrease, requiring active restoration attempts to shift the system back to its open, grassy state (Holling, 1973; Lett and Knapp, 2005) (Figure 1).

A shift from an herbaceous to woody functional type as a consequence of shrub encroachment has numerous ecological consequences. Animal species that require open, grassy areas for hunting or nesting may be outcompeted by those that depend on the standing biomass of woody shrubs (Mutch et al., 2005). For example, the increased shrub cover led to the federally-endangered aplomado falcons (*Falco femoralis* Temminck) being preyed upon by great horned owls (*Bubo virginianus* Gmelin) that use the high-density shrub cover for habitat (Jenny et al., 2004). Furthermore, a shift from prairie vegetation to woody shrubs increases carbon recalcitrance and allocation from belowground storage in prairie grass root systems to aboveground storage in woody shrub biomass (Knapp et al., 2008), where the potential for the carbon being released into the atmosphere is greater than it would be if it were stored in the fibrous underground roots of grasses (Goodale and Davidson, 2002). Thick, extensive roots of prairie grasses also serve to stabilize soil, without which the chances for soil erosion due to wind and runoff increase (Van Auken, 2000). Many encroaching woody shrubs have also been shown to alter soil chemistry, such as the leguminous mesquite (*Prosopis glandulosa* Benth.) that has symbiotic associations with N-fixing bacteria that can increase soil nitrogen over time (Tiedemann and Klemmedson, 1973; Tiedemann and Klemmedson, 1977; Huxman et al., 2005). Woody shrubs also have long tap roots that reach deep into the ground for water, altering soil hydrology at the expense of shallow-rooted grasses and forbs (Ansley et al., 1997). The consequences of shrub encroachment are varied and interact across all levels of ecosystem structure and function. If left unmanaged, the effects may be potentially irrevocable (Humphrey, 1958; White, 1979; Mack and D'Antonio, 1998; Lett and Knapp, 2005; Archer, 2009; Liu et al., 2013).

Along the Western Gulf coast of the United States, shrub encroachment is a primary factor causing the degradation of coastal prairie ecosystems (Archer, 1987; Grover and Musick, 1990; United States Geological Survey-National Wetlands Research Center, 2015). Once covering 3.8 million ha, < 0.1% of Gulf coastal prairie currently remains due to land use changes associated with urbanization and agriculture (USGS-NWRCS, 2015; Smeins et al., 1991), and remnant prairies are relegated to small, isolated fragments, which are often degraded due to woody, arborescent shrubs outcompeting and supplanting the prairie's grassy matrix and associated vegetation (Folke et al., 2004; Van Auken, 2009). Gulf coastal prairies are similar to other grassland ecosystems in that they are dominated by C_4 grasses, especially Gulf cordgrass (*Spartina spartinae* (Trin.) Merr. Ex Hitchc.), and have wildfire as their primary natural disturbance (USGS-NWRCS, 2015). Gulf coastal prairies are especially important from an ecological perspective because they support high biodiversity and provide habitat for several threatened and endangered species, including the federally-endangered Attwater's prairie chicken (*Tympanuchus cupido attwater* Bendire). In Texas, where most of these prairies are found (USGS-NWRC, 2015), they also support the aforementioned federally-endangered northern aplomado falcons. Coastal prairies also serve to prevent erosion and regulate hydrology (USGS-NWRCS, 2015; Stambaugh et al. 2014) because the grasses tend to have high belowground root biomass that holds loose soil in place (Van Auken, 2000). Therefore, the conversion of coastal prairies to shrubland could cause numerous ecological changes.

In deep South Texas, shrub encroachment by honey mesquite and huisache (*Acacia farnesiana* (L.) Wight & Arn.) is a major factor influencing Gulf coastal prairies within the Bahía Grande wetland complex, located within the U.S. Fish & Wildlife Service (USFWS) Laguna Atascosa National Wildlife Refuge (LANWR). Prior to purchase by USFWS in 2000, this area experienced an array of anthropogenic activities that likely facilitated the spread and proliferation of shrubs on this site, including anthropogenic wildfire suppression, cattle ranching and changes in hydrology and soil salinity caused by eliminating the area's tidal exchange with the Laguna Madre (Buffington and Herbel, 1965; Archer, 1989;Van Auken, 2000; Liu et al., 2013; Staumbach et al., 2014). Although the exact causes remain unknown, the shift from an open, grassy prairie to a woody shrubland is having detrimental impacts on the aplomado falcon, a species of primary concern for USFWS. Once abundant in this region, this species was extirpated in the 1950's due to a combination of factors, including habitat loss and shrub encroachment (Jenny et al., 2004). In response, the Peregrine Fund introduced 812 individual aplomado falcons in 1993 (Jenny et al., 2004), and the USFWS has initiated several management practices across these prairies in an attempt to curtail the shrub encroachment. Management typically uses a variety of methods, including mechanical (to remove standing woody biomass), herbicide (to prevent woody growth from resprouting), and prescribed fire (to keep woody regrowth in check and mimic the natural disturbance regime). The aforementioned shrub removal methods attempt to reduce the shrub's ability to respond and recover to removal treatments (which are essentially man-made disturbances), while directing the successional trajectory back towards an open, grassy prairie (Holling et al., 1973; Chapin et al., 2002). Walker et al. (2004) defined ecosystem resilience as the capacity of a system to absorb disturbance and reorganize while undergoing change to maintain essentially the same structure and function. While these management approaches have proven successful in other grasslands (Box and White, 1969; Patch et al., 1998; Lett and Knapp, 2005; Rook et al., 2011; Bowles and Jones, 2013), their impacts on shrub mortality and grass recovery have yet to be evaluated in the coastal prairies of South Texas where the climate and flora differ from other inland grasslands.

Even though these prairie rehabilitation techniques address the issues of standing shrub biomass and shrub regrowth, shrub presence on the landscape for extended periods may leave behind legacy effects that hinder grassland recovery even after shrubs are removed. The bare patches in shrub understories created as a consequence shrub establishment can promote invasion by both undesired native species, including new shrubs, and non-native invasive species (Mack and D'Antonio, 1998), and these effects may be most pronounced in areas with greater degrees of shrub encroachment prior to removal. Thus, management practices that seek to promote coastal prairie recovery must evaluate the effectiveness of the shrub removal method in combination with potential legacy effects left behind due to level of shrub encroachment prior to removal.

This study seeks to fill these knowledge gaps by addressing two overarching objectives: (1) characterize the potential effects of shrub canopy cover on understory microclimate and grass cover; and (2) assess the effects of four different combinations of mechanical, herbicide, and prescribed fire shrub removal treatments and degree of shrub encroachment prior to removal on coastal prairie regeneration and growth. Understory light intensity, soil temperature and air temperature were expected to decrease with increasing shrub canopy cover because larger shrub clusters with more canopy cover intercept more light and generate more shade than smaller shrub clusters. In response, there would be less Gulf cordgrass cover underneath large compared to small shrub clusters or areas devoid of any shrub coverage due to the darker and cooler microclimates. It was also hypothesized that areas with less shrub encroachment and subsequently treated with mechanical, herbicide and fire would have would have the fastest recovery rates and abundance of Gulf cordgrass. Small patches left behind by low levels of shrub encroachment inherently have less area and are readily colonized by seed rain from surrounding Gulf cordgrass, while larger patches depend on dispersed propagules from further away to fill in the large area (Barrat-Segretain and Amoros, 1996). Combining all three shrub removal treatments first prepares the area for revegetation by mechanically shredding aboveground woody biomass into mulch, removing woody debris and leaf litter with fire, and killing any shrub resprouts with herbicide. By monitoring conditions in established shrub clusters and measuring the revegetation of an area following shrub removal, this study establishes baseline data that reflect the relationship between shrub cover and grass cover in South Texas coastal prairies and provides information on grassland recovery following shrub removal methods and degree of shrub encroachment prior to removal. This information is essential for determining the most efficient methods for managing and restoring coastal prairies.

CHAPTER II

METHODS

Research was conducted at the USFWS Bahía Grande Unit of the LANWR in South Texas. Located approximately 9 km inland from the Gulf of Mexico, the project area was an 8,600 ha coastal wetland complex acquired by USFWS in 2000. Prior to its acquisition, the land was privately held range land used for cattle grazing (National Oceanic and Atmospheric Administration, 2009). The bays and wetlands in Bahía Grande were cut off from their natural tidal exchange with the Laguna Madre and Gulf of Mexico with the construction of major highways in the area around the 1930's. Consequences for the landscape were devastating as the bays dried up, causing massive fish kills and problematic dust storms and erosion. The tidal exchange was restored with a manmade channel in 2005, with a rapid reappearance of some of the area's estuarine flora and fauna (USFWS-LANWR, 2015).

This area of South Texas has a semi-arid and subtropical climate based on the Koppen climate classification, with a 50-yr average mean annual precipitation of 66 cm, and mean temperatures that have ranged from 16 ^{o}C in winter to 29 ^{o}C in summer (USFWS, 2003). Total precipitation during the study period was 59.7 cm in 2014 and 42.4 cm in 2015, with peaks in September 2014 and May 2015 (Figure 2). The average high temperature was 29.7 ^{o}C, and average low temperature was 18.6 ^{o}C, with an annual precipitation of 70 cm (U.S. Climate Data; Figure 2). The natural vegetation community in the Bahía Grande coastal prairie is comprised a grassy matrix of Gulf cordgrass (*S. spartinae* (Trin.) Merr. Ex Hitchc.) with interspersed low-growing shrubs (e.g., *Borrichia frutescens* (L.) DC., *Prosopis pubescens* Benth.), cacti (e.g., *Opuntia lindheimer* Engelm.) and Spanish dagger (*Yucca treculeana* Carreire). Laredo silty clay loam and Sejita silty clay loam were the predominant soils in the area (USDA-NRCS, 2013).

Shrub impacts on grass cover and microclimate

To test the hypothesis that grass cover is inhibited by increasing shrub canopy cover, these variables were quantified in three non-contiguous, untreated 40 x 40-m plots, with each plot containing varying sizes and numbers of mesquite and huisache clusters. The specific control plots used for this study were chosen because they were the only untreated areas with standing shrubs that remained after all other shrubs had been mechanically removed for this and a previous study (Verderber, 2015). Ten transects separated by 4 m were established within each plot. At 4 m intervals along each of these transects, shrub canopy cover was measured using a convex spherical densiometer, and grass cover was visually estimated using a 0.5-m^2 quadrat, for a total of 110 data points per plot (Figure 3). All measurements were taken in April 2015 when canopy leaves were fully emerged and grass was actively growing.

To test the hypothesis that understory microclimate in shrub clusters differ from that in pure grass cover, small (3 – 4 m diameter), medium (5 – 7 m diameter) and large (> 9 m) shrub clusters were identified within the same three 40 x 40-m plots used above and within a shrub-free grass area of Gulf cordgrass located near (~ 10 m away) each plot. In the center of each of these clusters (found by measuring the longest transect within the cluster from one edge of the cluster's canopy cover to the furthest edge of canopy cover on the opposite side) and grass areas, iButtons (Maxim Integrated, San Jose, California) and HOBO data loggers (Onset Computer Corporation, Bourne, Massachusetts) were installed in May 2014. iButtons were buried 3 cm below the soil's surface to record soil temperature (°C) continuously at 4-hr intervals for 16 mo from May 2014 to August 2015. HOBO data loggers were suspended 45 cm above the iButtons and facing north to record light (lumens per m^2, hereafter lux) and ambient air temperature (°C) at 3-hr intervals continuously over the same 16 mo time period. Data were retrieved from the devices every 4 mo (August 2014, January 2015. April 2015 and August 2015) and downloaded using the logger's software. Suspended at 45 cm, the HOBO data loggers in the Gulf cordgrass control plots eventually came to hang at the grass's understory-open air interface as the Gulf cordgrass grew taller over the course of the project.

Effects of shrub encroachment and removal treatments on vegetation recovery and soil conditions

To test the hypothesis that areas with less shrub encroachment and then subsequently treated with mechanical, fire and herbicide will have the greatest regrowth of herbaceous vegetation – especially Gulf cordgrass – four shrub removal treatments were applied to Bahía Grande's coastal prairies: (1) mechanical only, (2) mechanical and herbicide, (3) mechanical and prescribed fire, and (4) mechanical, prescribed fire and herbicide (Figure 4). Mechanical only treatments were conducted in November 2013 using a Barko 930 Industrial Tractor (Barko Hydraulics, LLC, Superior, Wisconsin) that instantly shreds any aboveground, standing, woody biomass and leaves behind mulched material on the ground. The tractor was driven around different parts of study plots in an approximate back-and-forth, lawnmower fashion. A prescribed fire was conducted in February 2014 according to USFWS policy and prescribed fire plan: air temperatures between 0-37 °C, relative humidity of 30-50%, and wind speed and direction of 6-10 knots out of the northwest. Weather forecasts and on-site weather conditions were evaluated by NOAA-National Weather Service and met the requirements for USFWS ground personnel prior to burning. Fire was ignited using drip torches (3:1 diesel-gasoline mixture) using a backfire (upwind), flanking fire and head fire (downwind). Herbicide treatments were applied in June 2014 and June 2015 using a solution of 20% Remedy Ultra herbicide (Dow AgroSciences, Indianapolis, Indiana) and 80% basal bark oil. Remedy Ultra, or triclopyr, is a systemic, foliar herbicide that kills the target plant by inhibiting metabolic processes. Target plants in this study were resprouts from mesquite and huisache stumps leftover from the mechanical treatment. Herbicide was applied by hand using a backpack sprayer.

In April 2014, three small (< 4 m diameter), medium (4.1 – 7.9 m diameter) and large (> 8 m diameter) bare patches caused by varying levels of shrub encroachment and left behind following shrub removal were identified within each of the four shrub removal treatments. Patch-makers (shrubs responsible for creating the bare patch) were identified to species based on bark texture, thorn arrangement and leaf patterns of resprouts. Basal diameter of each patch-maker was measured using a meter tape and converted to basal area to confirm the relationship between degree of shrub encroachment and bare patch area.

Vegetation recovery within each bare patch following shrub removal and coincident changes in bare patch substrate cover were quantified every 4 mo from April 2014 to August 2015. These parameters were assessed within cross-hair transects within each bare patch, running north to south and east to west, with the intersection of the transects located at the center of the bare patch (Figure 5). Transects were ran ~1.5 m beyond the obvious bare patch center to encompass the bare patch – grass interface, and were categorized as “inside” and “outside” patch areas. Vegetation outside of the bare patch was presumed to have experienced different environmental conditions than vegetation inside the bare patch because vegetation inside the bare patch had previously been underneath the shrub canopy before it was removed; measuring vegetation, substrate and soil parameters outside of the bare patch accounted for potential differences. Beginning at the center of each patch, a metal pin was dropped every 0.5 m along the cross-hair transects. Any vegetation touching the pin was identified to the lowest possible taxonomic level and recorded along with ground surface substrate. Potential substrates included woody debris, leaf litter and mineral soil.

To determine if patch size and shrub removal method influenced soil conditions that could be important for vegetation regrowth (Huxman et al., 2005), soil moisture, conductivity and temperature were quantified at the center of each patch. On each vegetation sampling date, instantaneous measurements of soil moisture and conductivity were measured at the same 0.5-m intervals along the same transect as the vegetation using a ProCheck Sensor Read-Out and Storage System (Decagon Devices, Pullman, Washington). iButtons, buried 3 cm beneath the soil's surface at the center of each patch, were permanently installed to record soil temperature every 4 hrs for 41 wks from September 2014 to August 2015.

Data and statistical analyses

To determine shrub impacts on grass cover, relationships between shrub canopy cover and grass cover and between shrub basal area and bare patch size were explored using a regression approach (SigmaPlot v 12.3; JMP v 12). For the former analysis, data were combined from all three study plots combined (330 points total), and for the latter, total patch-maker basal area was used and summed for each bare patch across all shrub removal treatments versus mean grass cover for that patch. Because the data exhibited somewhat curvilinear trends, the data were first fit with a linear model and then subsequently fit with logarithmic and exponential models to determine if these models generated a better fit based on $R^2$and AIC values. If a curvilinear model improved R^2 value, and produced AIC values > 5 units lower than the linear model, results were presented for the curvilinear model only (Bozdogan, 1987). Otherwise, the more parsimonious linear model was used.

To assess the effects of shrub cluster size and sampling period on understory microclimate (air and soil temperature and light intensity), a two-way ANOVA was used with cluster size, sampling period, and their interaction as fixed effects and plot as a random effect (JMP v 12). Plot was the experimental unit (n = 3). When significant fixed effects were found, a post-hoc Tukey test was performed to determine which treatments differed significantly (P < 0.05) from each other. Normality of the data was checked using a Shapiro-Wilk test and homoscedasticity with Levene's test. No transformations were necessary for this data.

Impacts of shrub cover prior to removal (i.e., bare patch size), shrub removal treatment, and sampling period on understory vegetation cover, soil substrate, soil moisture, and soil temperature were determined using a three-way ANOVA with bare patch size, shrub removal treatment, sampling period and all their interactions as fixed effects (JMP v 12). Bare patch was the experimental unit (n = 3 for each patch size*removal treatment combinations). All data were checked for normality with the Shapiro-Wilk test and homoscedasticity with Levene's test. Vegetation and substrate % cover were all transformed using log+1, and % woody debris data square-root transformed, to better meet these underlying assumptions. A Tukey's post-hoc test was used to determine significant (P < 0.05) differences among treatment effects. Means and standard errors (SE) presented in figures and tables represent untransformed data.

CHAPTER III

RESULTS

Shrub impacts on grass cover and microclimate

As predicted, grass cover declined as shrub cover increased. Gulf cordgrass cover exhibited a significant exponential decrease with increasing shrub canopy cover ($R^2 = 0.26$, $P < 0.0001$; Figure 6). Furthermore, large, medium and small bare patches left behind after shrubs were mechanically removed from the Bahía Grande wetland complex had significantly different abundances of individual shrubs prior to shrub removal, ($P < 0.0001$; Table 1). Large bare patches had more shrubs than medium ($P = 0.04$) and small ($P < 0.0001$) bare patches, with 12 – 40 individuals per large patch. Medium bare patches had significantly different amounts of individual shrubs than large and small ($P < 0.001$) patches, ranging from 14 – 22 individuals per medium patch. Small patches ranged from 1 – 8 individuals. Bare patch area showed a significant linear decrease with increasing shrub basal area ($R^2 = 0.33$, $P < 0.001$, Figure 7). Large bare patches had significantly larger shrubs than small bare patches ($P < 0.001$; Table 1). Bare patches of small, medium and large sizes were also significantly different from each other (all $P < 0.0001$; Table 3).

Cluster size had no significant effect on mean, maximum or minimum soil temperatures; only sampling date significantly impacted these microclimate variables ($P < 0.0001$ for all; Table

2). Mean soil temperatures during spring and summer 2014 and 2015 were significantly higher than those in fall and winter 2014 (P < 0.0001). The lowest recorded mean temperature of 5.6 ^{o}C was in winter 2014, while the highest mean temperature of 37 ^{o}C occurred in summer 2014. Maximum soil temperatures in spring and summer 2014 and 2015 were significantly higher than temperatures recorded in fall and winter 2014 (P < 0.0001 for both comparisons). The lowest maximum temperature of 7 ^{o}C was recorded in winter 2014, while the highest maximum temperature of 61 ^{o}C was recorded in spring 2014. Minimum soil temperatures beneath shrub clusters during spring and summer 2014 and 2015 were significantly higher from temperatures recorded in fall and winter 2014 (P < 0.0001 for both comparisons). The lowest minimum temperature of 4 ^{o}C was recorded in winter 2014, while the highest minimum temperature of 33 ^{o}C was recorded in summer 2014.

Shrub cluster size significantly impacted mean air temperatures, but this effect depended on sampling date (Cluster size*Date; P = 0.02; Table 2; Figure 8). Mean air temperatures beneath small, medium and large shrub cluster canopies were lower than mean air temperatures measured in controls in all sampling dates (P < 0.0001 for all comparisons), but mean temperature rarely differed between shrub cluster sizes within the same sampling date. The lowest mean air temperature of 3.9 ^{o}C was recorded in a large shrub cluster in winter 2014, while the highest mean air temperature of 35.5 ^{o}C was recorded in a medium shrub cluster in summer 2015.

Maximum understory ambient air temperatures were significantly affected by the interaction of shrub cluster size and sampling date (Cluster size*Date; P < 0.0001; Table 2; Figure 9). Maximum air temperatures beneath small, medium and large shrub cluster canopies were significantly higher than maximum air temperatures measured in controls in all sampling dates (P < 0.0001 for all comparisons), but maximum temperature rarely differed between shrub cluster sizes within the same sampling date. Differences in maximum air temperatures between shrub cluster sizes ranged from 5.3 ^{o}C in small shrub clusters in winter 2014 to 50.5 ^{o}C in control plots during summer 2015 (Figure 9). Large shrub clusters had the coolest maximum air temperatures in 5 out of 6 sampling dates, with the exception found in fall 2014 (Figure 9). Control plots in pure cordgrass cover had the warmest maximum temperatures in 5 out of 6 sampling dates, the exception being winter 2014 (Figure 9).

Minimum understory ambient air temperatures were significantly different by cluster size (P < 0.0001) and sampling date (P < 0.0001; Table 2). Minimum air temperatures in control plots were significantly cooler than minimum air temperatures in large (P < 0.0001), medium (P = 0.006) and small (P = 0.003) shrub clusters. Minimum air temperatures were significantly different between all seasons (P < 0.0001) except summer 2014 and 2015 (P = 1). Minimum air temperatures were as low as -1.7 ^{o}C in control plots in winter 2014 and as high as 27.5 ^{o}C in large plots in summer 2015.

Mean and maximum light intensity (lux) were significantly different between cluster sizes during different sampling dates (Cluster size*Date; P < 0.001; Table 2; Figure 10). Mean and maximum light intensity were significantly lower in large clusters (P < 0.0001) compared to controls in all sampling dates. Mean and maximum light intensity were significantly less in small shrub clusters (P < 0.0001; Figure 10) compared to controls in all sampling dates except winter 2014 (P = 1) and summer 2015 (P = 0.21). Medium shrub clusters had significantly more light than small and large clusters in summer 2015 (P < 0.0001 for both comparisons). Minimum light in all categories was 0 for measurements recorded at night.

Effects of shrub encroachment and removal on vegetation recovery and soil conditions

As Gulf cordgrass recolonized the bare patches over the course of the study, there were significant differences in cordgrass abundance (Table 3) between patch sizes ($P < 0.0001$), treatments ($P < 0.0001$) and sampling dates ($P < 0.0001$). Small patches had significantly higher percentages of Gulf cordgrass than medium ($P = 0.009$) and large ($P < 0.0001$) patches. Patches treated with fire had significantly higher percentages of Gulf cordgrass than patches treated only mechanically ($P < 0.0001$) and with mechanical+herbicide ($P < 0.001$). Furthermore, patches treated with fire had approximately 100% Gulf cordgrass abundance after 16 mo, whereas patches without fire treatments had Gulf cordgrass abundances as low as 50% in mechanical and herbicide plots and 66% in mechanical only plots (Figure 11). There were no significant differences in Gulf cordgrass recovery rates between treatments or patch sizes at 1 yr or 1.25 yr (Table 4).

Mesquite and huisache abundances were significantly affected my treatment, but only during certain sampling dates (Treatment*Date, P <0.0001; Table 3). Patches treated with mechanical, fire and herbicide had significantly less mesquite and huisache than patches treated only mechanically in fall 2014 ($P = 0.01$) and spring 2015 ($P = 0.03$). At the end of the 16 mo sampling period in summer 2015, patches treated with mechanical+ herbicide had significantly less mesquite and huisache shrubs compared to patches treated only mechanically ($P = 0.01$) and with mechanical+fire ($P = 0.001$; Figure 12). At the first sampling date in April 2014, the highest shrub abundance was found in small patches treated with mechanical+herbicide at 20%; all other patches had < 10% or 0% shrub abundance at the first sampling. However, patches treated with mechanical+herbicide yielded 0% shrub abundance after 16 mo, and mechanical+fire+herbicide patches yielded <7% shrub abundance after 16 mo. Mechanical only patches had shrub abundances as high as 35% after 16 mo in summer 2015. Patches treated with mechanical+fire+herbicide had significantly lower shrub abundance after 16 mo than patches treated with mechanical+fire ($P = 0.03$). Over the course of the study, patches treated with herbicide had at least 6% less mesquite and huisache and at most 35% less mesquite and huisache than patches not treated with herbicide.

Invasive grass abundance was significantly different by treatment ($P = 0.02$; Table 4), where patches treated with mechanical+fire+herbicide had significantly more invasive grass than did other treatments ($P = 0.03$). A single medium-sized patch in the mechanical+fire+treatment area accounts for most of the invasive grass encountered during the study, where invasive grass % abundance in this patch was 38% at the final sampling in August 2015 (Figure 13).

Woody debris soil substrates were significantly affected by patch size in certain treatments (Patch size*Treatment, $P < 0.0001$; Table 5). At the beginning of the study in spring 2014, small, medium and large patches treated with fire had significantly less woody debris substrate than large mechanical only patches ($P < 0.0001$) and medium and large mechanical+herbicide patches ($P < 0.0001$ for all comparisons). At the end of the study, all patch sizes treated with fire had significantly less woody debris than mechanical only patches ($P < 0.0001$ for all comparisons) and mechanical+herbicide patches ($P < 0.0001$ for all comparisons). Patches treated with fire had at most 26% woody debris substrate (large mechanical+fire), whereas patches treated without fire had woody debris substrate percentages as high as 84% (large mechanical+herbicide) (Figure 14). At the end of the study in summer 2015, patches treated with fire had a woody debris substrate percentages ranging from 0% (small mechanical+fire) to 11% (small mechanical+fire+herbicide), while patches without fire ranged from 32% (small mechanical+herbicide) to 57% (large mechanical) (Figure 14).

Leaf litter ($P < 0.0001$) and mineral soil ($P < 0.001$) substrates were both significantly impacted by the interaction of treatment and sampling date (Treatment*Date; Table 6). Leaf litter in patches treated with prescribed fire was significantly lower than in patches without fire in spring 2015 ($P < 0.0001$) and summer 2015 ($P < 0.0001$). Leaf litter abundance was also impacted by the interaction of patch size and sampling date (Patch size*Treatment, $P = 0.007$; Table 6), where large patches treated with fire had significantly less leaf litter than large patches treated without fire ($P < 0.0001$), and large and medium mechanical and mechanical+herbicide patches had significantly less leaf litter than small patches in all treatments ($P < 0.0001$). Leaf litter abundance was as high as 100% in small patches with mechanical+fire+herbicide treatments in spring 2015 and summer 2015, and < 50% in large patches with mechanical and mechanical+herbicide treatments during the same sampling dates. Fire treatments also had significantly more mineral soil in spring 2014 than in all other treatments in all other sampling dates ($P < 0.0001$). Mineral soil abundance in patches treated with fire was as high as 79% in spring 2014, while 46% was the highest abundance of mineral soil in patches treated without fire in spring 2014.

Soil moisture and soil conductivity measured in all bare patches were significantly affected by the interaction of treatment and sampling date (Treatment*Date, $P < 0.0001$; Table 6), with most treatments differing significantly from one another as moisture steadily increased each sampling after spring 2014 ($P < 0.0001$; Figure 15). Patches treated with fire had significantly wetter ($P < 0.0001$) soils with higher conductivity than patches treated without fire

($P < 0.0001$ for all comparisons). Likewise, soil conductivity varied significantly by treatment ($P < 0.0001$; Table 6) for all sampling dates after the first in spring 2014 (Figure 16).

Mean soil temperatures measured in each patch size in each treatment were significantly affected by the interaction of treatments and sampling dates (Treatment*Date, $P = 0.008$; Table 7), where temperatures were significantly different by treatments ($P < 0.0001$) as sampling dates progressed. Mean soil temperatures were as high as 35.1 ^{o}C in mechanical+fire patches in fall 2014, and as low as 5.8 ^{o}C in mechanical+fire plots during winter 2014 (Figure 17). Maximum soil temperatures in all plots were significantly affected by the interaction of patch size, treatment and sampling date (Patch size*Treatment*Date, $P < 0.0001$; Table 7). Small patches treated with only mechanical shrub removal methods patches were significantly different from other patches and treatments in winter 2014, fall 2014 and spring 2015 ($P < 0.0001$), and small, mechanical+herbicide patches were significantly different from other patch sizes and treatments in winter 2014, spring 2015 and summer 2015. The highest maximum soil temperatures in patches treated without fire were 26.5 ^{o}C in winter 2014, and 31 ^{o}C in patches treated with fire during the same sampling date (Figure 18). The highest maximum soil temperature recorded in spring 2015 in patches treated without fire was 54 ^{o}C, while 34.5 ^{o}C was the highest recorded maximum temperature in patches treated with fire in the same sampling date (Figure 18).

CHAPTER IV

DISCUSSION

Land use changes, including urbanization and agriculture, have reduced Gulf coastal prairies to < 1% of their original extent (USGS-NWRCS, 2015; Smeins et al. 1991). The small fragments of coastal prairie that remain have been subjected to intense cattle grazing, fire suppression and, hydrologic modifications, leading to a fundamental shift from open prairie to mesquite and huisache shrubland with potentially irrevocable changes in ecosystem structure and function (Humphrey, 1958; White, 1979; Mack and D'Antonio, 1998; Lett and Knapp, 2005; Archer, 2009; Liu et al., 2013). Examining the effects of shrub encroachment and shrub removal addresses critical gaps in our understanding of this important ecosystem.

As hypothesized, increased shrub encroachment led to decreased cover of native grasses and increased bare area. Shrubs in coastal prairies creates a positive feedback in which shrubs tend to restrict grass growth but promote the growth of new shrubs (Schlesinger et al., 1990; Archer et al. 1995; Barnes and Archer, 1996), and the size of bare area around shrubs has been shown to be proportional in size to the size of the shrub itself (Buffington and Herbel, 1965). Overtime, individuals or small clusters of shrubs coalesce to form dense clusters that can protect shrubs inside of the cluster from fire, providing another positive feedback that facilitates shrub encroachment (Briggs et al. 2005).

Large shrub clusters tended to moderate microclimate (i.e., reduce temperatures and light) more so than open grassy areas, especially during summer; however, small shrub cluster had no effect on microclimate, and medium shrub clusters often accentuated microclimate. The lack of Gulf cordgrass beneath shrub canopies is potentially a consequence of altered microclimates in shrub understories. This study showed that shrubs alter their understory microclimates as they grow and coalesce, possibly creating an inhospitable environment with less light for coastal prairie flora such as Gulf cordgrass beneath the shrub's canopy while simultaneously promoting the recruitment and growth of more shrubs (Schlesinger et al., 1990; Archer et al. 1995; Barnes and Archer, 1996). This cycle creates a feedback cycle in which shrubs beget more shrubs.

As expected, bare patches left behind by shrubs following shrub removal and then subsequently treated with three successive treatments (mechanical – fire – herbicide) exhibited the fastest rates of Gulf cordgrass recovery. In these areas, Gulf cordgrass cover was nearly 100% after 16 mo. Grass recovery was also notably slower in patches without fire than with treatments including fire. The region in which Bahía Grande is located in South Texas historically had a wildfire at least once every 5 yr (Stambaugh et al., 2014), suggesting that natural coastal prairie flora such as Gulf cordgrass is ecologically dependent on wildfire to the point that fire has a regenerative effect on the herbaceous vegetation (Box and White, 1969).

While the removal of fire is at least partially responsible for the establishment of mesquite and huisache in South Texas coastal prairies (Box et al., 1967), the use of fire alone is no longer a viable option for halting shrub encroachment (Briggs et al., 2005). After decades of anthropogenic fire suppression, the mesquite and husiache have grown substantially and coalesced into clusters, allowing the shrubs to withstand a fire by virtue of their size and by forming a protective barrier against fire for shrubs inside the cluster (Briggs et al., 2005). Fire, then, is no longer able to fully eradicate shrubs (Briggs et al., 2005), and mechanical treatments are necessary (Box and White, 1969) to effectively remove the established, aboveground woody biomass and increase its surface area via mechanical shredding. Box and White (1969) found that while burning reduced shrub cover when compared to unburned controls plots, a mechanical pretreatment followed by a fire was more effective in reducing shrub cover and increasing herbaceous vegetation.

Mechanical treatments, however, leave behind a layer of woody debris on the ground that obstructs grass seed germination and growth. Mechanical treatments also leave belowground meristematic tissues untouched (Patch et al., 1998), allowing mesquite and huisache shrubs to resprout (Briggs et al., 2005). Thus, fire following mechanical treatment incinerates woody debris and leaf litter that could otherwise create an impediment for grass regeneration and germination (Knapp and Seastedt, 1986) and kills ground-level buds, minimizing resprouting. Herbicide following mechanical and fire treatments then affords long-term shrub removal and control by accounting for shrub resprouts that emerge from underground meristems. Patch et al. (1998) found that patches treated with triclopyr had the greatest mean reduction in shrub resprouts compared to other resprout control methods such as light occlusion. Rook et al. (2011) found that using herbicide after a fire led to lower abundances of exotic, invasive species and higher abundance of native species. Therefore, herbicide in addition to mechanical and fire is necessary for effective shrub removal. After an initial treatment with all three methods, restoring periodic fire to the system at an interval that mimics the natural fire regime is likely the best way to keep shrub encroachment in check. A prescribed burn program that mimics the area's historic fire return interval holds woody and invasive species in check, removes detritus, revitalizes natural prairie flora growth, increases biodiversity and potentially reduces the dependence on mechanical and chemical means of management (Bowles and Jones, 2013).

The study area received an unusually high amount of precipitation in spring 2014, causing extremely wet conditions with several centimeters of standing water during the sampling date. The copious amount of water could have had a profound impact on the abundance of the vegetation monitored during the study as precipitation, moisture and evaporation are reliable predictors of total above ground net primary production (Briggs and Knapp, 1995; Briggs and Knapp, 2000). As a result, the flora abundances presented in this study may be markedly higher than similar studies conducted in similar arid environments, or the same study conducted in a different year. Furthermore, the extreme variability between dry and wet conditions encountered in the study area brings the ecological significance of the soil moisture and soil conductivity measurements into question. Caution should be taken when reading the soil moisture measurements in this study, as the measurements were instantaneous and highly correlated to the amount of precipitation in the study area around the time of sampling. Soil conductivity measurements, in turn, were highly correlated to soil moisture measurements because conductivity as measured with the Pro-check device used in this study is an instantaneous measurement of mobile ions in the soil; more water moving through the soil mobilizes more ions. Therefore, the timing of soil samplings with the highly variable weather conditions during samplings could be considered confounding factors for this part of the study.

Guineagrass (*Megathyrsus maximus* (Jacq.) R. Webster) is a non-native invasive (Everitt et al., 2011) that was found occasionally in this study. However, any occurrence of guineagrass may be due to its establishment prior to the study, as the plant did not appear to spread during the course of sampling. The fact that this plant did not spread and other invasive species were not found in this area of Bahía Grande is likely due, in part, to the competitiveness of the native coastal prairie flora, namely Gulf cordgrass, which has been shown in this study to recovery quickly and fully, leaving little time and space for invasive plant species to become established. The salinity of soil in Bahía Grande may also mitigate invasion of less saline-tolerant non-native grasses such as guineagrass (Vasquez et al., 2006). The bare patches in this study, which would be more susceptible to invasion, did not see any new invasive plants because the bare patch was surrounded by thick Gulf cordgrass that easily disperses its seeds into the adjacent bare patches (Kotanen, 1997). Furthermore, the soils in Bahía Grande were relatively undisturbed, and USFWS takes measures to prevent invasive species threats such as spot-spraying herbicide and regularly washing vehicles that drive through the area. The relatively pristine state of Bahía Grande underscores the importance of controlling the spread of mesquite and husiache in the coastal prairie.

If Bahía Grande is used as a biogeographical case study determining that mesquite and huisache are likely to cause economic or environmental harm (U.S. Department of Agriculture-National Invasive Species Information Center, 2015), then the shrubs should be classified as "invasive" (Colautti and MacIsaac, 2004) despite the fact that they are native to South Texas. Common definitions limit the invasive denomination to non-native species (Van Auken, 2009; NOAA, 2014), yet this study has shown that without proper management, native species (i.e., mesquite and huisache) can overrun a landscape with potentially irreversible changes to the ecosystem. Similar cases of woody plant encroachment into grasslands involve other native plants species in the western U.S., such as Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), pinyons (*Pinus* spp.) and junipers (*Juniperus* spp.), which are encroaching and dominating landscapes that were once grasslands (Van Auken, 2000; Lett and Knapp, 2005). The problem is perhaps more pressing in South Texas because mesquite has been found to have one of the highest rates of encroachment across the western United States compared to other species of woody encroachers (Barger, 2011). As awareness of the problem increases, the importance of using the “invasive” label despite the plant’s native status could trigger a more immediate response from the general public. If it becomes common knowledge that these native plant species can become invasive without proper management, then there exist grounds on which to build public support for addressing the problem of woody shrub encroachment.

Yet, woody plant encroachment into grasslands is hardly a problem confined to the western U.S. Cases are being observed and recorded worldwide, including Africa, Asia, Australia and South America (Archer, 1989; Archer et al., 1998; Van Auken, 2009). The shift from open grasslands to woody shrublands in these bioregions only emphasizes the urgent need to address this issue as ecologically and economically valuable grasslands continue to disappear. The documentation of mesquite and huisache encroachment into the coastal prairie in this study is a small but important step in understanding the mechanisms that lead to landscape degradation occurring around the world.

This study has shown that the synergistic effects of integrating mechanical, prescribed fire and herbicide techniques for shrub removal leads to faster Gulf cordgrass recovery rates, improved shrub control and, therefore, a more efficient coastal prairie management plan in which the long-term ecological benefits could outweigh initial overhead monetary costs (Verderber 2015). Approaches to ecosystem restoration and management must adapt to a dynamic global environment in which humans and nature are intimately entwined and susceptible to the influences of the other. While the shrub removal and coastal prairie restoration scenario examined in this project may not completely solve the problem of shrub encroachment, it provides a baseline with which to adapt future management strategies as more information becomes available.

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TABLES

Table 1: Average bare patch area (±SE) and patch-maker abundance and size (±SE) by shrub removal treatment and bare patch size category within the Bahía Grande wetland complex in South Texas. Shrub removal treatments were mechanical (M), prescribed fire (F) and herbicide (H). Letters next to numbers indicate significant differences across patch sizes within a treatment.

	M			MH			MF			MFH		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Mean patch area (m^2)	8.1 A	24 B	109.8 C	8.4 A	34 B	85.1 C	8.9 A	28.1 B	100.4 C	9 A	32.4 B	78 C
	(0.1)	(0.3)	(4)	(0.4)	(2.1)	(4)	(1)	(3.6)	(2.5)	(0.7)	(1.7)	(0.5)
Patch-maker abundance (#)	3 A	15 B	28 C	5 A	22 B	12 C	5 A	4 B	40 C	8 A	18 B	25 C
	(1)	(1)	(0)	(0.7)	(0.9)	(0.6)	(0.7)	(0.6)	(3.5)	(0.7)	(0.9)	(0.6)
Patch-maker basal area (cm^2)	1.8 A	2.6 B	10 B	4.9 A	23.2 B	29.9 B	2.6 A	7.8 B	21.1 B	4.1 A	10.8 B	20.2 B
	(1)	(0.2)	(0.8)	(0.6)	(3.4)	(5.2)	(0.3)	(0.5)	(0.5)	(0.5)	(0.5)	(0.6)

Table 2: Two-way analysis of variance (ANOVA) for shrub cluster size and sampling date on mean, maximum and minimum air temperature (ºC), mean and maximum light (lux), and mean, maximum and minimum soil temperature (ºC) measured in shrub understories and control plots in Gulf cordgrass in the Bahía Grande wetland complex in South Texas. Statistics include degrees of freedom (df), F-ratio and *P*-values for measurements taken over 16 mo, from May 2014 to August 2015.

		Mean air temp		Max air temp		Min air temp		Mean light		Max light		Mean soil temp		Max soil temp		Min Soil temp	
	df	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Cluster size	3	16.4	***	144.3	***	9.6	***	4.44	0.06	3.69	0.08	0.4	0.76	0.22	0.88	0.62	0.63
Date	5	1686.8	***	905.5	***	1230.1	***	12.86	**	6.11	*	274.15	***	127.6	***	253.5	***
Cluster size*Date	15	1.9	**0.02**	6.5	***	1.2	0.26	27.83	*	2.21	**0.03**	0.34	0.98	0.91	0.57	0.46	0.94

***** $P < 0.01$
****** $P < 0.001$
******* $P < 0.0001$

Table 3: Three-way analysis of variance (ANOVA) results for plant functional group % cover and bare ground % cover in small, medium and large patches (Patch size) treated with four different combinations of mechanical, prescribed fire and herbicide shrub removal methods (Treatment) sampled every 4 months from April 2014 to August 2015 (Date) in the Bahía Grande coastal prairie in South Texas. Statistics including degrees of freedom (df), F-ratio and *P*-value for functional groups and bare ground. Significant results indicated in bold and/or with asterisks.

		Gulf cordgrass		Mesquite/ huisache		Forb/ shrub		Invasive grass		Bare	
	df	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Patch size	2	10.6	***	0.6	0.54	3.8	**0.03**	1.7	0.19	8.1	**
Treatment	3	20.8	***	21.7	***	28.7	***	3.3	**0.02**	4.9	*
Date	4	48	***	8.3	***	12.6	***	0.8	0.51	64.7	***
Patch size*Treatment	6	2.1	0.06	0.5	0.78	0.4	0.89	1.7	0.13	1.4	0.23
Patch size*Date	8	1.3	0.25	0.6	0.74	0.2	0.99	0.4	0.94	0.7	0.71
Treatment*Date	12	1.6	0.12	3.6	**	1.9	**0.04**	0.6	0.88	1.9	**0.04**
Patch size*Treatment*Date	24	0.2	1	0.6	0.9	0.4	0.99	0.3	0.1	0.4	1

***** $P < 0.01$
****** $P < 0.001$
******* $P < 0.0001$

Table 4: Gulf cordgrass recovery rates (% month^{-1} (±SE)) by patch size (small, medium and large) and combinations of shrub removal treatments (mechanical, prescribed fire and herbicide) 1 year after treatment applications and 16 months after treatment applications in the Bahía Grande wetland complex in South Texas. There were no significant differences between patch sizes or treatments, and 1 yr. Gulf cordgrass recovery rate in mechanical patches is n=1 because of flooding during sampling .

	Mechanical			Mechanical +Herbicide			Mechanical +Fire			Mechanical +Fire +Herbicide		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
1 yr. Gulf cordgrass recovery rate	1.28 -	2.5 -	3.96 -	3.56 (1.12)	3.55 (1.44)	2.66 (1.16)	5.42 (1.24)	5.19 (0.19)	5.75 (0.80)	5.19 (0.83)	5.46 (0.70)	6.32 (0.38)
1.25 yr. Gulf cordgrass recovery rate	2.99 (1.54)	2.38 (0.92)	3.25 (0.83)	3.4 (0.76)	2.83 (0.94)	2.54 (0.61)	3.97 (0.31)	4.58 (0.10)	4.54 (0.58)	3.9 (0.62)	4.25 (0.41)	5.1 (0.27)

Table 5: Three-way analysis of variance (ANOVA) results for soil substrates in small, medium and large patches (Patch size) treated with combinations of mechanical, prescribed fire and herbicide shrub removal treatments (Treatment) sampled every four months from April 2014 to August 2015 (Date) in the Bahía Grande wetland complex in South Texas. Statistics including degrees of freedom (df), F-ratio and *P*-value. Significant results are bold or indicated with asterisks.

		Woody debris		Leaf litter		Mineral soil	
	df	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Patch size	2	24.4	***	29.7	***	8.5	**
Treatment	3	141.1	***	25.3	***	36.7	***
Date	4	2.9	**0.03**	30.8	***	35.8	***
Patch size*Treatment	6	8.7	***	3.2	*	1.5	0.2
Patch size*Date	8	2	0.06	1.3	0.26	0.3	0.96
Treatment*Date	12	1.3	0.23	4	***	3.2	**
Patch size*Treatment*Date	24	1	0.51	0.7	0.86	0.8	0.76

* $P < 0.01$
** $P < 0.001$
*** $P < 0.0001$

Table 6: Three-way analysis of variance (ANOVA) results including degrees of freedom (df), F-ratio and *P*-value for soil moisture (m^3/m^3), conductivity (dS/m) and soil temperature (ºC) by patch size (small, medium and large), treatment (4 different combinations of mechanical, prescribed fire and herbicide shrub removal methods) sampled every fourth months from April 2014 to August 2015 (Date) in the Bahía Grande wetland complex in South Texas. Significant differences are indicated with asterisks.

		Soil moisture		Soil conductivity		Mean temp.		Max temp.		Min temp.	
	df	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Patch size	2	0.8	0.48	0.5	0.6	0.7	0.5	122.8	***	4.8	*
Treatment	3	25.7	***	17.8	***	6	**	33.2	***	1.5	0.23
Date	3	453.4	***	279.4	***	1806.9	***	1099	***	1686.5	***
Patch size*Treatment	6	0.1	1	0.8	0.59	1.6	0.14	17.5	***	4.4	**
Patch size*Date	6	0.5	0.78	0.9	0.53	0.2	0.97	24.3	***	0.7	0.69
Treatment*Date	9	10.3	***	16	***	2.5	*	57.7	***	4.7	***
Patch size*Treatment*Date	18	0.2	1	0.7	0.84	0.6	0.88	12.4	***	0.7	0.8

* $P < 0.01$
** $P < 0.001$
*** $P < 0.0001$

FIGURES

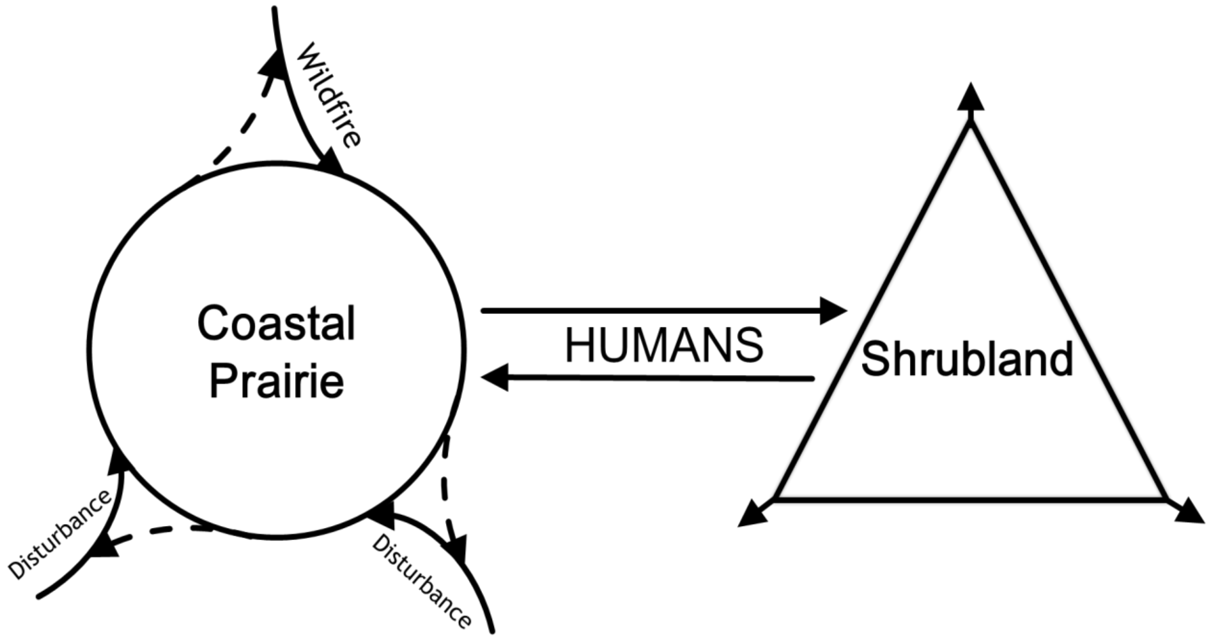

Figure 1: Conceptual model in which wildfire and other disturbances maintain feedback cycles that exclude woody shrubs from encroaching onto coastal prairies. Anthropogenic pressures, including wildfire suppression, remove these necessary disturbances and cause a shift to a self-reinforcing shrubland comprised of mesquite and huisache. Anthropogenic input in the form of prairie rehabilitation and restoration may be necessary to force the system back to a coastal prairie.

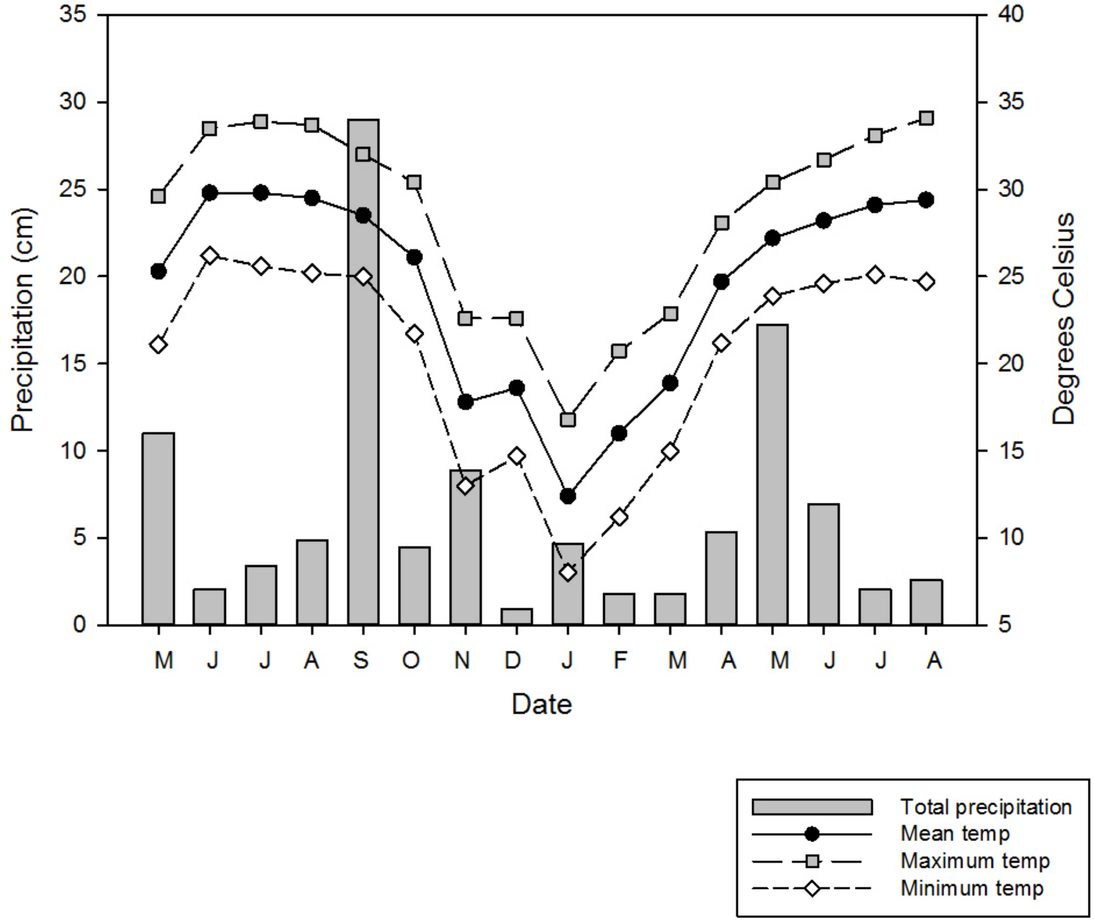

Figure 2: Climate data from Port Isabel, Cameron County Airport, TX (26.16583°, -97.34583°) located 9 km north of the Bahía Grande wetland complex in South Texas. Total precipitation (cm) from May 2014 to August 2015 is shown with bars, and mean, maximum and minimum temperatures (^{o}C) are shown with lines.

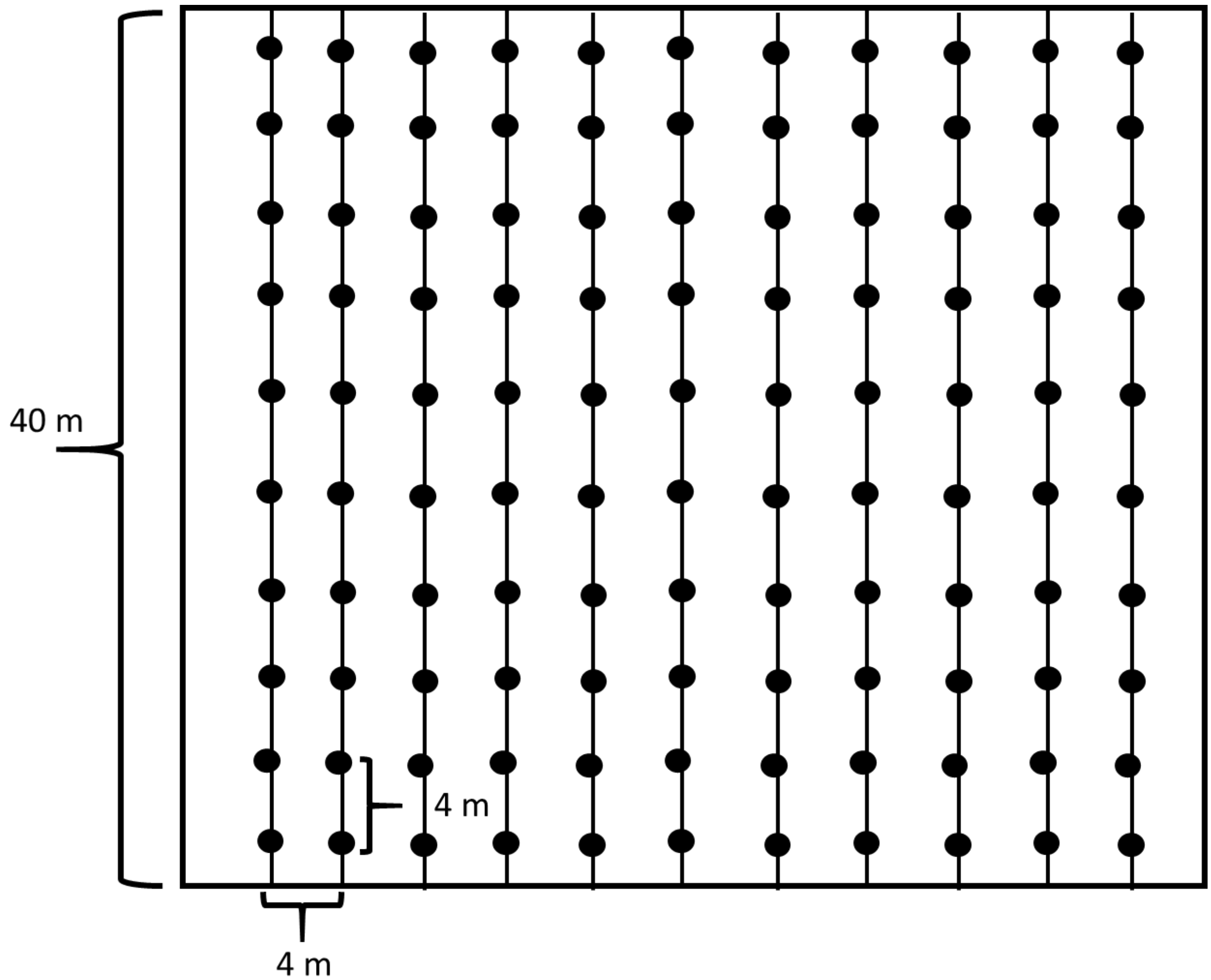

Figure 3: Schematic of sampling design for measuring Gulf cordgrass abundance and canopy cover in three 40 x 40 m plots in the Bahía Grande wetland complex in South Texas. Each plot had ten transects that were spaced 4 m apart. Gulf cordgrass % cover was recorded using a $0.5m^2$ quadrat and % canopy cover was measured using a densiometer every 4 m along each transect.

Figure 4: A map of study area in the Bahía Grande wetland complex in South Texas showing the four different treatments and treatment areas used for the project. Mechanical (M) treatments were applied in November 2013, prescribed fire (F) treatments were applied in February 2014 herbicide (H) was applied in June 2014 and June 2015. The three smaller, hollow squares represent the location of the three 40 x 40 m plots used for measuring understory Gulf cordgrass cover, shrub canopy cover and understory microclimates.

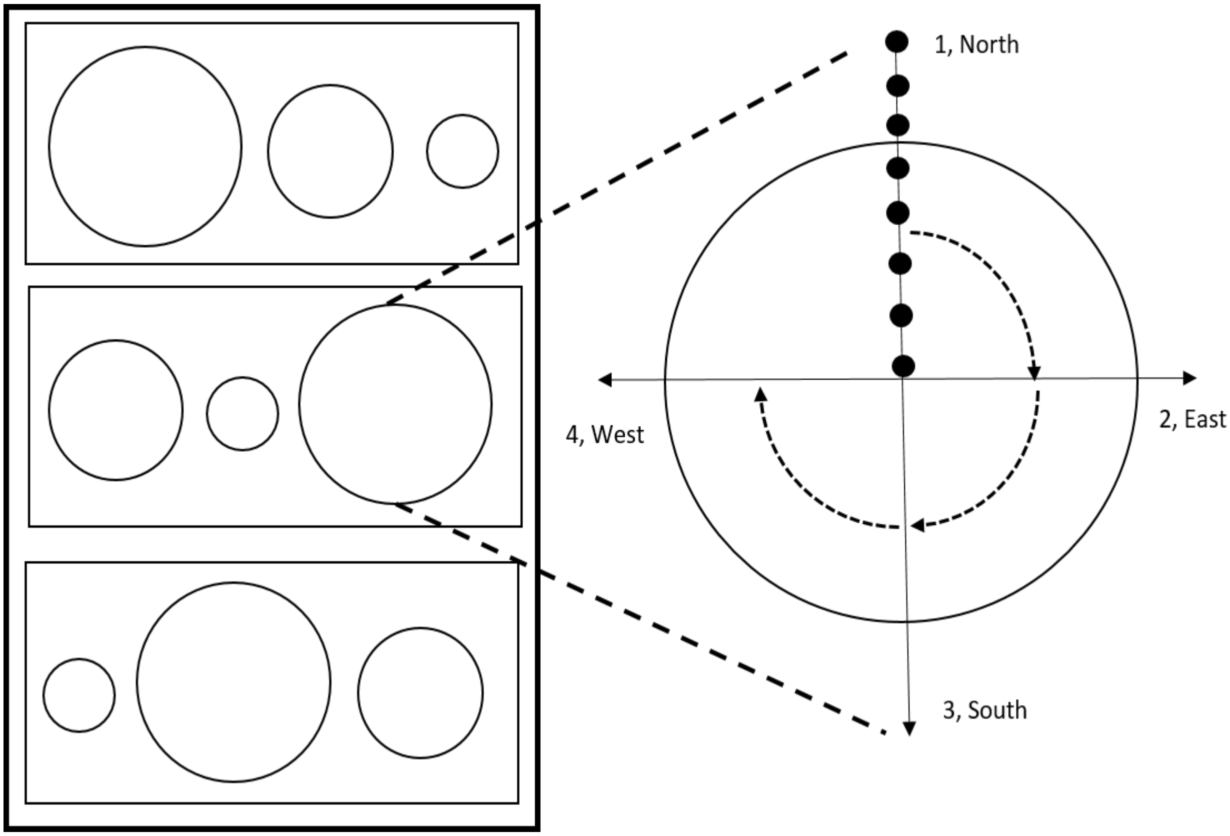

Figure 5: Schematic of sampling protocol for bare patches in the Bahía Grande wetland complex in South Texas. Small, medium and large bare patches identified and replicated 3 times (n = 3) in 4 different treatment areas using mechanical, prescribed fire and herbicide shrub removal methods singly or in combination. Cross-hair transects were laid out running north to south and east to west in each bare patch with a metal pin dropped ever 0.5 m along each transect and with vegetation and soil substrate touching the pin recorded every four months from April 2014 to August 2015. Soil moisture and conductivity were also instantaneously measured at the same 0.5 m intervals, and an iButton was buried at the center of each patch to record soil temperature every 4 hours from September 2014 to August 2015.

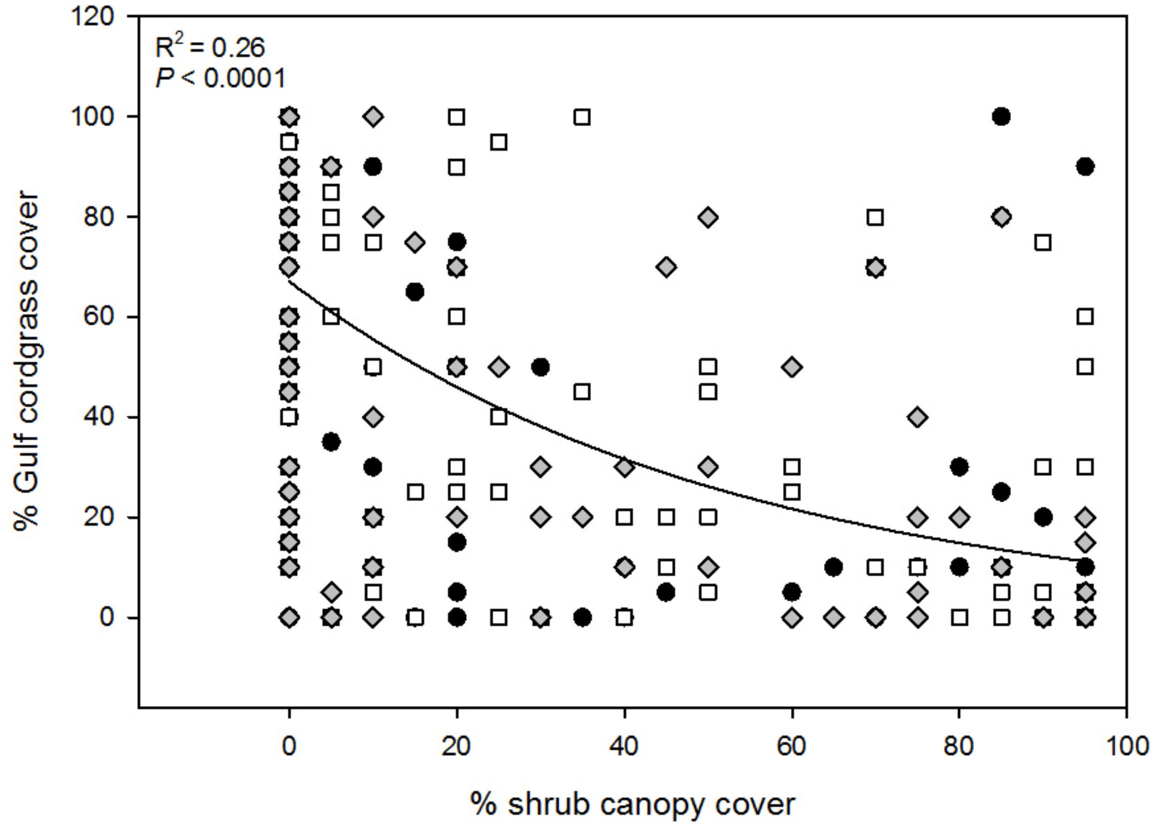

Figure 6: Gulf cordgrass percent cover in response to increasing shrub canopy cover measured in three 40 x 40 m plots within the Bahía Grande wetland complex in South Texas. Gulf cordgrass and shrub canopy cover were measured at 110 points in each of the three plots (data points from different plots are identified with different symbols) with varying degrees of shrub encroachment.

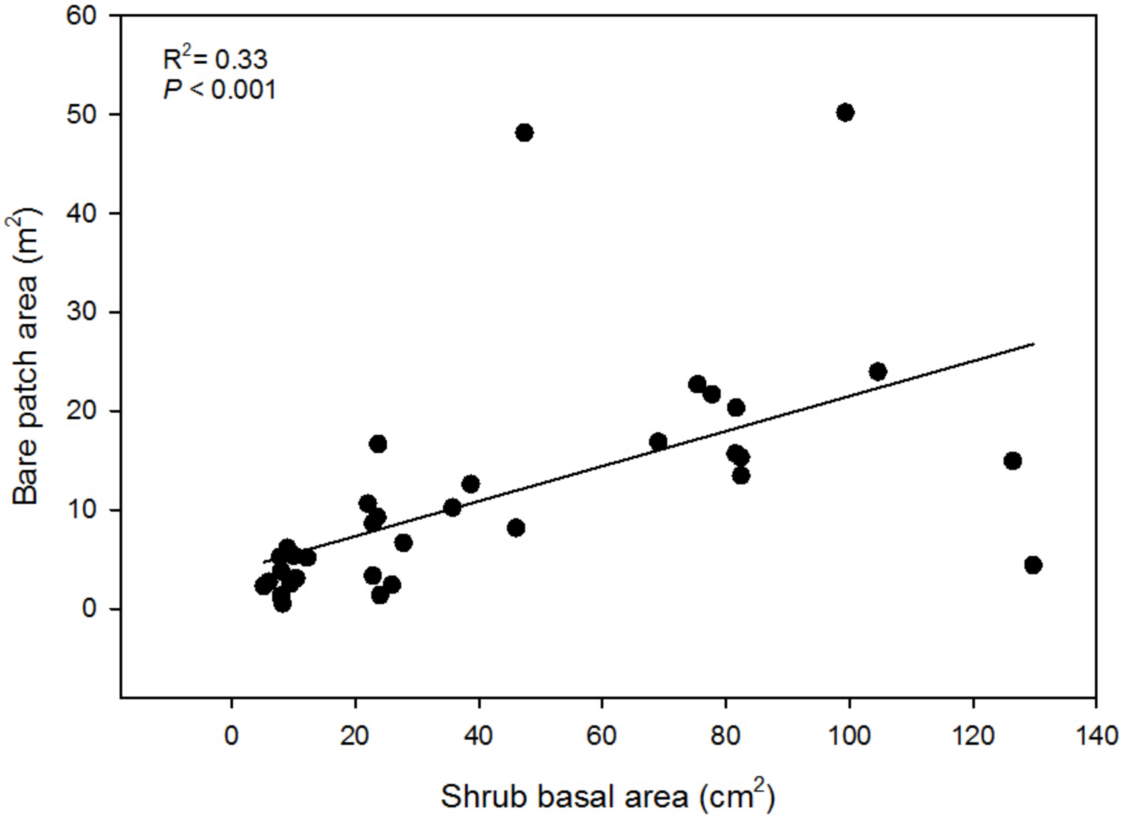

Figure 7: Bare patch area in response to increasing shrub basal areas as measured in April 2014 in bare patches treated with mechanical, prescribed fire and herbicide shrub removal methods singly or in combination in the Bahía Grande Coastal wetland complex in South Texas.

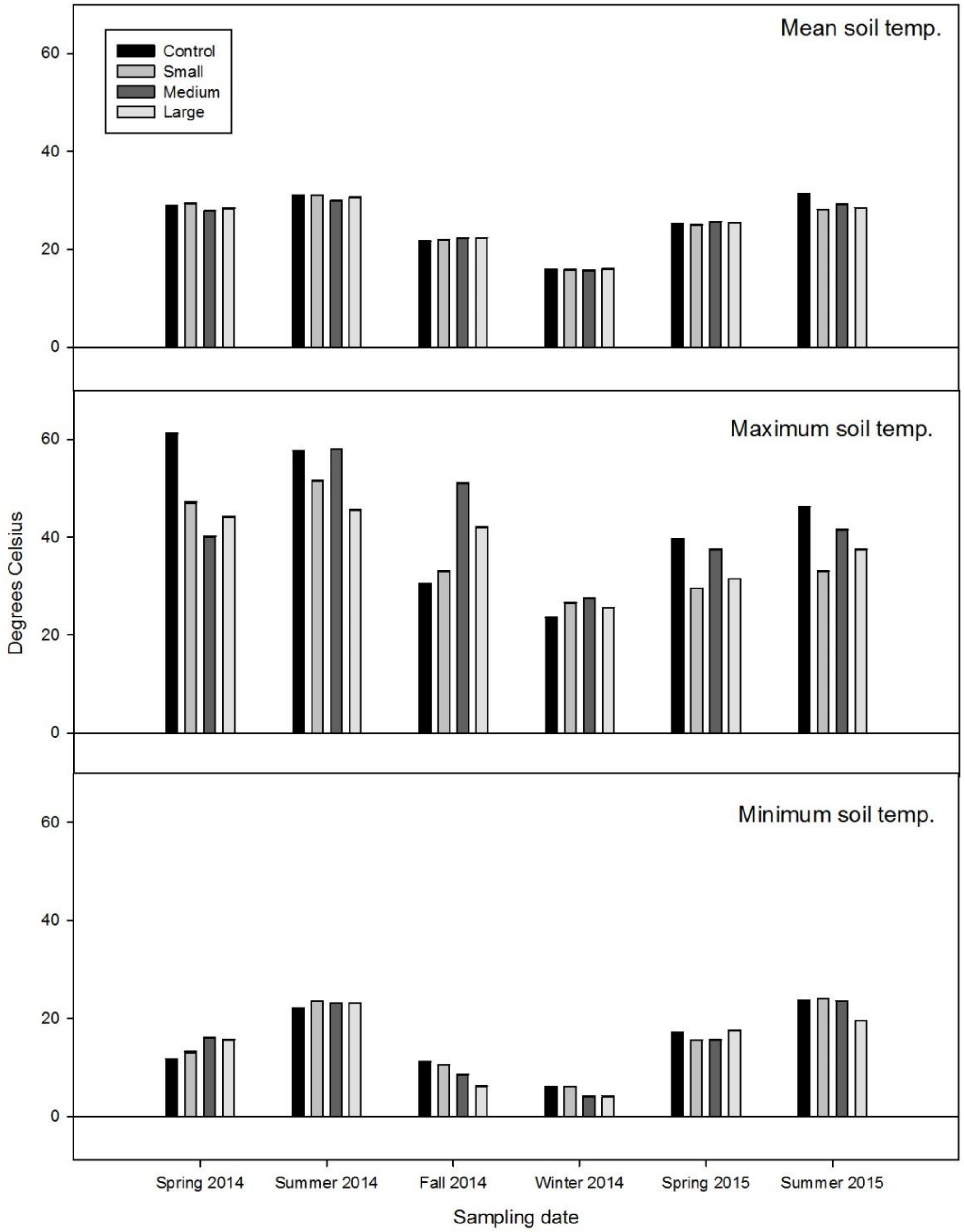

Figure 8: Soil temperature (^{o}C ±SE) measured beneath small, medium and large shrub cluster canopies and controls in pure Gulf cordgrass cover every 4 hrs for 16 mo, from May 2014 to August 2015 in the Bahía Grande wetland complex in South Texas. No significant differences were found among clusters of different sizes.

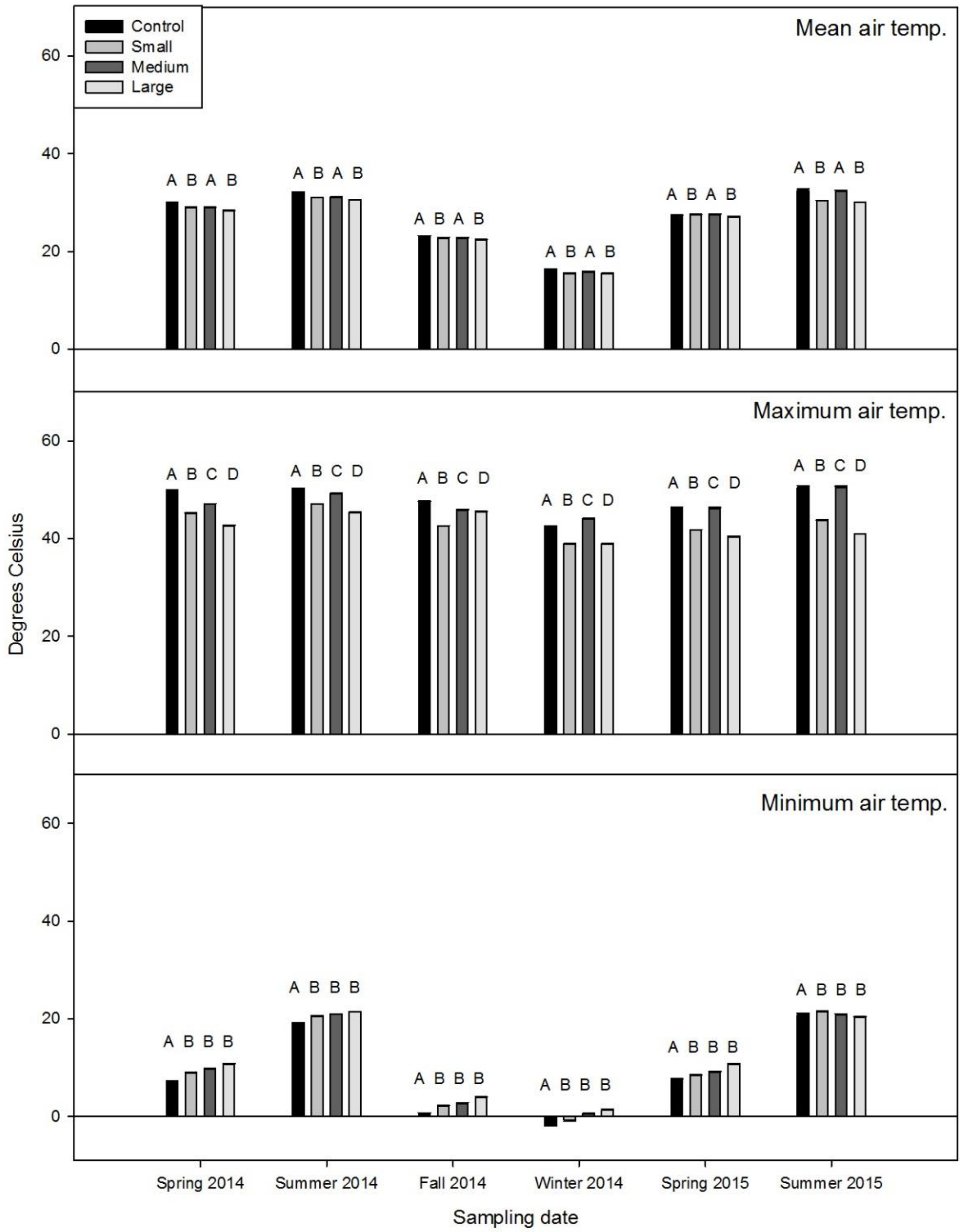

Figure 9: Air temperature (ºC ±SE) measured beneath small, medium and large shrub cluster canopies and controls in pure Gulf cordgrass cover every 4 hr for 16 mo, from May 2014 to August 2015 in the Bahía Grande wetland complex in South Texas. Different letters indicate significant differences by cluster size.

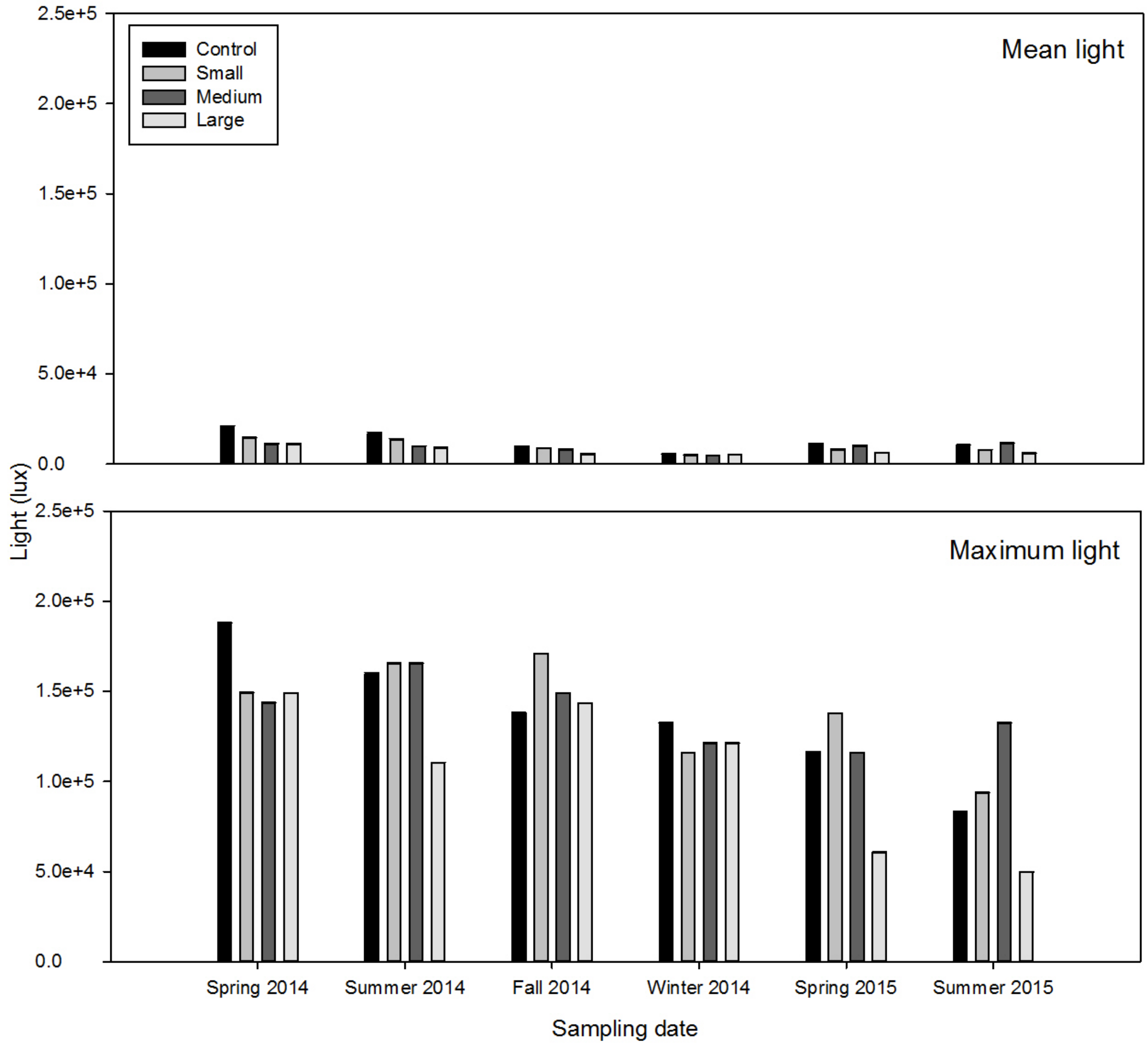

Figure 10: Light (lux ±SE) measured beneath small, medium and large shrub cluster canopies and controls in pure Gulf cordgrass cover every 4 hr for 16 mo, from May 2014 to August 2015 in the Bahía Grande wetland complex in South Texas. No significant differences were found among clusters of different sizes.

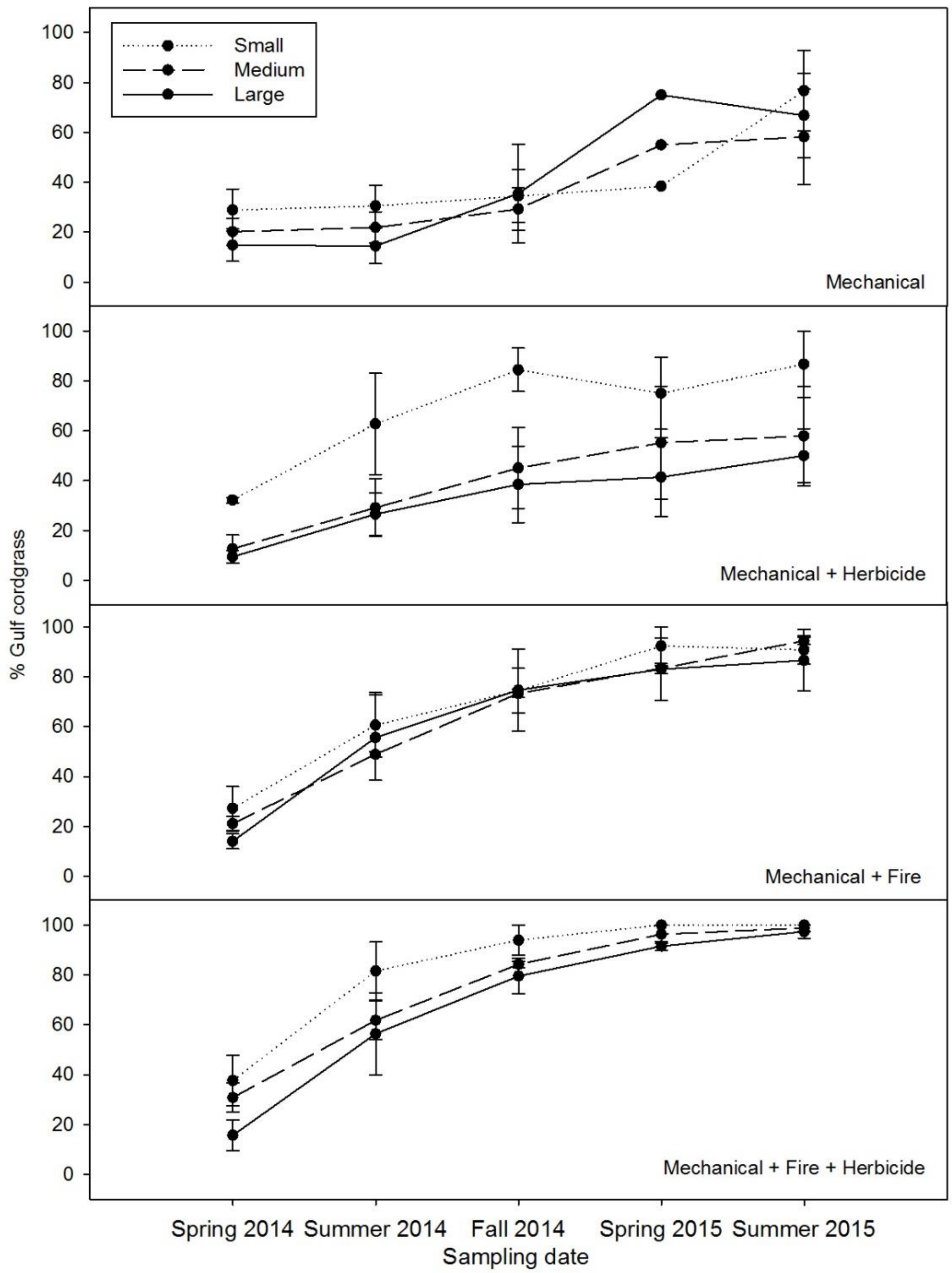

Figure 11: Gulf cordgrass percent cover (±SE) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from April 2014 to August 2015 within the Bahía Grande wetland complex in South Texas.

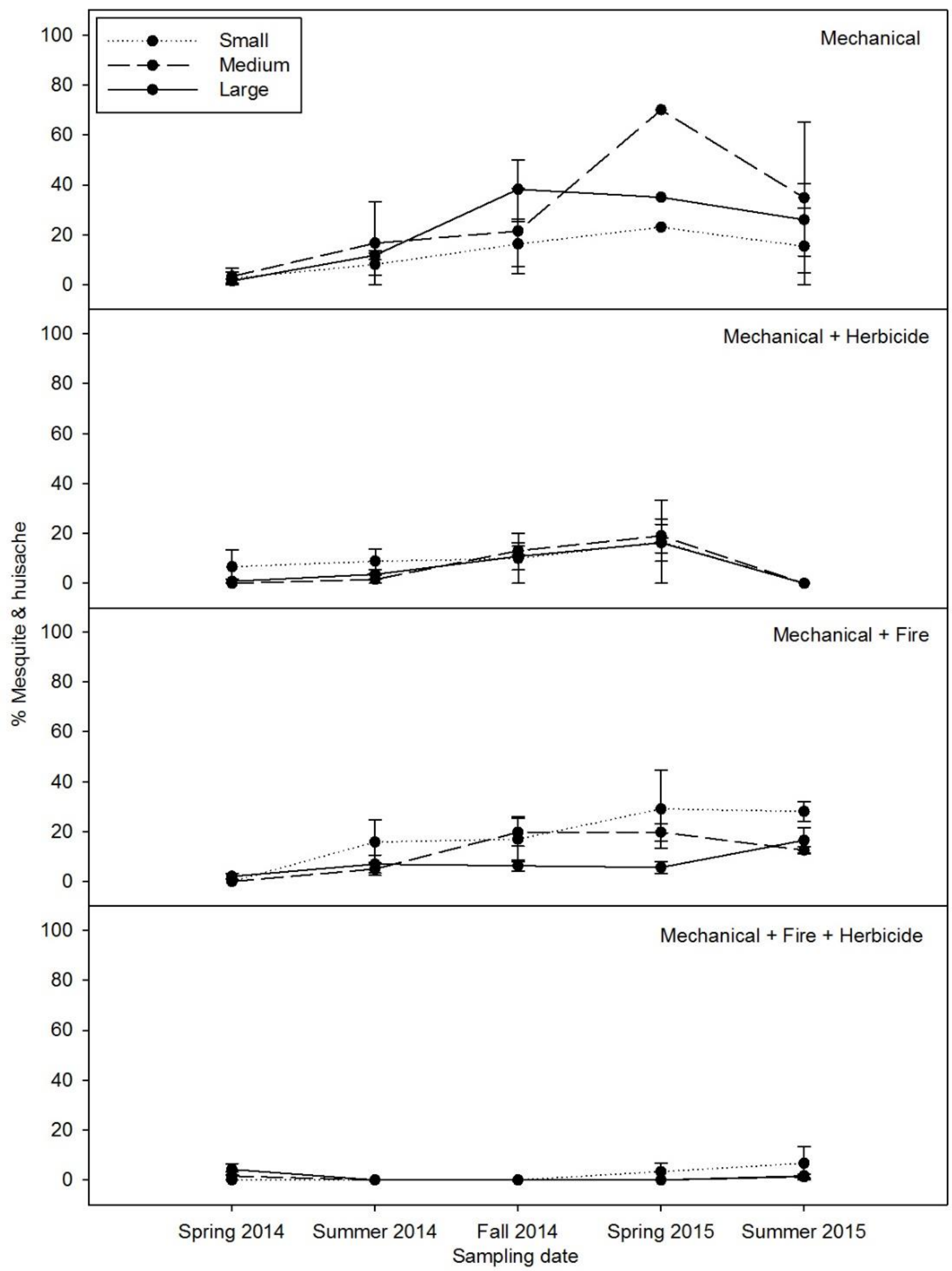

Figure 12: Mesquite and huisache percent cover (±SE) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from April 2014 to August 2015 within the Bahía Grande wetland complex in South Texas.

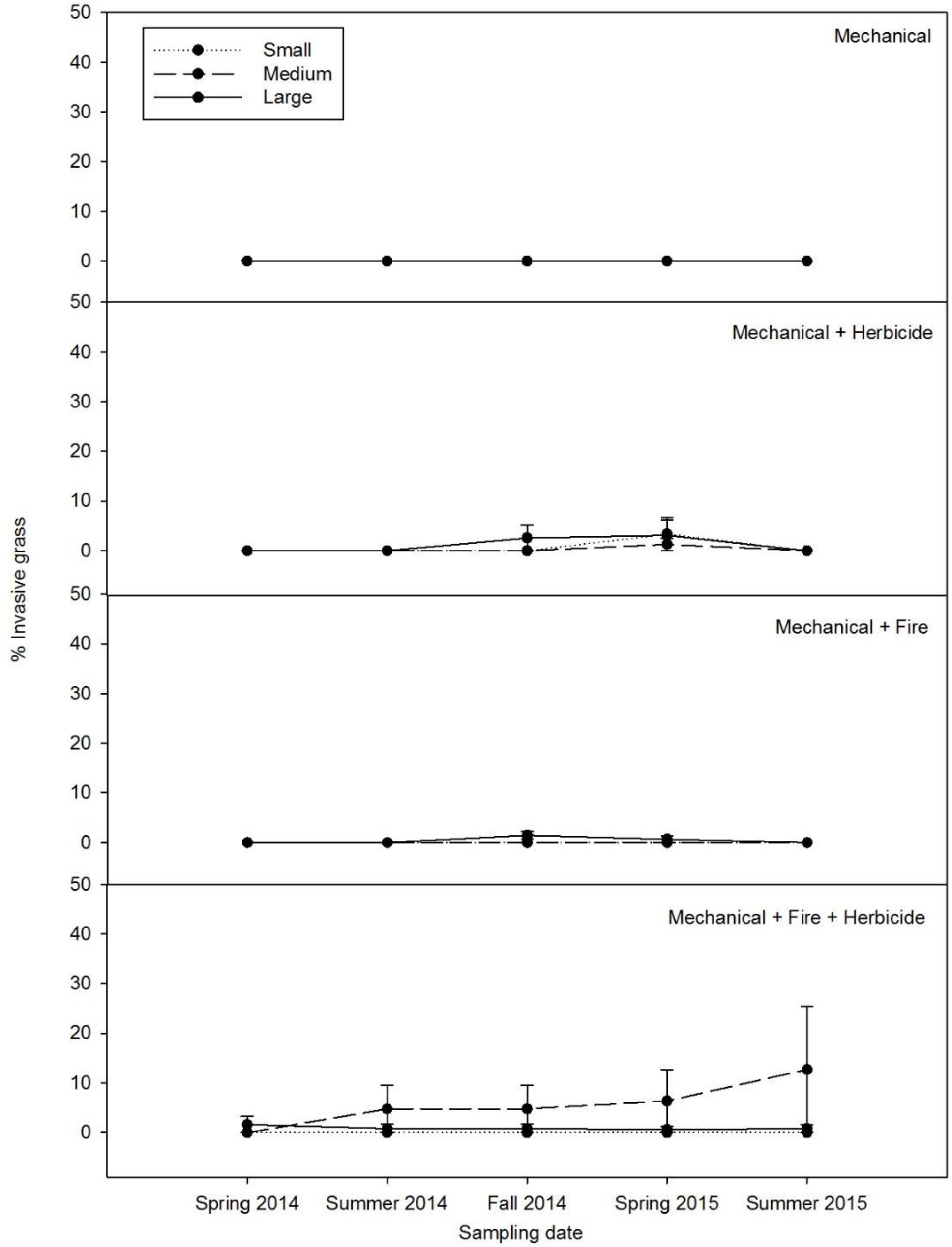

Figure 13: Invasive grass percent cover (±SE) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from April 2014 to August 2015 within the Bahía Grande wetland complex in South Texas.

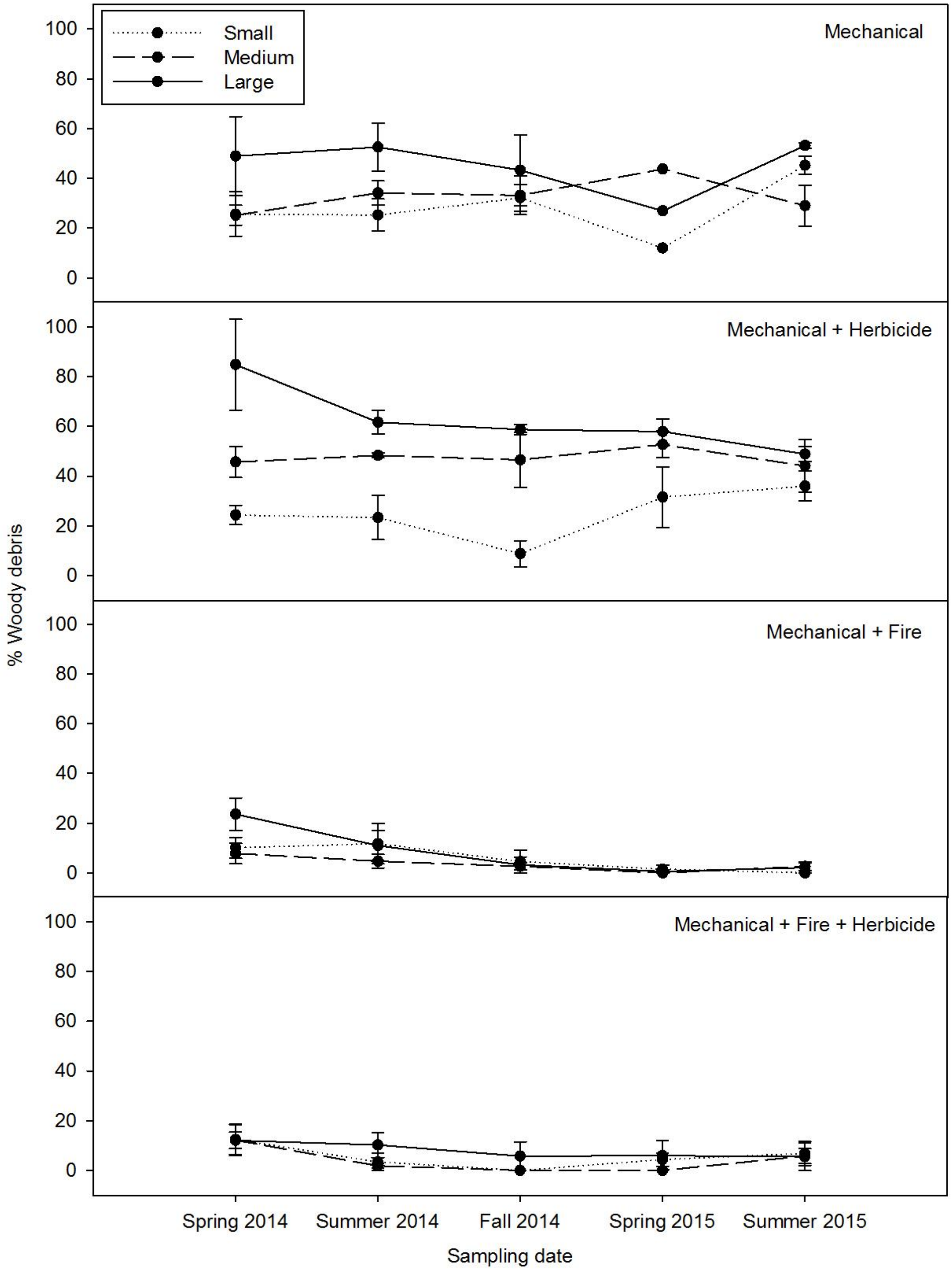

Figure 14: Woody debris substrate percent cover (±SE) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from April 2014 to August 2015 within the Bahía Grande wetland complex in South Texas.

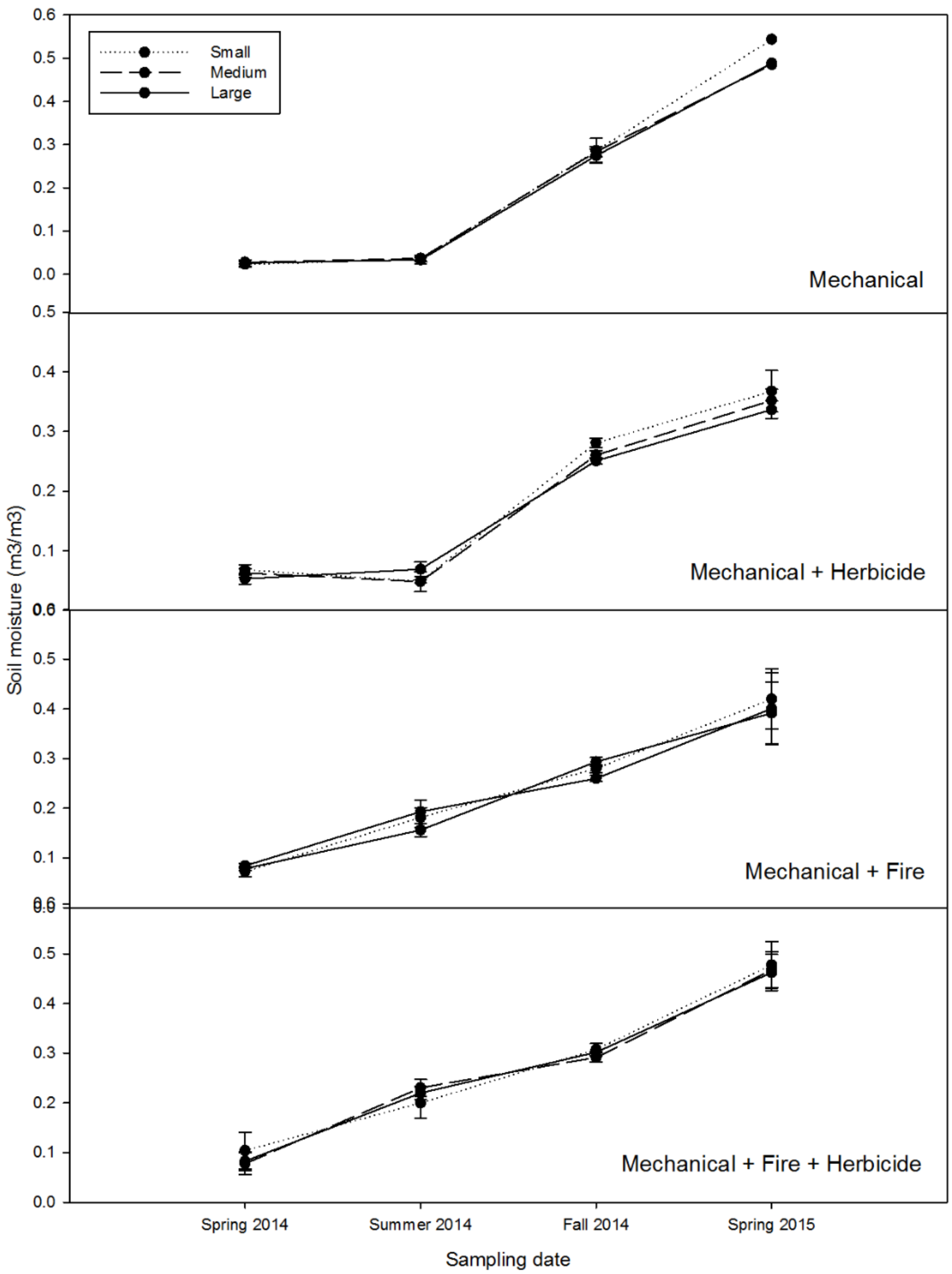

Figure 15: Soil moisture (m^3/m^3 (±SE)) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from April 2014 to April 2015 within the Bahía Grande wetland complex in South Texas.

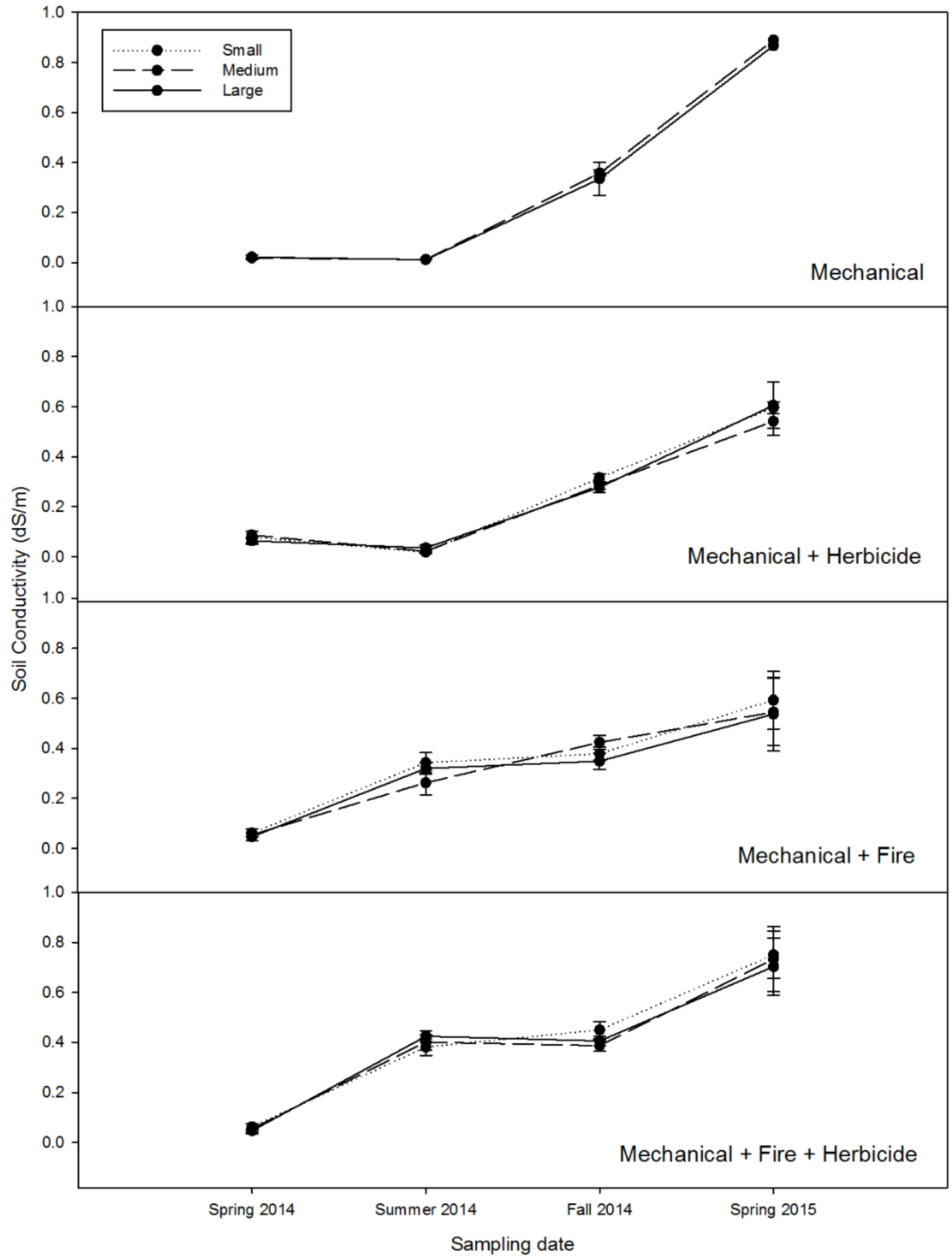

Figure 16: Soil conductivity (dS/m (±SE)) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from April 2014 to April 2015 within the Bahía Grande wetland complex in South Texas.

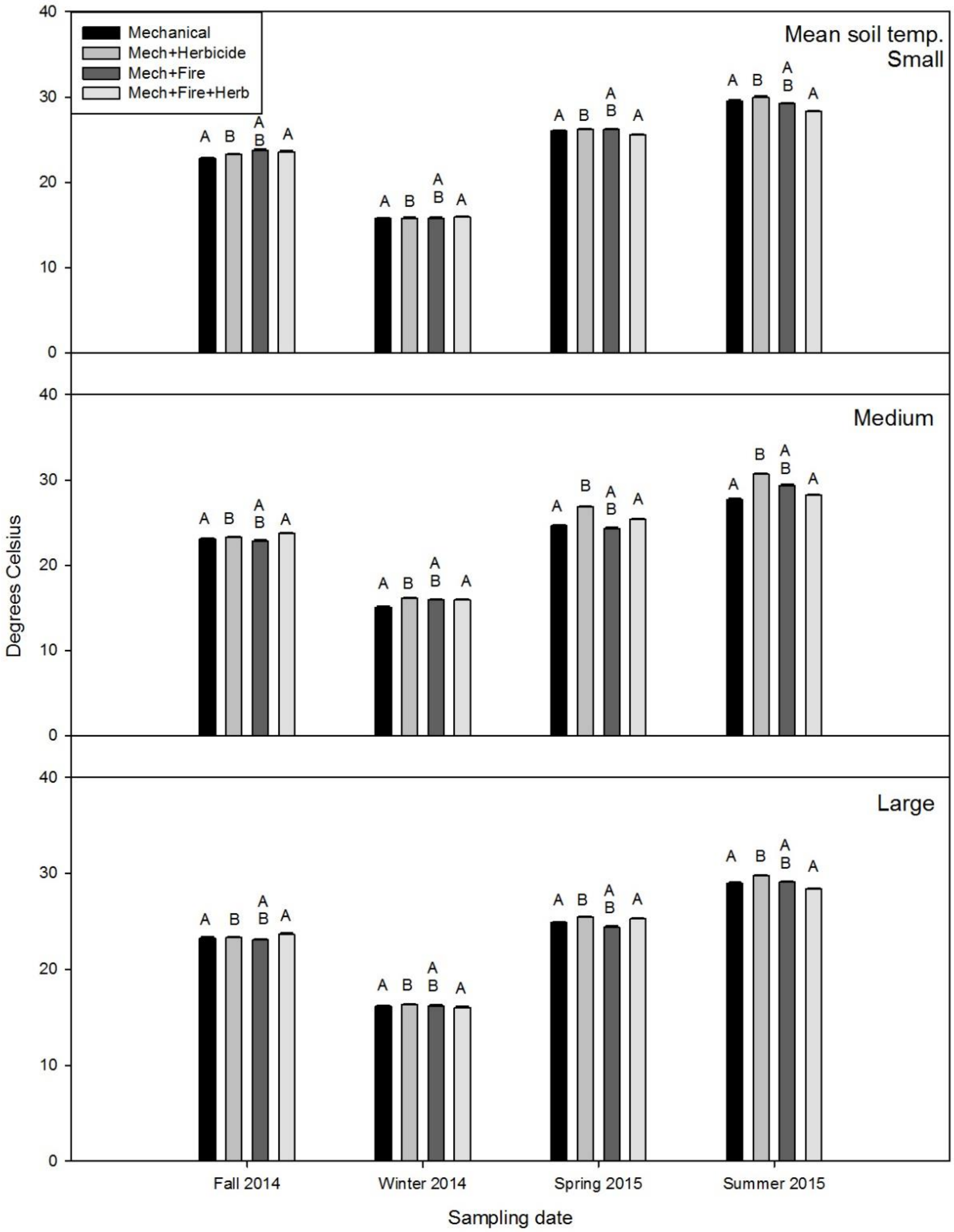

Figure 17: Mean soil temperature (±SE) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from September 2014 to August 2015 within the Bahía Grande wetland complex in South Texas. Different letters indicate significant differences among shrub removal treatments.

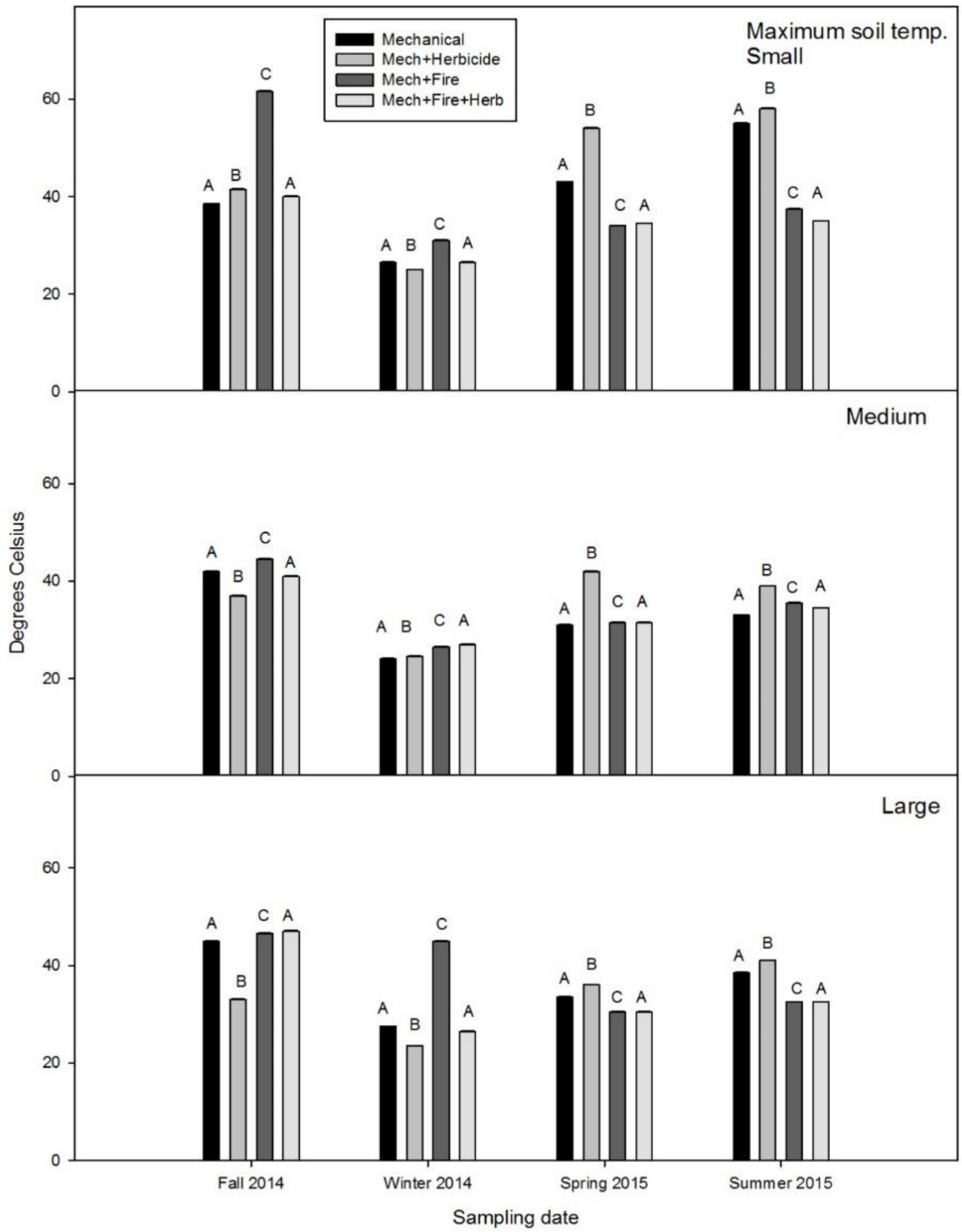

Figure 18: Maximum soil temperature (±SE) within small, medium and large bare patches created by shrubs and treated with mechanical, mechanical and herbicide, mechanical and fire, and mechanical, fire and herbicide shrub removal methods from September 2014 to August 2015 within the Bahía Grande wetland complex in South Texas. Different letters indicate significant differences among shrub removal treatments.

BIOGRAPHICAL SKETCH

Parker Alex Watson was born and raised in Des Moines, Iowa. He graduated from the University of Iowa with a Bachelor of Science degree in Environmental Sciences in December 2010 and the University of Texas Rio Grande Valley with a Master of Science degree in Biology in December 2015.

Parker joined the United States Peace Corps in Ecuador in 2011 as a natural resources volunteer. He then worked in Montana as a field technician for MPG Ranch; Oregon as a field crew member for Ash Creek Forest Management; Iowa as a natural resources technician for the City of Des Moines; Minnesota as a forest ecology intern for the University of Minnesota; and Kentucky as a natural areas intern for Bernheim Arboretum and Research Forest. At press time, Parker's mailing address is: 1 West University Blvd., Brownsville, TX 78520.