

Prescribed Extreme Fire Effects on Richness and Invasion in Coastal Prairie

Dirac Twidwell, William E. Rogers, Elizabeth A. McMahon, Bryce R. Thomas, Urs P. Kreuter, and Terry L. Blankenship*

Widely-held, untested assumptions in many prairies are that high-intensity fires conducted during droughts will decrease native herbaceous species richness and lead to rapid invasions by alien species. We compared native and exotic herbaceous species richness and aboveground herbaceous biomass one year following the application of high-intensity growing-season fires in Texas coastal prairie. Fires were conducted in June 2008, when precipitation was 96% below the long-term monthly average, at the end of a severe 5-mo drought, resulting in high fire intensities within treatment units. Native forb species richness was greater in burned than unburned areas. In contrast, species richness of native grasses, exotic forbs, and the frequency of King Ranch (KR) bluestem [*Bothriochloa ischaemum* (L.) Keng.] did not significantly differ between burned and unburned treatments. The potential to use prescribed extreme fire to maintain native herbaceous species richness while not increasing KR bluestem provides preliminary evidence that growing season fires conducted during droughts can be a viable management strategy in coastal prairies.

Nomenclature: King Ranch bluestem, *Bothriochloa ischaemum* (L.) Keng.

Key words: Conservation-invasion fire dilemma, diversity, fire ecology, grassland restoration, invasive grass, plant community conservation.

Introductions of herbaceous species to new continents are occurring at an unprecedented rate (Mooney et al. 2005) and pose a serious threat to the biodiversity, productivity, and economic profitability of the world's grasslands (DiTomaso 2000; Mack et al. 2000; Pimentel et al. 2005). Hence, understanding the reasons for invasion of exotic herbaceous plants is of considerable importance to scientists and managers. One of the more alarming recent global trends is the capacity for exotic plants to rapidly colonize and invade grasslands following fire (D'Antonio and Vitousek 1992; Keeley 2001). The more notorious exotic invaders of recently burned grasslands are cheatgrass (*Bromus tectorum* L.) in the northwestern United States (Harnis and Murray 1973; Mack 1981); gamba grass (*Andropogon gayanus* Kunth) in Australia (Rossiter et al. 2003); and buffelgrass [*Pennisetum ciliare* (L.) Link] in

Australia (Butler and Fairfax 2003), Mexico (Franklin et al. 2006), and the southwestern United States (Mayeux and Hamilton 1983; Stevens and Falk 2009). Invasions by these species have led to widespread detrimental impacts to native ecosystems that include severe losses in native diversity (Clarke et al. 2005; Fairfax and Fensham 2000; Knapp 1996; Sands et al. 2009), lower forage quality and quantity for livestock (McHenry and Murphy 1985), and drastically modified fire regimes (D'Antonio and Vitousek 1992; Martin et al. 1999; Rossiter et al. 2003). Such undesirable effects have created a management dilemma in grasslands. Fire is considered to be a critical factor in the conservation and management of the world's grasslands (Bond 2008). Yet, the catastrophic examples of fire triggering widespread invasion of exotic plants might prevent managers from using fire for the conservation of other grassland ecosystems where invasive herbaceous species are present (Keeley 2006).

The conservation-invasion fire dilemma is a pressing management concern in the coastal tallgrass prairie ecological region located along the Gulf of Mexico (USA). The coastal tallgrass prairie represents one of the rarest and most diverse community types in North America (Grace 1998). Coastal prairie is estimated to have once occupied between 3.4 to 8.0 million ha (8.4 to 19.8 million acres) in the United States along the Gulf of Mexico (Diamond and Smeins 1988; Smeins et al. 1991).

DOI: 10.1614/IPSM-D-12-00017.1

*First, second, third, fourth, and fifth authors: Instructor and Graduate Student, Associate Professor, Undergraduate Student, Graduate Student, and Professor, Department of Ecosystem Science and Management, Texas A&M University, College Station, TX 77843; Sixth author: Director, Rob and Bessie Welder Wildlife Foundation, Sinton, TX 78387. Current address of first author: Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078. Corresponding author's E-mail: dirac.twidwell@okstate.edu

Management Implications

King Ranch (KR) bluestem is an invasive C_4 grass introduced from Europe and Asia that has led to declines in the richness of plant, avian, and arthropod species in prairie ecosystems. Managers in Texas Gulf coastal prairies are concerned that using fire to manage woody plant encroachment will trigger rapid invasion by KR bluestem and decrease native herbaceous species richness. The objective of this study was to compare the rapid responses of native and exotic herbaceous species in burned and unburned treatments in a huisache–mesquite-invaded coastal tallgrass prairie. In this study, prescribed fires were conducted in the growing season with special permission during a county-mandated burn ban initiated by a severe, prolonged drought that caused considerable grass curing and the potential for high fire intensities (referred to as prescribed extreme fire). Our results counter previously unsubstantiated assumptions in coastal tallgrass prairies and show that prescribed extreme fire increased native forb species richness while maintaining the richness of native grasses, and not increasing King Ranch bluestem significantly. Because other research has shown burning in the dormant season is more likely to facilitate rapid invasion by KR bluestem, prescribed extreme fires in the growing season might be more effective at maintaining herbaceous species richness in coastal prairies prone to KR bluestem invasion.

Today, less than 1% of this ecosystem remains in a nonagricultural or nonurban state, and rapid shrub encroachment threatens to convert the remaining coastal prairie remnants to shrubland (Bruce et al. 1995; Scifres et al. 1982). Conservation organizations and scientists recognize that such widespread transitions jeopardize the high biodiversity of the ecoregion and threaten endangered species that depend on coastal tallgrass prairie, such as the whooping crane (*Grus americana*) and Attwater's greater prairie chicken (*Tympanuchus cupido attwateri*) (Grace 1998; Grossman et al. 1994). Fire historically was critical to the maintenance of coastal prairies (Grace 1998) and presently often is used to kill small woody plants, decrease the canopy cover of mature shrubs, and limit further grassland degradation by preventing the establishment of new woody individuals (Bond 2008; Van Auken 2000). However, the emergence of numerous alien invasive grass and forb species has many conservation managers concerned that fire might facilitate their invasion (Grace et al. 2001).

One of the major invasive threats in Gulf coastal prairie is King Ranch (KR) bluestem [*Bothriochloa ischaemum* (L.) Keng] (Grace et al. 2001), an invasive C_4 grass introduced in the 1920s and 1930s from Europe and Asia (Gould 1975). KR bluestem has led to declines in the richness of plant, avian, and arthropod species in areas it has invaded (Hickman et al. 2006; Johnson et al. 2008). It therefore is important to determine whether the use of fire for the conservation of coastal prairie will inadvertently trigger rapid KR bluestem invasion. Experimental studies in other ecosystems have shown KR bluestem responds favorably to

fires applied during dormant periods of plant growth (Gabbard and Fowler 2006), whereas fires conducted during the growing season have reduced KR bluestem (Ruckman et al. 2011; Simmons et al. 2007) with the greatest reductions occurring during periods of drought (Simmons et al. 2007). Growing-season fires therefore might present a favorable management option for coastal prairie conservationists. However, much of our knowledge on how herbaceous species respond to fire is limited to the dormant season, which is consistent with conventional fire management practices in tallgrass coastal prairie (Hansmire et al. 1988) and elsewhere in the Great Plains (Howe 1994; Pavlovic et al. 2011). As a result, numerous uncertainties limit the use of growing-season fires in restoration and management of Gulf coastal prairies. The two primary concerns are that fire will decrease native herbaceous species richness (e.g., Abrams 1987) and facilitate invasions of alien invasive grass and forb species (Grace et al. 2001).

The objective of our experiment was to compare the rapid responses of native and exotic herbaceous species in burned and unburned treatments in a coastal tallgrass prairie with high levels of shrub encroachment. In this study, prescribed fires were conducted in the growing season during a severe, prolonged drought that caused considerable grass curing (for details on grass curing, see Cheney and Sullivan 1997; Luke and McArthur 1978; Wittich 2011) and the potential for high fire intensities (hereafter these fires are referred to as prescribed extreme fires). Our study was designed to test hypotheses associated with previously unsubstantiated assumptions in coastal tallgrass prairies that (1) prescribed extreme fire will decrease native herbaceous species richness and (2) prescribed extreme fire will trigger rapid increases in alien species.

Materials and Methods

Study Site. The experiment was established at the Rob and Bessie Welder Wildlife Refuge and Foundation, located approximately 11 km north of Sinton, Texas. The 3,150 ha (7,783 acre) Welder Wildlife Refuge functions as a working ranch and wildlife reserve (<http://www.welderwildlife.org>). Traditional grassland management practices, such as fire and cattle grazing, play an integral role in conserving the numerous plant and animal species on the refuge. Prescribed fire is used to maintain grassland dominance and productivity and to control woody plant encroachment. Cattle are rotated among the fenced pastures on the refuge, consistent with the long-term grazing practices of the region. Average annual rainfall at the site is 900 mm (35.4 inches), with peak rainfall occurring in the months of May through June and September (Janecka et al. 2007). Soils are mainly Victoria clays, deep, well-drained, and relatively hydrophobic soils, and range from 0 to 1% in slope (Hansmire et al. 1988).

The upland areas of the Welder Wildlife Refuge were characterized historically as coastal tallgrass prairie, but lack of fire in some areas has increased woody vegetation cover to its current condition of a high density, thorn-scrub woodland (Scifres et al. 1982). We selected a 60 ha section of the refuge dominated by honey mesquite (*Prosopis glandulosa* Torr.) and huisache [*Acacia farnesiana* (L.) Willd.], interspersed with shrub clusters of lime prickly ash [*Zanthoxylum fagara* (L.) Sarg.], spiny hackberry [*Celtis ehrenbergiana* (Klotzsch) Liebm.], and Brazilian bluewood [*Condalia hookeri* M. C. Johnst.] (Box 1961). Primary native perennial grasses include vine mesquite (*Panicum obtusum* Kunth), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], buffalograss [*Bouteloua dactyloides* (Nutt.) J. T. Columbus], and bristle grass (*Setaria* spp.), among others. Common native forbs include noseburn (*Tragia* spp.), limestone wild petunia (*Ruellia strepens* L.), yellow puff [*Neptunia lutea* (Leavenworth) Benth.], and blue mist flower [*Conoclinium coelestinum* (L.) DC.]. Introduced noxious plants include bindweed (*Convolvulus arvensis* L.), woodsorrel (*Oxalis* spp.), and KR bluestem. Cattle were removed prior to initiation of this experiment and were excluded for its duration.

Experimental Design and Treatments. Prescribed fire and herbicide treatments were applied in eighteen plots, each 30 m by 20 m (98.4 ft by 65.6 ft), using a split-plot experimental design (Figure 1a). Burned and unburned plots were assigned randomly at the whole-plot level. Three herbicide treatments were randomly assigned to one of three subplots within each whole plot to treat woody plants (Figure 1a). Each subplot was 20 m by 10 m. Herbicide treatments included: (1) herbicide in 2007, which was timed to occur 1 yr prior to conducting the burn treatment; (2) herbicide in 2009, which was timed to occur when resprouting stems from burned mesquite trees were approximately 0.5 m in length; and (3) no herbicide, which served as a control.

At the time of these analyses, the experimental design consisted of 12 replicate burned plots and six replicate unburned plots. There were 12 replicate plots in the burned treatment to allow half the burned plots to be assigned different fire frequency treatments in the future. This resulted in an unbalanced design for the present analyses. A blocked experimental design was not used in this study because plots were located on a relatively homogeneous upland site on the refuge. Every whole plot was surrounded by at least a 15-m-wide bare-ground firebreak (Figure 1b). Each burned plot therefore was ignited independently of other burned plots and served as true replicates.

Herbicide was applied to all woody plants by spraying a 75% diesel : 25% Remedy Ultra mix (triclopyr; Dow Agrosciences, Indianapolis, IN) at the base of their stems.

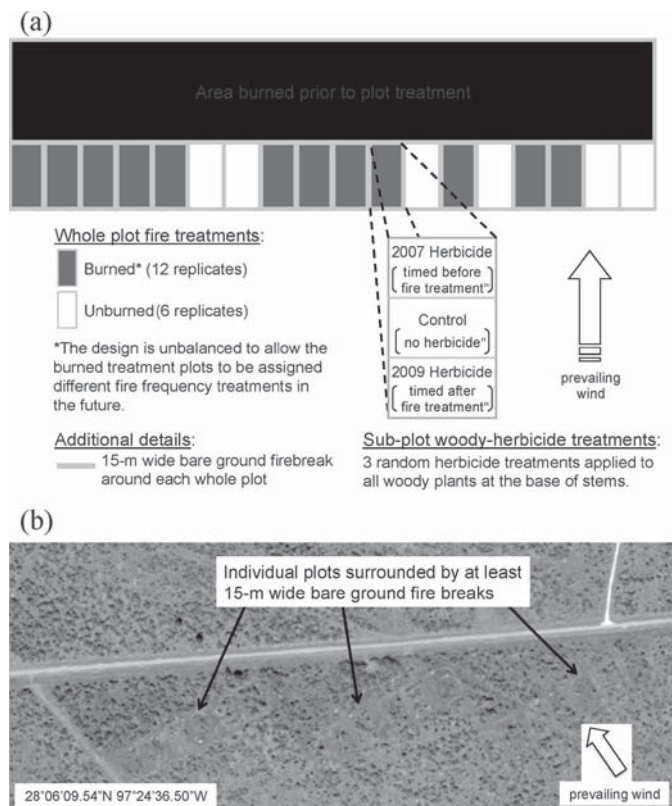


Figure 1. (a) Illustration showing the conceptual framework for the split-plot experimental design and (b) aerial photograph from Google Earth showing the actual layout of the 18 plots at the Welder Wildlife Refuge. Prior to fire treatments, a large area was burned downwind of the plots (not shown by Google Earth in panel b) to remove surface fuels and prevent spot fires when conducting extreme fire treatments.

The herbicide was not sprayed directly on herbaceous vegetation. At the time of establishing this experiment, basal application of this herbicide mixture was regarded as the best approach for killing mesquite (McGinty et al. 2000; McGinty and Ueckert 1997) and other invasive woody plants (McGinty et al. 2000), and has been widely adopted by Texas landowners as a preferred management practice for controlling shrub encroachment (Kreuter et al. 2001).

Plots were burned with headfires in the direction of a large buffer area that was burned in mild fuel and fire weather conditions (i.e., high fine-fuel moisture, low temperature, high relative humidity, low wind speed) prior to conducting the extreme fire treatment (Figures 1a and 1b). The purpose of the buffer area was to remove surface fuels and provide sufficient space to prevent firebrands from starting spot fires outside the burn unit. The size of the buffer area was determined using generally-accepted rules established for rangelands by Wright (1974) and comparing those guidelines to quantitative predictions of

spot-fire distance in flat terrain using methods from Albini (1979, 1981).

Fireline intensity and fire temperatures were measured in each subplot. Ocular estimates of mean and maximum flame length were recorded in each subplot, and fireline intensities were calculated for each subplot using the methodology outlined in Rothermel and Deeming (1980). Maximum fire temperatures were recorded using ceramic tile pyrometers. Tiles were painted with 25 temperature-indicating lacquers (OMEGALAQ® Liquid Temperature Lacquers; Omega, Inc., Stamford, CT, 2011) that melted from 79 C to 1,038 C. A temperature of 1,038 C represents the second-highest temperature-indicating lacquer sold by Omega. The highest temperature lacquer, 1,093 C, was not available in sufficient quantities at the time of purchase. Lacquers were chosen at approximately 50 C to 100 C increments, depending on the products available, to achieve a relatively even distribution of temperature indicators. Tile pyrometers were located at the base of a large tree (> 1.5 m). Three trees were randomly selected in each subplot. At the base of each tree, a tile pyrometer was placed on the ground (0-cm [0-inch] height) and another at a height of 150 cm (59.1 inches) by affixing the tile to a piece of metal conduit that was pounded into the ground. This protocol was established for research objectives that are beyond the purview of this analysis; however, the fire temperature data are useful in characterizing the fire temperatures produced in this experiment and in making comparisons to temperatures reported in other studies. A total of 216 tile pyrometers were used in this study (two tiles per location/tree [one tile at 0 cm + one tile at 150 cm] by three locations per subplot by three subplots per plot by 12 burned plots). The side of the tile with lacquers was oriented upwards, which might have resulted in an insulating effect because ceramic tiles were used (Kennard et al. 2005). Pyrometers at a height of 150 cm therefore might have underestimated the actual fire temperatures produced in this study, which should be taken into account when comparing fire temperatures produced in other studies.

Due to the number of burned plots, the amount of preparation required to set up pyrometers prior to burning each plot, the time required to burn each plot individually, and the amount of monitoring associated with conducting fires during burn bans, it took 3 d to burn 12 plots. Fires were conducted from June 17 to 19, 2008. Minimum and maximum temperature, relative humidity, and wind speed at the time of conducting fires were 35.0 C and 38.3 C, 28.9% and 43.3%, and 1.1 km h^{-1} and 14.6 km h^{-1} , respectively.

Vegetation Sampling. Vegetation sampling was conducted 1 yr after the prescribed fires by clipping all the herbaceous material within three randomly located 0.25-m^2 quadrats

in each subplot. A total of 162 quadrats were sampled. Each live herbaceous individual was identified to species, with the exception of *Carex* spp., *Eragrostis* spp., *Oxalis* spp., *Croton* spp., *Tragia* spp., *Setaria* spp., and *Paspalum* spp., which could only be identified to genus because they did not exhibit necessary vegetation characteristics for more detailed identification and were generally in low abundance. After species identification, samples were dried (70 C, 48 h) to measure aboveground productivity.

Statistical Analysis. Testing for differences in herbaceous species richness and aboveground herbaceous biomass as a result of the application of herbicide on woody plants using non-balanced split-plot ANOVA revealed no significant differences among subplot treatments ($F = 1.75$, $P = 0.18$). Therefore data from each herbicide-treated subplot were pooled in each whole plot (i.e., three quadrats per subplot by three subplots = nine quadrats per whole plot) to test for differences between burned and unburned treatments. Species richness (number of species per 0.25 m^2 quadrat) data were averaged for all quadrats in a plot, and the averaged values were analyzed using an independent samples t -test with unequal sample sizes of equal variance and normal distribution. Data for herbaceous biomass were square-root transformed to meet assumptions of normality. Levene's test indicated unequal variances for the herbaceous biomass data ($F = 9.88$; $P = 0.006$), so these data were analyzed using an independent samples t -test that did not assume homogeneity of variances. Nonmetric multidimensional scaling (NMS) was used to visualize differences in the herbaceous plant community between burn treatments. NMS ordinations were produced with PC-ORD (McCune and Mefford 1999) using Bray-Curtis distances with random starting configurations, three dimensions, 100 runs of real data with 500 iterations per run, and a stability criterion of 0.00001. Individual species were not included in the NMS if they occurred in less than 5% of all treatment units, following the recommendations by McCune and Grace (2002). Statistical analyses assumed plots were not different prior to treatment because pretreatment data were not collected due to the presence of adequate controls, the assignment of completely randomized treatments, and a relatively homogeneous study area (visual observation). Multiple pair-wise comparisons were performed using Tukey HSD to test for differences in fire temperatures as a result of the herbicide treatments applied to each subplot.

Results and Discussion

Weather and Fire Intensity. Prescribed fires were conducted in environmental conditions that led to remarkably high fire intensities for this ecosystem. The research site had been in an extended drought for nearly

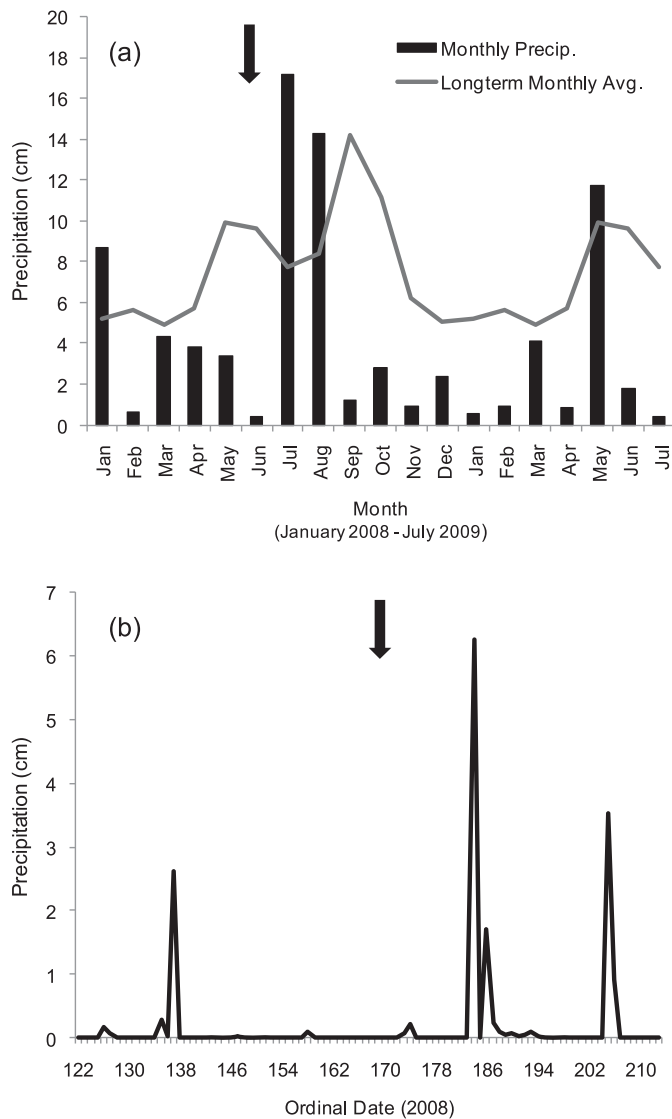


Figure 2. (a) Monthly and long-term average precipitation and (b) daily precipitation before and after fires were conducted at Welder Wildlife Refuge from January 2008 to July 2009. Arrows show dates prescribed fires were conducted (June 17 to 19, 2008). Samples were collected in July 2009.

5 mo at the time of burning in June 2008 (Welder Wildlife Refuge station records). Total precipitation was less than the long-term monthly average from February through June (Figure 2a). When fires were conducted, the site had not received a substantial rain event for 46 d (Figure 2b) and total precipitation in June was only 0.41 cm, which was 96% below the long-term monthly average. The shortage of rainfall resulted in nearly complete grass curing (D. Twidwell and T. L. Blankenship, personal observations; Cheney and Sullivan 1997; Luke and McArthur 1978; Wittich 2011) and contributed to high fire temperatures and intensity levels. Fire temperatures averaged 886 C at ground level and 461 C at a height of

150 cm. The temperature of the highest indicating lacquer (1,038 C) was reached on 88% of pyrometers at ground level (95 of 108). As a result, the tile pyrometers likely underestimated the actual mean fire temperatures produced at ground level in these fires. Mean fireline intensity across all burned plots was $897 \pm 124 \text{ kJ m}^{-1} \text{ s}^{-1}$; however, maximum flame lengths observed in this study were 5 m, producing fireline intensities of approximately $8500 \text{ kJ m}^{-1} \text{ s}^{-1}$ in localized areas of multiple plots.

The fire temperatures recorded in this study are far above values typically observed in other fire studies in the Gulf coastal prairie. Few studies have directly measured and reported fire temperature or intensity data in Gulf coastal prairie ecosystems. An earlier study at the Welder Wildlife Refuge observed maximum fire temperatures ranging from 330 C to 460 C at ground level in a plant community similar to this experiment (i.e., thorn-scrub woodland) and 689 C to 820 C at ground level in a bunchgrass-dominated area where herbaceous fuel load was higher (Scifres et al. 1988). Maximum fire temperatures averaged 235 C and 280 C for fires conducted in 2 different yr in Texas coastal tallgrass prairie (range was 110 to 300 C for fires in both years; Hartley et al. 2007). In other studies, peak fire temperatures ranged between 150 C to 500 C for a single fire in Texas coastal prairie (values approximated from figure; Grace et al. 2005) and 116 C to 525 C in Louisiana coastal marsh (Owens et al. 2007).

Applying herbicide on woody plants 1 yr before conducting fires in 2008 did not result in greater fire temperatures or fireline intensities than other subplots (Tukey's HSD, $P = 0.99$ and $P = 0.14$ for temperatures in herbicide after fire and no herbicide treatments, respectively; $P = 1.00$ and $P = 1.00$ for fireline intensities in herbicide after fire and no herbicide treatments). Mean fire temperatures were 846 C, 863 C, and 949 C in herbicide before fire (2007), herbicide after fire (2009), and no herbicide subplots, respectively. Mean fireline intensities were $913 \text{ kJ m}^{-1} \text{ s}^{-1}$, $870 \text{ kJ m}^{-1} \text{ s}^{-1}$, and $909 \text{ kJ m}^{-1} \text{ s}^{-1}$ in herbicide before fire (2007), herbicide after fire (2009), and no herbicide subplots, respectively.

Coastal Prairie Species Composition. Overall, this herbaceous plant community was dominated by relatively few species (Table 1). Perennial grasses comprised the majority of plant species. Of these, KR bluestem and vine mesquite were the most frequently observed plants in both the burned and unburned treatments. Texas wintergrass, a perennial C_3 grass, ranked third in frequency of occurrence. Only one annual grass, prairie threeawn (*Aristida oligantha* Michx.), was found, and only with infrequent occurrences in the burned treatment. The dominant forbs were yellow puff, noseburn, blue mistflower, and trailing krameria (*Krameria lanceolata* Torr.). Two introduced forbs, field bindweed and wood sorrel, occurred infrequently in the plots.

Table 1. List of species observed in this experiment at the Welder Wildlife Refuge, their growth characteristics, and the frequencies (% of quadrats) and Pearson correlations (r) with nonmetric multidimensional scaling (NMS) axis 1 of each plant species in burned ($n = 12$) and unburned ($n = 6$) treatments.

Scientific species name	Common name	Acronym ^a	Provenance ^b	Growth form ^b	Periodicity ^b	Frequency (%)		r^c
						Burned	Unburned	
<i>Bothriochloa ischaemum</i>	King Ranch bluestem	BOIS	I ^d	G	P	20.37	16.67	0.53
<i>Convolvulus arvensis</i>	field bindweed	COAR4	I ^d	F	P	0.31	0.62	—
<i>Oxalis</i> spp.	woodsorrel	OXCO	I	F	P	0.31	0	—
<i>Bothriochloa laguroides</i>	silver beardgrass	BOLA	N	G	P	0	1.23	—
<i>Bouteloua dactyloides</i>	buffalograss	BODA2	N	G	P	2.47	1.85	0.39
<i>Chloris × subdolichostachya</i>	shortspike windmill grass	CHSU3	N	G	P	1.54	3.09	-0.59
<i>Coelorachis cylindrica</i>	cylinder jointtail grass	COCY	N	G	P	0	0.62	—
<i>Dichanthelium oligosanthes</i>	rosette grass	DIOL	N	G	P	0.31	0	—
<i>Eragrostis intermedia</i>	plains lovegrass	ERIN	N	G	P	0.31	0	—
<i>Hilaria belangeri</i>	curly mesquite	HIBE	N	G	P	0.31	0	—
<i>Nassella leucotricha</i>	Texas wintergrass	NALE3	N	G	P	1.85	5.56	-0.34
<i>Panicum obtusum</i>	vine mesquite	PAOB	N	G	P	9.88	12.35	-0.55
<i>Steinchisma bians</i>	gaping grass	STHI3	N	G	P	3.70	1.23	0.38
<i>Paspalum</i> spp.	paspalum	PASE	N	G	P	1.23	0	—
<i>Schizachyrium scoparium</i>	little bluestem	SCSC	N	G	P	1.23	0	—
<i>Setaria</i> spp.	bristlegrass	SETAR	N	G	P	3.09	1.85	0.33
<i>Tridens albescens</i>	white tridens	TRAL2	N	G	P	0.93	0.62	—
<i>Aristida oligantha</i>	prairie threecawn	AROL	N	G	A	0.31	0	—
<i>Ambrosia psilostachya</i>	Cuman ragweed	AMPS	N	F	A/P	0	0.62	—
<i>Eupatorium coelestinum</i>	blue mistflower	COCO13	N	F	P	4.01	6.79	-0.41
<i>Krameria lanceolata</i>	trailing krameria	KRLA	N	F	P	5.25	3.70	0.43
<i>Neptunia lutea</i>	yellow puff	NELU2	N	F	P	12.35	6.17	0.60
<i>Ruellia strepens</i>	limestone wild petunia	RUST2	N	F	P	0.93	0	—
<i>Rubus trivialis</i>	dewberry	RUTR	N	F	P	0	0.62	—
<i>Solanum elaeagnifolium</i>	silverleaf nightshade	SOEL	N	F	P	0.93	0.62	—
<i>Tragia</i> spp.	noseburn	TRAGI	N	F	P	14.51	3.09	0.50

^a Acronyms are from PLANTS database (USDA, NRCS 2011).

^b Abbreviations are: I = Introduced; N = Native; G = Graminoid; F = Forb; A = Annual; P = Perennial.

^c Species without correlations (shown by a dash) were present in less than 5% of all plots and were excluded from the ordination. Only correlations with NMS axis 1 are shown because other axes did not separate groups according to differences between treatments.

^d Listed as noxious plants in Texas (USDA, NRCS 2011).

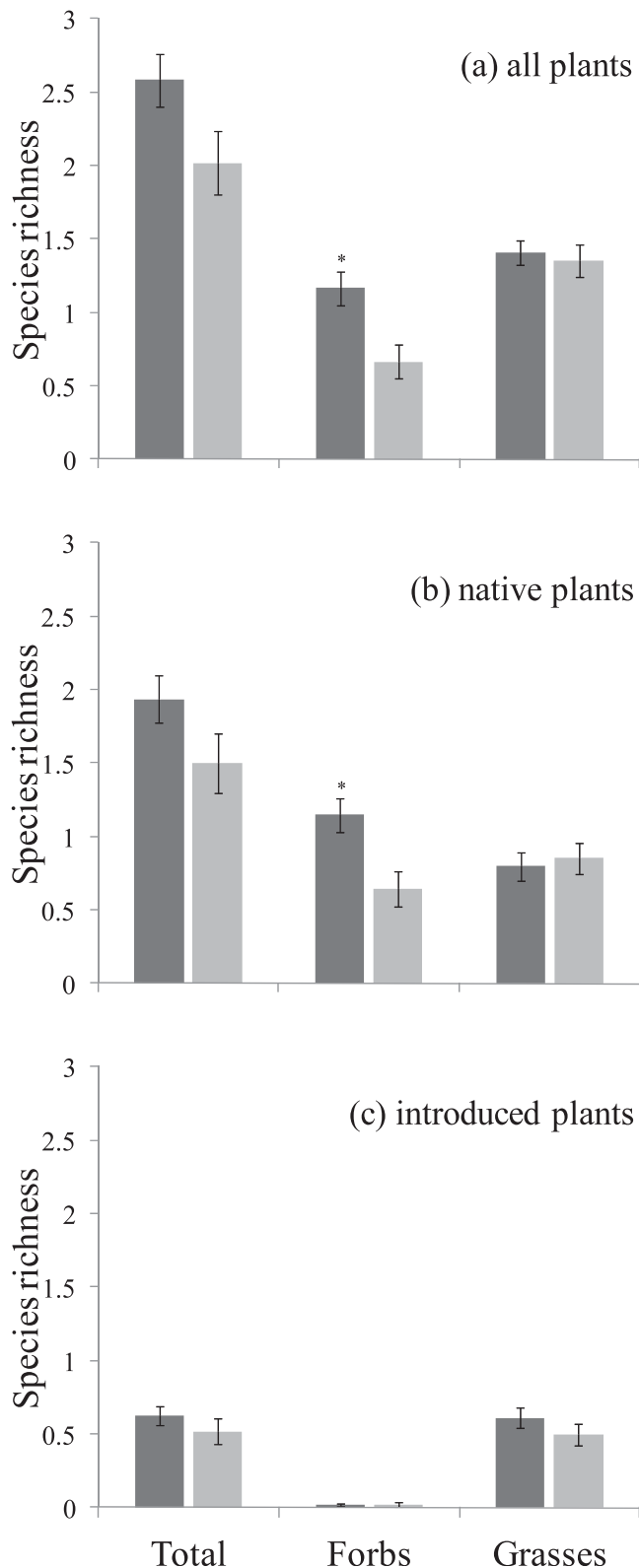


Figure 3. Mean (+ SE) species richness (No. species 0.25 m⁻²) of forbs and perennial grasses in burned (dark gray) and unburned (light gray) treatments for (a) all plants, (b) native plants, and (c) introduced plants. * indicates significant differences at $P < 0.05$, compared to the unburned controls of each functional group.

The number of species was low in this coastal tallgrass prairie relative to its potential richness. Over 900 plant species have been documented throughout the coastal tallgrass prairie range, with a large proportion of its diversity owed to a high number of forb species (Grace 1998). In contrast, coastal prairie in our study area was dominated by a few perennial grasses species, particularly in the unburned control, and had only one annual grass species. Perennial species dominance commonly reduces the number of annuals (Pickett 1982). In addition, many coastal prairie ecosystems are undergoing a regime shift to shrub forest or woodland, leading to extensive species displacement (Bruce et al. 1995; Grace et al. 2000). These factors are leading to widespread shifts in species composition and losses in species richness throughout prairie ecosystems (Howe 1994; Leach and Givnish 1996; Sluis 2002), and likely explain why only 19 native species were observed in unburned coastal prairie in this study.

Fire Effects on Herbaceous Species. Contrary to widely held assumptions and the prediction of our first hypothesis, conducting prescribed extreme fires in the growing season did not decrease native species richness (Figure 3). Rather, native forb species richness was greater in burned areas compared to unburned areas ($t = 2.65$, $df = 16$, $P = 0.02$; Figure 3b) and the richness of native grass species did not differ between treatments ($t = -0.35$, $df = 16$, $P = 0.73$; Figure 3b). Total species richness did not differ between burned and unburned treatments ($t = 1.91$, $df = 16$, $P = 0.07$; Figure 3a), and no other native or introduced functional group differed between treatments ($P > 0.10$; Figure 3b, 3c). Aboveground herbaceous biomass was significantly lower in the burned treatment ($t = -3.17$, $df = 6$, $P = 0.02$; Figure 4).

Forb-driven increases in species richness often is observed following growing season burns in other prairies (Biondini et al. 1989; Copeland et al. 2002; DiTomaso et al. 1999; Towne and Kemp 2008); however, the number of species can vary considerably following fire (Suding and Gross 2006), so no universal pattern between fire and species richness has emerged. Regardless, a fire-stimulated increase in richness is typically short-lived and decreases with time since fire (Gibson and Hulbert 1987; Kyser and DiTomaso 2002), often as a result of long-term accumulation of grass litter (Hobbs and Huenneke 1992; Shay et al. 2001; Tilman 1993). Managers therefore will need to consider the frequency with which fires are to be reapplied in coastal prairie ecosystems if fire management programs are to successfully maintain high levels of species richness.

Although the richness of native forbs was the only functional group to differ between burned and unburned treatments (Figures 3b and 3c), many herbaceous species within a functional group differed in their response to fire. Differential responses among species were shown by NMS

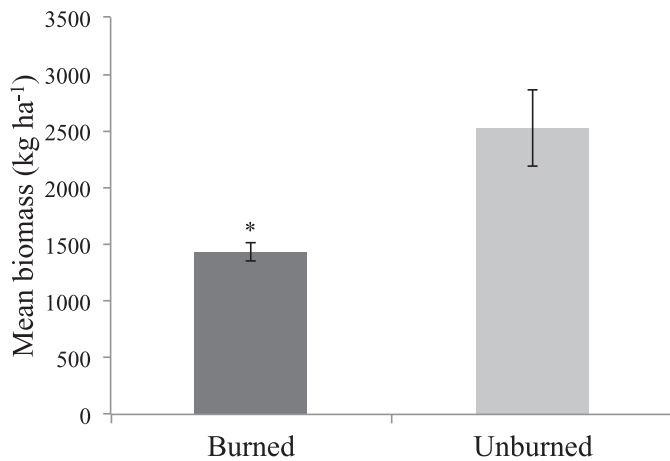


Figure 4. Mean (+ SE) aboveground herbaceous biomass in burned and unburned treatments (* indicates statistically significant difference at $P < 0.05$ compared to unburned control).

ordination, which generally separated unburned and burned treatment units along NMS axis 1 (Figure 5). Total species richness and native forb species richness were positively correlated in the direction of burned plots along axis 1 ($r = 0.48$ and 0.64 , respectively). The dominant native forbs that accounted for this trend were noseburn, yellow puff, and trailing krameria. Such species were found in considerably greater abundances in burned areas than in unburned areas and were highly correlated with NMS axis 1 (Table 1; Figure 5). In contrast, blue mistflower was negatively associated with burned sites and NMS axis 1 (Table 1; Figure 5). KR bluestem was positively associated with the direction of burned plots, whereas the dominant native species, vine mesquite and Texas wintergrass, along with shortspike windmill grass, were negatively associated with axis 1 (Table 1; Figure 5). Buffalograss, bristlegrass, and gaping grass [*Steinchisma bians* (Elliott) Nash] were positively associated with axis 1 (Table 1; Figure 5).

Introduced plant species did not differ significantly between burned and unburned treatments after 1 yr, which counters our second hypothesis and challenges the widely held concern that prescribed extreme fires will promote rapid invasion by undesirable exotic grasses and forbs. The richness of introduced forbs did not differ significantly between burned and unburned treatments ($t = 0.00$, $df = 16$, $P = 1.00$; Figure 3c). The occurrence of KR bluestem, the only introduced grass species observed in this study, did not differ significantly between burned and unburned treatments after one year ($t = 0.32$, $df = 16$, $P = 0.32$; Figure 3c) but was positively associated with the direction of burned plots in NMS ordination (Figure 5, Table 1). Two separate studies support our findings that KR bluestem does not rapidly invade prairies burned by prescribed extreme fires (Ruckman et al. 2011; Simmons

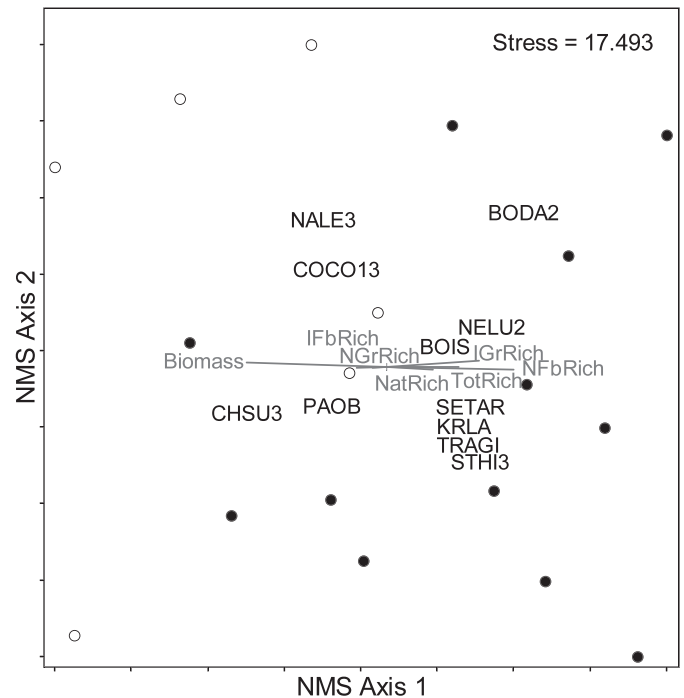


Figure 5. Nonmetric multidimensional scaling (NMS) ordination showing the differences in the distribution of the herbaceous plant community in burned (filled circles) and unburned (hollow circles) treatments. NMS ordinations were rotated in the direction of total richness. Biplots show the direction and strength of relationships between ordination scores and total richness (TotRich), native richness (NatRich), native grass richness (NGrRich), native forb richness (NFbRich), introduced grass richness (IGrRich), and introduced forb richness (IFbRich). Species are plotted by their acronyms; full names for species acronyms are given in Table 1.

et al. 2007). KR bluestem has been reduced by fires conducted early in the growing season, when the phenological development of the plant is less advanced (Ruckman et al. 2011), and the greatest reductions have occurred when growing season fires are conducted during drought (Simmons et al. 2007). In contrast, KR bluestem has responded favorably to fires conducted in milder conditions during dormant periods of plant growth (Gabbard and Fowler 2006; Pase 1971). However, this experiment and all the aforementioned studies characterize the short-term effect of fire on KR bluestem and research has yet to establish its response over longer time intervals in a postfire environment.

Conclusions and Conservation Implications. The potential to use prescribed extreme fire to increase native forb species richness while not increasing KR bluestem suggests that prescribed fires conducted during droughts in the growing season might be more effective than dormant-season fires at meeting native coastal prairie conservation

goals. This counters the majority of fire management practices in tallgrass prairie (Howe 1994; Pavlovic et al. 2011). Most prescribed fires in coastal prairie are ignited in December through February when plants are dormant (Hansmire et al. 1988), often with the intent of increasing forbs for wildlife species (Chamrad and Box 1968; Lehman 1984). Such a strategy is likely to produce the opposite effect in coastal prairies invaded by KR bluestem. Burning during the dormant season is more likely to facilitate KR bluestem invasion (Gabbard and Fowler 2006; Pase 1971; Ruckman et al. 2011), which can lead to decreases in the composition and richness of plants and animals across multiple trophic levels (Hickman et al. 2006; Johnson et al. 2008). In contrast, burning during drought periods in the growing season increased forb richness and did not significantly increase KR bluestem occurrence in this study and decreased KR bluestem in previous research (Ruckman et al. 2011; Simmons et al. 2007). This information, coupled with research showing prescribed fire can reduce woody plant dominance in coastal prairie (Allain and Grace 2001; Grace 1998; Twidwell 2012) and cause high levels of woody plant mortality in other ecosystems (Taylor et al. 2012; Twidwell et al. 2009), provides preliminary evidence that prescribed extreme fires conducted in the growing season can be a viable management strategy in coastal prairies.

Acknowledgments

We thank Baldemar Martinez, Lynn Drawe, and others for their assistance in planning for and conducting prescribed extreme fires. We thank Carissa Wonkka for her contributions to this manuscript. This research was supported by United States Department of Agriculture Natural Resource Conservation Service (Conservation Innovation Grant 68-3A75-5-180), the Rob and Bessie Welder Wildlife Foundation (WWF contribution #709), Tom Slick Foundation, and Texas A&M AgriLife Research.

Literature Cited

- Abrams, M. D. and L. C. Hulbert. 1987. Effect of topographic position and fire on species in tallgrass prairie in northeast Kansas. *Am. Midl. Nat.* 117:442–445.
- Albini, F. A. 1979. Spot Fire Distance from Burning Trees: A Predictive Model. USDA Forest Service Research Paper INT-56. 73 p.
- Albini, F. A. 1981. Spot Fire Distance from Isolated Sources. Extensions of a Predictive Model. USDA Forest Service Research Note INT-309. 10 p.
- Allain, L. and J. B. Grace. 2001. Changes in density and height of the shrub *Baccharis halimifolia* following burning in coastal tallgrass prairie. *Proc. North Am. Prairie Conf.* 17:66–72.
- Biondini, M. E., A. A. Steuter, and C. E. Gryciel. 1989. Seasonal fire effects on the diversity patterns, spatial distribution, and community structure of forbs in the Northern Mixed Prairie. *Vegetatio* 85:21–31.
- Bond, W. J. 2008. What limits trees in C_4 grasslands and savannas? *Annu. Rev. Ecol. Evol. Syst.* 39:641–659.
- Box, T. W. 1961. Relationships between plants and soil of four range plant communities in south Texas. *Ecology* 42:794–810.
- Bruce, K. A., G. N. Cameron, and P. A. Harcombe. 1995. Initiation of a new woodland type on the Texas Coastal Prairie by the Chinese tallow tree (*Sapium sebiferum* (L.) Roxb.) *Bull. Torrey Bot. Club* 122: 215–225.
- Butler, D. W. and R. J. Fairfax. 2003. Buffel grass and fire in a Gidgee and Brigalow woodland; a case study from central Queensland. *Ecol. Manag. Restor.* 4:120–125.
- Chamrad, A. D. and T. W. Box. 1968. Food habits of white-tailed deer in south Texas. *J. Range Manag.* 21:158–164.
- Cheney, P. and A. Sullivan. 1997. Grassfires: Fuel, Weather and Fire Behaviour. Collingwood, Australia: CSIRO Publishing. 160 p.
- Clarke, P. J., P. K. Latz, and D. E. Albrecht. 2005. Long-term changes in semi-arid vegetation: invasion of an exotic perennial grass has larger effects than rainfall variability. *J. Veg. Sci.* 16:237–248.
- Copeland, T. E., W. Sluis, and H. F. Howe. 2002. Fire season and dominance in an Illinois tallgrass prairie restoration. *Restor. Ecol.* 10: 315–323.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annu. Rev. Ecol. Syst.* 23:63–87.
- Diamond, D. D. and F. E. Smeins. 1988. Gradient analysis of remnant true and upper coastal prairie grasslands of North America. *Can. J. Botany* 66:2152–2161.
- DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Sci.* 48:255–265.
- DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. *Weed Sci.* 47:233–242.
- Dow Agrosiences. Range and Pasture. <http://www.dowagro.com/range/products/treatments/low.htm>. Accessed: December 6, 2010.
- Fairfax, R. J. and R. J. Fensham. 2000. The effect of exotic pasture development on floristic diversity in central Queensland, Australia. *Biol. Conserv.* 94:11–21.
- Franklin, K. A., K. Lyons, P. L. Nagler, D. Lampkin, E. P. Glenn, F. Molina-Freaner, T. Markow, and A. R. Huete. 2006. Buffelgrass (*Pennisetum ciliare*) land conversion and productivity in the plains of Sonora, Mexico. *Biol. Conserv.* 127:62–71.
- Gabbard, B. L. and N. L. Fowler. 2006. Wide ecological amplitude of a diversity-reducing invasive grass. *Biol. Invasions* 9:149–160.
- Gibson, D. J. and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72:175–185.
- Gould, F. W. 1975. The Grasses of Texas. College Station, TX: Texas A&M University Press. 654 p.
- Grace, J. B. 1998. Can prescribed fire save the endangered coastal prairie ecosystem from Chinese tallow invasion? *Endangered Species UPDATE* 15:70–76.
- Grace, J. B., L. Allain, and C. Allen. 2000. Factors associated with plant species richness in a coastal tallgrass prairie. *J. Veg. Sci.* 11:443–452.
- Grace, J. B., A. Owens, and L. Allain. 2005. Fireloggers User's Manual. U.S. Geological Survey Open-File Report 2005–1212. 24 p.
- Grace, J. B., M. D. Smith, S. L. Grace, S. L. Collins, and T. J. Stohlgren. 2001. Interactions between fire and invasive plants in temperate grasslands of North America. Pages 40–65 in K.E.M. Galley and T. P. Wilson, eds. *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species*. Misc. Publ. 11. Tallahassee, FL: Tall Timbers Research Station.
- Grossman, D. H., K. L. Goodin, and C. L. Reuss. 1994. Rare Plant Communities of the Conterminous United States. Arlington, VA: The Nature Conservancy. 620 p.
- Hansmire, J. A., D. L. Drawe, D. B. Wester, and C. M. Britton. 1988. Effects of winter burns on forbs and grasses of the Texas coastal prairie. *Southwest. Nat.* 33:333–338.

- Harnis, R. O. and R. B. Murray. 1973. 30 years of vegetal change following burning of sagebrush-grass range. *J. Range Manag.* 26: 322–325.
- Hartley, M. K., W. E. Rogers, E. Siemann, and J. Grace. 2007. Responses of prairie arthropod communities to fire and fertilizer: balancing plant and arthropod conservation. *Am. Midl. Nat.* 157: 92–105.
- Hickman, K. R., G. H. Farley, R. Channell, and J. E. Steier. 2006. Effects of old world bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. *Southwest. Nat.* 51:524–530.
- Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity and invasion: implications for conservation. *Conserv. Biol.* 6:324–337.
- Howe, H. F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. *Conserv. Biol.* 8:691–704.
- Janecka, J. E., T. L. Blankenship, D. H. Hirth, C. W. Kilpatrick, M. E. Tewes, and L. I. Grassman, Jr. 2007. Evidence of male-biased dispersal in bobcats *Lynx rufus* using relatedness analysis. *Wildl. Biol.* 13:38–47.
- Johnson, S. D., K. C. Horn, A. M. Savage, S. Windhager, M. T. Simmons, and J. A. Rudgers. 2008. Timing of prescribed burns affects abundance and composition of arthropods in the Texas hill country. *Southwest. Nat.* 53:137–145.
- Keeley, J. E. 2001. Fire and invasive species in Mediterranean-climate ecosystems of California. Pages 81–94 in K.E.M. Galley and T. P. Wilson, eds. *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species*. Misc. Publ. 11. Tallahassee, FL: Tall Timbers Research Station.
- Keeley, J. E. 2006. Fire management impacts on invasive plants in the western United States. *Conserv. Biol.* 20:375–384.
- Kennard, D. K., J. J. O'Brien, and K. Outcalt. 2005. Comparing techniques for estimating fire temperature and intensity. *Fire Ecol.* 1: 70–84.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. *Global Environ. Change* 6:37–52.
- Kreuter, U. P., H. E. Amestoy, D. N. Ueckert, and W. A. McGinty. 2001. Adoption of brush busters: results of Texas county extension survey. *J. Range Manag.* 54:630–639.
- Kyser, G. B. and J. M. DiTomaso. 2002. Instability in a grassland community after the control of yellow starthistle (*Centaurea solstitialis*) with prescribed burning. *Weed Sci.* 50:648–657.
- Leach, M. K. and T. J. Givnish. 1996. Ecological determinant of species loss in remnant prairies. *Science* 273:1555–1558.
- Lehman, V. M. 1984. Bobwhites in the Rio Grande Plain of Texas. College Station, TX: Texas A&M University Press. 544 p.
- Luke, R. H. and A. G. McArthur. 1978. Bushfires in Australia. Canberra, Australia: Australian Government Publishing Service. 359 p.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145–165.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10:689–710.
- Martin, M., J. Cox, F. Ibarra, D. Alston, R. Banner, and J. Malecheck. 1999. Spittlebug and buffelgrass responses to summer fires in Mexico. *J. Range Manag.* 52:621–625.
- Mayeux, H. S., Jr. and W. T. Hamilton. 1983. Response of common goldenweed (*Isocoma coronopifolia*) and buffelgrass (*Cenchrus ciliaris*) to fire and soil. *Weed Sci.* 31:355–360.
- McCune, B. and J. B. Grace. 2002. Analysis of Ecological Communities. Gleneden Beach, OR: MjM Software Design. 300 p.
- McCune, B. and M. J. Mefford. 1999. PC-ORD: Multivariate Analysis of Ecological Data. Ver. 4.41. Medford, OR: MjM Software Design. 6 p.
- McGinty, A. and D. N. Ueckert. 1997. Brush Busters: How to Beat Mesquite. College Station, TX: Texas Agricultural Extension Service & Texas Agricultural Experiment Station. Leaflet L-5144. 2 p.
- McGinty, A., J. F. Cadenhead, W. Hamilton, W. C. Hanselka, D. N. Ueckert, and S. G. Whisenant. 2000. Chemical Weed and Brush Control Suggestions for Rangeland. College Station, TX: Texas Agricultural Extension Service Bulletin B-1466. 27 p.
- McHenry, W. B. and A. H. Murphy. 1985. Weed management of California rangeland. Pages 413–423 in E. A. Kurtz and F. O. Colbert, eds. *Principles of Weed Control in California*. Fresno, CA: Thomson Publishing.
- Mooney, H. A., R. N. Mack, J. A. McNeely, L. E. Neville, P. J. Schei, and J. K. Waage. 2005. *Invasive Alien Species: A New Synthesis*. Washington, DC: Island Press. 368 p.
- Omega, Inc. 2011. OMEGALAQ® Liquid Temperature Lacquers. <http://www.omega.com/pptst/LAQ.html>. Accessed: November 14, 2011.
- Owens, A. B., C. E. Proffitt, and J. B. Grace. 2007. Prescribed fire and cutting as tools for reducing woody plant succession in a created salt marsh. *Wetland Ecol. Manag.* 15:405–416.
- Pase, C. P. 1971. Effects of a February burn on Lehmann lovegrass. *J. Range Manag.* 24:454–456.
- Pavlovic, N. B., S. A. Leicht-Young, and R. Grundel. 2011. Short-term effects of burn season on flowering phenology of savanna plants. *Plant Ecol.* 212:611–625.
- Pickett, S.T.A. 1982. Population patterns through twenty years of old field succession. *Vegetatio* 49:45–59.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52:273–288.
- Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Divers. Distrib.* 9:169–176.
- Rothermel, R. C. and J. E. Deeming. 1980. Measuring and interpreting fire behavior for correlation with fire effects. Washington, DC: US Dept of Agriculture, Forest Service, General Technical Report INT-93. 3 p.
- Ruckman, E. M., S. Schwinning, and K. G. Lyons. 2011. Effects of phenology at burn time on post-fire recovery of an invasive C₄ grass. *Restor. Ecol.* doi: 10.1111/j.1526-100X.2011.00830.x.
- Sands, J. P., L. A. Brennan, F. Hernández, W. P. Kuvlesky, J. F. Gallagher, D. C. Ruthven, and J. E. Pittman. 2009. Impacts of buffelgrass (*Pennisetum ciliare*) on a forb community in South Texas. *Invasive Plant. Sci. Manag.* 2:130–140.
- Scifres, C. J., J. L. Mutz, R. E. Whitson, and D. L. Drawe. 1982. Interrelationships of huisache canopy cover with range forage on the coastal prairie. *J. Range Manag.* 35:558–562.
- Scifres, C. J., T. W. Oldham, P. D. Teel, and D. L. Drawe. 1988. Gulf Coast tick (*Amblyomma maculatum*) populations and responses to burning of coastal prairie habitats. *Southwest. Nat.* 33:55–64.
- Shay, J., D. Kunec, and B. Dyck. 2001. Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Manitoba. *Plant Ecol.* 155:157–167.
- Simmons, M. T., S. Windhager, P. Power, J. Lott, R. K. Lyons, and C. Schwoppe. 2007. Selective and non-selective control of invasive plants: the short-term effects of growing-season prescribed fire, herbicide and mowing in two Texas prairies. *Restor. Ecol.* 15:662–669.
- Sluis, W. J. 2002. Patterns of species richness and composition in a re-created grassland. *Restor. Ecol.* 10:677–684.
- Smeins, F. E., D. D. Diamond, and C. W. Hanselka. 1991. Coastal prairie. Pages 269–290 in R. T. Coupland, ed. *Natural Grasslands: Introduction and Western Hemisphere. Ecosystems of the World*. Vol. 8A. Amsterdam, The Netherlands: Elsevier.
- Stevens, J. and D. A. Falk. 2009. Can buffelgrass invasions be controlled in the American southwest? Using invasion ecology theory to understand buffelgrass success and develop comprehensive restoration and management. *Ecol. Restor.* 27:417–427.

- Suding, K. N. and K. L. Gross. 2006. Modifying native and exotic species richness correlations: the influence of fire and seed addition. *Ecol. Appl.* 16:1319–1326.
- Taylor, C. A., Jr., D. Twidwell, N. E. Garza, C. Rosser, J. K. Hoffman, and T. D. Brooks. 2012. Long-term effects of fire, livestock herbivory removal, and weather variability in Texas semiarid savanna. *Rangeland Ecol. Manag.* 65:21–30.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179–2191.
- Towne, E. G. and K. E. Kemp. 2008. Long-term response patterns of tallgrass prairie to frequent summer burning. *Rangeland Ecol. Manag.* 61:509–520.
- Twidwell, D. 2012. From Theory to Application: Extreme Fire, Resilience, Restoration, and Education in Social-Ecological Disciplines. Ph.D. dissertation. College Station, TX: Texas A&M University.
- Twidwell, D., S. D. Fuhlendorf, D. M. Engle, and C. A. Taylor, Jr. 2009. Surface fuel sampling strategies: linking fuel measurements and fire effects. *Rangeland Ecol. Manag.* 62:223–229.
- USDA, NRCS. 2011. The PLANTS Database. National Data Center, Baton Rouge, Louisiana. <http://plants.usda.gov>. Accessed: May 2011.
- Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annu. Rev. Ecol. Syst.* 31:197–215.
- Wittich, K. P. 2011. Phenological observations of grass curing in Germany. *Int. J. Biometeorol.* 55:313–318.
- Wright, H. A. 1974. Range burning. *J. Range Manag.* 27:5–11.

Received March 8, 2012, and approved April 6, 2012.