The Dissertation Committee for Emily Mary Booth certifies that this is the approved version of the following dissertation:

Factors Determining Post-Wildfire Plant Community Recovery Trajectories in Central Texas

Committee:

Norma Fowler, Supervisor

Kenneth Dunton

Christine Hawkes

Shalene Jha

Stanley Roux

Factors Determining Post-Wildfire Plant Community Recovery Trajectories in Central Texas

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Emily Mary Booth

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Dedication

Pour mon oncle, Philippe Plailly, dont l’esprit aventureux, l’énergie implacable, et l’amour de la science et de l’art m'inspirent pour toujours continuer à explorer.

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Factors Determining Post-Wildfire Plant Community Recovery Trajectories in Central Texas

Emily Mary Booth, Ph.D.
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Supervisor: Norma Fowler

Wildland fires are becoming more frequent and more severe in the United States, due in part to climate change and in part to long-term fire suppression and the subsequent build-up of fuels. Following wildfires of greater severity than what were historically present in an area, plant community recovery trajectories may diverge from the pre-disturbance plant community.

The Lost Pines region of central Texas supported the westernmost stands of loblolly pine (*Pinus taeda*) in the United States. In 2011, a wildfire burned most of Bastrop State Park (BSP), located in the Lost Pines. Pre-fire, BSP was a mostly closed-canopy forest dominated by loblolly pine and several species of oak (*Quercus* spp.), with sparse herbaceous vegetation and a dense mid-canopy of yaupon (*Ilex vomitoria*). Most plants in BSP were either killed or top-killed in the wildfire. We studied pre- and post-fire plant community dynamics to understand and predict post-fire plant community recovery trajectories.

Top-killed oak species sprouted vigorously in more severely-burned plots (Chapter 1, Chapter 2); yaupon sprouted in all burn severity classes (Chapter 3). Loblolly pine, which can only recruit from seed, established more slowly than sprouting species, in part due to the transitory inhibitory effect of an erosion control product (Chapter 3). In the first year after the fire, it appeared that oak sprouts might out-compete loblolly pine seedling recruitment. However, in 2015, a large loblolly pine recruitment event occurred following a year of unusually high precipitation (Chapter 1, Chapter 2). These results indicate recovery trajectories towards continued survival of the loblolly pine population in BSP, although with a potentially greater abundance of oak species than what was present pre-fire. Furthermore, yaupon is likely to re-form dense thickets such as those present pre-fire without measures to prevent woody plant encroachment.

Immediately post-fire, the herbaceous plant community increased in abundance, richness and diversity, likely due to greater canopy openness (Chapter 4). Very few invasive species were present either pre- or post-fire (Chapter 5). Alternate trajectories towards open-canopy savanna with a diverse understory community and lower mid-story tree abundance could be maintained by management actions such as prescribed fire or mechanical thinning.

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ABSTRACT

Objective

Alterations to historic disturbance regimes can have lasting effects on plant community trajectories. The Lost Pines region of central Texas supports the westernmost stands of loblolly pine (*Pinus taeda*) in the United States. In 2011, a wildfire burned most of Bastrop State Park (BSP), located in the Lost Pines region of central Texas. Pre-fire, the Lost Pines was dominated by loblolly pine and several species of oak (primarily *Quercus margaretta* and *Q. marilandica*), and historically was likely maintained by frequent, low-severity fire. Post-fire recovery trajectories could move the Lost Pines back towards the pre-fire pine-oak forest community, oak-dominated woodland, or pine-oak savanna. We studied pre- and post-fire tree dynamics to better understand and predict post-disturbance woody plant community recovery trajectories.

Methods

Fifty-six 20m x 50m permanent plots were established in Bastrop State Park and surveyed between 1999-2015. Data were collected on three tree size classes in size-dependent subplots: seedlings (loblolly pine) / basal sprouts (oaks), saplings, and mature trees. Within each subplot, individuals were identified to species and counted. We combined these data with information about burn severity, soil types, canopy cover, elevation, and aspect.

Results

Most woody plants were killed or top-killed in the fire, and oaks sprouted vigorously where top-killed. Burn severity and canopy cover are negatively correlated, which is expected, because burn severity is partly determined by mature tree mortality. Mature loblolly pine and sand post oak numbers were negatively related to one or the other of these variables in each post-fire year. Unexpectedly, we did not find any relationship between burn severity or canopy cover on loblolly pine seedling or oak basal sprout numbers. In 2015, following heavy rainfall, there was a large recruitment event of loblolly pine seedlings, and significantly greater numbers of loblolly pine seedlings in areas with more loblolly pine mature trees.

Conclusions

Recovery trajectories in the Lost Pines were not apparent immediately post-fire due to a time lag in pine recruitment. Initial oak sprouting appeared to outpace loblolly seedling recruitment, which suggested a trajectory towards oak domination; three years after the fire, pine recruitment made this future much less likely. Trajectories towards an oak-pine savanna is more likely, especially with management interventions to maintain the open canopy, such as prescribed burning. Our results illustrate the importance of understanding the complexity of pre- and post-fire plant community dynamics to better predict future trajectories and develop more effective restoration plans.

INTRODUCTION

Disturbances, such as wildland fire, shape plant community composition and structure over time (Bond and Keeley 2005, Hanberry 2014, Hernandez-Serrano et al. 2013, Hessburg et al. 2005, Naiman et al. 1993, Nowacki and Abrams 2008, Ward et al. 1999). Wildland fire can play many different roles: surface fires maintain many savannas (Bond and Keeley 2005, Fill et al. 2015, Nowacki and Abrams 2008, Peterson and Reich 2001, van Langevelde et al. 2003), crown fires often re-start succession (Turner et al. 1999, Turner et al. 2003), and some fires, particularly those different in severity from the historical fire regime, may lead a plant community towards a new trajectory (Kane et al. 2013, Urza and Sibold 2017). The drivers of ecosystem change following large wildfires are poorly understood; our study examines recovery trajectories following a wildfire of unprecedented severity to elucidate these drivers and additional complexities.

Changes to historical fire regimes can change plant community composition, which in turn may alter fire behavior and subsequent vegetation recovery trajectories (Stevens-Rumann et al. 2004, Turner 2010). Trajectories of community change after disturbance can be understood in part through legacy effects (James et al. 2007, Carillo et al. 2012, Cuddington 2011). Legacy effects are lasting impacts of a species or management action that affect future biotic community composition (Cuddington 2011, Foster et al. 2003). They may include instances in which early successional species affect future plant community composition (Kepfer-Rojas et al. 2015) by altering plant-soil feedbacks (Kardol et al. 2007, van de Voorde et al. 2011), soil microbial relationships with plants (Grove et al. 2012), or seed availability (Brown et al. 2015, Larson and Franklin 2005). Land-use history, such as logging, agriculture or anthropogenically altered fire regimes can also have persistent impacts on vegetation, soil, and nutrient dynamics (Bellemare and

Motzkin 2002, Foster et al. 2003, Kepfer-Rojas et al. 2015, McGranahan et al. 2015). Here, we address legacy effects as biotic or abiotic conditions that persist after disturbance.

Transient dynamics can also be a helpful concept for understanding population dynamics (Ellis and Crone 2013) in systems that experience frequent disturbance (Hastings 2004, Koons et al. 2005, Fukami and Nakajima 2011). Transient dynamics include time lags, in which response to disturbance is delayed. Time-lagged responses to disturbance can occur across taxa (Abrahamson and Layne 2002, Crooks 2005, du Toit et al. 2016, Milchunas and Lauenroth 1995, Verdenschot et al., Willig et al. 2010), often with species-specific responses. Post-disturbance establishment of plant species varies by life history traits, timing of establishment in relation to other species, and severity of disturbance (Zobel and Antos 2009). Transient dynamics and time-lagged responses can provide opportunities for earlier-establishing species to out-compete later-establishing species, potentially affecting future plant community assemblages following disturbance.

Wildland fires are disturbances which, as much of the US become warmer and drier, are becoming more frequent (Dennison et al. 2014; Settele et al. 2014; Westerling et al. 2006) and more severe (Banner et al. 2010, Dillon et al. 2011, IPCC 2013, Miller and Safford 2012). Wildland fire can influence community assembly by shaping the traits and organisms found within an environment (Bond and Keeley 2005), and by altering spatial patterns of vegetation (Menges and Hawkes 1998, Ooi et al. 2006). Fire intensity and burn severity (the effects of fire on biotic and abiotic characteristics of the burned area) partly determine future trajectories of biotic communities (Bernhardt et al. 2011, Collins 1992, Duguy and Vallejo 2008, Freeman and Kobziar 2011, Hartnett 2007, Turner et al. 1997).

We investigated the effects of a mixed-severity wildfire that killed or top-killed most trees in a mostly closed-canopy pine-oak woodland in central Texas. We analyzed data from the first four years after the wildfire to describe the changes that occurred during that period and to help predict possible future trajectories for the developing plant community. As disturbance regimes and ecosystem responses to disturbance change (Turner 2010), it is increasingly important that we study plant community responses to more frequent and more severe fires, and the complex ways in which wildland fire, legacies, and transient dynamics alter plant community recovery trajectories.

Our hypotheses were:

1) Areas of greater burn severity, and so a more open canopy, will have more pine seedlings where there are sources of pine seeds, and more oak basal sprouts.
2) The gravelly upland soils will favor oaks, while sandy soils downslope will favor pines.
3) The initial post-fire colonists or survivors will maintain dominance and affect the trajectory in future years. As a result, chance and legacy effects will play an important role in post-fire trajectories.

METHODS

Study Area

The Lost Pines of central Texas are the westernmost stands of loblolly pine (*Pinus taeda* L.) in the United States. They support a diverse plant community that includes several native species of oak, including sand post oak (*Quercus margaretta* [Ashe] Small), blackjack oak (*Q. marilandica* Münchh.), and post oak (*Q. stellata* Wangenh.), as well as loblolly pine. Bastrop State Park (BSP), in the Lost Pines, was logged between 1900 and 1940 and largely fire-suppressed until 2011 (Stambaugh *et al*. 2017). In September 2011, the Bastrop County Complex wildfire burned much of the Lost Pines, including almost all of BSP, during a record drought and heat wave (Hoerling *et al*. 2013), and most mature trees were killed or top-killed. Following the fire, the recovery of the pine population was of substantial public and management concern.

It is thought that the vegetation of the Lost Pines region historically had more open canopies, that is, savannas rather than forests, and perhaps more oak than it had pre-fire, in 2011 (Stambaugh *et al*. 2017). These savannas would have been maintained by frequent, low-intensity surface fires (Stambaugh *et al*. 2014).

Data Collection

Forty-six 20m x 50m permanent plots were established in Bastrop State Park (Fig. 1.1, QGIS 2.18.9, QGIS Development Team 2009, Open Source Geospatial Foundation) between 1999-2012 and surveyed following Fire Monitoring Handbook (FMH) protocols (USDI National Park Service 2003). Each plot included three subplots, one for each size class (Fig. 1.2). In each subplot we we recorded all individuals of the given size classes of tree species: seedling or basal sprout (diameter at breast height [DBH]<2.5cm, 5m x 10m subplot), sapling (DBH ≥2.5 and ≤15cm, 20m x 10m subplot), and mature (DBH>15cm, 20m x 50m full plot). We here refer to *P. taeda* individuals in the first size class as 'seedlings', following language found in the FMH; these 'seedlings' had germinated after the fire, though developmentally they were not necessarily still seedlings at the time of our surveys. We refer to oak stems in the first size class as 'basal sprouts' because all observed stems in this size class had sprouted after the fire from the base of a parent tree. FMH protocols do not distinguish between stems from the same parent tree and stems from another parent tree in the same subplot. In each subplot, individuals (or basal sprouts, in the case of the first oak size class) of all size classes were identified to species and counted. Mature trees were tagged and the same trees were re-measured each year. Annual samples of each plot were irregularly made from 1999 through 2011, on dates that varied from May through October. Each plot was sampled once a year from 2012 through 2015, in May, June, or July.

Burn severity of plots was determined immediately post-fire in September 2011, using the FMH assessment protocol (USDI National Park Service 2003), which is based on degree of consumption of vegetation and substrate. Plots were assigned one of five burn severity classes (in order from least to greatest severity: unburned, scorched, light, moderate, and heavy). No plots surveyed post-fire were unburned. Canopy cover was measured at multiple points per plot in some pre-fire and all post-fire surveys using a canopy densiometer, then averaged for each plot each year.

Soil data was obtained from the Soil Survey Geographic (SSURGO) Database. SSURGO soil types were first ground-truthed and modified where necessary to accurately reflect local soil texture, then re-classified as either ‘sandy’ or ‘gravelly’ (Appendix A) for increased statistical power and ease of interpretation. Elevation, slope, and aspect were extracted from topographic maps provided by BSP (G. Creacy).

Statistical Analyses

Pre-fire data from 1999-2011 were pooled into one ‘year’ to compare with post-fire data. We pooled these data rather than using only data from 2010, one year before the fire, because not all plots were surveyed every year pre-fire. When necessary to obtain larger sample sizes, data from each burn severity class were pooled into two new classes: scorched or light burn, and moderate or heavy burn. We examined the effects of burn severity, soil type, elevation, slope, aspect, and previous year’s abundance on the numbers of individuals or basal sprouts of loblolly pines and oaks in each size class in each year. Killed and top-killed trees were not included in our statistical models of mature tree numbers. The effects of canopy cover and mature tree numbers were only used as predictor variables in analyses of seedling and basal sprout numbers. Interaction terms were tested, and but did not have enough effect to be included in the final models. Only the first size class (basal sprouts <2.5cm DBH) of blackjack oak had sample sizes sufficient for these analyses. No size class of post oak had sufficient sample sizes for these analyses.

Statistical analyses were completed using the GLIMMIX procedure of SAS 9.2 (SAS Institute, Cary, North Carolina, USA). Generalized linear models using the negative binomial distribution with the default log link function were fit to each species - size class - year combination separately. Preliminary analyses found that the Poisson and normal distributions did not give good fits to the data, while the negative binomial did. For each species - size class - year combination, the best model was determined by forward selection, adding one variable at a time. At each step, the AICc values of all possible models with one additional variable were compared, and the variable that most decreased AICc was added to the model. No additional variables were added to a model if AICc did not decrease by two or more. Once the best model for a given response variable had been identified by this procedure, we examined the significance (*P*-value) of each included predictor variable in this final model.

Because of the large number of models, we used a Bonferroni correction to determine a suitable alpha. There were 3 size classes x 5 years of loblolly pine and sand post oak, plus 1 size class x 5 years of blackjack oak, for a total of 35 models, and therefore an adjusted alpha of $p = 0.0014$ was used. Predicted means and confidence limits were back-transformed for tables and figures.

RESULTS

66.4% of the mature oak trees present in the plots before the fire were killed or top-killed by 2013 (Table 1.1); almost all of these were only top-killed and had basal sprouts. 87.4% of the mature *P. taeda* trees present in the plots before the fire were killed by the fire by 2013 (Table 1.1). We calculated these comparing pre-fire numbers to numbers in 2013, instead of numbers immediately post-fire, to account for delayed mortality due to fire damage and drought.

Seedlings and basal sprout densities of all species increased (Table 1.1). Loblolly pine seedling numbers increased greatly in lower burn severity classes between pre-fire and 2015, with an almost 200-fold increase in scorched plots (Table 1.1).

After the fire, there was relatively little loblolly pine recruitment until an unusually wet 12 month period (1173 mm July 2014 through June 2015, versus 644 mm to 792 mm in the preceding three July-June periods, Table 1.2), when there was a significant positive relationship between the number of loblolly pine seedlings and numbers of mature trees in

2015. Estimated loblolly pine seedling densities in 2015 ranged from 535.6 seedlings/ha in the most severely burned areas to 79,400 seedlings/ha in the lightly burned areas (Table 1.1). If no further recruitment were to occur, moderate survival rates would be sufficient to replace the pre-fire trees in all but the most heavily burned areas (Table 1.3).

More loblolly pine mature trees were found pre-fire in plots at higher elevations (Table 1.4), although the elevational range was small (62m), indicating that elevation may be standing in for another variable, likely moisture availability. Greater numbers of pre-fire mature sand post oak mature trees and of 2015 blackjack oak basal sprouts were found in plots with gravelly, rather than sandy, soils (Fig. 1.3, Tables 1.5 and 1.6).

The sampling design involved re-sampling the same subplots in each plot each year and so surviving individuals were re-sampled in subsequent years. Therefore we expected, and found, that the number of individuals or stems in the previous year, which was a covariate tested for inclusion in each model, was often an excellent predictor of the number of individuals or stems the following year (Fig. 1.4, Tables 1.4-1.6). A consequence of this is that an environmental factor may be significant only in the first year; after that its role in the model may be taken by numbers of individuals or basal sprouts in the previous year. This may explain why the effects of elevation on loblolly pine mature trees and soil type on sand post oak mature trees only reached significance in the pre-fire models, for which previous year numbers were not available.

We did not find significant effects in any year of burn severity on seedlings, basal sprouts, or saplings. There were few saplings of any species, so detecting any effects on them was problematic, and none were detected.

Burn severity and canopy cover were negatively correlated in every year (Table 1.7), which is expected because burn severity is partly determined by tree mortality. Either burn severity or the resulting low canopy cover were each closely related with the number of post-fire mature loblolly pine and sand post oak trees (Fig. 1.5, Tables 1.4 and 1.5). The expected negative association between burn severity and mature tree numbers reached significance for loblolly pine in 2014 and for sand post oak in 2014 and 2015 (Tables 1.5 and 1.6).

Less expected was the lack of consistent relationship between oak basal sprouts and numbers of mature (and not top-killed) trees in the same year. This relationship was weakly positive for sand post oak basal sprouts in 2013 and 2015, and weakly negative for sand post oak basal sprouts in 2012 and blackjack oak basal sprouts in 2012 and 2013 (Tables 1.5 and 1.6). We expected that a greater number of mature trees in a plot would produce more basal sprouts. However, because so many oaks were top-killed, most basal sprouts were growing on top-killed trees.

DISCUSSION

Post-fire sprouting of oaks from parent plant material provides evidence consistent with legacy effects due directly to pre-fire conditions. In the first three post-fire years, it appeared that oak sprouts might outcompete pine seedlings, which would be consistent with our hypothesis that initial post-fire colonists or survivors would remain dominant in the future. However, pine seedling recruitment was time-lagged: seeds were water-limited rather than light-limited, and germinated in large numbers following an unusually rainy year in 2015. This indicates that while legacy effects and initial post-fire plant establishment may play a role in determining future plant community trajectories, time lags related to stochastic events may play a larger role in this case. Therefore, it is important to consider limiting factors to the establishment of dominant species and the ways in which they might be affected by weather and other disturbance events when predicting future trajectories.

Legacy effects

We define legacy effects as those due, directly or indirectly, to pre-fire conditions. For example, the pre-fire plant community structure can affect burn severity, which in turn can affect post-fire plant communities (Harris and Taylor 2015, Keyser et al. 2008, Lee et al. 2009). In our plots, burn severity was negatively related to pre-fire canopy cover (r_s = -0.47, Table 8). Canopy cover was not measured consistently pre-fire, and was measured in only 26 out of 56 total plots pre-fire. There may have been more plots with lower pre-fire canopy cover that burned more severely by chance. The fire was large and fast-moving enough that even in areas with was slightly less canopy, the crown fire would have been maintained.

The most evident legacy was the surviving oak trees. Enough survived without being top-killed to create a significant positive relationship between the number of mature sand post oak trees pre-fire and the number of mature sand post oak trees post-fire. Although many oaks were top-killed, almost all of these trees sprouted vigorously. Many other oak species sprout vigorously after high-severity fire (Cocking et al. 2014, Fulé et al. 2000, Hammett et al. 2017, Maguire and Menges 2011, Varner et al. 2016). Sprouting plant species can produce shoots by drawing on resources from the live root starch reserves of the parent tree, even when top-killed (Chapin et al. 1990; Schutz et al. 2009), which can allow them to out-compete conifers (Barton 2002, Goforth and Minnich 2008). These basal sprouts can be considered another legacy. There was no observed regeneration of any oak species from seeds in our plots, but the vigorous sprouting of each oak species make it likely that their densities will be maintained in the future, even with a degree of self-thinning.

We expected to see a relationship between numbers of pre-fire sand post oak mature trees and numbers of post-fire basal sprouts of this species, but there was no evidence of such a relationship. However, data were collected using a protocol that counted individual sprouts, instead of sprouts per tree (see Methods), and variation among individual trees in sprout numbers may have hidden such a relationship.

Permanent environmental factors, such as soil type and elevation, may create legacy effects via their effects on the pre-fire plant community, but they can also have direct post-fire effects; the two are not mutually exclusive. Based on verbal reports and our own casual observations, we expected to find that gravelly upland soils would favor oak species, and that sandy downslope soils would favor loblolly pine. However, elevation and soil type had a very weak relationship, if any, among our plots ($N = 56$, $F = 0.37$, $p = 0.5$). Pre-fire, there were significantly more loblolly pine mature individuals at higher elevations, and significantly more sand post oak mature trees in sandy soils. In another study (Booth 2017), we found that loblolly pine seedlings were larger in gravelly soils. A study in the Lost Pines by Brown et al. (2014) found that post-fire survivorship of planted loblolly pine seedlings was higher in gravelly soils. After the fire, sprouts of sand post oak tended to be more common in sandy soils, and sprouts of blackjack oak tended to be more common in gravelly soils, suggesting the possibility of some degree of niche separation between these two oak species. There may also be some niche separation between loblolly pine and sand post oak, with former favored by gravelly soils and the latter by sandy soils.

Time lags and transient dynamics

Prior to 2015, there was concern that loblolly pine seedlings might be outcompeted by vigorously sprouting blackjack oak (Stambaugh et al. 2017). However, loblolly pine seedling numbers increased sharply in lower burn severity plots in 2015. The time-lagged loblolly pine seedling recruitment can be partly explained by the increase in rainfall (Table 3), allowing more seeds to germinate and survive. Timing of rainfall has been shown cause time-lagged seedling emergence in other ecosystems (Arredondo et al. 2016, Reichmann et al. 2013) on both seasonal (Ooi et al. 2004) and decadal (Tomback et al. 1993) timescales. The lag may also have been partially due to temporal variation in pine seed production, which is known to vary among years (Calama and Montero 2007; Koenig and Knops 2000; Krannitz and Duralia 2004). In 2014 and 2015, loblolly pine trees produced more seed than usual (G. Creacy, pers. comm.).

Loblolly pine seeds require high light availability to germinate and establish (Mclemore 1971, Mitchell et al. 1999). We expected higher loblolly pine seedling counts in plots with higher burn severity and therefore lower canopy cover and fewer mature loblolly pine trees, because there would be increased light availability and less competition from surviving plants in those plots (Dzwonko et al. 2015). However, the number of loblolly pine seedlings was positively correlated with the number of mature loblolly pine trees in 2015, and a trend for there to be more loblolly pine seedlings in less severely burned plots. The mostly likely explanation is that the greater number of surviving mature trees in and near the less severely burned plots received more loblolly pine seeds than did the more severely burned plots, and that the effects of seed input outweighed those of competition. Seed limitation is a common factor influencing post-disturbance seedling recruitment (Landis et al. 2005, Weyenberg et al. 2004), and post-fire conifer seedling densities are often low in high burn severity areas due increased distance to seed trees (Borchert et al. 2003, Kemp et al. 2016, Pierce and Taylor 2011, Rother and Veblen 2016, Welch et al. 2016). Our results are also consistent with results from another study in BSP by Lee and Chow (2015), which found that NDVI levels increased more quickly in areas burned at a lower severity.

Burn severity was not a significant predictor of sand post oak or loblolly pine mature tree numbers until 2014, when significantly fewer mature trees were found in higher burn severity plots than in lower burn severity plots, as expected. The delay likely occurred because initial mature tree counts included fire-injured trees defined as 'live' using the FMH burn classification system, that later died. Delayed mortality post-fire is common and occurs across woody plant genera (Engber and Varner 2012, Fulé et al. 2007, Ganio and Progar 2017).

Alternate trajectories

In old-field plant community studies in the southeastern U.S., loblolly pine often acts as an early woody dominant (De Steven 1991) within the framework of the classic deterministic model of succession, in which plant assemblages move linearly towards a predictable climax community (Clements 1916). However, the Lost Pines ecoregion differs from old-field communities in composition and structure, and instead may be more analogous to longleaf pine (*Pinus palustris* Mill.)-wiregrass (*Aristida stricta* Michx.) systems of the southeastern U.S. and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson)-gambel oak (*Quercus gambelii* Nutt.) forests of the southwestern U.S. These systems are better described by vegetation-fire feedback models, in which a persistent biotic community is maintained by fire cycles (Fill et al. 2015). The fire return interval in the Oak Woods and Prairies ecoregion of Texas, in which the Lost Pines region is located, likely had relatively frequent and low severity fires, with a mean fire interval between 2.4-10.9 years (Stambaugh et al. 2014, Stambaugh et al. 2017). This is similar to historical fire regimes in ponderosa pine-gambel oak forests in the southwestern U.S. (Guiterman et al. 2015) and *P. palustris* savannas in the southeastern U.S. (Chapman 1932, Glitzenstein et al. 1995). These low severity fires were likely more often surface fires than crown fires, and likely killed few mature pine trees.

The Lost Pines was extensively logged and fire suppressed in the 20th century (Stambaugh et al. 2017). Post-wildfire recovery trajectories may follow novel pathways which diverge from pre-fire or pre-logging plant communities. Previous studies have shown that high-severity wildland fire may promote transitions from conifer dominance to sprouting oak dominance in pine-oak woodlands and forests (Cocking et al. 2014, Martin-Alcón and Coll 2016). Re-establishment of loblolly pine as the dominant woody plant species Lost Pines will depend partly on loblolly pine seedlings and trees surviving drought (Brown et al. 2014), and partly on competitive outcomes between species and on future management techniques. Loblolly pine seedlings were planted along roadways between 2013-2015, and their survival rate has been approximately 15%-65%, and greater in gravelly soils than in sandy soils (G. Creacy, pers. comm.). According to loblolly pine seedling densities in our plots, survival of natural regeneration would need to be 0.4% in order to replace pre-fire mature tree densities (Table 4). If the management goal was a more open-canopy savanna, loblolly seedling survival could be lower and still attain this goal. Because the 'seedlings' in the 2015 data were, for the most part, established juvenile plants rather than developmentally seedlings, adequate survival rates may be attained if no further fires occur. Additionally, oak basal sprouts appear to be self-thinning (Table 2). Therefore, it appears that loblolly pines are unlikely to be outcompeted by oak species in the future.

Immediately post-fire, the Lost Pines plant community had the potential to develop towards pine domination, towards oak domination, or towards a mixture of these species. By 2015, the latter seemed most likely, although the ratio of pines to oaks will depend upon pine seedling survival rates and whether or not regeneration by pines, by oaks, or by both occurs in the future. The future trajectory of BSP and the Lost Pines region, however, will depend primarily on management: will a closed canopy be allowed to develop? or will prescribed fire and/or mechanical thinning allow an oak-pine savanna to develop and persist? The latter would have the advantages of greater biodiversity (Booth 2017) and a lower risk of crown fires and, therefore, less wildfire danger to housing developments and other structures in the region. However, the public response to the fire has largely been to express a strong desire to have a closed-canopy forest throughout the Lost Pines, supported by vigorous volunteer efforts to plant pine seedlings (Harmon 2012). In our plots, natural regeneration combined with an absence of prescribed fire and mechanical thinning would probably produce such a forest without the need for planting pines. Future management decisions will therefore be critical.

CONCLUSIONS

Disturbance regimes can influence species composition (Scholtz et al. 2016), and management actions taken prior to and following disturbance can alter recovery trajectories (Dale et al. 1998). In developing restoration and other treatment plans, it is important to create appropriate disturbance regimes that are specific to management goals. Due to the difficulty in predicting responses to disturbance, some restoration efforts may be less successful than others, often depending on how success is defined for the study (Zedler 2007). Attempts to restore a system to a goal state can be helped by understanding factors influencing community assembly prior to disturbance. Legacy effects, time lags, and disturbance characteristics can shape post-fire community dynamics, and understanding potential alternative states in an ecosystem can be useful in determining restoration actions (Suding et al. 2004). Research linking plant community ecology and ecological restoration has only developed recently (Young et al. 2005). Our results illustrate the importance of understanding the complexity of pre- and post-fire plant community dynamics to better predict future trajectories and develop more effective restoration plans. More work is needed to clarify the relationships between legacies, short-term and long-term dynamics following novel disturbances in a changing climate.

Table 1.1. Mean stems ha-1 per plot of each size class of each species pre-fire, in 2013, and in 2015. Pre-fire densities are taken from the last year of data collection before the wildfire. Percent change is calculated between stem densities pre-fire and 2015.

		Scorched				Light burn			
Species	Size class	Pre-fire	2013	2015	% change	Pre-fire	2013	2015	% change
P. taeda	seedling	400.0	1,575.0	79,400.0	**19,750.0**	920.0	1,575.0	4,512.7	**390.5**
P. taeda	sapling	93.0	15.0	26.7	**-71.3**	120.0	0.0	163.6	**36.3**
P. taeda	adult	300.0	206.5	195.7	**-34.8**	300.0	41.3	45.6	**-84.8**
Q. margaretta	basal sprout	300.0	1,875.0	1,233.3	**311.1**	560.0	1,075.0	781.8	**39.6**
Q. margaretta	sapling	593.0	165.0	66.7	**-88.8**	280.0	30.0	101.8	**-63.6**
Q. margaretta	adult	246.9	145.7	121.7	**-50.7**	212.5	97.8	137.0	**-35.5**
Q. marilandica	basal sprout	0.0	50.0	66.7	**--**	480.0	2,775.0	1,327.3	**176.5**
Q. marilandica	sapling	60.0	15.0	13.3	**-77.8**	144.0	0.0	101.8	**-29.3**
Q. marilandica	adult	37.5	19.6	17.4	**-53.6**	50.0	2.2	4.3	**-91.4**

Table 1.1, continued. Mean stems ha-1 per plot of each size class of each species pre-fire, in 2013, and in 2015. Pre-fire densities are taken from the last year of data collection before the wildfire. Percent change is calculated between stem densities pre-fire and 2015.

		Moderate burn				Heavy burn			
Species	Size class	Pre-fire	2013	2015	% change	Pre-fire	2013	2015	% change
P. taeda	seedling	2,700.0	1,350.0	1,036.4	**-61.6**	750.0	25.0	535.6	**-28.6**
P. taeda	sapling	80.0	0.0	192.7	**140.9**	210.0	0.0	17.8	**-91.5**
P. taeda	adult	484.4	0.0	0.0	**-100.0**	881.3	0.0	0.0	**-100.0**
Q. margaretta	basal sprout	200.0	600.0	236.4	**18.2**	350.0	125.0	688.9	**96.8**
Q. margaretta	sapling	0.0	0.0	43.6	**--**	140.0	0.0	22.2	**-84.1**
Q. margaretta	adult	43.8	10.9	8.7	**-80.1**	121.9	0.0	0.0	**-100.0**
Q. marilandica	basal sprout	300.0	1,325.0	1,381.8	**360.6**	1,050.0	2,825.0	1,526.7	**45.4**
Q. marilandica	sapling	100.0	0.0	214.6	**114.6**	100.0	0.0	131.1	**31.1**
Q. marilandica	adult	34.4	4.4	6.5	**-81.1**	90.6	0.0	0.0	**-100.0**

Table 1.1, continued. Mean stems ha-1 per plot of each size class of each species pre-fire, in 2013, and in 2015. Pre-fire densities are taken from the last year of data collection before the wildfire. Percent change is calculated between stem densities pre-fire and 2015.

		Total			
Species	Size class	Pre-fire	2013	2015	% change
P. taeda	seedling	4,770.0	4,525.0	85,484.7	**1,692.1**
P. taeda	sapling	503.0	15.0	400.8	**-20.3**
P. taeda	adult	1,965.7	247.8	241.3	**-87.7**
Q. margaretta	basal sprout	1,410.0	3,675.0	2,940.4	**108.5**
Q. margaretta	sapling	1,013.0	195.0	234.3	**-76.9**
Q. margaretta	adult	625.1	254.4	267.4	**-57.2**
Q. marilandica	basal sprout	1,830.0	6,975.0	4,302.5	**135.1**
Q. marilandica	sapling	404.0	15.0	460.8	**14.1**
Q. marilandica	adult	212.5	26.2	28.2	**-86.7**

Table 1.2. Total monthly precipitation, 2011-2015 (mm) (NOAA 2016).

Month	2011	2012	2013	2014	2015
January	86.1	74.7	76.2	20.3	81.3
February	11.4	93	29.5	18	22.6
March	7.1	105.7	14.5	51.8	153.7
April	1.3	23.6	89.2	19.1	144.3
May	45	106.2	73.2	175	284.2
June	45.2	32.8	44.7	63	119.1
July	9.7	105.2	58.7	40.4	18.3
August	8.4	36.1	36.8	22.4	34
September	29.7	120.4	147.1	98.8	51.3
October	54.4	26.7	135.6	44.7	202.7
November	40.6	10.7	50.5	113.3	73.9
December	87.6	18	17	48.5	59.9

Table 1.3. Density of mean pre-fire *P. taeda* trees and post-fire (2015) *P. taeda* seedlings. Required survival rate is the percentage of seedlings that would need to survive to maturity in order to replace the pre-fire population.

	Stem number ha^{-1}	Survival rate for replacement (%)
Mean pre-fire mature trees	300.0	N/A
2015 seedlings, scorched	79,400.0	0.4
2015 seedlings, light burn	4,512.7	6.6
2015 seedlings, moderate burn	1,036.4	28.9
2015 seedlings, heavy burn	535.6	56.0
2015 seedlings, all burn classes	85,484.7	0.4

Table 1.4. Summary of generalized linear model results by functional group, with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect), are reported as 'F, p'; results for continuous predictor variables (numbers in same or different size class and year, canopy cover in same or different year, and elevation) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Size class	Year	N	Burn severity	Soil type	Aspect	Number in same size class in previous year
P. taeda	seedling	pre-fire	26	NI	NI	3.3, 0.03	N/A
P. taeda	seedling	2012	17	0.4, 0.7	NI	NI	NI
P. taeda	seedling	2013	46	3.5, 0.03	NI	NI	**0.2, 20.9, 0.0001**
P. taeda	seedling	2014	46	1.4, 0.2	NI	NI	**0.2, 62.1, <0.0001**
P. taeda	seedling	2015	46	2.2, 0.1	NI	NI	NI
P. taeda	saplings	pre-fire	37	NI	9.6, 0.004	3.0, 0.03	N/A
P. taeda	saplings	2012	17	NI	NI	NI	NI
P. taeda	saplings	2013	32	NI	NI	NI	NI
P. taeda	saplings	2014	46	NI	NI	NI	NI
P. taeda	saplings	2015	46	3.2, 0.03	NI	NI	2.5, 0.1
P. taeda	adults	pre-fire	37	NI	NI	NI	N/A
P. taeda	adults	2012	11	NI	NI	NI	0.2, 4.8, 0.1
P. taeda	adults	2013	17	NI	NI	NI	**0.1, 29.6, <0.0001**
P. taeda	adults	2014	46	**11.7, <0.0001**	1.7, 0.2	NI	**0.1, 134.7, <0.0001**
P. taeda	adults	2015	46	3.9, 0.01	2.3, 0.1	NI	**0.1, 17.2, 0.0002**

Table 1.4, continued. Summary of generalized linear model results by functional group, with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect), are reported as 'F, p'; results for continuous predictor variables (numbers in same or different size class and year, canopy cover in same or different year, and elevation) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Size class	Year	N	Previous year canopy cover	Canopy cover, same year	Number of mature trees in previous year	Number of mature trees in same year	Elevation
P. taeda	seedling	pre-fire	26	N/A	0.004, 0.01, 0.9	N/A	NI	NI
P. taeda	seedling	2012	17	NI	NI	0.2, 0.7	NI	NI
P. taeda	seedling	2013	46	NI	NI	NI	0.05, 9.1, 0.005	NI
P. taeda	seedling	2014	46	NI	NI	NI	NI	NI
P. taeda	seedling	2015	46	NI	0.04, 7.5, 0.009	NI	**0.1, 13.0, 0.0009**	NI
P. taeda	saplings	pre-fire	37	N/A	NI	N/A	NI	NI
P. taeda	saplings	2012	17	NI	NI	NI	NI	NI
P. taeda	saplings	2013	32	NI	NI	NI	NI	NI
P. taeda	saplings	2014	46	NI	NI	NI	NI	NI
P. taeda	saplings	2015	46	NI	NI	NI	NI	NI
P. taeda	adults	pre-fire	37	N/A	N/A	N/A	N/A	**0.03, 16.3, 0.0003**
P. taeda	adults	2012	11	N/A	N/A	N/A	N/A	-0.09, 2.9, 0.1
P. taeda	adults	2013	17	N/A	N/A	N/A	N/A	NI
P. taeda	adults	2014	46	N/A	N/A	N/A	N/A	NI
P. taeda	adults	2015	46	N/A	N/A	N/A	N/A	NI

Table 1.5. Summary of generalized linear model results by functional group, with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect), are reported as 'F, p'; results for continuous predictor variables (numbers in same or different size class and year, canopy cover in same or different year, and elevation) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Size class	Year	N	Burn severity	Soil type	Aspect	Number in same size class in previous year
Q. margaretta	seedling	pre-fire	40	NI	3.4, 0.08	NI	N/A
Q. margaretta	seedling	2012	11	0.7, 0.5	NI	NI	0.6, 0.3, 0.6
Q. margaretta	seedling	2013	32	2.6, 0.08	NI	NI	**0.3, 20.3, 0.0001**
Q. margaretta	seedling	2014	46	NI	4.7, 0.04	NI	0.4, 9.6, 0.003
Q. margaretta	seedling	2015	46	NI	0.01, 0.9	NI	**0.3, 14.9, 0.0004**
Q. margaretta	saplings	pre-fire	37	NI	8.9, 0.005	NI	N/A
Q. margaretta	saplings	2012	11	NI	NI	NI	0.08, 22.5, 0.0015
Q. margaretta	saplings	2013	17	NI	NI	NI	**0.1, 27.9, 0.0001**
Q. margaretta	saplings	2014	46	NI	NI	NI	0.2, 3.7, 0.06
Q. margaretta	saplings	2015	46	NI	NI	NI	0.2, 5.4, 0.02
Q. margaretta	adults	pre-fire	37	NI	**12.3, 0.0013**	NI	N/A
Q. margaretta	adults	2012	11	0.2, 0.6	NI	NI	**0.09, 29.9, 0.0006**
Q. margaretta	adults	2013	17	2.9, 0.1	NI	NI	**0.1, 71.5, <.0001**
Q. margaretta	adults	2014	46	**22.3, <.0001**	NI	NI	**0.1, 18.6, <.0001**
Q. margaretta	adults	2015	46	**22.8, <.0001**	NI	NI	**0.1, 24.9, <.0001**

Table 1.5, continued. Summary of generalized linear model results by functional group, with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect), are reported as 'F, p'; results for continuous predictor variables (numbers in same or different size class and year, canopy cover in same or different year, and elevation) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Size class	Year	N	Previous year canopy cover	Canopy cover, same year	Number of mature trees in previous year	Number of mature trees in same year	Elevation
Q. margaretta	seedling	pre-fire	40	N/A	NI	N/A	NI	0.01, 0.4, 0.5
Q. margaretta	seedling	2012	11	NI	NI	NI	0.06, 0.5, 0.5	NI
Q. margaretta	seedling	2013	32	NI	-0.002, 3.5, 0.07	NI	0.05, 1.3, 0.3	NI
Q. margaretta	seedling	2014	46	NI	NI	NI	NI	NI
Q. margaretta	seedling	2015	46	NI	NI	NI	0.08, 11.3, 0.0017	NI
Q. margaretta	saplings	pre-fire	37	N/A	NI	N/A	NI	NI
Q. margaretta	saplings	2012	11	NI	NI	NI	0.08, 4.0, 0.08	NI
Q. margaretta	saplings	2013	17	NI	NI	0.07, 6.1, 0.03	NI	NI
Q. margaretta	saplings	2014	46	NI	NI	NI	NI	NI
Q. margaretta	saplings	2015	46	NI	NI	NI	NI	NI
Q. margaretta	adults	pre-fire	37	N/A	N/A	N/A	N/A	NI
Q. margaretta	adults	2012	11	N/A	N/A	N/A	N/A	NI
Q. margaretta	adults	2013	17	N/A	N/A	N/A	N/A	NI
Q. margaretta	adults	2014	46	N/A	N/A	N/A	N/A	NI
Q. margaretta	adults	2015	46	N/A	N/A	N/A	N/A	NI

Table 1.6. Summary of generalized linear model results by functional group, with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect), are reported as 'F, p'; results for continuous predictor variables (numbers in same or different size class and year, canopy cover in same or different year, and elevation) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Size class	Year	N	Burn severity	Soil type	Aspect	Number in same size class in previous year	Previous year canopy cover
Q. marilandica	seedling	pre-fire	26	NI	10.6, 0.004	3.1, 0.04	N/A	N/A
Q. marilandica	seedling	2012	11	NI	NI	NI	**5.3, 22.6, 0.0014**	NI
Q. marilandica	seedling	2013	17	NI	NI	NI	**0.3, 36.2, <.0001**	NI
Q. marilandica	seedling	2014	46	NI	NI	NI	0.3, 10.3, 0.002	NI
Q. marilandica	seedling	2015	46	NI	**12.9, 0.0008**	NI	**0.3, 12.3, 0.0011**	NI

Table 1.6, continued. Summary of generalized linear model results by functional group, with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect), are reported as 'F, p'; results for continuous predictor variables (numbers in same or different size class and year, canopy cover in same or different year, and elevation) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Size class	Year	N	Canopy cover, same year	Number of mature trees in previous year	Number of mature trees in same year	Elevation
Q. marilandica	seedling	pre-fire	26	0.05, 0.4, 0.5	N/A	NI	NI
Q. marilandica	seedling	2012	11	NI	NI	0.1, 2.1, 0.2	NI
Q. marilandica	seedling	2013	17	NI	NI	-1.5, 9.6, 0.004	NI
Q. marilandica	seedling	2014	46	NI	NI	NI	NI
Q. marilandica	seedling	2015	46	NI	NI	NI	NI

Table 1.7. Spearman correlation coefficients, p-values, and sample sizes for burn severity and canopy cover in each year.

	Mean pre-fire canopy cover			Canopy cover 2012			Canopy cover 2013		
	r_s	p	n	r_s	p	n	r_s	p	n
Mean pre-fire canopy cover	1	--	26						
Canopy cover 2012	0.81	0.0007	13	1	--	32			
Canopy cover 2013	0.57	0.003	25	0.46	0.008	32	1	--	46
Canopy cover 2014	0.53	0.007	25	0.56	0.0009	32	0.39	0.008	46
Canopy cover 2015	0.59	0.002	25	0.68	<0.0001	32	0.46	0.001	46
Burn severity	-0.47	0.01	26	-0.61	0.0002	32	-0.51	0.0003	46

Table 1.7, continued. Spearman correlation coefficients, p-values, and sample sizes for burn severity and canopy cover in each year.

	Canopy cover 2014			Canopy cover 2015			Burn severity		
	r_s	p	n	r_s	p	n	r_s	p	n
Mean pre-fire canopy cover									
Canopy cover 2012									
Canopy cover 2013									
Canopy cover 2014	1	--	46						
Canopy cover 2015	0.91	<0.0001	46	1	--	46			
Burn severity	-0.73	<0.0001	46	-0.76	<0.0001	46	1	--	46

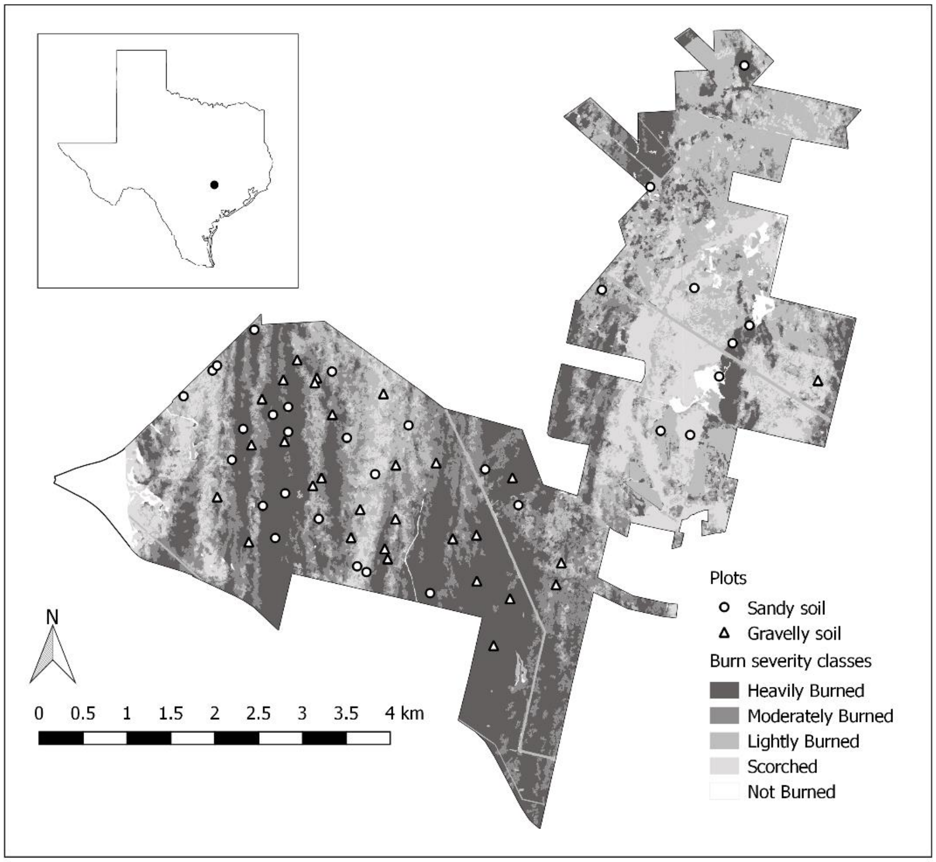


Figure 1.1. Map of Bastrop State Park (BSP) with burn severity classes and permanent plot locations. Soil type is indicated for each plot by point shape.

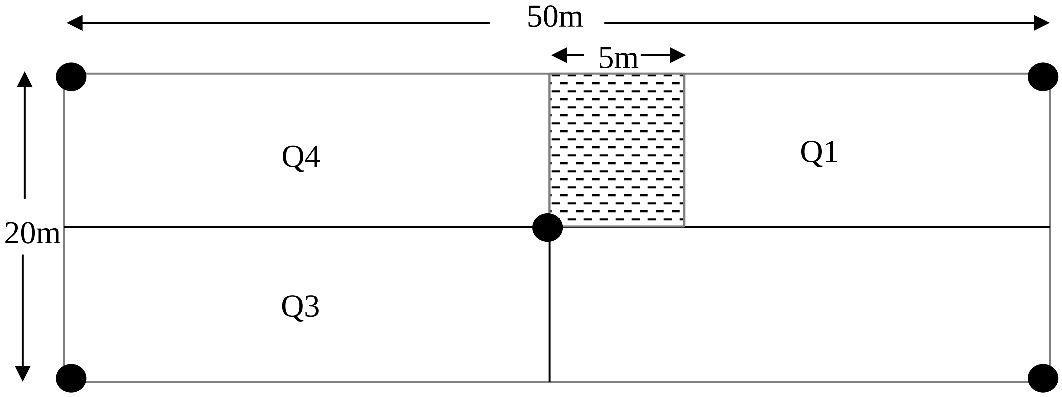


Figure 1.2. Data were collected from permanent plots as follows: seedlings and basal sprouts (subplot within Q1 with dashed lines); saplings (Q1 and Q4); mature trees (Q1-Q4); canopy cover (facing four directions at each of the black circles).

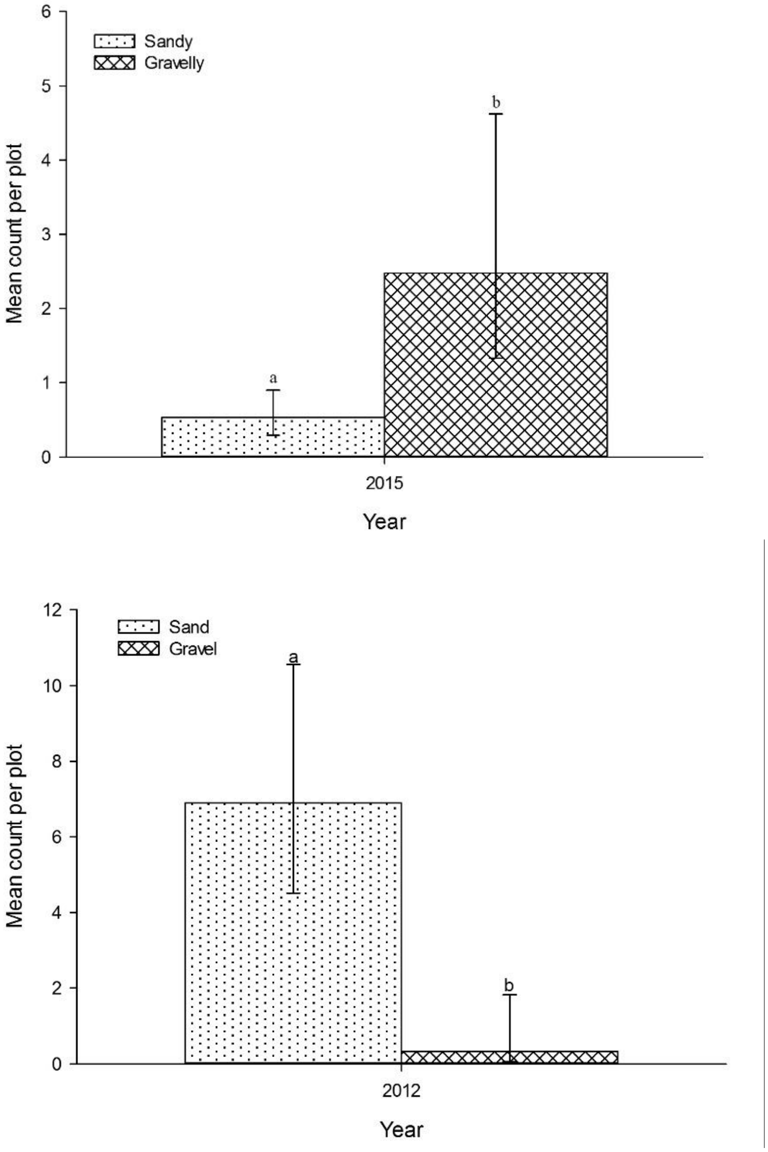


Figure 1.3. Mean number of blackjack oak basal sprouts (top) sand post oak mature trees (bottom) in each soil category. Each year is a separate model. Letters over 95% confidence intervals represent significant differences between treatments within a year; there are no letters where the model was not significant (*P*>0.05). Soil type was not a predictor of loblolly pine seedling numbers.

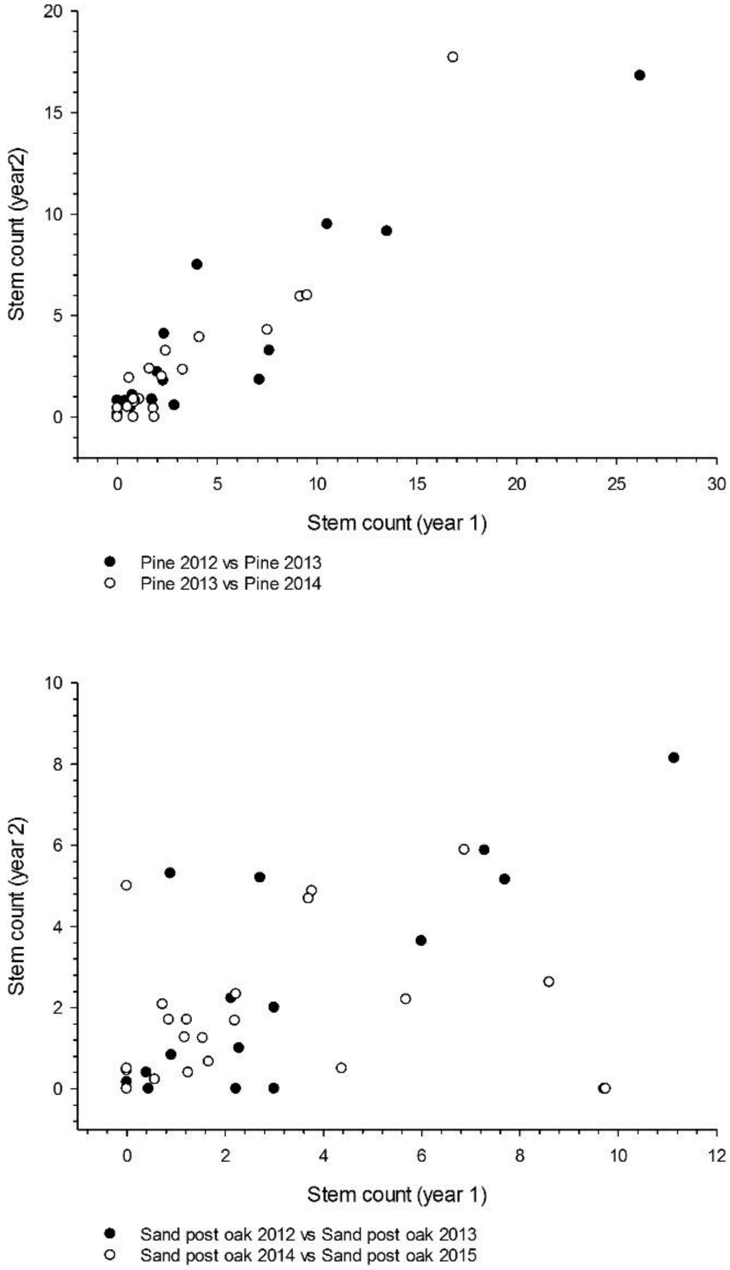


Figure 1.4. Year-to-year stem counts of loblolly pine seedlings (top), sand post oak basal sprouts and (middle), blackjack oak basal sprouts (bottom).

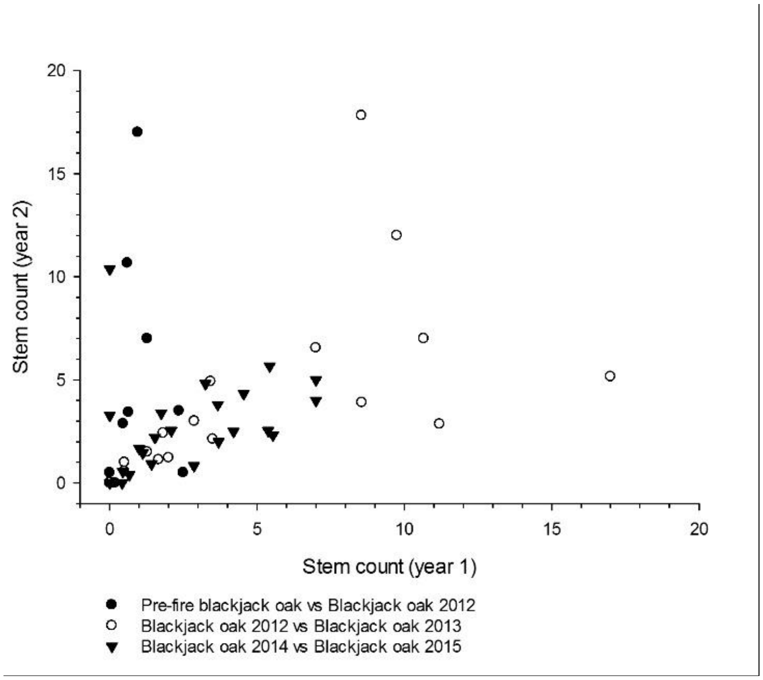
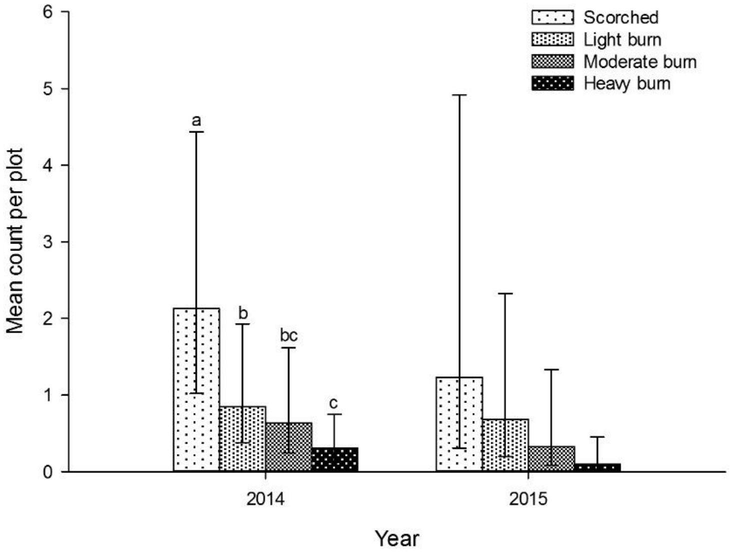


Figure 1.4, continued. Year-to-year stem counts of loblolly pine seedlings (top), sand post oak basal sprouts and (middle), blackjack oak basal sprouts (bottom).



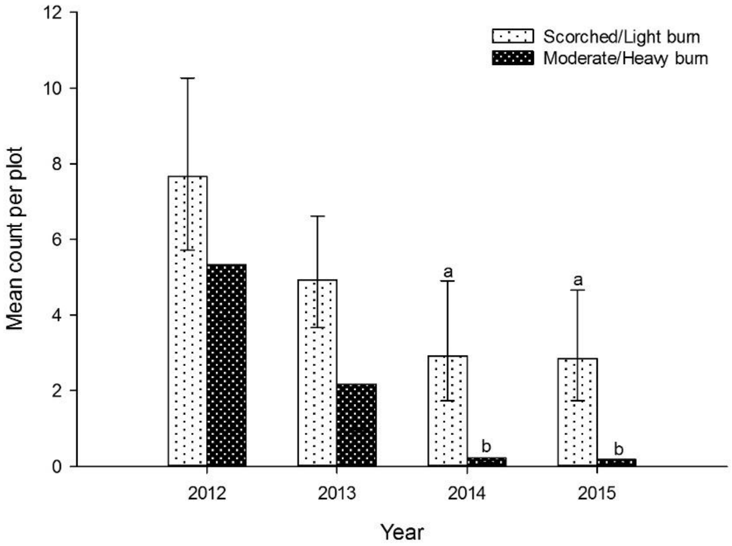


Figure 1.5. Mean number of loblolly pine mature trees (top) and sand post oak mature trees (bottom) in each burn severity. Each year is a separate model. Letters over 95% confidence intervals represent significant differences between treatments within a year; there are no letters where the model was not significant (*P*>0.05). Burn severity was not a predictor for blackjack oak sprout numbers.

Chapter 2: Wildland fire stimulates growth of overstory and mid-story woody species in a pine-oak woodland

ABSTRACT

Objective

The Lost Pines region of central Texas supports the westernmost stands of loblolly pine (*Pinus taeda*) in the United States, which co-dominates with blackjack oak (*Quercus marilandica*), sand post oak (*Q. margaretta*), and yaupon (*Ilex vomitoria*). In 2011, during a record drought, a wildfire burned most of Bastrop State Park, which is in the Lost Pines region. The fire, predominantly a crown fire, was more severe than those that typically maintain pine-oak savannas and woodlands, partly due to heat and drought, and partly due to fuels buildup after decades of fire suppression. Our objective was to characterize post-fire recovery of the dominant woody species using demographic data.

Methods

We used a stratified randomized design: points were randomly located in one of two soil types (sandy soils or gravelly soils), combined with one of three burn severities (unburned, low severity, or high severity), in a factorial design. The individual of each species that was nearest to a randomly-located point, and <15cm basal diameter, was tagged. We measured number of stems per individual, height of the tallest stem and up to four additional stems, and basal diameter of the largest stem, which was converted to basal area. We also measured canopy cover at each point. Each individual was measured twice, once between November 2014 and January 2015, and once in January 2016.

Results

Burn severity and canopy cover were negatively correlated. Canopy cover was negatively related to basal area and average stem height of each species. Yaupon had more stems and possibly higher survival at burned points, and blackjack oak had larger basal area, more stems, greater height, and higher survival at burned points. The other species did not detectably respond to the burn treatment. Yaupon was taller at unburned points, which may reflect a morphological response to lower light levels there.

Conclusions

Our results point to potential shifts in woody plant composition, which may develop into an open-canopy savanna instead of the closed-canopy woodland that was present pre-fire. This is especially likely if management strategies are implemented to maintain an open canopy and mid-story, such as prescribed burning. Maintenance of a more open canopy and mid-story in this and other pine-oak savannas is important to prevent dense growth of mid-story fuels and reduce the risk of crown fire in the future, as large wildfires become more severe and more frequent.

INTRODUCTION

Disturbances, such as wildland fire, shape plant community composition and structure over time (Bond and Keeley 2005, Hanberry 2014, Hernandez-Serrano *et al.* 2013, Hessburg *et al.* 2005, Naiman *et al.* 1993, Nowacki and Abrams 2008, Ward *et al.* 1999). Wildland fire can play many different roles: surface fires maintain many savannas (Bond and Keeley 2005, Fill *et al.* 2015, Nowacki and Abrams 2008, Peterson and Reich

2001, van Langevelde *et al*. 2003), crown fires often re-start succession (Turner *et al*. 1999, Turner *et al*. 2003), and some fires, particularly those different in severity from the historical fire regime, may lead a plant community towards a new trajectory (Kane *et al*. 2013).

As much of the US becomes warmer and drier, wildfires are becoming more frequent (Dennison *et al*. 2014; Settele *et al*. 2014; Westerling *et al*. 2006) and more severe (Banner *et al.* 2010, Dillon *et al*. 2011, Miller and Safford 2012). Climate change can alter the frequency, characteristics, and effects of wildfire (Parks et al. 2016), which can be further exacerbated by years of fire suppression (Shang *et al*. 2007, Stephens *et al*. 2009). Long-term fire suppression can also lead to shifts in plant community composition (Andruk *et al*. 2014, Shang *et al*. 2007) and build-up of fuels, including mid-story 'ladder' fuels.

Ladder fuels often intensify fires and cause them to reach the canopy (Hessburg *et al*. 2016, Menning and Stephens 2007, Shang *et al*. 2007). Models of ladder fuels (Kramer *et al*. 2014, Kramer *et al*. 2016) are thus critical to predicting wildland fire behavior, but these rely on an understanding mid-story plant growth patterns and their response to fire. Whereas there are many studies on post-fire mid-story tree dynamics (Dey and Hartman 2005, Grady and Hoffmann 2012, Reemts and Hansen 2008, Taft 2003), the link between mid-story plant response to disturbance and their role as ladder fuels is poorly understood (Gordon *et al*. 2017).

Here, we took advantage of a severe wildfire in the Lost Pines region of central Texas to examine the effects of this wildfire on the dominant woody species and their role in ladder fuels, in part to predict possible future trajectories for this community and also to offer management guidance. The Lost Pines region was probably mostly savanna dominated by oaks and loblolly pines (*Pinus taeda* L.) pre-settlement (Stambaugh 2017). However, after it was logged in the 1930s and 1940s, it re-grew as a closed canopy, pine-dominated forest. It also developed an understory of yaupon (*Ilex vomitoria* Aiton), which is a highly flammable species, especially when covered with dropped pine needles ('needle drape') (Fig. 2.1). Yaupon has long been a plant of management concern in Texas (Bovey *et al*. 1972, Duncan and Scifres 1983, Meyer and Bovey 1985).

In unusually hot, dry weather in 2011, combined with strong winds caused by Tropical Storm Lee, a large portion of the Lost Pines burned in a wildfire. The wildfire was likely an example of the potential long-term effects of fire suppression, and perhaps climate change. The weather conditions, combined with continuous canopy and a dense flammable mid-story to carry the fire to the tree crowns, resulted in an intense crown fire.

The four dominant tree species we studied were loblolly pine, blackjack oak (*Quercus marilandica* Münchh.), sand post oak (*Q. margaretta* [Ashe] Small), and yaupon. All are native, and all were abundant before the fire (Chapter 1). Yaupon remains an understory tree; the others reach the canopy. Loblolly pine regenerates only from seed, but both oak species and yaupon produce basal sprouts after being top-killed by fire, if live tissue remains at the base of the trunk. Top-killed sprouting woody species, like these oaks and yaupon, produce shoots by drawing on resources from the live root starch reserves of the parent tree (Chapin *et al*. 1990; Schutz *et al*. 2009), enabling them to regenerate quickly post-fire.

Our goals were to better understand post-fire recovery of the four woody plant species, to help predict the future trajectory of this ecosystem and to improve our understanding of the factors that determine it. These factors, including ladder fuels, resprouting versus reseeding species, and the effects of fire severity and differences among soil type, will help to illustrate the importance of studying mid-story ladder fuel regeneration.

METHODS

Study Area

The Lost Pines of central Texas are the westernmost stands of loblolly pine in the United States. This study was conducted in Bastrop and Buescher State Parks, within the Lost Pines region. Before 2011, both parks had dense, continuous canopies composed of loblolly pine trees and several oak species, with a yaupon mid-story. In September 2011, during a record drought and heat wave (Hoerling *et al*. 2013), at the Bastrop County Complex Fire (BCCF) burned much of the Lost Pines, including almost all of Bastrop State Park. The BCCF was a crown fire in most parts of Bastrop State Park, killing or top-killing most vegetation and consuming litter and duff. A similar fire, the Hidden Pines wildfire, burned parts of Buescher State Park in October 2015.

It is thought that the vegetation of the Lost Pines region historically had more open canopies, that is, savannas rather than forests, and perhaps more oak than it had pre-fire, in 2011 (Stambaugh *et al*. 2017). These savannas would have been maintained by frequent, low-intensity surface fires (Stambaugh *et al*. 2014).

Data Collection

We measured the size and growth of the four common woody species mentioned in the introduction: loblolly pine, blackjack oak, sand post oak, and yaupon. We used a stratified randomized sampling design, in which points were randomly located in one of two soil types (sandy soils or gravelly soils) combined with one of three burn severities (unburned in 2011, low severity fire in 2011, or high severity fire in 2011), a total of six combinations in a factorial design. Twenty points were randomly located for each combination, using ArcGIS (ESRI, Redlands, California, USA) and burn severity and soil maps (see below) of Bastrop and Buescher State Parks (Fig. 2.2, QGIS 2.18.9, QGIS Development Team 2009, Open Source Geospatial Foundation) . Both soil type and burn severity were very patchy, and neither factor was randomly distributed across the landscape. We therefore cannot rule out correlated and likely unknown spatial factors.

At each randomly-located point, the individual of each of the four species less than 15cm in basal diameter that was nearest to the point was permanently marked. For each individual of each species, we measured number of stems, height of the tallest stem and height of up to four additional haphazardly-selected stems, and basal diameter of the largest stem. Stem height was averaged for each individual, and basal diameter was converted to basal area. Initial measurements were made between November 2014 and January 2015; marked plants were re-located and, if still alive, re-measured in January 2016.

Canopy cover was estimated with a densiometer held at a height of approximately 1.2m. Two canopy cover measurements were taken at each point, facing in opposite directions, and then averaged.

Burn severity in Bastrop State Park was determined immediately following the wildfire in September, 2011 using FMH assessment definitions (USDI National Park Service 2003), which are based on degree of consumption of vegetation and substrate. Points were initially assigned one of five burn severity classes (in order from least to greatest severity: unburned, scorched, light, moderate, and heavy). We grouped scorched and lightly burn areas into a ‘low burn’ class, and moderate and heavily burn areas into a ‘high burn’ class.

Buescher State Park provided the ‘unburned’ points in our original design. However, some of these points were burned in the Hidden Pines wildfire of 2015 and were therefore discarded from the study (Table 2.1). Plots were also discarded when they were unreachable or unusable (ex. in the middle of a road, on private property, in a body of water); 319 plots were used in the final analyses.

Soil data were obtained from the Soil Survey Geographic (SSURGO) Database. SSURGO soil types were first ground-truthed and modified where necessary to accurately reflect local soil texture, then re-classified as either ‘sandy’ or ‘gravelly’ (Appendix A) for increased statistical power and ease of interpretation.

Statistical Analyses

Analyses were completed using SAS 9.4 (SAS Institute, Cary, North Carolina, USA). Basal area, mean height, stem count in both years, and survival (presence of a marked plant in the second year) were used as response variables, with the exceptions that stem count was not analyzed for loblolly pine seedlings because they grow one stem only.

Generalized linear models (SAS GLIMMIX procedure) were used to accommodate non-normal distributions. The binomial distribution with logit link function was used to construct models of survival, and the negative binomial with log link function to construct all other models except sand post oak stem count in the first year, for which the Poisson distribution gave a better fit. We used forward selection to build these models, adding variables one by one. At each step, the AICc values of all possible models with one additional variable were compared, and the variable that most decreased AICc was added to the model. No additional variables were added to a model if AICc did not decrease by two or more. Once the best model for a given reponse variable had been identified by this procedure, we examined the significance (*P*-value) of each included predictor variable in this final model.

We used a Bonferroni correction to determine a suitable alpha value. There were a total of 24 final models: 4 species x (2 years basal area + 2 years mean height + 2 years stem number + 1 survival interval), minus the three exceptions noted above. We therefore used an adjusted alpha of $p \leq 0.002$. Predicted means and confidence limits were back-transformed for tables and figures.

RESULTS

Mean basal area and stem height increased or stayed the same from year 1 to year 2 for all species except for blackjack oak, which decreased in size (Fig. 2.3). Yaupon, blackjack oak, and sand post oak all had fewer stems in year 2 than in year 1 (Fig. 2.3).

As expected, canopy cover was negatively related to burn severity (Table 2.2) because burn severity was determined partly by overstory tree mortality (USDI National Park Service 2003). Also as expected, the size of an individual in the first year was positively related to its size in the second year (Table 2.3).

Canopy cover was negatively related to at least two measures of size, basal area and average height, of each species (Tables 2.4 and 2.5). It did not have a detectable relationship with stem count (Table 2.6), and it had a weak positive relationship with yaupon survival (Table 2.7).

Yaupon had more stems and possible higher survival at burned points (Table 2.7), and blackjack oak had larger basal area (Fig. 2.4, Table 2.4), more stems (Fig. 2.5, Table 2.6), greater height (Fig. 2.6, Table 2.5), and higher survival at burned points (Fig. 2.6, Table 2.7); the other species did not detectably respond to the burn treatment. Yaupon was taller at unburned points (Fig. 2.6, Table 2.5), which may reflect a morphological response to lower light levels there.

The only relationship detected with soil type was that loblolly pines has greater basal area in gravelly soils than in sandy soils (Fig. 2.7, Table 2.4). None of the interaction terms had sufficient effect on AICc to be included in the final models

DISCUSSION

Our results suggest that recovery from the 2011 fire is proceeding rapidly. The four measured species were abundant before the fire (Chapter 1) and appear to be on trajectories that will ensure their continued abundances in the future. Several years following the BCCF, there was concern that the oak species might outcompete the returning loblolly pines, due to their vigorous sprouting and rapid recruitment relative to pine seedlings (Stambaugh *et al*. 2017). However, decreasing oak stem counts and blackjack oak basal area (Fig. 2.3) combined with abundant loblolly recruitment in 2015 has diminished that concern (Chapter 1).

All four of the measured species were favored directly by fire or indirectly by the lower canopy cover that resulted from fire, in size and/or survival. Because fire history and canopy cover were correlated, it is difficult to assign causality. It is likely that reduced competition for light, water, and nutrients was the underlying causal mechanism. We did not detect effects on growth rate, which would have appeared in our analyses of the three size variables as differences among burn severity classes in the slope of size year 2 versus size year 1. The observed differences among burn severity classes and the relationships with canopy cover therefore must have been due to differential effects on size before our data were collected, via difference in growth rates (faster growth in burned areas) and/or differences in plant age (older plants in burned areas).

Sprouting in blackjack oak and post oak (*Q. stellata*, which is also found in the Lost Pines) has been shown to be stimulated by fire (Backoulou *et al*. 1999, DeSantis and Hallgren 2011). Our results are also consistent with findings that immature oaks and pines have higher survival rates in higher light conditions (Karki and Hallgren 2015, Mclemore 1971, Mitchell *et al*. 1999, Royse *et al*. 2010), and that immature oak growth rates can be positively correlated with light availability (Dobrowolska 2008). While longleaf pine (*Pinus palustris*) seedlings can become moisture-stressed under high light conditions and be facilitated by mid-story oak canopy (Loudermilk *et al*. 2016), loblolly seedling growth can be stimulated by disturbance through reduction of competition (Glencross *et al*. 2016, Graham *et al*. 2012, Linkevičius *et al*. 2014, Sanchez-Salguero *et al*. 2015). The ecological role of loblolly pine in North Carolina, where it invades fields as soon as they are abandoned (De Steven 1991), is also consistent with its behavior in this study.

Loblolly pine was the only species in this study that was affected by soil type; seedlings had greater mean basal area in gravelly soils than in sandy soils (Fig. 2.7). Another post-fire study in the Lost Pines (Brown *et al*. 2014) found that short-term post-fire survival of planted loblolly seedlings was primarily dictated by soil type, and that post-fire survival of seedlings was higher in gravelly soils. We found no detectable effect of soil type on survival of loblolly pines; it may be that gravelly soils encourage survival of planted seedlings but that the effect is not great enough to be detected in natural regeneration, which typically has higher survival rates than planted seedlings. Size is typically correlated with age in plants (Niklas *et al*. 2003), so larger loblolly stems in gravelly soils in this study may indicate earlier establishment and longer survival in gravelly soils.

Long-term fire suppression may lead to altered fuel structures, but historical plant communities and disturbance regimes can, in some cases, be restored within 50-75 years by re-introducing the historical fire regime, or by an unusually large fire (Baker 1994). The BCCF was an unusually large fire for the Lost Pines. If prescribed burning or mechanical thinning is not used in the future, our results suggest that yaupon will once again form thickets, providing ladder fuels and the conditions for another crown fire. With appropriate management strategies, especially prescribed surface fires that check yaupon growth, the future plant community structure could be more similar to the more open pre-logging conditions than the conditions in 2011 that favored a severe crown fire.

MANAGEMENT IMPLICATIONS

Re-establishment of appropriate disturbance regimes is important to maintain plant communities which are resistant and resilient to disturbance. For the Lost Pines, resistance and resilience to fire are closely related to the control of mid-story fuel, especially yaupon. Ladder fuels can be reduced by thinning and burning (Agee and Skinner 2005, Fulé and

Laughlin 2006), but there are many financial and logistic constraints on treating buildup of fuels (Collins *et al*. 2010). However, because the Lost Pines region is rapidly developing, the financial incentives to prevent crown fires and associated losses of houses are great and increasing. Future warming of the climate combined with a dense mid-story will increase the probability of intense fires and therefore the economic value of preventing crown fires in this region.

Ideally, mid-story fuel reduction would be coupled with prescribed surface fires frequent enough to create savannas rather than closed forests, and therefore increase the likelihood that future wildfires would be surface fires instead of crown fires. This management would also probably increase biodiversity, because the vegetation would be closer to what it was pre-settlement (Stambaugh *et al*. 2014), and would at least increase the diversity of the herbaceous layer (Chapter 4). Varying the fire regime both spatially and temporally would also probably increase diversity by creating spatial mosaics in which plant species with different life-history strategies may coexist (Menges 2007).

Table 2.1. Number of observations of each species in each combination of burn severity and soil type. Observations in the first two columns are from unburned points in year one to show how many unburned points were discarded per species in year 2.

	Year 1		Year 2						
	Gravelly soil, no burn	Sandy soil, no burn	Gravelly soil, no burn	Sandy soil, no burn	Gravelly soil, low burn	Sandy soil, low burn	Gravelly soil, high burn	Sandy soil, high burn	Total (year 2 only)
I. vomitoria	20	21	12	10	19	19	20	17	97
P. taeda	3	3	0	2	19	19	22	19	81
Q. marilandica	9	10	1	7	20	16	20	19	83
Q. margaretta	1	1	0	0	11	9	19	19	58
Total	33	35	13	19	69	63	81	74	319

Table 2.2. Spearman correlation coefficients and p-values for burn severity and canopy cover (N = 319).

	Burn severity	Canopy cover, year 1	Canopy cover, year 2
Burn severity	1		
Canopy cover, year 1	-0.67, <0.0001	1	
Canopy cover, year 2	-0.68, <0.0001	0.79, <0.0001	1

Table 2.3. Spearman correlation coefficients and p-values for growth and survival variables (N=319).

	Mean height 1	Mean height 2	Stem count 1	Stem count 2	Basal area 1	Basal area 2	Survival
Mean height 1	1						
Mean height 2	0.57, <.0001	1					
Stem count 1	0.16, 0.003	-0.04, 0.4	1				
Stem count 2	0.14, 0.01	0.33, <.0001	0.67, <.0001	1			
Basal area 1	0.75, <.0001	0.44, <.0001	0.38, <.0001	0.28, <.0001	1		
Basal area 2	0.53, <.0001	0.82, <.0001	0.21, 0.0001	0.56, <.0001	0.57, <.0001	1	
Survival	NA	0.45, <.0001	NA	0.48, <.0001	NA	0.47, <.0001	1

Table 2.4. Summary of basal area model results, with explanatory variables in columns. Results for categorical predictor variables (burn severity and soil type), are reported as 'F, p'; results for continuous predictor variables (canopy cover and area) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Year	N	Burn severity	Soil type	Previous year canopy cover	Same year canopy cover	Previous year area	Previous year area x burn severity
I. vomitoria	1	97	NI	NI	N/A	**-0.01, 23.1, <0.0001**	N/A	N/A
I. vomitoria	2	97	NI	NI	NI	NI	**0.04, 45.5, <0.0001**	NI
P. taeda	1	81	NI	NI	N/A	**-0.03, 18.8, <0.0001**	N/A	N/A
P. taeda	2	81	2.3, 0.01	**12.5, 0.0007**	NI	NI	**0.05, 21.1, <0.0001**	NI
Q. marilandica	1	83	3.6, 0.03	NI	N/A	-0.01, 2.94, 0.09	N/A	N/A
Q. marilandica	2	83	**13.3, <0.0001**	NI	NI	NI	**0.02, 14.3, 0.0003**	NI
Q. margaretta	1	58	NI	NI	N/A	-0.02, 5.62, 0.02	N/A	N/A
Q. margaretta	2	58	NI	NI	NI	NI	**0.008, 14.8, 0.0003**	NI

Table 2.5. Summary of height model results, with explanatory variables in columns. Results for categorical predictor variables (burn severity and soil type), are reported as 'F, p'; results for continuous predictor variables (canopy cover and height) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Year	N	Burn severity	Soil type	Previous year canopy cover	Same year canopy cover	Previous year height	Previous year height x burn
I. vomitoria	1	97	**10.6, <0.0001**	NI	N/A	-0.006, 5.4, 0.02	N/A	N/A
I. vomitoria	2	97	NI	NI	NI	NI	0.006, 6.6, 0.01	NI
P. taeda	1	81	NI	NI	N/A	**-0.01, 16.7, 0.0001**	N/A	N/A
P. taeda	2	81	NI	NI	NI	NI	**0.005, 12.0, 0.0008**	NI
Q. marilandica	1	83	NI	NI	N/A	**-0.007, 12.0, 0.0008**	N/A	N/A
Q. marilandica	2	83	5.5, 0.005	NI	NI	NI	0.005, 4.8, 0.03	NI
Q. margaretta	1	58	NI	NI	N/A	**-0.02, 16.7, 0.0001**	N/A	N/A
Q. margaretta	2	58	NI	NI	NI	NI	0.005, 7.4, 0.008	NI

Table 2.6. Summary of stem count model results, with explanatory variables in columns. Results for categorical predictor variables (burn severity and soil type), are reported as 'F, p'; results for continuous predictor variables (canopy cover and stem count) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Year	N	Burn severity	Soil type	Previous year stem count	Previous year canopy cover	Same year canopy cover
I. vomitoria	1	97	6.36, 0.003	NI	NI	NI	NI
I. vomitoria	2	97	NI	NI	**0.2, 97.9, <0.0001**	NI	NI
Q. marilandica	1	83	N/A	N/A	N/A	N/A	N/A
Q. marilandica	2	83	**9.09, 0.0003**	NI	**0.1, 92.56, <0.0001**	NI	NI
Q. margaretta	1	58	NI	0.87, 0.4	NI	NI	NI
Q. margaretta	2	58	NI	NI	**0.2, 24.76, <0.0001**	NI	NI

Table 2.7 Summary of survival model results, with explanatory variables in columns. Results for categorical predictor variables (burn severity and soil type), are reported as 'F, p'; results for continuous predictor variables (canopy cover) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	N	Burn severity	Soil type	Previous year canopy cover	Same year canopy cover
I. vomitoria	97	3.8, 0.02	NI	NI	0.05, 3.7, 0.05
P. taeda	81	0.4, 0.6	NI	NI	5.5, 0.02, 0.8
Q. marilandica	83	**7.5, 0.001**	NI	NI	NI
Q. margaretta	58	2.5, 0.1	NI	NI	NI

Figure 2.1. Yaupon (*I. vomitoria*) covered in dried pine needle drape.

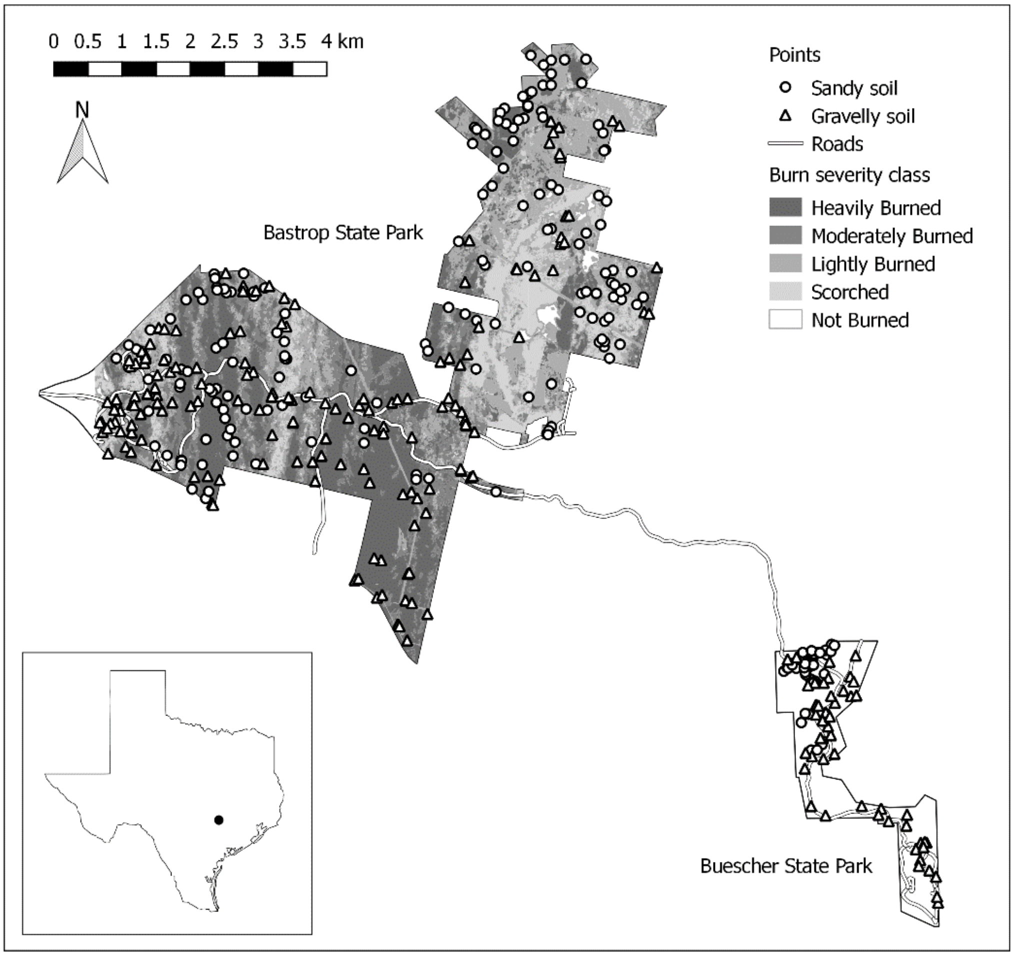


Figure 2.2. Map of Bastrop State Park and Buescher State Park with burn severity classes and point locations. Soil type is indicated for each point by shape.

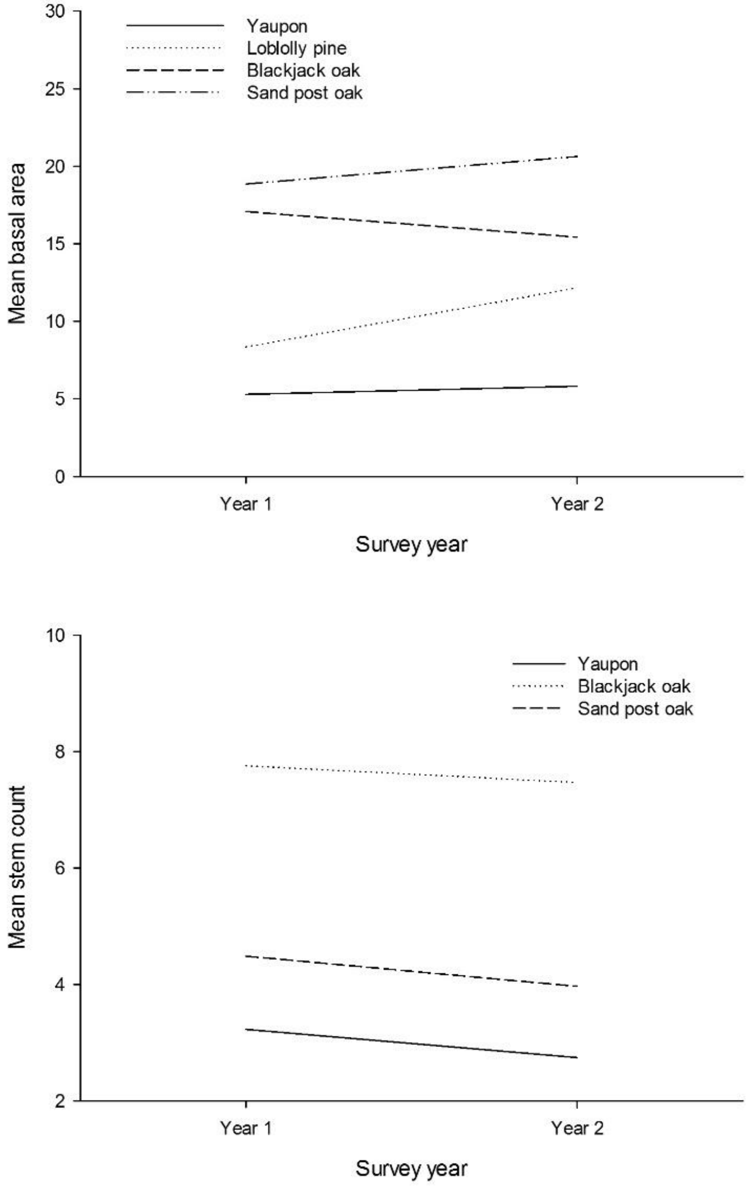


Figure 2.3. Mean basal area (top), stem count (middle), and height (bottom) for each species each year.

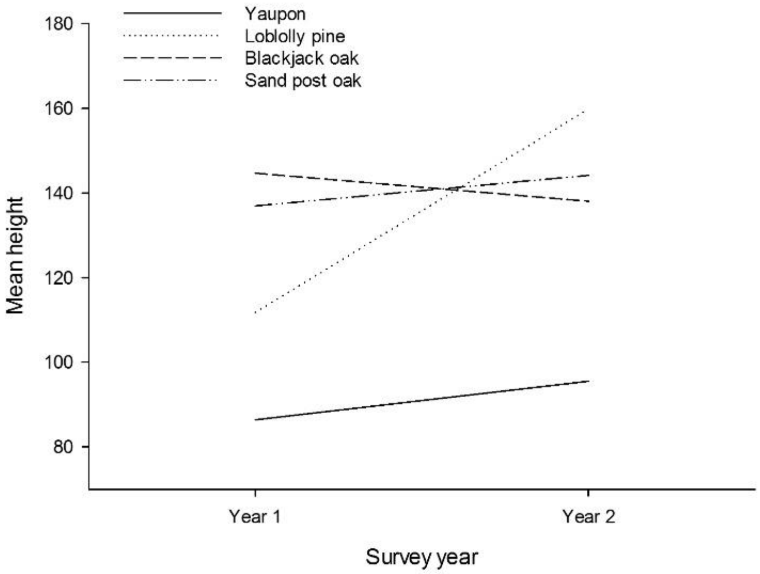


Figure 2.3, continued. Mean basal area (top), stem count (middle), and height (bottom) for each species each year.

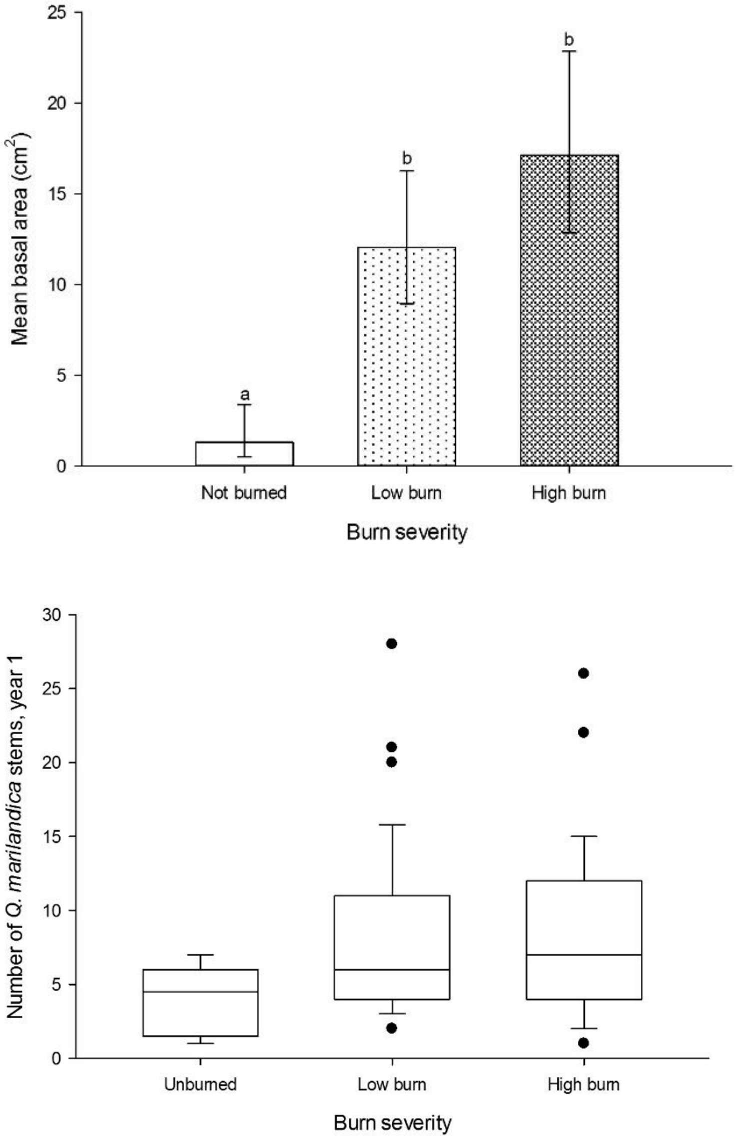


Figure 2.4. Top: Effect of burn severity on mean basal area in the second census year for *Q. marilandica* (n = 83, F = 13.3, $p < 0.0001$). Letters over 95% confidence intervals represent significant differences between treatments within a year. Bottom: Boxplot of the number of *Q. marilandica* stems in year one in each burn severity class. Burn severity was not a predictor of basal area of any other of the focal species.

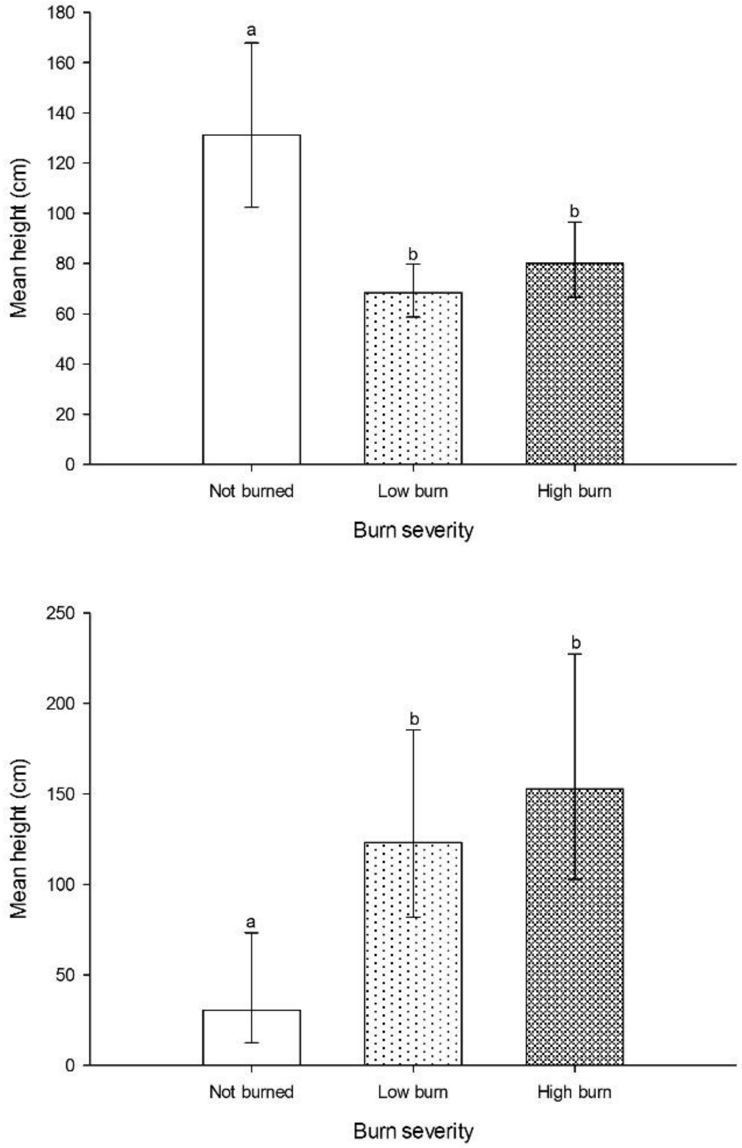


Figure 2.5. Effect of burn severity on mean stem height in year 1 for *I. vomitoria* (top, n = 97, F = 10.64, p = <0.0001), and in year 2 for *Q. marilandica* (bottom, n = 83, F = 5.48, p = 0.005). Letters over 95% confidence intervals represent significant differences between treatments within a year. Burn severity was not a predictor of stem height of any other of the focal species.

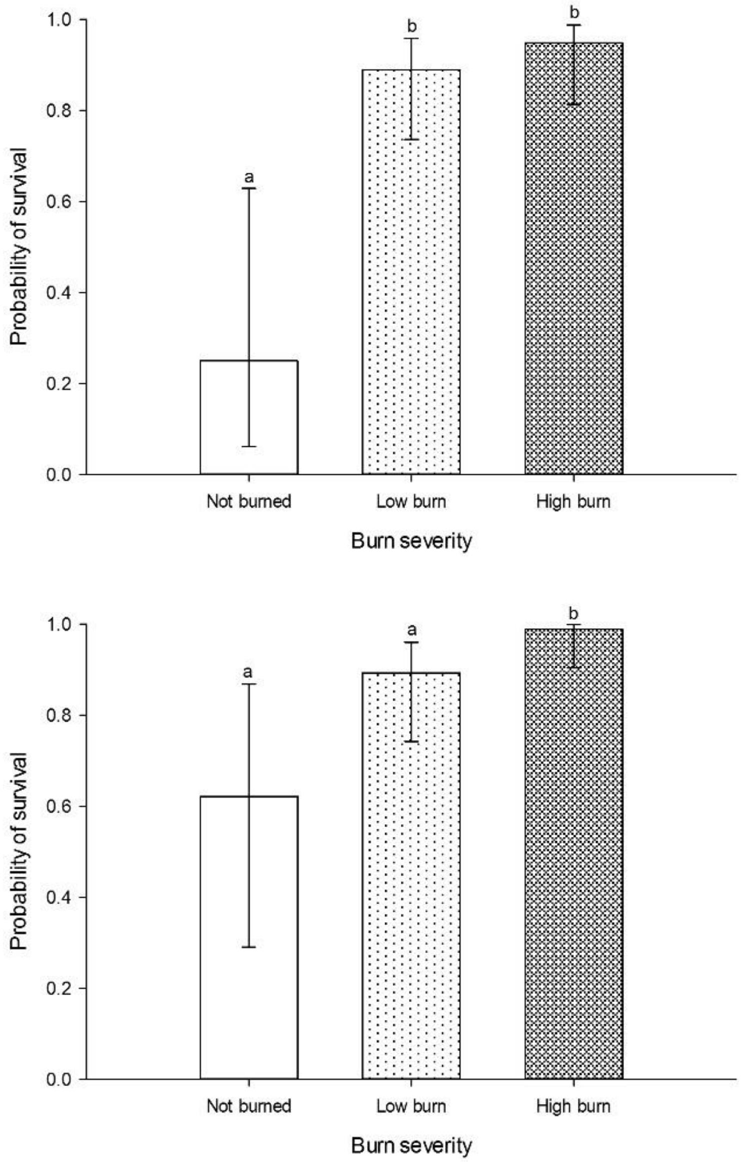


Figure 2.6. Effect of burn severity on probability of survival for *Q. marilandica* (top, n = 83, F = 7.5, p = 0.001) and *I. vomitoria* (bottom, n = 97, F = 3.8, p = 0.02). Letters over 95% confidence intervals represent significant differences between treatments within a year. Burn severity was not a predictor of probability of survival of any other of the focal species.

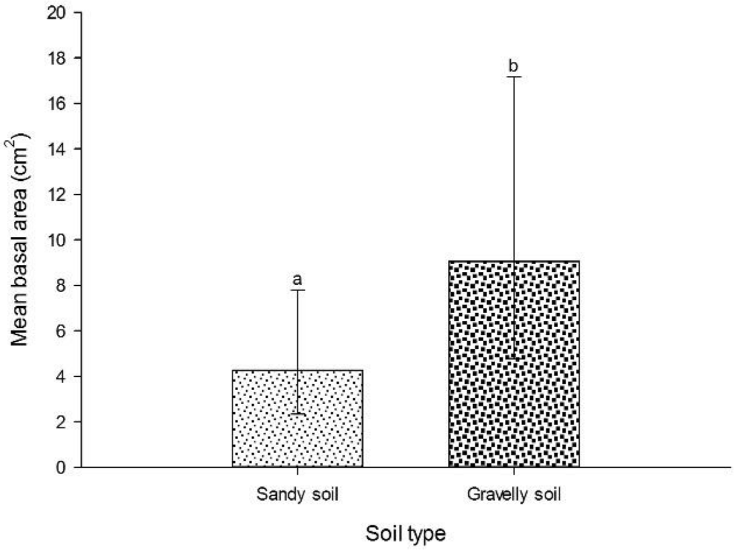


Figure 2.7. Effect of soil type on mean basal area in the second census year for *P. taeda* (*n* = 81, *F* = 19.82, $p < 0.0001$). Letters over 95% confidence intervals represent significant differences between treatments within a year. Soil type was not a predictor of basal area of any other of the focal species.

Chapter 3: Burn severity and post-fire erosion control affect post-fire woody plant recruitment

ABSTRACT

As wildfires become more frequent and severe in the United States, effective post-fire intervention is increasingly important for soil and plant conservation. Post-fire erosion control is often necessary in severely burned areas, but methods vary in effectiveness and impacts on vegetation. Little is known about the effects of hydroseed, an erosion control product, on post-fire plant recovery trajectories. Hydroseed was applied to control erosion of sandy soils after the 2011 wildfire in the Lost Pines region of Texas. Pre-fire, the region was dominated by loblolly pine (*Pinus taeda*), an obligate-seeder, and several species of sprouting oak, including sand post oak (*Quercus margaretta*). We investigated the effects of hydroseed and burn severity on post-fire pine and oak recovery in Bastrop State Park, within the Lost Pines. Fifty-six permanent plots were surveyed 1999-2015; hydroseed was applied to 15 plots post-fire. Hydroseed inhibited *P. taeda* regeneration in the first post-fire year, but had no effect on *P. taeda* seedling numbers after that, and no effect on *Q. margaretta* basal sprout numbers in any year. *P. taeda* seedling counts were greatest in lightly and moderately burned plots in the first post-fire year, and increased in scorched and lightly burned plots following heavy rain in 2015. *Q. margaretta* basal sprout numbers were greatest in moderately and heavily burned plots in the first post-fire year. While hydroseed may reduce initial post-wildfire woody plant recruitment, it is unlikely to permanently alter long-term woody plant community recovery in this region; burn severity may be a more important factor.

INTRODUCTION

When a disturbance regime changes, management strategies must also change to remain effective in reaching conservation goals. Large wildfires have become more frequent (Dennison *et al*. 2014; Settele *et al*. 2014; Westerling *et al*. 2006) and more severe (Dillon *et al*. 2011; Miller and Safford 2012) in the United States in the past several decades, in part due to past management practices (Bowman *et al* 2011) and in part due to climate change (Westerling *et al*. 2006). High levels of soil erosion (Certini 2005; Marcos *et al*. 2000; Scott and Van Wyk 1990), increases in non-native invasive species (Coffman *et al*. 2010; Dodge *et al*. 2006; Rew and Johnson 2008), and increases in undesired native species often follow these wildfires. As a result, land management agencies and private landowners are increasingly concerned with mitigating the effects of severe wildfires (Brunson and Tanaka 2011; Hesseln *et al*. 2003; Jones *et al*. 2016; Penman *et al*. 2016).

Post-fire rehabilitation treatments are costly and their effects on plant communities are sometimes controversial or poorly understood (Richards *et al*. 1998; Robichaud *et al*. 2000). Post-fire treatment decisions can be complex; fortunately tools that help assess fire effects and create management plans are becoming increasingly available to land managers (Napper 2006; Reinhardt and Dickinson 2010; Robichaud and Ashmun 2013). Post-fire treatments may have both desirable and undesirable effects. For example, salvage logging can help recover economic losses after a wildfire, but may reduce species diversity and inhibit post-fire recovery of native plant species (Leverkus *et al*. 2014). Less aggressive approaches, such as partially cutting trees and lopping branches from downed trees, may aid seedling recruitment and erosion control (Castro *et al*. 2011; Leverkus *et al*. 2012; Maranon-Jiminez *et al*. 2013) because they remove less plant material from the site.

Erosion control is one of the most common and urgent concerns following wildland fire. The most severe fires kill all vegetation and consume surface cover, including litter, duff, and downed woody debris, leaving the soil unprotected. Consumption of surface cover may change soil porosity and repellency (Doerr *et al*. 2006; Stoof *et al*. 2015; Wittenberg 2012), which can further increase rates of post-fire erosion and run-off (Johansen *et al*. 2001; Larsen *et al*. 2009). Rates of erosion are generally greatest immediately post-fire, especially in the most severely-burned areas (Myronidis *et al*. 2010). Rapid application of erosion control treatments may be essential to avoid loss of soil, especially on steep slopes and in more severely burned areas. However, erosion control treatments may alter future plant communities by affecting post-fire recruitment of plant species.

Mulching and application of synthetic polymers are common treatments used to decrease post-fire erosion and run-off (Babcock and McLaughlin 2013; Inbar *et al*. 2015; Lado *et al*. 2016; Morgan *et al*. 2014). Hydroseed, sometimes called hydromulch, is a class of erosion control products that contain mulch, tackifier (a bonding agent which adheres the mulch to itself and to the ground), and usually seed. Hydroseed was first developed in the late 1940s to control erosion and run-off on construction sites and road-cuts (California Department of Transportation 2003; Prats *et al*. 2016), and became more common following the 1977 Surface Mining Control and Reclamation Act (Committee on Surface Mining and Reclamation 1979). When used after wildland fire, it is important that the seed mix not introduce non-native invasive species.

Most research on hydroseed has investigated its effectiveness as an erosion control product (Babcock and McLaughlin 2013; Hubbert *et al*. 2012; Prats *et al*. 2016; Robichaud *et al*. 2013a, 2013b). The very few studies on the ways in which hydroseed affects post-fire vegetation dynamics (Hubbert *et al*. 2012; McCullough and Endress 2012; Morgan *et al*. 2014), especially on comparative effects on sprouting and non-sprouting woody species, have had mixed results, including no effect on woody plant community recovery (Hubbert *et al*. 2012; McCullough and Endress 2012), alteration of herbaceous species diversity and richness (Morgan *et al*. 2014), and accelerated growth of forbs (Hubbert *et al*. 2012). Top-killed sprouting woody species produce shoots by drawing on resources from the live root starch reserves of the parent tree (Chapin *et al*. 1990; Schutz *et al*. 2009), enabling them to regenerate quickly post-fire. Non-resprouting woody species regenerate only by germinating from seed, and may be slower to establish but better able persist after disturbance (Thomas and Davis 1989). Post-fire hydroseeding may alter competitive dynamics between sprouting and non-sprouting woody plant species, leading to alternative plant community recovery trajectories. We investigated the effects of hydroseeding and burn severity on post-wildfire recruitment of sprouting oaks and non-sprouting pines in the Lost Pines region of Texas, where the pine population was of special concern.

METHODS

Study Area

Bastrop State Park (BSP) is in the Lost Pines region of Texas, so named because it this region has the westernmost stands of loblolly pine (*Pinus taeda* L.), separated from the rest of this species' range in the southeastern United States. In September 2011, the Bastrop County Complex Fire burned most of BSP during a record drought and heat wave (Hoerling *et al*. 2013). 64.2% of mature trees were either killed or top-killed, and herbaceous vegetation, litter, and duff were completely consumed in most of the park (Keith and Creacy 2011).

Following the fire, increased rainfall (Table 3.1) accelerated post-fire soil erosion in BSP. Hazard trees were cut, and a hydroseed mix (22.68kg sterile non-native triticale [x *Triticosecale* Wittm. ex A. Camus (*Secale* x *Triticum*)] seed/acre; 0.45kg non-sterile native green sprangletop [*Leptochloa dubia* (Kunth) Nees, a native species] seed/acre; 680.39kg Rainier Fiber™ wood fiber mulch/acre; 90.72kg Patriot Environmental Clinker-Tack™ or Rantec Corporation Super Tack® tackifier/acre) was applied to areas of BSP which were the most severely burned and to slopes greater than 15°, between February and March, 2012. Hydroseed was also applied to easily accessible areas and areas which would simplify treatment unit boundaries.

Data Collection

Fifty-six 20m x 50m permanent plots were established in BSP (Figure 3.1) in 1999 and 2012 and surveyed following Fire Monitoring Handbook (FMH) protocols (USDI National Park Service 2003). Each permanent plot contained a 5m x 10m subplot from which vegetation data for this study were collected. Plots were surveyed occasionally between the months of May and October, 1999-2011, and yearly between the months of May and July, 2012-2015. In each subplot, immature trees (<2.5cm diameter at breast height [dbh]) were identified to species and counted.

Burn severity of plots was determined immediately post-fire in September, 2011 using the FMH visual assessment (USDI National Park Service 2003). Burn severity here refers to the effects of fire on soil and vegetation (Simard 1991; Karau and Keane 2010).

Plots were assigned one of five burn severity classes (in order from least to greatest severity: not burned, scorched, light, moderate, heavy). Presence or absence of hydroseed in plots was recorded between May and July, 2012.

We examined the effects of burn severity and hydroseed application on counts of immature *P. taeda* individuals, and on counts of immature 'individuals' of *Quercus margaretta* [Ashe] Small (sand post oak). There was not enough *Q. marilandica* Münchh. (blackjack oak) or *Q. stellata* Wangenh.(post oak) in each treatment for these two species to be analyzed statistically (Table 3.2). We here refer to immature *P. taeda* individuals as 'seedlings', following language found in the FMH, to indicate that these plants originated from seed. We refer to immature oak individuals as 'basal sprouts' because almost all individuals we found had sprouted from the base of a parent tree.

Statistical Methods

Statistical analyses were completed using SAS software v.9.2 (SAS Institute, Inc., Cary, North Carolina, USA). Generalized linear models (SAS GLIMMIX procedure) were used because our data were counts. Preliminary analyses found that the Poisson distribution did not give good fits. The negative binomial distribution with the log link function was used to fit all models to avoid over-dispersion and provide good fits. The negative binomial distribution, like the Poisson distribution, is not symmetric, so a few high values ('outliers') do not affect the results unduly. Predicted means and their confidence limits were back-transformed for tables and figures; note that confidence limits are asymmetric.

Pre-fire data from 1999 through 2011 were pooled to compare with post-fire data. No scorched plots received a hydroseed treatment, and no plots were unburned; analyses were therefore conducted on two overlapping subsets of the data (Table 3.3) to avoid including empty cells in analyses or discarding data. Subset *A* included plots with all burn severity classes but only plots without hydroseed. Subset *B* included only plots in the light, moderate, and heavy burn severity classes, but included all hydroseed treatments. Within each data subset, a separate analysis was done for each species, each year.

RESULTS

Data Subset A (all fire intensities; no hydroseed)

Pre-fire *P. taeda* seedling counts were significantly greater in moderately burned plots than in scorched or heavily burned plots pre-fire and remained so in 2012, approximately one year after the fire. *P. taeda* seedling counts were relatively low in all burn severity classes in both 2013 and 2014, and remained relatively low in moderately and heavily burned plots in 2015, probably due to low numbers of live parent trees. *P. taeda* seedling counts were significantly greater in scorched and lightly burned plots than in moderate and heavy burn plots in 2015, following heavy rainfall several months before sampling.

Pre-fire *Q. margaretta* basal sprout counts were significantly greater in moderately burned plots than in scorched or lightly burned plots pre-fire. Post-fire basal sprout counts were not significantly related to burn severity.

Data Subset B (± hydroseed; light to heavy burn severities only)

Interactions between burn severity and hydroseed were not significant in any model. Hydroseed application significantly inhibited *P. taeda* seedling recruitment in 2012

(Table 3.5, Figure 3.3). *Q. margaretta* did not appear to be affected by hydroseed treatment in any year (Tables 3.5, Figure 3.3).

DISCUSSION

Post-fire hydroseeding in BSP temporarily inhibited *P. taeda* seedling recruitment, likely because the hydroseed shaded seedlings or acted as a physical barrier to emergence. Competition with temporary sterile grass populations from the hydroseed seed mix may also have been partly responsible for poor recruitment of *P. taeda* seedlings in the first post-fire year. This latter hypothesis is consistent with research showing that seeding of soil-holding grasses and forbs can reduce conifer regeneration (Schoennagel and Waller 1999; Dodson and Peterson 2009) and native plant cover (Keeley 2004).

After 2012, hydroseed no longer inhibited *P. taeda* seedling emergence, likely due to the breakdown of hydroseed and die-back of some of the seeded sterile grasses. Hydroseed breaks down rapidly after application (Hubbert *et al*. 2012; Robichaud *et al*. 2013a), decomposing within five to twelve months (Prats *et al.* 2016). By contrast, dry wood strand mulch decomposes more slowly than hydroseed slurry (Robichaud *et al*. 2013a) and straw mulch decomposes more rapidly (Brockway *et al.* 2009). Straw mulch and hydroseed may also increase post-fire woody plant counts by increasing soil moisture retention (Brockway *et al.* 2009; Prats *et al*. 2016). Seeding alone may not be effective at reducing erosion in every case (Robichaud et al 2006; Vega et al 2015; Groen and Woods 2008), though it can help prevent colonization by invasive species (Pyke *et al*. 2013).

Following heavy spring rain in 2015, *P. taeda* seedling counts increased substantially in lower burn-severity plots, where more seed trees survived. Pine seed production, which varies year to year (Calama and Montero 2007; Koenig and Knops 2000; Krannitz and Duralia 2004), may also have contributed to the 2015 increase in seedling counts: pine seed production was low in 2013 and increased in 2014 and 2015 (G. Creacy, pers. comm.).

Hydroseeding had no discernible effect on *Q. margaretta* basal sprout counts. Where live root tissue remained, trees sprouted vigorously regardless of burn severity, which is typical of the response to hydroseeding of other sprouting woody plant species (Hubbert *et al*. 2012; McCullough and Endress 2012). *P. taeda* seedling counts were significantly higher in moderately burned plots pre-fire and in the first post-fire year, and *Q. margaretta* basal sprout counts were (non-significantly) higher in moderately burned plots pre-fire, indicating that these plots may have characteristics not addressed in this study which promoted seedling and basal sprout recruitment.

Sprouters and obligate-seeders can co-exist where the patchy nature of wildland fire creates spatial mosaics (Stephens *et al*. 2008) that may favor different life-history strategies (Bellingham and Sparrow 2000; Keeley and Zedler 1978). In our study, *P. taeda* seedlings were present but less abundant in more severely burned plots than in less severely burned plots. At least in the less severely burned plots, it is unlikely that *P. taeda* will be outcompeted by *Q. margaretta*.

CONCLUSION AND MANAGEMENT IMPLICATIONS

Post-fire application of hydroseed did not appear to have lasting effects on the recovery of the two dominant tree species, although it may have delayed pine seedling recruitment. Strong recruitment of pine seedlings four years after the fire, combined with their subsequent rapid growth (Booth, pers. obs.), suggests that both species will remain abundant in the future. Any long-term negative effects of hydroseeding therefore apparently did not involve the dominant tree species.

We cannot say at this time whether or not hydroseeding will have similar effects in other plant communities, other fire histories, or other environmental conditions. Effects of hydroseeding on woody plant regeneration may also be affected by the components of the hydroseed mix. Higher seeding rates and larger amounts of tackifier than were used in BSP might have a greater impact on seedling and basal sprout emergence.

Given the rapid rate of hydroseed decomposition, vegetation may only need to be monitored for 2-3 years after application to ascertain whether the post-fire plant community recovery trajectory will be directly affected by hydroseed applications. After that, any effects would be a secondary consequence of the immediate post-fire effects. .

Land managers are often confronted with difficult decisions immediately following wildfire which can influence future vegetation trajectories. These decisions are especially critical when recovery of a particular species is of concern. Post-fire assessment tools are valuable resources, but are most effectively used with an understanding of the impacts that specific post-fire interventions might have on vegetation recovery trajectories. More research is needed on the effects of hydroseed and other erosion control treatments in other plant communities, and it should be made available to the public.

Table 3.1. Total monthly precipitation, 2011-2015 (mm) (NOAA 2016).

Month	2011	2012	2013	2014	2015
January	86.1	74.7	76.2	20.3	81.3
February	11.4	93	29.5	18	22.6
March	7.1	106	14.5	51.8	154
April	1.3	23.6	89.2	19.1	144
May	45	106	73.2	175	284
June	45.2	32.8	44.7	63	119
July	9.7	105	58.7	40.4	18.3
August	8.4	36.1	36.8	22.4	34
September	29.7	120	147	98.8	51.3
October	54.4	26.7	136	44.7	203
November	40.6	10.7	50.5	113	73.9
December	87.6	18	17	48.5	59.9

Table 3.2. Average basal area of mature individuals of the four most abundant tree species in all plots in 2010 (one year pre-fire).

Species	Average basal area (m^2/ha)
Pinus taeda	16.3
Quercus margaretta	2.3
Quercus stellata	1.6
Quercus marilandica	0.9

Table 3.3. Numbers of permanent plots of each type. Data were separated into two overlapping subsets, which were analyzed separately. Subset *A*: all burn severity levels, hydroseed absent; subset *B*: light, moderate, and heavy burn severity levels, all hydroseed treatments.

	Burn severity					
Mulch treatment	Unburned	Scorched	Light	Moderate	Heavy	Total
Hydromulch absent	0	5^{A}	9^{AB}	6^{AB}	11^{AB}	31
Hydromulch present	0	0	1^{B}	4^{B}	10^{B}	15
Total	0	5	10	10	21	46

Table 3.4 (subset *A*). Back-transformed mean stem counts (lower confidence limit, upper confidence limit) of *P. taeda* seedlings and *Q. margaretta* basal sprouts in scorched, light, moderate, and heavy burn severity levels *P*-values from generalized linear models (see Methods).

				Burn severity				
	N	df	χ^2	Scorched	Light	Moderate	Heavy	*P*
P. taeda counts:								
pre-fire	31	3	7.9	4.3 (1.2, 15.2)	15.2 (6.1, 37.6)	75.0 (10.3, 543.6)	5.0 (1.7, 14.6)	*0.04*
2012	15	3	7.9	8.7 (2.5, 29.3)	1.7 (0.3, 9.9)	74.0 (7.9, 685.9)	0.5 (0.06, 9.6)	*0.04*
2013	31	3	4.2	9.0 (1.9, 40.9)	17.5 (7.4, 41.1)	9.8 (3.7, 25.4)	2.6 (0.6, 10.4)	*0.24*
2014	31	3	2.1	17.0 (1.9, 151.5)	12.0 (5.2, 27.6)	9.0 (3.3, 24.4)	3.6 (0.9, 14.3)	*0.56*
2015	31	3	21.1	164.8 (48.4, 560.9)	214.2 (81.3, 564)	17.2 (4.9, 59.4)	7.3 (3.1, 17.2)	*0.0001*
Q. margaretta counts:								
pre-fire	31	3	10.0	2.6 (0.8, 8.0)	11.1 (5.7, 21.5)	44.4 (15.0, 131.2)	7.0 (1.3, 37.3)	*0.01*
2012	15	3	0.4	1.2 (0.3, 4.4)	1.2 (0.2, 6.4)	0.5 (0.03, 8.0)	1.0 (0.09, 11.0)	*0.94*
2013	31	3	2.4	8.0 (2.6, 23.7)	18.6 (8.2, 41.7)	8.0 (2.1, 30.2)	5.0 (0.7, 35.3)	*0.48*
2014	31	3	4.8	8.3 (4.0, 16.9)	19.0 (11.5, 31.3)	9.0 (3.8, 21.2)	5.0 (1.2, 19.2)	*0.18*
2015	31	3	0.2	7.4 (3.4, 15.7)	6.8 (3.1, 14.5)	8.0 (2.4, 26.0)	5.0 (0.8, 28.9)	*0.97*

Table 3.5 (subset *B*). Back-transformed mean stem counts (lower confidence limit, upper confidence limit) of *P. taeda* seedlings and *Q. margaretta* basal sprouts in scorched, light, moderate, and heavy burn severity levels. *P*-values from generalized linear models (see Methods).

	N	df	χ^2	Hydromulch		*P*
				Absent	Present	
P. taeda counts:						
pre-fire	41	1	2.7	14.7 (7.4, 29.3)	34.1 (16.9, 68.6)	*0.1*
2012	19	1	9.9	11.8 (4.3, 31.9)	0.1 (0.01, 1.2)	*0.001*
2013	41	1	2.0	8.5 (4.6, 15.5)	3.2 (1.1, 9.3)	*0.1*
2014	41	1	0.1	7.5 (4.1, 13.6)	6.4 (2.1, 18.8)	*0.8*
2015	41	1	1.9	29.5 (17.0, 51.2)	10.5 (2.9, 37)	*0.1*
Q. margaretta counts:						
pre-fire	41	1	0.4	15.3 (7.0, 33.2)	22.7 (10.6, 48.7)	*0.5*
2012	19	1	2.5	1.7 (0.8, 3.8)	0.9 (0.2, 2.9)	*0.2*
2013	41	1	0.0	9.9 (4.8, 20.3)	10.7 (4.7, 24.7)	*0.8*
2014	41	1	0.0	13.2 (6.4, 27.1)	12.2 (3.7, 40.5)	*0.9*
2015	41	1	0.2	7.2 (3.6, 14.4)	10.2 (3.5, 29.6)	*0.6*

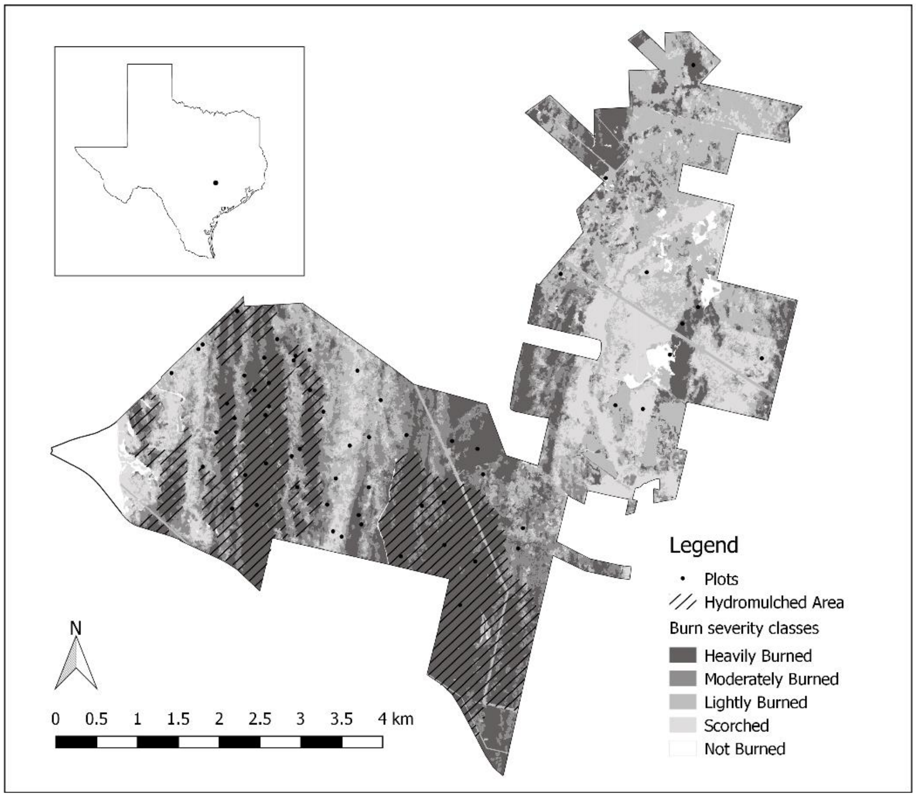


Figure 3.1. Map of Bastrop State Park and location within Texas, with permanent plots and burn severity classes. Hatched lines show hydroseeded area.

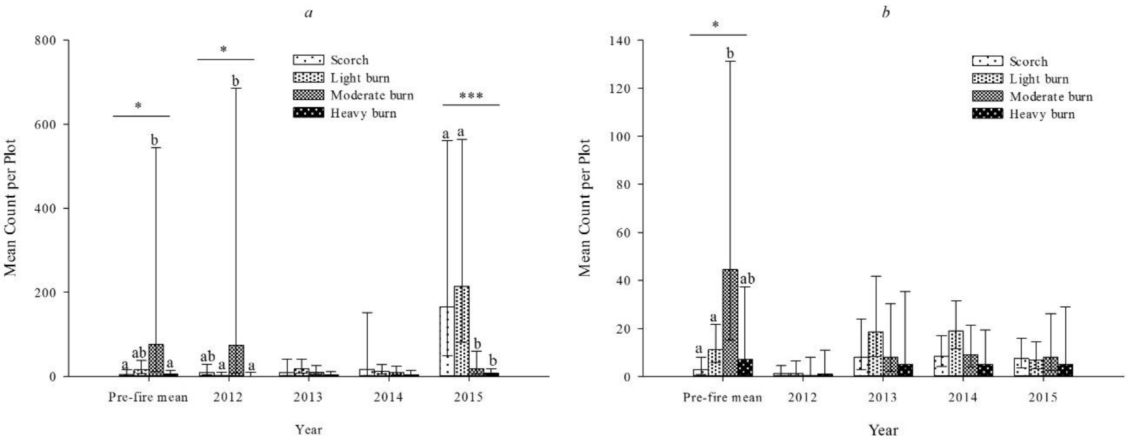


Figure 3.2 (subset *A*). Back-transformed mean counts per plot of *P. taeda* (a) and *Q. margaretta* (b), in scorch, light, moderate, and heavy burn levels. Model significance is indicated by asterisks (*: p=.05, **: p<0.01, ***: p<0.001, ****: p<0.0001). Letters over 95% confidence intervals represent significant differences between treatments within a year.

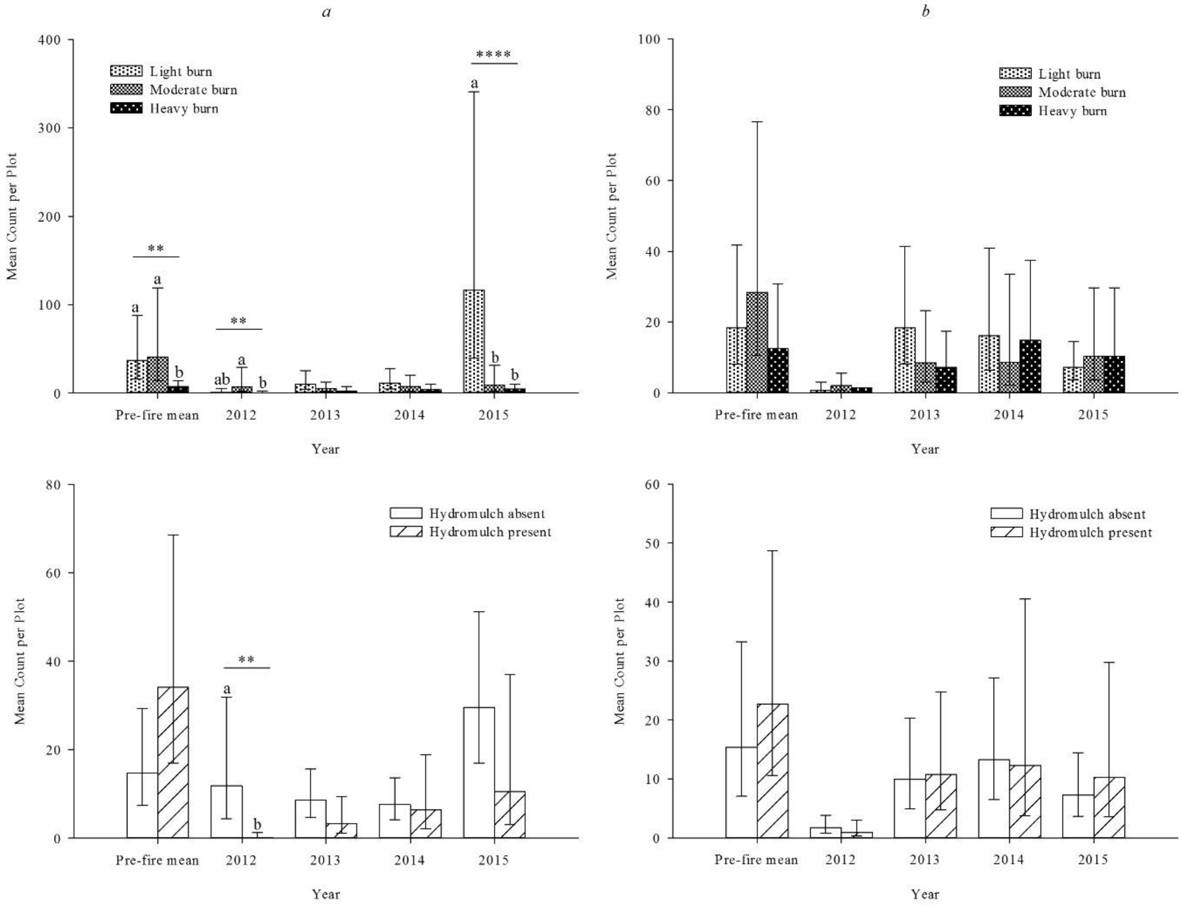


Figure 3.3 (subset *B*). Back-transformed mean counts per plot of *P. taeda* (a) and *Q. margaretta* (b). Top row shows mean count per plot in light, moderate, and heavy burn severity levels; bottom row shows mean count per plot in plots where hydroseed was absent or present. Model significance is indicated by asterisks (*: p=.05, **: p<0.01, ***: p<0.001, ****: p<0.0001). Letters over 95% confidence intervals represent significant differences between treatments within a year.

Chapter 4: Herbaceous plant community recovery after a high-severity wildfire

ABSTRACT

Objective

The Lost Pines region of central Texas supports the westernmost stands of loblolly pine (*Pinus taeda*) in the United States. In 2011, during a record drought, a wildfire burned most of Bastrop State Park (BSP), which is in the Lost Pines region. Before the fire, the tree canopy was continuous in many areas, which decreased understory light availability. The continuous canopy also allowed the fire to spread rapidly through the canopy, and most trees and herbaceous vegetation were consumed in the fire, which created large, open-canopy patches. Our objective was to quantify the effects of burn severity, soil types, and other abiotic factors on herbaceous species recovery trajectories in the Lost Pines.

Methods

Fifty-six 20m x 50m permanent plots were established in Bastrop State Park and surveyed between 1999-2015. Ten 1m^2 quadrats were placed along the long edges of each plot. In each quadrat, all herbaceous plants were identified to species, and forb stems and graminoid tillers counted. Canopy cover was measured at each plot. Forb stems, graminoid tillers, and relative abundances of forb species and graminoid species were analyzed separately, and six of the most abundant species were analyzed individually.

Results

Pre-fire, herbaceous plant abundance was low. Forb and graminoid abundance, species richness and diversity increased rapidly in the first two years after the fire. Graminoid tiller numbers decreased in 2014 and 2015, but abundance, richness, and diversity of forbs and graminoids continued to increase. Forbs and graminoids were more abundant in more severely burned plots than in less severely burned plots. Forbs and graminoids were both more abundant in gravelly soil plots than in sandy soil plots. Responses of the six individually-analyzed species to environmental variables were species-specific.

Conclusions

Our results suggest that the increased abundance, richness, and diversity of forbs and graminoids was likely due to decreased competition and greater light availability resulting from severe fire. The rapid post-fire colonization of many native herbaceous species in even the most severely burned areas indicates conditions favorable to post-fire plant community regeneration. In order to maintain a diverse herbaceous plant community in the future, continued management actions such as prescribed burns will be required to maintain an open canopy.

INTRODUCTION

Disturbance regimes shape plant community composition and structure over time (Bond and Keeley 2005, Hanberry 2014, Hernandez-Serrano *et al*. 2013, Hessburg *et al*. 2005, Naiman *et al*. 1993, Nowacki and Abrams 2008, Ward *et al*. 1999). The type and severity of a disturbance partly determines its effects on canopy structure, soil properties, and understory vegetation, which in turn affect future plant community composition (Roberts 2004).Wildland fire is a disturbance that can maintain certain types of ecosystems; many savannas and some woodlands are maintained by low-severity surface fires (Bond and Keeley 2005, Fill *et al*. 2015, Nowacki and Abrams 2008, Peterson and Reich 2001, van Langevelde *et al*. 2003). Long-term fire suppression in ecosystems typically maintained by fire can lead to altered plant communities and reduction of herbaceous plant diversity (Abrahamson and Abrahamson 1996, Menges *et al*. 1993).

Severe wildland fire creates a more open canopy by killing or top-killing overstory species. While extensive plant mortality can increase the risk of erosion, it also increases light availability to the understory, which is a limiting factor in seedling recruitment in many species (Lichter 1998). Herbaceous species cover, richness and diversity generally increase after severe fire, partly due to increased canopy openness (Gálhidy *et al*. 2005, Kunst et al 2003), and partly due to decreased competition and litter biomass (Burton *et al*. 2011), although the effect may be short-term (Fulbright 2004, Roberts 2007).

Different functional groups may also respond differently to fire; forbs and graminoids often increase in abundance after fire (Abella and Fornwalt 2015, Shryock *et al*. 2014) due to increased light availability. By contrast, cacti may decrease in abundance after fire (Shryock *et al*. 2014) due to mortality from fire damage. Species that sprout from underground rhizomes or bulbs may be more likely to remain where they survive in lower burn severity or unburned areas (Morgan *et al*. 2015) than to disperse into a severely burned area.

Competitive dynamics in the herbaceous community may contribute to the success or failure of woody plant regeneration (Carr and Krueger 2001, Gilliam 2007, McCarthy *et al*. 2001, Pitt *et al*. 2011), though not in all systems (Davis *et al*. 2017). It is therefore important to consider post-disturbance herbaceous species dynamics to better understand the effects of site characteristics on long-term vegetation trajectories (Gilliam 2007).

We investigated the effects of a severe wildfire in central Texas on forb and graminoid plant community dynamics. We analyzed data from the first four years after the wildfire, to describe the changes that occurred during that period and to help predict possible future trajectories for the developing plant community.

METHODS

Study Area

The Lost Pines of central Texas are the westernmost stands of loblolly pine (*Pinus taeda* L.) in the United States. The region has diverse flora and fauna (Appendix B) due to its soil and geographical properties, and includes western, eastern, northern, and southern species (Taber 2008). In September 2011, a crown fire burned much of the Lost Pines, including almost all of Bastrop State Park (BSP), during a record drought and heat wave (Hoerling *et al*. 2013). In most areas of BSP, above-ground vegetation, litter and duff were completely consumed.

To control erosion following the fire, a hydromulch mix (22.68kg sterile non-native triticale [x *Triticosecale* Wittm. ex A. Camus (*Secale* x *Triticum*)] seed/acre; 0.45kg non-sterile native green sprangletop [*Leptochloa dubia* (Kunth) Nees, a native species] seed/acre; 680.39kg Rainier Fiber^{TM} wood fiber mulch/acre; 90.72kg Patriot

Environmental Clinker-Tack^{TM} or Rantec Corporation Super Tack$^{®}$ tackifier/acre) was applied to the areas of BSP that were the most severely burned and to slopes greater than 15° between February and March, 2012. Hydromulch was applied on 15 plots.

Data Collection

Fifty-six 20m x 50m permanent plots were established in Bastrop State Park (Fig. 4.1, QGIS 2.18.9, QGIS Development Team 2009, Open Source Geospatial Foundation) between 1999-2012 and surveyed following Fire Monitoring Handbook (FMH) protocols (USDI National Park Service 2003). Quadrats (1m^2 each) were placed at 10m intervals along two 50m transects on the long edges of each plot, for a total of ten quadrats per plot. In each quadrat, all herbaceous plants were identified to species, and forb stems and graminoid tillers were counted for each species separately (Fig. 4.2). Annual samples of each plot were irregularly made from 1999 through 2011, on dates that varied from May through October. Each plot was sampled once a year from 2012 through 2015, in May, June, or July. Stem and tiller counts from all the quadrats in a given plot were added to obtain one value of each variable for each plot in each year. All densities are therefore per 10 m^2.

We here use ‘stems’ to refer to number of forb stems and ‘tillers’ to refer to number of graminoid tillers. Per FMH protocol, each tiller was counted as a separate individual, rather than as tillers per individual, which inflated the number of graminoids relative to forbs in each quadrat. Generally, forb individuals had a small number of stems, but most graminoids had many tillers.

Burn severity of plots was determined immediately post-fire in September, 2011 using the FMH assessment (USDI National Park Service 2003), which is based on degree of consumption of vegetation and substrate. Plots were assigned to one of 5 burn severity classes (in order from least to greatest severity: unburned, scorched, light, moderate, and heavy). No plots were unburned.

Soil data was obtained from the Soil Survey Geographic (SSURGO) Database. SSURGO soil types were first ground-truthed and modified where necessary to accurately reflect local soil texture, then re-classified as either ‘sandy’ or ‘gravelly’ (Appendix A) for increased statistical power and ease of interpretation. Canopy cover was measured at multiple points per plot (Fig. 4.2) in some pre-fire and all post-fire surveys using a canopy densiometer held approximately 1.2m from the ground, then averaged for each plot each year. Elevation, slope, and aspect were extracted from topographic maps provided by BSP.

Statistical Analyses

Pre-fire plot data from 1999-2011 were pooled as one ‘year’ to compare with post-fire data, in all analyses. We pooled these data rather than using only data from 2010, one year before the fire, because not all plots were surveyed every year pre-fire. To increase sample sizes in each burn category, burn severity classes were pooled into two classes: low burn (scorched and light burn plots), and high burn (moderate and heavy burn plots). Statistical analyses were made using SAS 9.4 (SAS Institute, Cary, North Carolina, USA) or RStudio 1.0.143 with R 3.3.3 (R Core Development Team 2011, Vienna, Austria).

Three sets of analyses were made, using different subsets of the data:

- Functional groups: Data subset A grouped individual species into two functional groups, forbs and graminoids. No other functional groups (e.g., succulents) were included.
- Individual species: Data subset B retained species identity information, but included only the five most abundant herbaceous species (*Dichanthelium linearifolium* [Scribn. ex Nash) Gould, *Dichanthelium oligosanthes* [Schult.] Gould var. *oligosanthes*, *Dichanthelium sphaerocarpon* [Elliot] Gould, *Heterotheca subaxillaris* [Lam.] Britton & Rusby var. *latifolia* [Buckley] Gandhi & R.D. Thomas, *Lechea tenuifolia* Michx.), and *Leptochloa dubia*. *L. dubia* was analyzed in years 2013-2015 because it was included in post-fire hydromulch applications; plots with hydromulch were not surveyed in 2012.
- Community metrics: Data subset C included relative abundances of individual species in each plot in each functional group each year (i.e., the relative abundances of all species in a given functional group in a given year in a given plot added to 1.0).

Generalized linear models were used to analyze functional groups and individual species. The response variable was number of stems per plot in a given functional group (data subset A) or of a given species (data subset B). The GLIMMIX procedure of SAS was used, specifying a negative binomial distribution (except for *H. subaxillaris*, which could be fit with a Poisson distribution). The potential predictor variables were burn severity, soil type, aspect, presence or absence of hydromulch, canopy cover, elevation, and slope. Each response variable in each year was analyzed separately. We used forward selection to build these models, adding variables one by one. At each step, the AICc values of all possible models with one additional variable were compared, and the variable that most decreased AICc was added to the model. No additional variables were added to a model if AICc did not decrease by two or more. Once the best model for a given reponse variable had been identified by this procedure, we examined the significance (*P*-value) of each included predictor variable in the final model. Due to the large number of final models, we used the Bonferroni correction of alpha. There was a total of 38 final models (forbs, graminoids, and 5 species = 7 x 5 years, + 1 additional species x 3 years) and we therefore used an adjusted alpha value of $p \leq 0.0013$. Predicted means and confidence limits were back-transformed for tables and figures.

Calculation of community metrics used data subset C. All species were pooled into ten datasets including only forbs or only graminoids in each year, which were analyzed separately. These data sets were used to create ordination plots and to perform PERMANOVA analyses. Ordination plots were constructed using the R functions ‘metaMDS’, ‘ordiplot’, and ‘orditorp’ from the ‘vegan’ package with Bray-Curtis dissimilarity indices. PERMANOVA analyses were done using the R function ‘adonis’ from the ‘vegan’ package. We used backward selection to build these models. Starting with a model that included all predictor variables, variables were dropped one at a time, and the variable that least reduced R^2 was permanently dropped. This process was repeated until dropping any variable reduced R^2 by more than 0.1.

RESULTS

General

By 2013, the severely burned plots had developed a herbaceous layer that was continuous or close to continuous (Fig. 4.3). Plots that were only lightly burned had much less herbaceous cover, but more than they had had before the 2011 fire. After 2013, the herbaceous community continued to develop: diversity and richness increased and the dominance of early species such as *D. linearifolium* decreased (Fig. 4.4), while the herbaceous layer did not thin.

Burn severity

There were more forb stems in more severely burned plots than in less severely burned plots (Fig. 4.5, Table 4.1). We did not detect a significant relationship between total graminoid tiller numbers and burn severity in any year. However, average numbers of *D. linearifolium* and *L. dubia* tillers, as well as of *L. tenuifolia* stems, were greater in more severely burned plots (Fig. 4.6, Table 4.2).

When species were analyzed via PERMANOVA, burn severity was a significant predictor of forb and graminoid species relative abundances in every post-fire year, and accounted for 15-20% of model variance for forbs and 14-29% of model variance for graminoids (Fig. 4.7, Table 4.3).

Soil type

There were more forb stems and graminoid tillers in gravelly soils than in sandy soils (Fig. 4.8, Table 4.1). In the PERMANOVA (Fig. 4.7, Table 4.3), soil type was a significant predictor of post-fire forb and pre-and post-fire graminoid species relative abundances, accounting for 5% of model variance for forbs and 6-8% of model variance for graminoids.

Canopy Cover

Pre-fire graminoid tiller and forb stem numbers and post-fire forb stem and graminoid tiller numbers were negatively related to same-year canopy cover (Table 4.1). Mean *H. subaxillaris* stem numbers were positively related to canopy cover in 2014, but negatively related to canopy cover in 2015 (Table 4.2). *D. linearifolium* tiller numbers were negatively related to canopy cover pre-fire, but positively related to canopy cover post-fire (Table 4.2). In the PERMANOVA, canopy cover was only a significant predictor of forb species relative abundances pre-fire and in 2015, and accounted for 8% and 3% of model variance, respectively (Fig. 4.7, Table 4.3). There was a statistically significant negative relationship between canopy cover and burn severity ($r_s = -0.50$, $p < 0.0001$), as would be expected, because burn severity was partly defined by overstory tree mortality.

Hydromulch

As expected, hydromulch was associated with greater stem density of *L. dubia* (Fig. 4.9, Table 4.2), which was part of the seed mixture in the hydromulch. The greater number of graminoid tillers in hydromulched plots reflected this (Fig. 4.9, Table 4.1). Hydromulch was a significant predictor of graminoid relative abundances in 2013 and 2014, and accounted for 9% and 3% of model variance, respectively (Fig. 4.7, Table 4.3).

Slope, aspect, elevation

Slope had little effect; the only effect detected was a negative one in pre-fire *H. subaxillaris* abundance (Table 4.2). No relationship was detected between aspect or elevation and any response variable.

Interactions

No interaction terms in the generalized linear models were significant. In the PERMANOVA, there were significant post-fire interactions from 2013-2015 for forb and graminoid relative abundances (Table 4.3). An interaction for forbs between burn severity and soil type may have been detected due to unknown physical or topographical properties of these soil types (see below), or because of sample size issues, in which there were fewer gravelly soil plots in lower burn severity classes (Table 4.4). The interaction for graminoids between burn severity and hydromulch application probably resulted from hydromulch only being applied in the most severely burned areas.

DISCUSSION

Pre-fire herbaceous abundances were so low that differences between soil types were not detected. Post-fire, however, gravelly soils consistently had more forb stems, more graminoid tillers, and greater abundances of the two most common herbaceous species than did sandy soils. This was unexpected, and its cause is unclear. Gravelly soils also had more pines, yaupon, and some oak species than did sandy soils (Chapter 1). Gravelly soils are more common on ridgetops and slopes, while the sandy soils are more often found in dry drainages, which one might expect to have higher soil moisture.

After the 2011 wildfire, the herbaceous community in our permanent plots flourished. Pre-fire, the pine-oak stands in the Lost Pines region had very little herbaceous vegetation (Fig.4.3), likely due to the fact that the canopy had been closed for decades. A continuous or nearly continuous herbaceous layer had developed in many severely burned plots by 2013, two years post-fire. In the 460 m^2 that were covered by the permanent plots, we recorded 173 herbaceous species (forbs and graminoids) pre-fire, and 250 herbaceous species post-fire (Appendix B). Some of the new species were non-native, but most were native species that had not been observed in any pre-fire plots, and may have been excluded due to low light levels. The post-fire herbaceous community was consistently densest (with the most tillers and stems) where the fire was most severe, including plots in which underground roots burned and the soil was apparently near-sterilized. We therefore suspect that, especially in the most severely burned plots, re-colonization by forbs and graminoids was primarily via seed dispersal rather than sprouting from surviving rhizomes or bulbs.

The most likely reason for the increased herbaceous species abundance and richness (Table 8) in more severely burned plots was the higher light levels there. It may also have been in part due to reduced underground competition from woody plants, which were either killed or top-killed in severely burned plots (Chapter 1). Graminoid cover and richness has been shown to increase with greater burn severity or canopy openness in other ecosystems (Laughlin *et al*. 2006, Moore *et al*. 2006, Pinno and Errington 2016, Rhoades and Fornwalt 2015, Sabo *et al*. 2009).

Initially, the herbaceous community was dominated by three perennial grass species in the genus *Dichanthelium*, the annual or biennial forb species *H. subaxillaris* (Asteraceae), and the perennial forb species *L. tenuifolia* (Cistaceae). As expected, *L.*

dubia, a perennial grass, was very abundant in and near hydromulched and severely burned areas because it was included in the hydromulch mix that was applied to severely burned areas. Over time, *L. dubia* and the *Dichanthelium* species declined in abundance, while richness and diversity of both forbs and graminoids continued to increase (Fig. 4.4, Table 4.5).

Herbaceous species response to fire can be species-specific (Turner *et al*. 1997). *H. subaxillaris* is known to colonize disturbances (Keever 1955, Tremmel and Peterson 1983), as is *Dichanthelium* spp. (Lonati *et al*. 2009, Mou *et al*. 2005), which increase in abundance in full sun (Flory *et al*. 2007). By contrast, *L. tenuifolia* is not generally thought of as an early colonizer of recent disturbances (Edgin *et al*. 2004). Many of the weedy plant species common in the region, such as *Conyza canadensis* (L.) Cronquist (Asteraceae) and *Gamochaeta* spp. Weddell (Asteraceae), which grow one or very few stems per individual, were not abundant in our plots. This is in part due to our use of stem and tiller counts, which emphasizes species in which an individual commonly has multiple stems or tillers, which is true of all six of the most abundant species. It may also reflect the unusual edaphic conditions in the Lost Pines, or the depauperate condition of the herbaceous community pre-fire.

After the initial increase in herbaceous biomass and diversity, graminoid abundance declined while both forb and graminoid diversity and richness continued to increase (Fig. 4.4, Table 4.5). If the increase in herbaceous biomass and diversity was due to release from competition with woody plants, it will likely not be maintained in the future, unless repeated surface fires or mechanical thinning maintain a savanna in place of the pre-fire closed canopy. However, if future management prevents a closed canopy from re-forming, we would expect herbaceous biomass and diversity to continue to increase as the existing population increases and new species arrive in these plots.

Management actions that maintain an open canopy, such as frequent prescribed burns and thinning, can help increase or maintain herbaceous species richness and cover (Burton *et al*. 2011, Collins *et al*. 2007, Glitzenstein *et al*. 2003, Lepik *et al*. 2004, Lettow *et al*. 2014, Peterson and Reich 2008, Platt *et al*. 2006), and can increase diversity and abundance of native species in other taxa (Brown *et al*. 2015, Taber *et al*. 2008). The future of the biotic community will depend primarily upon future management decisions, though climate change, species invasions, and natural community dynamics will undoubtedly also play roles.

Table 4.1. Summary of generalized linear model results by functional group, with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect, and hydromulch), are reported as 'F, p'; results for continuous predictor variables (canopy cover, elevation, and slope) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Functional group	Year	N	Burn severity (four classes)	Soil type	Aspect	Hydroseed	Same year canopy cover	Elevation	Slope
forbs	pre-fire	25	NI	3.3, 0.09	4.3, 0.01	NI	**-0.06, 19.15, 0.0004**	NI	NI
forbs	2012	32	1.9, 0.2	NI	NI	NI	NI	NI	NI
forbs	2013	46	**6.7, 0.0011**	12.1, 0.0014	4.5, 0.004	NI	NI	0.02, 4.7, 0.04	NI
forbs	2014	46	4.6, 0.008	NI	2.8, 0.04	NI	**-0.2, 16.9, 0.0002**	0.01, 5.6, 0.02	NI
forbs	2015	46	NI	**22.9, <0.0001**	4.6, 0.004	4.6, 0.04	NI	0.01, 5.1, 0.03	NI
graminoids	pre-fire	25	NI	NI	3.2, 0.04	NI	**-0.06, 26.9, <.0001**	NI	NI
graminoids	2012	32	NI	NI	3.3, 0.03	NT	NI	NI	NI
graminoids	2013	46	NI	7.9, 0.008	NI	**12.8, 0.0009**	-0.04, 7.9, 0.008	NI	NI
graminoids	2014	46	NI	**27.1, <.0001**	4.4, 0.005	NI	-0.01, 4.6, 0.04	NI	NI
graminoids	2015	46	NI	**15.4, 0.0003**	3.9, 0.01	NI	-0.007, 4.7, 0.04	NI	NI

Table 4.2. Summary of generalized linear model results by species (reported as 'F, p'), with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect, and hydromulch), are reported as 'F, p'; results for continuous predictor variables (canopy cover, elevation, and slope) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Year	N	Burn severity (two classes)	Soil type	Aspect	Hydroseed	Same year canopy cover	Elevation	Slope
D. linearifolium	pre-fire	25	NI	NI	NI	NI	-0.3, 7.7, 0.01	NI	NI
D. linearifolium	2012	31	11.9, 0.0017	NI	NI	NI	NI	NI	NI
D. linearifolium	2013	54	**22.2, <0.0001**	8.0, 0.007	NI	NI	NI	-0.1, 4.7, 0.04	NI
D. linearifolium	2014	46	**15.5, 0.0003**	7.9, 0.008	NI	NI	0.01, 0.2, 0.6	-0.09, 5.4, 0.03	NI
D. linearifolium	2015	46	10.3, 0.002	7.6, 0.009	NI	NI	0.005, 0.02, 0.9	-0.1, 6.8, 0.01	NI
D. oligosanthes	pre-fire	38	NI	6.9, 0.01	NI	NI	NI	NI	NI
D. oligosanthes	2012	31	6.4, 0.01	NI	NI	NI	NI	NI	NI
D. oligosanthes	2013	54	2.2, 0.1	2.2, 0.1	NI	NI	NI	0.009, 0.2, 0.6	NI
D. oligosanthes	2014	46	2.1, 0.2	4.1, 0.05	NI	NI	-0.01, 0.8, 0.05	0.01, 0.6, 0.4	NI
D. oligosanthes	2015	46	0.9, 0.4	1.6, 0.2	NI	NI	-0.004, 0.2, 0.7	0.01, 0.3, 0.6	NI
D. sphaerocarpon	pre-fire	25	NI	NI	NI	NI	-0.3, 7.3, 0.01	NI	NI
D. sphaerocarpon	2012	31	7.9, 0.009	NI	NI	NI	NI	NI	NI

Table 4.2, continued. Summary of generalized linear model results by species (reported as 'F, p'), with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect, and hydromulch), are reported as 'F, p'; results for continuous predictor variables (canopy cover, elevation, and slope) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Year	N	Burn severity (two classes)	Soil type	Aspect	Hydroseed	Same year canopy cover	Elevation	Slope
D. sphaerocarpon	2013	54	0.8, 0.4	0.7, 0.4	NI	NI	NI	-0.04, 1.8, 0.2	NI
D. sphaerocarpon	2014	46	0.04, 0.9	1.7, 0.2	NI	NI	-0.07, 4.0, 0.05	-0.08, 6.7, 0.01	NI
D. sphaerocarpon	2015	46	0.3, 0.6	1.6, 0.2	NI	NI	-0.04, 6.5, 0.01	-0.04, 4.8, 0.04	NI
H. subaxillaris	pre-fire	38	NI	NI	NI	NI	NI	NI	**-4.9, 115.1, <0.0001**
H. subaxillaris	2012	31	0.7, 0.4	NI	NI	NI	NI	NI	NI
H. subaxillaris	2013	54	9.6, 0.004	0.2, 0.8	NI	NI	NI	0.03, 0.9, 0.4	NI
H. subaxillaris	2014	46	0.7, 0.4	0.8, 0.4	NI	NI	**0.02, 28.8, <0.0001**	0.02, 1.2, 0.3	NI
H. subaxillaris	2015	46	0.9, 0.3	0.4, 0.5	NI	NI	**-0.07, 18.9, <0.0001**	0.01, 0.9, 0.4	NI
L. tenuifolia	pre-fire		NI	NI	NI	NI	NI	NI	NI
L. tenuifolia	2012	31	**33.9, <0.0001**	NI	NI	NI	NI	NI	NI

Table 4.2, continued. Summary of generalized linear model results by species (reported as 'F, p'), with explanatory variables in columns. Results for categorical predictor variables (burn severity, soil type, aspect, and hydromulch), are reported as 'F, p'; results for continuous predictor variables (canopy cover, elevation, and slope) are reported as 'estimate, F, p'. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface.

Species	Year	N	Burn severity (two classes)	Soil type	Aspect	Hydroseed	Same year canopy cover	Elevation	Slope
L. tenuifolia	2013	54	**23.6, <0.0001**	6.9, 0.01	NI	NI	NI	-0.02, 0.7, 0.4	NI
L. tenuifolia	2014	46	**14.6, 0.0004**	7.1, 0.01	NI	NI	-0.01, 0.2. 0.6	-0.02, 0.6, 0.5	NI
L. tenuifolia	2015	46	11.7, 0.0014	9.8, 0.003	NI	NI	-0.06, 5.2, 0.03	-0.03, 1.7, 0.2	NI
L. dubia	2013	45	**13.8, 0.0006**	NI	1.1, 0.4	NI	NI	NI	-0.3, 0.2, 0.6
L. dubia	2014	45	NI	NI	NI	**38.2, <0.0001**	NI	0.04, 3.7, 0.06	-0.1, 2.2, 0.1
L. dubia	2015	44	NI	NI	NI	NI	-0.22, 8.8, 0.005	NI	NI

Table 4.3. Summary of PERMANOVA model results (reported as 'p, R2'), with explanatory variables in columns. 'NI' indicates that the explanatory variable was not included in the final model. Significant results are in boldface. Only significant interactions are reported ('burn' = burn severity, 'soil' = soil type, 'hydr' = hydromulch application).

Functional group	Year	Burn severity	Soil type	Aspect	Hydroseed	Same year canopy cover	Elevation	Slope	Interactions	Residual R^2
forbs	pre-fire	NI	NI	0.8, 0.13	NI	**0.005, 0.08**	NI	NI	NS	0.61
forbs	2012	**0.002, 0.20**	NI	0.7, 0.09	NI	NI	NI	NI	NS	0.55
forbs	2013	**0.001, 0.15**	**0.002, 0.05**	NI	NI	NI	NI	NI	**burn*soil (0.005, 0.07)**	0.70
forbs	2014	**0.001, 0.16**	**0.002, 0.05**	NI	NI	NI	NI	NI	**burn*soil (0.002, 0.08)**	0.69
forbs	2015	**0.001, 0.20**	**0.002, 0.05**	**0.04, 0.10**	NI	**0.04, 0.03**	NI	NI	**burn*cover (0.01, 0.09)**	0.26
grams	pre-fire	NI	**0.01, 0.13**	0.6, 0.14	NI	NI	NI	NI	NS	0.67
grams	2012	**0.001, 0.29**	NI	NI	NI	NI	NI	NI	NS	0.70
grams	2013	**0.001, 0.17**	**0.002, 0.06**	NI	**0.001/0.09**	NI	NI	NI	**burn*hydr (0.01, 0.06)**	0.54
grams	2014	**0.001, 0.15**	**0.001, 0.07**	NI	**0.02/0.03**	NI	NI	NI	**burn*hydr (0.008, 0.06)**	0.57
grams	2015	**0.001, 0.14**	**0.001, 0.08**	NI	0.2/0.02	NI	NI	NI	**burn*hydr (0.01, 0.07)**	0.59

Table 4.4. Number of plots in each burn severity-soil type combination.

	Soil Type		
Burn severity	Sandy	Gravelly	*Total*
Scorched	10	0	*10*
Light	11	1	*12*
Moderate	7	4	*11*
High	16	7	*23*
Total	*44*	*12*	*56*

Table 4.5. Species richness and diversity for forbs and graminoids by year.

	Richness		**Diversity**	
Year	Forbs	Graminoids	Forbs	Graminoids
Pre-fire mean	14.70	7.83	1.50	1.18
2012	10.25	7.45	1.59	1.33
2013	14.44	8.99	1.53	1.24
2014	20.00	9.66	1.74	1.27
2015	23.58	11.54	1.96	1.47

Table 4.6. Mean post-fire species richness and diversity for forbs and graminoids by burn severity class.

	Richness		**Diversity**	
Burn severity	Forbs	Graminoids	Forbs	Graminoids
Scorched	16.21	8.44	1.90	1.35
Light	18.55	8.15	1.89	1.27
Moderate	18.50	7.62	1.59	1.24
Heavy	20.10	11.28	1.64	1.38

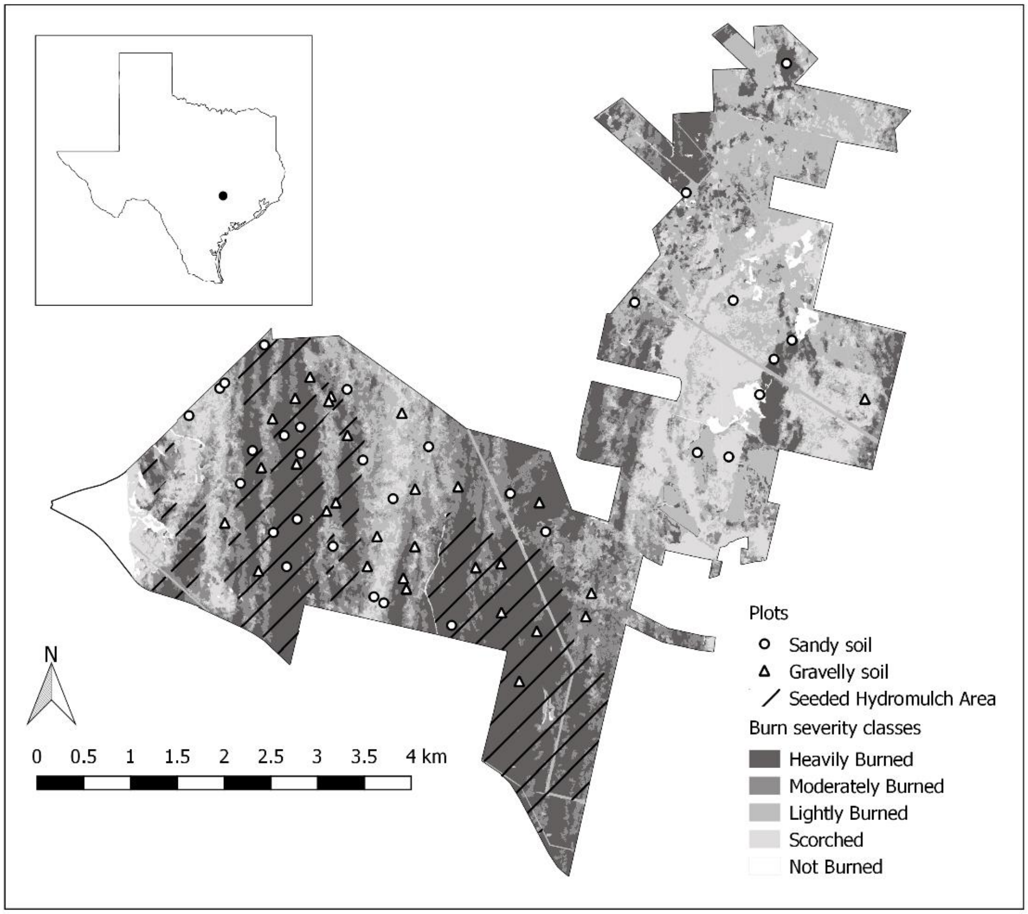


Figure 4.1. Map of Bastrop State Park (BSP) with burn severity classes and permanent plot locations. Soil type is indicated for each plot by point shape. Hatched lines show where hydromulch (seeded with *L. dubia*) was applied.

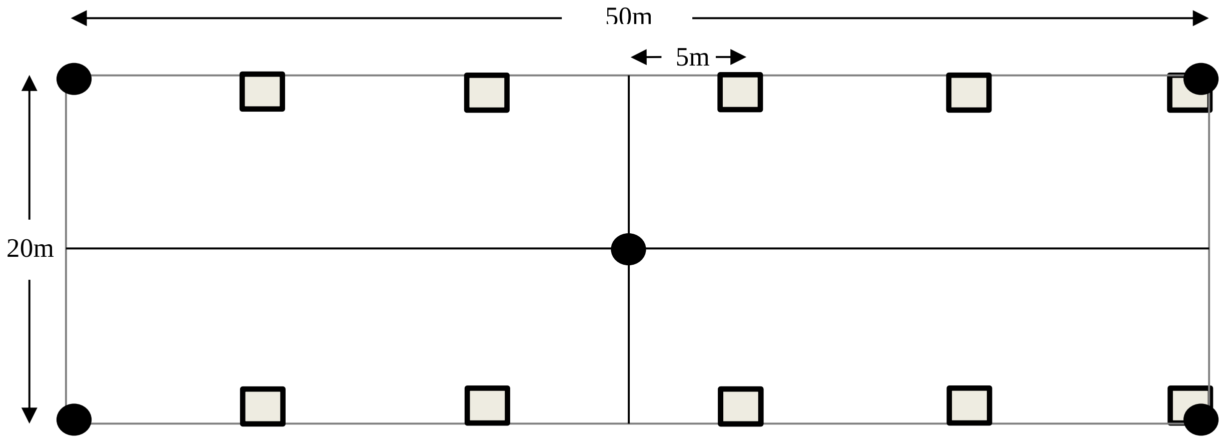


Figure 4.2. Permanent plot design. Herbaceous plant data were collected from 1m^2 quadrats along the long edges of plots, indicated by shaded squares. Canopy cover was collected facing in four directions at each corner and at plot center, as indicated by black circles.

Figure 4.3. Photographs of a heavily burned permanent plot, clockwise from top left: 2010 (pre-fire), 2011 (immediately post-fire), 2013, and 2015. All photographs were taken from the same location and facing the same direction every year. Photographs: Eric Keith.

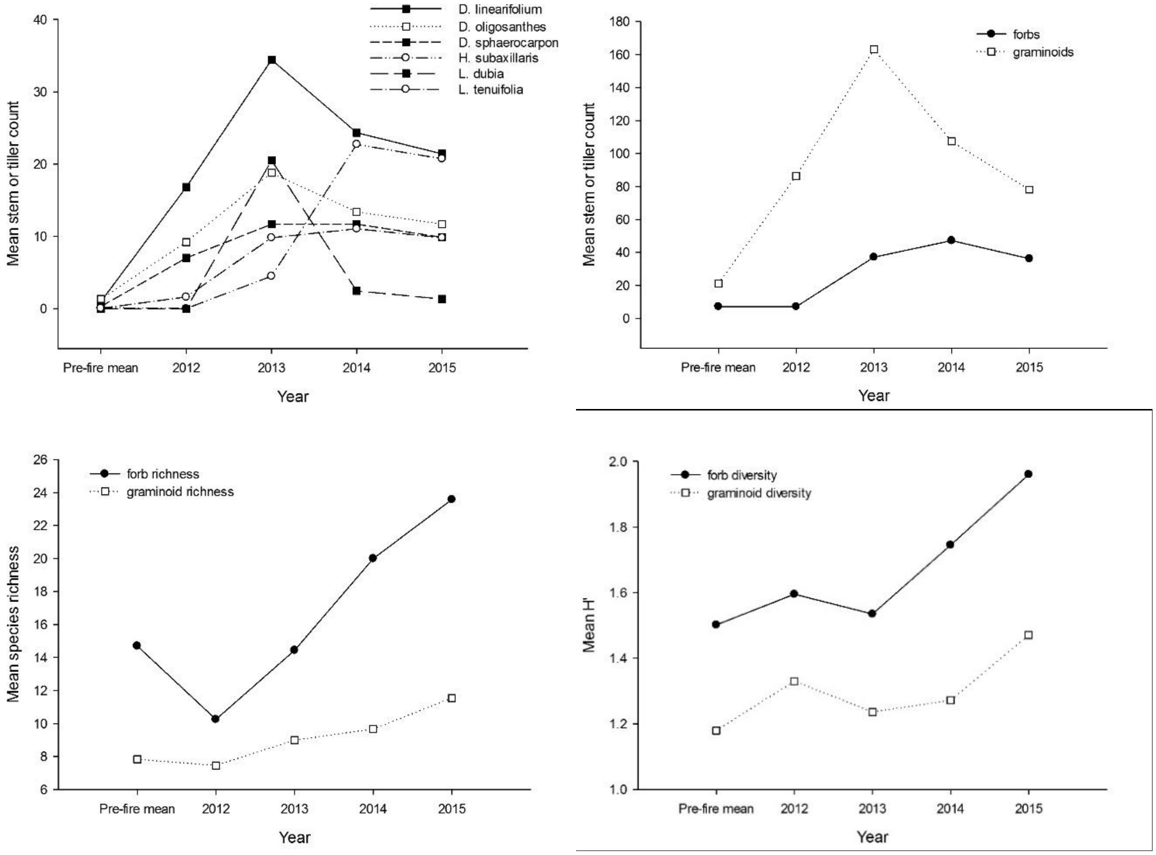


Figure 4.4. Top left: mean stem or tiller count of each individually-analyzed species per year. Top right: mean stem or tiller count of each functional group per year. Bottom left: Mean species richness of each functional group each year. Bottom right: Mean Shannon-Wiener Diversity Index (H’) of each functional group each year. Circles indicate forbs and forb species, and squares indicate graminoids and graminoid species.

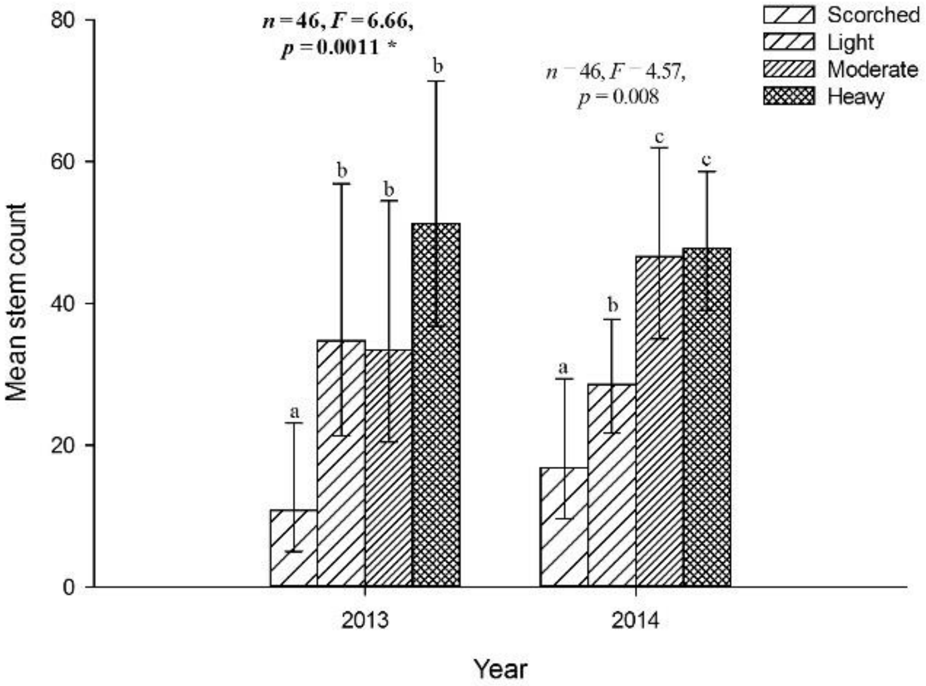


Figure 4.5. Effect of burn severity on mean forb stem counts. *n*, *F,* and *p*-values are shown above each year. Significant results are indicated by bold text and an asterisk.

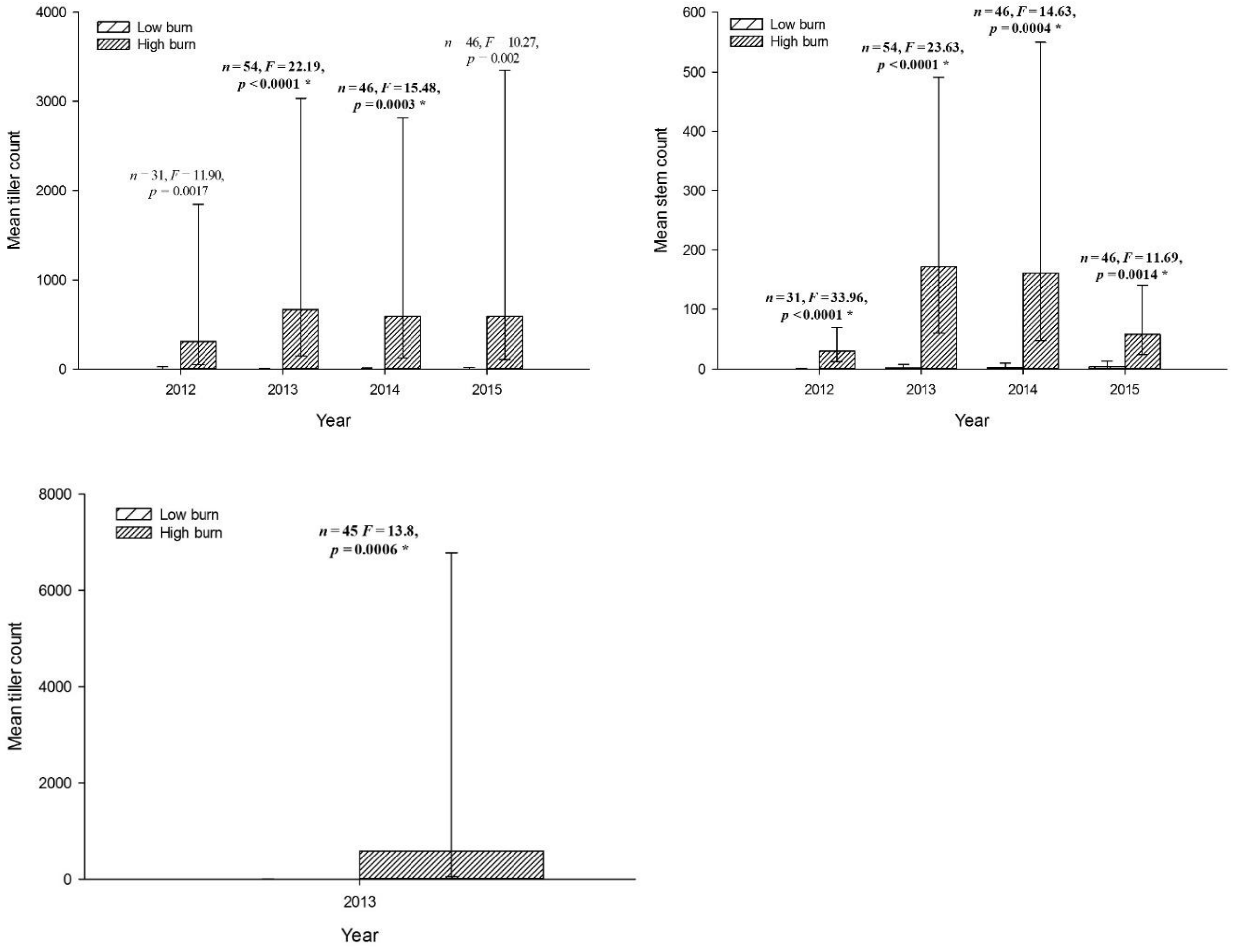


Figure 4.6. Effect of burn severity on mean *D. linearifolium* tiller (top), *L. tenuifolia* stem (middle), and *L. dubia* tiller (bottom) counts. *n*, *F*, and *p*-values are shown above each year. Significant results are indicated by bold text and an asterisk.

Chapter 5: Survey of non-native species following wildland fire in central Texas

ABSTRACT

Encroachment of invasive species, which can be native or non-native, is a major management concern following wildland fire. Wildland fires are becoming more frequent and more severe in the United States due in part to climate change, and in part to fuels build-up resulting from decades of fire suppression. Larger fires require more urgent firefighting response and intensified post-fire restoration efforts, which often lead to intentional or unintentional introduction and spread of invasive species. Monitoring of invasive or potentially invasive species following wildland fire is crucial to ensure early detection of introduction and spread of these species. Following the 2011 Bastrop County Complex Fire in the Lost Pines of central Texas, we surveyed edge habitat along roadways and powerlines to establish a baseline for post-fire non-native and invasive species monitoring in the area and to determine whether non-native invasive species required immediate control.

INTRODUCTION

Non-native invasive plant species are a concern for many reasons, which may include reductions in native biodiversity and increased risk of wildfire (Vilà *et al*. 2011). The introduction and spread of non-native invasive species often follows natural and anthropogenic disturbances (Mack *et al*. 2000). Rapid increases in non-native invasive species abundance are sometimes seen following wildland fire (Burke and Grime 1996, Crawley 1987, Tierney and Cushman 2006). Invasion of plant species may be favored by a fire-caused reduction in competition, but they can also be introduced or spread inadvertently along fuel breaks used during firefighting efforts (Keeley 2006), and are sometimes introduced by intentional post-fire seeding to control erosion (Keeley 2006).

The Wildland-Urban Interface (WUI), at the edges of human development, is especially susceptible to invasion (Bar-Massada *et al*. 2014, Gavier-Pizarro *et al*. 2010). Non-native invasive species abundances are often high along habitat edges such as roadways (Merriam 2003) and powerlines (Wagner *et al*. 2014). Monitoring non-native invasive species populations can help identify, prevent, and treat invasions (Mack *et al*. 2000), and is especially important in the WUI following wildland fire.

In 2011, a crown fire burned most of Bastrop State Park (BSP), located in the 'Lost Pines' region of central Texas. The Lost Pines is surrounded by development, and BSP has roads and buildings throughout its interior. The presence and general distribution of pre-fire non-native plant species were already known in BSP, but had not been quantified. We conducted a survey of non-native species three years after the wildfire. We chose to distinguish between native and non-native species instead of trying to distinguish between non-native non-invasive and non-native invasive plant species because most of the non-native plant species that we found in BSP are invasive elsewhere in the region. While there are some native species in BSP that could be considered to be over-abundant in the region, such as *Ilex vomitoria* Aiton, we restrict the term invasive species to non-native species. The objective of the survey was to quantify invasive species abundance and spatial distribution relative to high-risk features (roads and powerlines) in BSP. The survey was intended to provide baseline information on invasive species in the area and to help determine what, if any, control measures might be required.

METHODS

Study Area

The Lost Pines of central Texas are the westernmost stands of loblolly pine (*Pinus taeda* L.) in the United States. In September 2011, the Bastrop County Complex wildfire burned much of the Lost Pines, including almost all of BSP, during a record drought and heat wave (Hoerling *et al*. 2013). In most areas of BSP, this killed or top-killed vegetation and consumed litter and duff. Throughout firefighting efforts and post-fire rehabilitation treatments, bulldozing, clearcutting, and other mechanical disturbances were kept to a minimum. Mulch was applied at the edges of some roads to reduce erosion potential, especially in the most severely burned areas. This mulch included triticale [x *Triticosecale* Wittm. ex A. Camus (*Secale* x *Triticum*)], a non-native sterile grass species, which did not persist.

Data Collection

Burn severity was determined immediately following the wildfire in September, 2011 using FMH assessment definitions (USDI National Park Service 2003), which are based on degree of consumption of vegetation and substrate. All of BSP was classified into one of five burn severity classes (in order from least to greatest severity: unburned, scorched, light, moderate, and heavy).

Soil data was obtained from the Soil Survey Geographic (SSURGO) Database. SSURGO soil types were first ground-truthed and modified where necessary to accurately reflect local soil texture, then re-classified as either ‘sandy’ or ‘gravelly’ (Appendix A) for increased statistical power and ease of interpretation.

We used a stratified randomized sampling design in which 500 points were randomly located in one of the five burn severity classes and two soil types (Fig. 5.1, QGIS Development Team 2009, Open Source Geospatial Foundation). Points were located within 30m of roads and powerlines in or sharing a border with BSP. Randomization and location of the points was completed using ArcGIS 10.2 (ESRI, Redlands, California, USA). Plots were discarded when they were unreachable or unusable (ex. in the middle of a road, on private property, in a body of water); 355 plots were used in the final analyses. The survey was completed in the summer of 2014.

Each point served as the center of a 2m-diameter circular plot. In each plot, we recorded a visual estimate of total plant cover and an estimate of non-native plant cover in 10% increments, the species names of the three most abundant native plant species and of all non-native plant species, stem or tiller count of each non-native plant species, and canopy cover. We calculated native plant cover and presence or absence of native or invasive species after the survey. Canopy cover was measured twice per plot in opposite directions using a canopy densiometer held at approximately 1.2m, then averaged.

Statistical Analyses

Analyses were completed using SAS 9.4 (SAS Institute, Cary, North Carolina, USA). Numbers of plots with each of the six non-native species in each treatment combination were too low for species to be analyzed separately (Tables 5.1 and 5.2). Instead, three response variables were calculated for each plot: (1) non-native species presence-absence; (2) the sum of all non-native species stems and tillers in each plot; and (3) the total cover of non-native species in each plot. Burn severity, soil type, canopy cover, native species cover and native species presence-absence were used as explanatory variables.

Generalized linear models (SAS GLIMMIX procedure) were used to accommodate non-normal distributions. The binomial distribution with logit link function was used to fit models predicting invasive species presence-absence, and the negative binomial distribution with log link function to fit models predicting invasive species cover and stem or tiller counts.

We used forward selection to build these models, adding variables one by one. At each step, the AICc values of all possible models with one additional variable were compared, and the variable that most decreased AICc was added to the model. No additional variables were added to a model if AICc did not decrease by two or more. Once the best model for a given reponse variable had been identified by this procedure, we examined the significance (*P*-value) of each included predictor variable in this final model. Predicted means and confidence limits were back-transformed for tables and figures.

RESULTS

Non-native species were present in very few plots and were scarce where native species were present (Table 5.3, Fig. 5.2). We observed six non-native species in our plots: *Bothriochloa ischaemum* (L.) Keng (King Ranch bluestem), *Cynadon dactylon* (L.) Pers. (Bermudagrass), *Melia azedarach* L. (Chinaberry), *Paspalum dilatatum* Poir. (dallisgrass), *Paspalum notatum* Flueggé (bahiagrass), and *Photinia serratifolia* (Desf.) Kalkm. (Taiwanese photinia).

As expected, the correlation between non-native cover and non-native stem and tiller counts was positive ($r_s = 0.99$, $p < 0.0001$, $N = 355$). Also as expected, canopy cover and burn severity were negatively correlated ($r_s = -0.50$, $p < 0.0001$, $N = 355$).

Plots were more likely to have at least one non-native species present if no native species were present. Non-native plant cover was greater in plots that had been burned less severely (Fig. 5.3, Table 5.4) and in plots with less native plant cover (Fig. 5.4, Table 5.4). Canopy cover and soil type were not significant predictors in any model.

DISCUSSION

Non-native species do not appear to be invading BSP at this time. This may be in part due to the rapid post-fire development of a dense and diverse native herbaceous plant community (Chapter 4). Non-native species were less likely to be present where native species were present; if present, non-native species cover was less where native species cover was greater. Other studies have also reported results that support the hypothesis that greater native plant species cover can help a community resist invasion (Abella *et al*. 2012, Simmons 2005, Phillips-Mao *et al* 2014), partly due to competition from native plants for open space (MacDougall and Turkington 2005, Stachowicz *et al*. 2002).

King Ranch bluestem, which was observed in BSP, is an invasive grass of Eurasian origin that grows nearly indiscriminately in central Texas, showing no preference for particular slopes, grazing regimes, or fire history (Gabbard and Fowler 2007). This species reduces inversely related to native species richness and invisibility at small scales (Gabbard and Fowler 2007, Alofs and Fowler 2013). Unlike the other five non-native species that we observed in plots with native species, King Ranch bluestem was never observed in a plot with any native species present (Table 5.5). This was likely due to the extremely high cover and biomass typical of King Ranch bluestem stands.

Unexpectedly, we observed the lowest non-native species cover in the most severely burned plots. The most severely burned roadside areas in BSP were mulched, either with wood chips or with a seeded hydromulch mix (Chapter 3). Non-native species may have been inhibited by the mulch application and competition with seeded species in these areas, as has been demonstrated in other systems (Kribeche *et al*. 2013, Penny and Neal 2003). This could also be the result of small sample sizes. Bermudagrass was the only non-native species observed in plots which were not burned (Table 5.2); these plots were often near lawns and structures, where firefighting efforts during the wildfire were the most intensive.

Also counter to expectation, canopy cover had no effect on any measure of non-native species. Most of our plots had very low canopy cover (average canopy cover was 9.5%), due to the effects of the wildfire and to the location of the plots on or adjacent to roads and powerlines. In many areas of BSP, fire-damaged trees along roads and trails were removed for public safety prior to this survey. Many invasive species thrive in open, disturbed habitat (Charbonneau and Fahrig 2004, Zenner and Berger 2008) and decrease in richness with distance from human development (Alston and Richardson 2006). This was our reason for collecting data only along roads and powerlines, and may also explain why we saw no effect of canopy cover: there likely was insufficient variation in canopy cover between plots to detect an effect. However, chinaberry was observed in plots with higher canopy cover than the other five non-native species (Table 5.5). Although chinaberry is not shade tolerant (Nock *et al*. 2009), it was found in plots located in draws and near creeks, with a greater abundance of native trees surrounding the plot. Chinaberry was not found in BSP prior to the wildfire, but appears to have dispersed to higher moisture areas following the fire.

In BSP, non-native invasive species were sparse both pre-disturbance (G. Creacy and E. Keith, pers. comm.) and post-disturbance. Efforts to minimize firefighting-related soil disturbance may have helped maintain low incidence of invasive species in BSP. Future surveys in this case may not need to be frequent, unless further invasion is detected.

Table 5.1. Number of plots with each observed non-native species in each burn severity class.

Species	Not burned	Scorched	Light burn	Moderate burn	Heavy burn	Total	% of plots
Bothriochloa ischaemum	0	0	2	2	0	4	1.13
Cynodon dactylon	3	0	1	0	1	5	1.41
Melia azedarach	0	2	0	1	0	3	0.85
Paspalum dilatatum	0	1	0	0	0	1	0.28
Paspalum notatum	0	0	2	0	1	3	0.85
Photinia serratifolia	0	0	0	1	0	1	0.28
Total non-native species records	3	3	5	4	2	17	4.79

Table 5.2. Number of plots with each observed non-native species in each soil type.

Species	Sandy soil	Gravelly soil	Total	% of plots
Bothriochloa ischaemum	1	3	4	1.13
Cynodon dactylon	5	0	5	1.41
Melia azedarach	1	2	3	0.85
Paspalum dilatatum	1	0	1	0.28
Paspalum notatum	2	1	3	0.85
Photinia serratifolia	1	0	1	0.28
Total non-native species	11	6	17	4.79

Table 5.3. Number of presences and absences observed for non-native and native species.

	Number of observations	
Category	present	absent
Non-native	16	339
Native	334	21

Table 5.4. Summary of model results (reported as 'F, p'), with explanatory variables in columns. 'NI' indicates that the explanatory variable was not included in the final model.

Response variable	N	Burn severity	Soil type	Canopy cover	Native species presence-absence	Native species cover
Non-native species presence-absence	355	NI	NI	NI	20.32, <0.0001	NI
Non-native species cover	355	2.40, 0.04	NI	NI	NI	11.03, 0.001
Non-native species stem or tiller count count	355	NI	2.83, 0.09	0.47, 0.4	1.05, 0.3	NI

Table 5.5. Number of observations of non-native species, mean non-native species stem count, mean non-native and native species cover, and percent canopy cover.

Species	Number of observations	Mean stem count per observation	Mean invasive species cover per observation	Mean native species cover per observation	Canopy cover (%)
Bothriochloa ischaemum	4	33.0	35.0	0.0	4.3
Cynodon dactylon	5	26.6	24.3	19.5	0.0
Melia azedarach	3	2.7	10.3	16.3	37.1
Paspalum dilatatum	1	28.0	50.0	20.0	0.0
Paspalum notatum	3	46.3	27.8	44.3	0.9
Photinia serratifolia	1	5.0	10.0	10.0	0.5

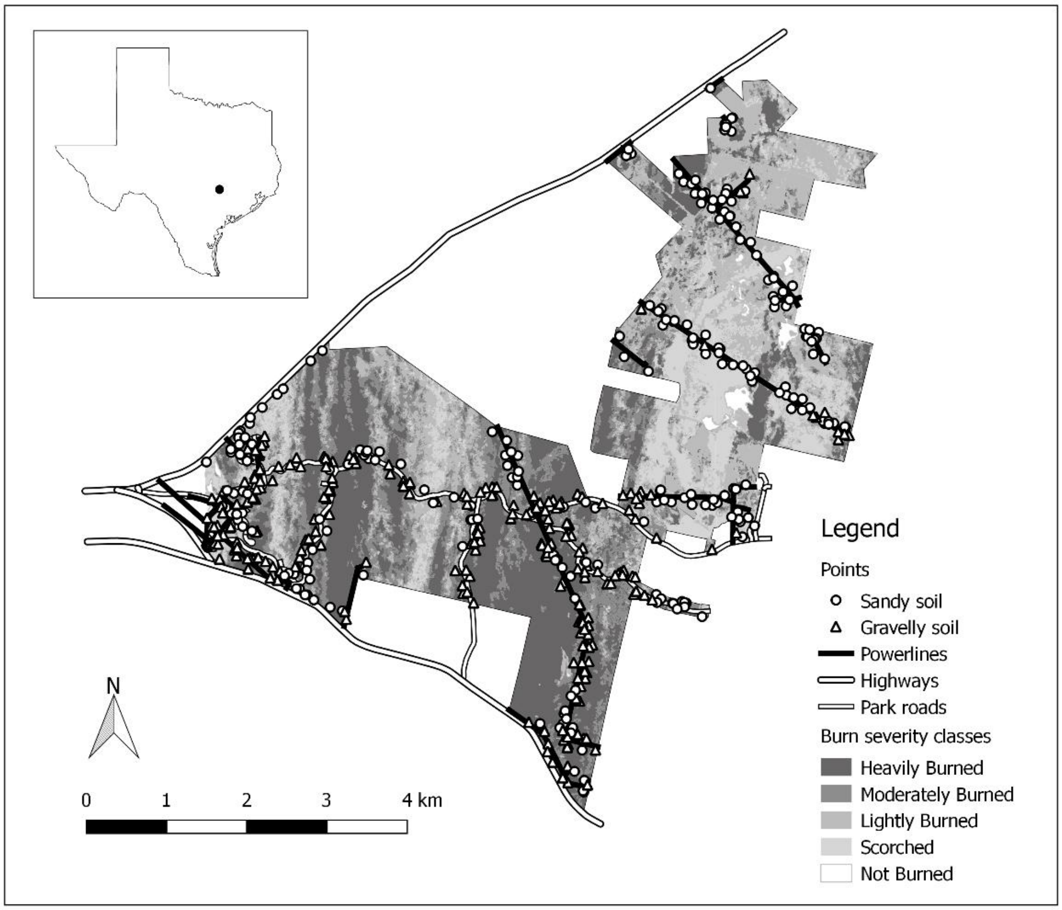


Figure 5.1. Map of Bastrop State Park (BSP) with burn severity classes, powerlines and roads. Soil type is indicated for each plot by shape.

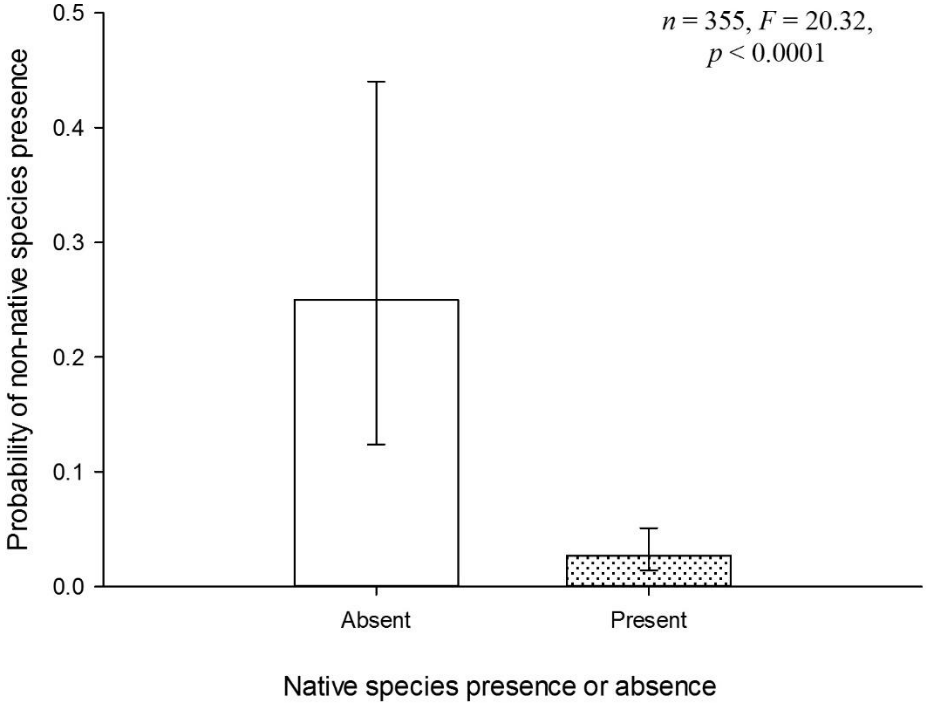


Figure 5.2. Effect of native species presence or absence on probability of non-native species presence.

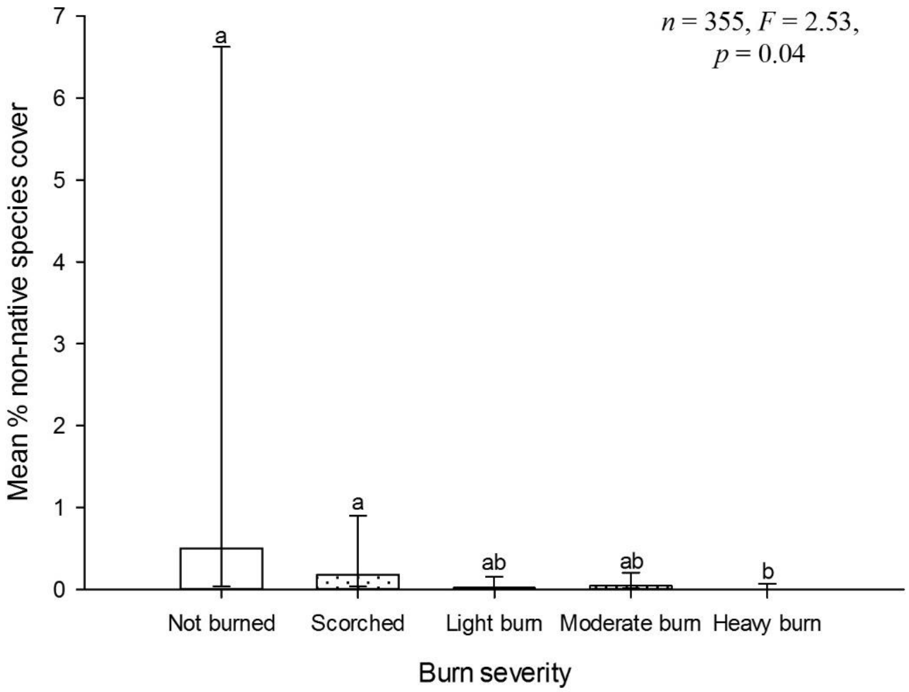


Figure 5.3. Effect of burn severity on mean percent invasive species cover.

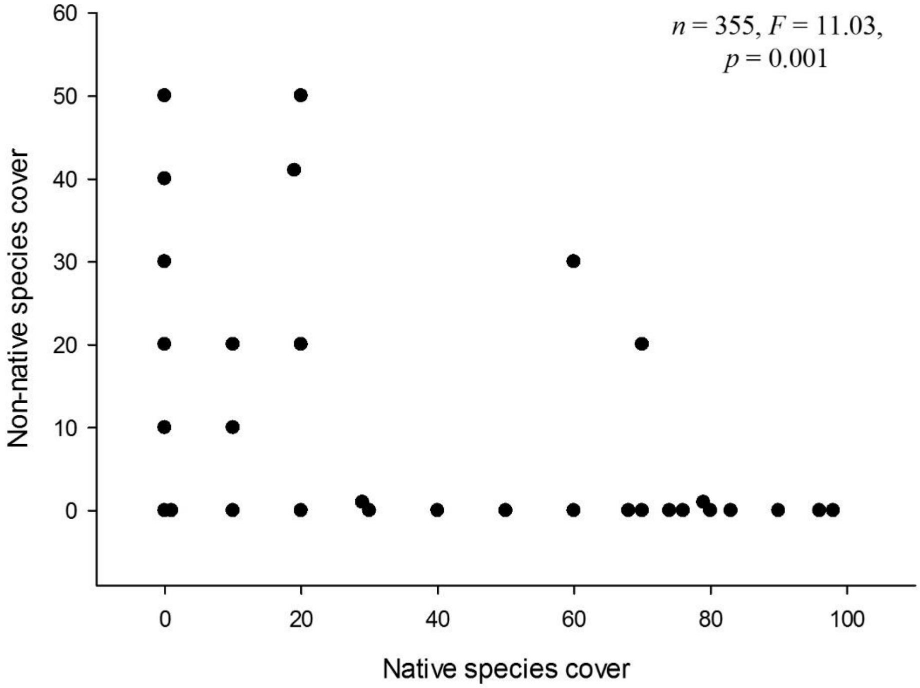


Figure 5.4. Relationship between native and non-native species cover.

Appendix A

Soil type in each plot. SSURGO soils types were re-classed into sandy or gravelly soils based on predominant texture.

Plot	SSURGO soil type	Re-classed soil type
1181	Padina fine sand	sandy
1186	Edge gravelly fine sandy loam	sandy
1188	Padina fine sand	sandy
1189	Jedd gravelly fine sandy loam	gravelly
1190	Padina fine sand	sandy
1191	Padina fine sand	sandy
1192	Edge gravelly fine sandy loam	gravelly
1193	Jedd gravelly fine sandy loam	sandy
1194	Padina fine sand	sandy
1195	Padina fine sand	sandy
1196	Padina fine sand	sandy
1197	Padina fine sand	sandy
1198	Padina fine sand	sandy
1199	Padina fine sand	sandy
1200	Jedd gravelly fine sandy loam	gravelly
1201	Padina fine sand	sandy
1202	Padina fine sand	sandy
1203	Jedd gravelly fine sandy loam	sandy
1204	Jedd gravelly fine sandy loam	sandy
1205	Padina fine sand	sandy
1206	Edge gravelly fine sandy loam	sandy
1207	Edge gravelly fine sandy loam	sandy
1208	Jedd gravelly fine sandy loam	gravelly
1209	Padina fine sand	sandy
1210	Edge fine sandy loam	sandy
1211	Tabor fine sandy loam	sandy
1212	Padina fine sand	sandy
1213	Jedd gravelly fine sandy loam	sandy
1214	Jedd gravelly fine sandy loam	sandy
1215	Padina fine sand	sandy
1216	Padina fine sand	sandy

1217	Padina fine sand	sandy
1218	Mabank loam	sandy
1219	Robco loamy fine sand	sandy
1220	Padina fine sand	sandy
1221	Edge gravelly fine sandy loam	gravelly
1222	Edge gravelly fine sandy loam	gravelly
1223	Edge fine sandy loam	sandy
1224	Tabor fine sandy loam	sandy
1225	Jedd gravelly fine sandy loam	sandy
1226	Robco loamy fine sand	sandy
1227	Jedd gravelly fine sandy loam	sandy
1228	Edge gravelly fine sandy loam	gravelly
1229	Edge gravelly fine sandy loam	sandy
1230	Jedd gravelly fine sandy loam	sandy
1231	Jedd gravelly fine sandy loam	gravelly
1232	Edge gravelly fine sandy loam	gravelly
1233	Edge gravelly fine sandy loam	sandy
1234	Edge fine sandy loam	sandy
1235	Edge gravelly fine sandy loam	gravelly
1236	Edge gravelly fine sandy loam	gravelly
1237	Edge gravelly fine sandy loam	sandy
1238	Edge gravelly fine sandy loam	sandy
1239	Edge gravelly fine sandy loam	gravelly
1240	Tabor fine sandy loam	sandy
5300	Tabor fine sandy loam	sandy

Appendix B

List of herbaceous species found in plots. Functional group was assigned after data collection. Number of observations indicates the number of times a species was observed in all plots and years.

USDA species code	Species name	Family	Functional group	Number of observations
RUHU6	*Ruellia humilis*	Acanthaceae	forb	8
FRFLx	*Froelichia floridana*	Amaranthaceae	forb	7
FRGR3	*Froelichia gracilis*	Amaranthaceae	forb	1
SACA1	*Sanicula canadensis*	Apiaceae	forb	1
SPINx	*Spermolepis inermis*	Apiaceae	forb	3
ARERx	*Aristolochia erecta*	Aristolochiaceae	forb	1
MADE3	*Matelea decipiens*	Asclepiadacea	forb	1
ASOEx	*Asclepias oenotheroides*	Asclepiadaceae	forb	1
ASTUx	*Asclepias tuberosa*	Asclepiadaceae	forb	1
GOGO2	*Gonolobus gonocarpos*	Asclepiadaceae	forb	3
AMAR2	*Ambrosia artemisiifolia*	Asteraceae	forb	2
AMPSx	*Ambrosia psilostachya*	Asteraceae	forb	3
CHIMx	*Chaetopappa imberbis*	Asteraceae	forb	3
CHPI8	*Chrysopsis pilosa*	Asteraceae	forb	76
CHTE1	*Chrysopsis texana*	Asteraceae	forb	6
CIHO2	*Cirsium horridulum*	Asteraceae	forb	1
CITE2	*Cirsium texanum*	Asteraceae	forb	46
COCA5	*Conyza canadensis*	Asteraceae	forb	155
COBA2	*Coreopsis basalis*	Asteraceae	forb	9
COTI3	*Coreopsis tinctoria*	Asteraceae	forb	6
COWR3	*Coreopsis wrightii*	Asteraceae	forb	1
CRDI1	*Croptilon divaricatum*	Asteraceae	forb	13
CRHOH	*Croptilon hookerianum var. hookerianum*	Asteraceae	forb	2
CRRI3	*Croptilon rigidifolium*	Asteraceae	forb	2
ELAN5	*Elephantopus angustifolius*	Asteraceae	forb	1
ERHI9	*Erechtites hieracifolia*	Asteraceae	forb	1
ERHI2	*Erechtites hieraciifolia*	Asteraceae	forb	1

ERGEx	*Erigeron geiseri*	Asteraceae	forb	1
ERST3	*Erigeron strigosus*	Asteraceae	forb	7
EUPI3	*Eupatorium pinnatifidum*	Asteraceae	forb	1
EUCO7	*Eupatorium compositifolium*	Asteraceae	forb	40
EUSEx	*Eupatorium semiserratum*	Asteraceae	forb	48
EUSE2	*Eupatorium serotinum*	Asteraceae	forb	1
EUHE1	*Eurybia hemispherica*	Asteraceae	forb	1
EVCAx	*Evax candida*	Asteraceae	forb	2
EVVEx	*Evax verna*	Asteraceae	forb	1
FAREx	*Facelis retusa*	Asteraceae	forb	8
GAAEx	*Gaillardia aestivalis*	Asteraceae	forb	1
GAPUx	*Gaillardia pulchella*	Asteraceae	forb	1
GAAMx	*Gamochaeta antilliana*	Asteraceae	forb	1
GAAN1	*Gamochaeta antilliana*	Asteraceae	forb	94
GAAR1	*Gamochaeta argyrinea*	Asteraceae	forb	127
GACA6	*Gamochaeta calviceps*	Asteraceae	forb	3
GAPE2	*Gamochaeta pensylvanica*	Asteraceae	forb	75
GAPU3	*Gamochaeta purpurea*	Asteraceae	forb	3
HEAMx	*Helenium amarum*	Asteraceae	forb	5
HEAN3	*Helianthus annuus*	Asteraceae	forb	1
HEDE4	*Helianthus debilis*	Asteraceae	forb	4
HELA5	*Heterotheca subaxillaris var. latifolia*	Asteraceae	forb	117
HIGR3	*Hieracium gronovii*	Asteraceae	forb	1
HYAR3	*Hymenopappus artemisiifolius*	Asteraceae	forb	4
HYGL2	*Hypochaeris glabra*	Asteraceae	forb	29
KRDAx	*Krigia dandelion*	Asteraceae	forb	2
KROCx	*Krigia occidentalis*	Asteraceae	forb	4
KRVIx	*Krigia virginica*	Asteraceae	forb	14
LAHIx	*Lactuca hirsuta*	Asteraceae	forb	6
LALUx	*Lactuca ludoviciana*	Asteraceae	forb	1
LASEx	*Lactuca serriola*	Asteraceae	forb	3
LIASx	*Liatris aspera*	Asteraceae	forb	11
LIELx	*Liatris elegans*	Asteraceae	forb	9
LIEL1	*Liatris elegans var. bridgesii*	Asteraceae	forb	3

PAHOx	*Palafoxia hookeriana*	Asteraceae	forb	7
PAROx	*Palafoxia rosea*	Asteraceae	forb	4
PLODx	*Pluchea odorata*	Asteraceae	forb	4
PSOB3	*Pseudognaphalium obtusifolium*	Asteraceae	forb	30
PTVI2	*Pterocaulon virgatum*	Asteraceae	forb	13
PYCA2	*Pyrrhopappus carolinianus*	Asteraceae	forb	17
PYMU2	*Pyrrhopappus multicaulis*	Asteraceae	forb	2
RUHI2	*Rudbeckia hirta*	Asteraceae	forb	16
SOAL6	*Solidago altissima*	Asteraceae	forb	13
SOCA6	*Solidago canadensis*	Asteraceae	forb	1
SORAx	*Solidago radula*	Asteraceae	forb	3
SOASx	*Sonchus asper*	Asteraceae	forb	29
SOOLx	*Sonchus oleraceus*	Asteraceae	forb	28
SYPA1	*Symphyotrichum patens*	Asteraceae	forb	7
TAOFx	*Taraxacum officinale*	Asteraceae	forb	1
VETE3	*Vernonia texana*	Asteraceae	forb	21
POPEx	*Podophyllum peltatum*	Berberidaceae	forb	1
LEAR3	*Lesquerella argyraea*	Brassicaceae	forb	1
POPR4	*Polypremum procumbens*	Buddlejaceae	forb	125
LOPUx	*Lobelia puberula*	Campanulaceae	forb	1
TRBI2	*Triodanis biflora*	Campanulaceae	forb	24
TRPE4	*Triodanis perfoliata*	Campanulaceae	forb	12
WAMAx	*Wahlenbergia marginata*	Campanulaceae	forb	2
POERx	*Polanisia erosa*	Capparaceae	forb	1
SACA1	*Sambucus canadensis*	Caprifoliaceae	forb	1
SIAN2	*Silene antirrhina*	Caryophyllace	forb	3
LOSQx	*Loeflingia squarrosa*	Caryophyllaceae	forb	1
PADRx	*Paronychia drummondii*	Caryophyllaceae	forb	1
POTEx	*Polycarpon tetraphyllum*	Caryophyllaceae	forb	3
HEGEx	*Helianthemum georgianum*	Cistaceae	forb	70
HERO2	*Helianthemum rosmarinifolium*	Cistaceae	forb	21
LEMU3	*Lechea mucronata*	Cistaceae	forb	74
LETEx	*Lechea tenuifolia*	Cistaceae	forb	92
HYDRx	*Hypericum drummondii*	Clusiaceae	forb	41

HYGEx	*Hypericum gentianoides*	Clusiaceae	forb	6
HYSEx	*Hypericum setosum*	Clusiaceae	forb	1
COERx	*Commelina erecta*	Commelinaceae	forb	16
TRHIx	*Tradescantia hirsutiflora*	Commelinaceae	forb	18
DICA3	*Dichondra carolinensis*	Convolvulacea	forb	1
STPI3	*Stylisma pickeringii*	Convolvulacea	forb	4
EVSEx	*Evolvulus sericeus*	Convolvulaceae	forb	5
JATAx	*Jacquemontia tamnifolia*	Convolvulaceae	forb	1
MEPE3	*Melothria pendula*	Cucurbitaceae	forb	2
JUCO1	*Juniperus coahuilensis*	Cupressaceae	graminoid	1
BUCA2	*Bulbostylis capillaris*	Cyperaceae	graminoid	7
BUCIx	*Bulbostylis ciliatifolia*	Cyperaceae	graminoid	14
CALE6	*Carex leavenworthii*	Cyperaceae	graminoid	3
CAMI5	*Carex microdonta*	Cyperaceae	graminoid	1
CAMI8	*Carex microrhyncha*	Cyperaceae	graminoid	40
CAMU4	*Carex muehlenbergii*	Cyperaceae	graminoid	8
CYPER	*Cyperus*	Cyperaceae	graminoid	1
CYCR6	*Cyperus croceus*	Cyperaceae	graminoid	24
CYEC2	*Cyperus echinatus*	Cyperaceae	graminoid	57
CYFI2	*Cyperus filiculmis*	Cyperaceae	graminoid	1
CYFI4	*Cyperus filiformis*	Cyperaceae	graminoid	1
CYHYx	*Cyperus hystricinus*	Cyperaceae	graminoid	24
CYLU2	*Cyperus lupulinus*	Cyperaceae	graminoid	31
CYPL3	*Cyperus plukenetii*	Cyperaceae	graminoid	4
CYRE2	*Cyperus reflexus*	Cyperaceae	graminoid	7
CYRE1	*Cyperus retroflexus*	Cyperaceae	graminoid	4
CYRE5	*Cyperus retrorsus*	Cyperaceae	graminoid	107
CYSUx	*Cyperus surinamensis*	Cyperaceae	graminoid	3
FIAU2	*Fimbristylis autumnalis*	Cyperaceae	graminoid	1
FIPUx	*Fimbristylis puberula*	Cyperaceae	graminoid	4
RHGL2	*Rhynchospora globularis*	Cyperaceae	graminoid	2
RHHAx	*Rhynchospora harveyi*	Cyperaceae	graminoid	42
SCCIx	*Scleria ciliata*	Cyperaceae	graminoid	113
SCOL2	*Scleria oligantha*	Cyperaceae	graminoid	7
PTAQx	*Pteridium aquilinum*	Dennstaedtiaceae	forb	12
DRAN3	*Drosera annua*	Droseraceae	forb	1

ACGR2	*Acalypha gracilens*	Euphorbiaceae	forb	85
CHAMx	*Chamaesyce ammannioides*	Euphorbiaceae	forb	1
CHAN5	*Chamaesyce angusta*	Euphorbiaceae	forb	1
CHCO1	*Chamaesyce cordifolia*	Euphorbiaceae	forb	4
CHMA1	*Chamaesyce maculata*	Euphorbiaceae	forb	2
CNTEx	*Cnidoscolus texanus*	Euphorbiaceae	forb	7
CRCA6	*Croton capitatus*	Euphorbiaceae	forb	27
CRGL2	*Croton glandulosus*	Euphorbiaceae	forb	28
CRWI5	*Croton michauxii*	Euphorbiaceae	forb	1
CRMI8	*Croton michauxii*	Euphorbiaceae	forb	3
CRMO6	*Croton monanthogynus*	Euphorbiaceae	forb	37
EUCO1	*Euphorbia corollata*	Euphorbiaceae	forb	113
EUDE1	*Euphorbia dentata*	Euphorbiaceae	forb	3
PHABx	*Phyllanthus abnormis*	Euphorbiaceae	forb	2
STSYx	*Stillingia sylvatica*	Euphorbiaceae	forb	3
TRBE4	*Tragia betonicifolia*	Euphorbiaceae	forb	1
TRRA5	*Tragia ramosa*	Euphorbiaceae	forb	29
TRUR2	*Tragia urticifolia*	Euphorbiaceae	forb	32
ASNU4	*Astragalus nuttallianus*	Fabaceae	forb	12
BABR2	*Baptisia bracteata*	Fabaceae	forb	5
CAFAx	*Cassia fasciculata*	Fabaceae	forb	2
CEVI2	*Centrosema virginianum*	Fabaceae	forb	125
CLMA4	*Clitoria mariana*	Fabaceae	forb	11
CRSA4	*Crotalaria sagittalis*	Fabaceae	forb	27
DADRx	*Dalea drummondiana*	Fabaceae	forb	4
DEAC3	*Desmanthus acuminatus*	Fabaceae	forb	2
DECIx	*Desmodium ciliare*	Fabaceae	forb	1
DELA2	*Desmodium laevigatum*	Fabaceae	forb	1
DESEx	*Desmodium sessilifolium*	Fabaceae	forb	4
GARE2	*Galactia regularis*	Fabaceae	forb	112
GAST2	*Galactia striata*	Fabaceae	forb	1
LEHI2	*Lespedeza hirta*	Fabaceae	forb	30
LERE2	*Lespedeza repens*	Fabaceae	forb	41
LESPE	*Lespedeza spp.*	Fabaceae	forb	4
LEST4	*Lespedeza striata*	Fabaceae	forb	5
LEST5	*Lespedeza stuevei*	Fabaceae	forb	1

LEVI7	*Lespedeza virginica*	Fabaceae	forb	1
MINU6	*Mimosa nuttallii*	Fabaceae	forb	7
NELU2	*Neptunia lutea*	Fabaceae	forb	5
RHMI4	*Rhynchosia minima*	Fabaceae	forb	3
STHE4	*Strophostyles helvola*	Fabaceae	forb	2
STLE6	*Strophostyles leiosperma*	Fabaceae	forb	2
STUM2	*Strophostyles umbellata*	Fabaceae	forb	1
STBI2	*Stylosanthes biflora*	Fabaceae	forb	8
TEONx	*Tephrosia onobrychoides*	Fabaceae	forb	2
TRBE3	*Trifolium bejariense*	Fabaceae	forb	2
VILE2	*Vicia leavenworthii*	Fabaceae	forb	5
VIMIx	*Vicia minutiflora*	Fabaceae	forb	1
SACA3	*Sabatia campestris*	Gentianaceae	forb	1
GECA5	*Geranium carolinianum*	Geraniaceae	forb	11
HELA6	*Herbertia lahue*	Iridaceae	forb	1
JUBRx	*Juncus brachycarpus*	Juncaceae	graminoid	11
JUDIx	*Juncus dichotomus*	Juncaceae	graminoid	8
JUMA4	*Juncus marginatus*	Juncaceae	graminoid	40
JUTEx	*Juncus tenuis*	Juncaceae	graminoid	10
JUVA2	*Juncus validus*	Juncaceae	graminoid	4
BRTRx	*Brazoria truncata*	Lamiaceae	forb	1
MOCIx	*Monarda citriodora*	Lamiaceae	forb	7
MOPUx	*Monarda punctata*	Lamiaceae	forb	5
SCCA4	*Scutellaria cardiophylla*	Lamiaceae	forb	1
TRDI2	*Trichostema dichotomum*	Lamiaceae	forb	1
ALCA3	*Allium canadense*	Liliaceae	forb	2
HYHI2	*Hypoxis hirsuta*	Liliaceae	forb	5
HYMI2	*Hypoxis micrantha*	Liliaceae	forb	1
NOBI2	*Nothoscordum bivalve*	Liliaceae	forb	2
LIME2	*Linum medium*	Linaceae	forb	1
CAIN2	*Callirhoe involucrata*	Malvaceae	forb	2
MOCAx	*Modiola caroliniana*	Malvaceae	forb	1
SIABx	*Sida abutifolia*	Malvaceae	forb	2
SICIx	*Sida ciliaris*	Malvaceae	forb	1
SILIx	*Sida lindheimeri*	Malvaceae	forb	7
SIRHx	*Sida rhombifolia*	Malvaceae	forb	1

MOVEx	*Mollugo verticillata*	Molluginaceae	forb	5
GABR2	*Gaura brachycarpa*	Onagraceae	forb	1
LURE2	*Ludwigia repens*	Onagraceae	forb	3
OELAx	*Oenothera laciniata*	Onagraceae	forb	4
OELIx	*Oenothera linifolia*	Onagraceae	forb	1
OXDI2	*Oxalis dillenii*	Oxalidaceae	forb	89
OXSTx	*Oxalis stricta*	Oxalidaceae	forb	6
ARAL3	*Argemone albiflora*	Papaveraceae	forb	1
PALU2	*Passiflora lutea*	Passifloracea	forb	2
PHAM4	*Phytolacca americana*	Phytolaccacea	forb	34
PLHOx	*Plantago hookeriana*	Plantaginaceae	forb	5
PLVIx	*Plantago virginica*	Plantaginaceae	forb	6
PLWRx	*Plantago wrightiana*	Plantaginaceae	forb	1
AGHYx	*Agrostis hyemalis*	Poaceae	graminoid	12
AIEL4	*Aira elegans*	Poaceae	graminoid	2
ANGL2	*Andropogon glomeratus*	Poaceae	graminoid	7
ANVI2	*Andropogon virginicus*	Poaceae	graminoid	10
ARDE3	*Aristida desmantha*	Poaceae	graminoid	9
ARLA6	*Aristida lanosa*	Poaceae	graminoid	11
ARLO1	*Aristida longespica*	Poaceae	graminoid	6
ARPU8	*Aristida purpurascens*	Poaceae	graminoid	3
ARPUP	*Aristida purpurea var. purpurea*	Poaceae	graminoid	1
BOLA2	*Bothriochloa laguroides*	Poaceae	graminoid	1
BOLAT	*Bothriochloa laguroides ssp. torreyana*	Poaceae	graminoid	1
BOHI2	*Bouteloua hirsuta*	Poaceae	graminoid	1
BRMI2	*Briza minor*	Poaceae	graminoid	1
BRJAx	*Bromus japonicus*	Poaceae	graminoid	1
CENCH	*Cenchrus*	Poaceae	graminoid	1
CESP4	*Cenchrus spinifex*	Poaceae	graminoid	3
CHSE2	*Chasmanthium sessiliflorum*	Poaceae	graminoid	1
DIACx	*Dichanthelium aciculare*	Poaceae	graminoid	14
DIAC2	*Dichanthelium acuminatum*	Poaceae	graminoid	34
DIAN4	*Dichanthelium angustifolium*	Poaceae	graminoid	91
DICO1	*Dichanthelium commutatum*	Poaceae	graminoid	4

DILA9	*Dichanthelium laxiflorum*	Poaceae	graminoid	1
DILI5	*Dichanthelium lindheimeri*	Poaceae	graminoid	3
DILI2	*Dichanthelium linearifolium*	Poaceae	graminoid	77
DIOLx	*Dichanthelium oligosanthes*	Poaceae	graminoid	184
DIOLS	*Dichanthelium oligosanthes var. oligosanthes*	Poaceae	graminoid	2
DIOVx	*Dichanthelium ovale*	Poaceae	graminoid	41
DIRAx	*Dichanthelium ravenelii*	Poaceae	graminoid	22
DISC3	*Dichanthelium scoparium*	Poaceae	graminoid	25
DISP2	*Dichanthelium sphaerocarpon*	Poaceae	graminoid	127
DIVI7	*Dichanthelium villosissimum*	Poaceae	graminoid	6
DICO6	*Digitaria cognata*	Poaceae	graminoid	11
ELIN3	*Eleusine indica*	Poaceae	graminoid	2
ERCUx	*Eragrostis curtipedicellata*	Poaceae	graminoid	1
ERHIx	*Eragrostis hirsuta*	Poaceae	graminoid	1
ERINx	*Eragrostis intermedia*	Poaceae	graminoid	2
ERSEx	*Eragrostis secundiflora*	Poaceae	graminoid	5
ERSE2	*Eragrostis sessilispica*	Poaceae	graminoid	1
ERSPx	*Eragrostis spectabilis*	Poaceae	graminoid	60
GYAMx	*Gymnopogon ambiguus*	Poaceae	graminoid	8
LEDUx	*Leptochloa dubia*	Poaceae	graminoid	40
LIARx	*Limnodea arkansana*	Poaceae	graminoid	2
PAANx	*Panicum anceps*	Poaceae	graminoid	2
PABR2	*Panicum brachyanthum*	Poaceae	graminoid	9
PAHI1	*Panicum hians*	Poaceae	graminoid	3
PANO2	*Paspalum notatum*	Poaceae	graminoid	2
PAPL3	*Paspalum plicatulum*	Poaceae	graminoid	29
PASE5	*Paspalum setaceum*	Poaceae	graminoid	34
PASEC	*Paspalum setaceum var. ciliatifolium*	Poaceae	graminoid	2
SCSCx	*Schizachyrium scoparium*	Poaceae	graminoid	64
SOEL3	*Sorghastrum elliottii*	Poaceae	graminoid	4
SONU2	*Sorghastrum nutans*	Poaceae	graminoid	4
SPOBx	*Sphenopholis obtusata*	Poaceae	graminoid	2
SPCLx	*Sporobolus clandestinus*	Poaceae	graminoid	13

SPCO1	*Sporobolus compositus*	Poaceae	graminoid	16
SPVAx	*Sporobolus vaginiflorus*	Poaceae	graminoid	2
STLE5	*Stipa leucotricha*	Poaceae	graminoid	3
TRBEx	*Tragus berteronianus*	Poaceae	graminoid	1
TRFL2	*Tridens flavus*	Poaceae	graminoid	9
TRFLC	*Tridens flavus var. chapmanii*	Poaceae	graminoid	1
TRFLF	*Tridens flavus var. flavus*	Poaceae	graminoid	1
TRPU4	*Triplasis purpurea*	Poaceae	graminoid	4
URCIx	*Urochloa ciliatissima*	Poaceae	graminoid	1
VUOCx	*Vulpia octoflora*	Poaceae	graminoid	15
GIINx	*Gilia incisa*	Polemoniaceae	forb	20
POPOx	*Polygala polygama*	Polygalaceae	forb	4
POVEx	*Polygala verticillata*	Polygalaceae	forb	1
ERLO5	*Eriogonum longifolium*	Polygonaceae	forb	2
ERMU4	*Eriogonum multiflorum*	Polygonaceae	forb	2
RUAL4	*Rumex altissimus*	Polygonaceae	forb	3
RUCO2	*Rumex conglomeratus*	Polygonaceae	forb	1
RUHA2	*Rumex hastatulus*	Polygonaceae	forb	9
CEMIx	*Centunculus minimus*	Primulaceae	forb	3
DECA3	*Delphinium carolinianum*	Ranunculaceae	forb	1
RHLAx	*Rhamnus lanceolata*	Rhamnaceae	forb	4
RUABx	*Rubus aboriginum*	Rosaceae	forb	1
DITE2	*Diodia teres*	Rubiaceae	forb	10
GAPI2	*Galium pilosum*	Rubiaceae	forb	13
HECR9	*Hedyotis crassifolia*	Rubiaceae	forb	1
HEGR1	*Hedyotis greenmanii*	Rubiaceae	forb	1
HENI4	*Hedyotis nigricans*	Rubiaceae	forb	1
OLBOx	*Oldenlandia boscii*	Rubiaceae	forb	10
AGFA2	*Agalinis fasciculata*	Scrophulariaceae	forb	2
NUCAx	*Nuttallanthus canadensis*	Scrophulariaceae	forb	19
NUTEx	*Nuttallanthus texanus*	Scrophulariaceae	forb	36
VEARx	*Veronica arvensis*	Scrophulariaceae	forb	1
SEARx	*Selaginella arenicola*	Selaginellaceae	forb	4
PHAN5	*Physalis angulata*	Solanaceae	forb	1
PHCI4	*Physalis cinerascens*	Solanaceae	forb	51
PHHE4	*Physalis hederifolia*	Solanaceae	forb	1

PHHE5	*Physalis heterophylla*	Solanaceae	forb	13
PHMO9	*Physalis mollis*	Solanaceae	forb	10
PHTEx	*Physalis texana*	Solanaceae	forb	1
SOAM4	*Solanum americanum*	Solanaceae	forb	2
SOPYx	*Solanum pyrifolium*	Solanaceae	forb	6
TYDOx	*Typha domingensis*	Typhaceae	graminoid	2
UNGR3	*Unknown grass 3*	Unknown	graminoid	1
PAPE5	*Parietaria pensylvanica*	Urticaceae	forb	6
VISOx	*Viola sororia*	Violaceae	forb	3

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