INTERACTIVE EFFECTS OF DROUGHT, NITROGEN DEPOSITION, AND FIRE ON HERBACEOUS COMMUNITIES IN A SEMI-ARID SAVANNA

A Thesis

by

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ABSTRACT

Understanding the responses of savanna communities to disturbance and altered resource conditions will gain importance under climate-change induced modifications to precipitation patterns and nutrient cycling. This study investigates 1) how an herbaceous community within a semi-arid savanna will respond to drought, nitrogen deposition, and prescribed fire and 2) how these factors will interact to alter those responses. Sixty-four 5 x 5 m, herbaceous-dominated plots were established at the Texas A&M AgriLife Research Station on the Edwards Plateau, a generally rocky, shallow-soil savanna ecoregion (latitude 31°N, longitude 100° W). A prescribed drought treatment (rainout shelter or ambient), nutrient treatment (nitrogen addition or control), and fire treatment (burned or control) was assigned to each plot in a full factorial, completely randomized experimental design. Vegetation and topsoil data were collected to evaluate the treatment effects on both the vegetative community and also on the soil and vegetation chemistry. The vegetative community responded rapidly to the treatments especially in terms of drought-reduced ANPP (ANOVA $p<0.05$) and a shift in community composition from the full combination of treatments (PERMANOVA $p<0.05$) after 8 months of treatments. After 12 months of treatments, forb ANPP was reduced by fires (ANOVA $p<0.01$) but increased by drought (ANOVA $p<0.05$). When dominated by annual plants in the early spring (12 months after treatment), the community failed to exhibit a statistically significant shift in community composition. The soil chemistry was more recalcitrant to change and did not demonstrate treatment effects during the study period. Vegetation N, on the other hand, exhibited increases only when it had previously been burned. Under future environmental conditions, the herbaceous communities may be expected to experience alterations in a short time-frame while soil chemistry remains unchanged in the short-term. These results will provide insights into how managers and ecologists can use the feedbacks between prescribed fire, drought, and soil fertility to maintain biodiversity, desirable cover ratios, biomass production, and protect semi-arid savanna systems from degradation.

DEDICATION

This work is dedicated to both of my grandfathers whose legacies inspired in me a love for nature and conservation.

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Undergraduate technicians assisted with field sample collection, soils processing, and biomass sorting prior to analysis. All other work conducted for the thesis was completed by the M.S. student.

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NOMENCLATURE

ANOVA	Analysis of Variance
ANPP	Above-ground Net Primary Productivity
C	Carbon
N	Nitrogen
NMDS	Non-metric Multi-dimensional Scaling
NUE	Nutrient Use Efficiency
PERMANOVA	Permutational multivariate analysis of variance
SLA	Specific Leaf Area
WUE	Water Use Efficiency

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Savannas account for one fifth of earth's land surface and hold both ecological and socioeconomic significance (Scholes 2003, Baudena et al. 2015). They are defined as having mostly continuous grassy cover with scattered individual and patches of trees (Scholes and Archer 1997). Many pastoral communities worldwide depend on savanna forage for livestock grazing. Unfortunately, both the ecological services and biodiversity of savannas are being increasingly threatened by the altered vegetation structure caused by woody encroachment, overgrazing, fire suppression, drought, and soil erosion.

Two primary theories have been suggested to explain the grass/tree coexisting community of savanna ecosystems: the resource-based and disturbance-based hypothesis (February et al. 2013). The resource-based hypothesis proposes that water partitioning (via differences in rooting depth) prevents competitive exclusion from occurring (Walter 1939, Weltzin and McPherson 2000, Fargione and Tilman 2005, Isbell et al. 2009). While tree roots penetrate to deep horizons, herbaceous roots are concentrated in the surface layer (Belsky 1994). Thus, trees exploit deep soil water and grasses and forbs utilize the surface soil moisture which can limit its supply to deeper horizons. Ward et al. (2013) found that this hypothesis, known as "Walter's two-layer hypothesis" is supported particularly well by studies within dry savannas. Consequently, the small precipitation events which are most characteristic of semi-arid environments hold great ecological significance both for rapid water and nutrient root uptake and biogeochemical cycling in the surface soil layers (Sala and Lauenroth 1982, van Langevelde et al. 2003). Through this interaction, particularly during drought, the herbaceous vegetation may directly inhibit woody seedling establishment.

On the other hand, the disturbance-based hypothesis of tree/grass coexistence attributes woody plant density maintenance to drought and fire (Weaver 1935, February et al. 2013). While droughts can reduce competition from grasses for woody seedling recruitment, fires can cause woody seedling mortality, thus limiting recruitment (Higgins et al. 2000). By governing the fuel load for fire frequency and intensity, the herbaceous layer indirectly regulates woody encroachment (Scholes and Archer 1997).

Using historical aerial photographs (Archer et al. 1988), isotope analysis (Boutton et al. 1998), and data from long-term vegetation plots (Fuhlendorf et al. 1996), a trend of increasing woody plant density has been documented in savannas and grasslands worldwide including those in Australia (Fensham et al. 2005) and South Africa (Kraaij and Ward 2006). Fire suppression has been identified as a leading cause for this phenomenon (Van Auken 2009).

Fires are one of the principal tools used to minimize woody encroachment in savannas and grasslands by inducing woody seedling mortality and limiting woody density (Hochberg et al. 1994, Bond and Keeley 2005, Higgins et al. 2007). Overgrazing in many regions has reduced the herbaceous fuel load to the point that effective, vegetative structure-maintaining fires are rare (Archer 1995). Proper grazing management is crucial to maintaining adequate fuels for effective fires. Savanna fires not only alter the structure and composition of the woody communities, but also the composition and growth of the herbaceous communities as different species and life forms display differential fire responses. Herbaceous responses are dependent upon fire intensity, season of growth, and post-fire conditions such as precipitation availability and soil nutrients (Solbrig et al. 1996, Buis et al. 2009, Mbatha and Ward 2010) as in Figure 1.

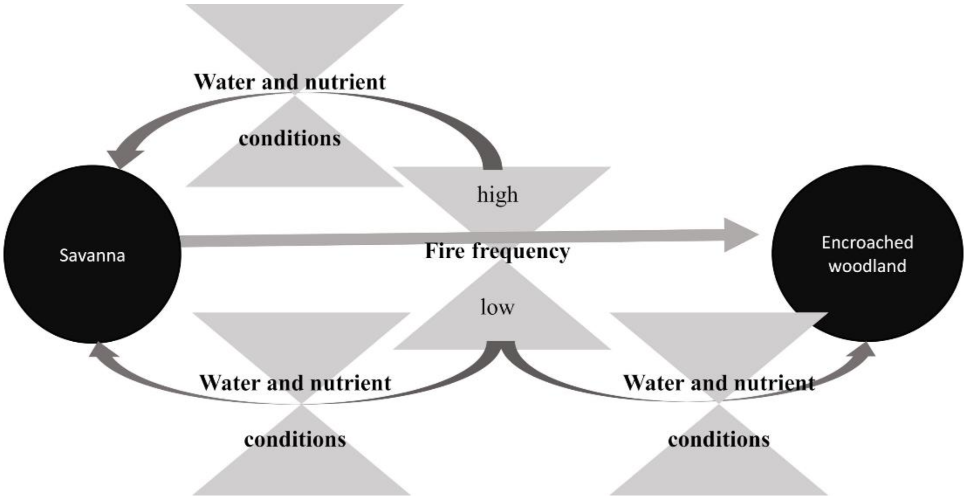

Figure 1. Relationships between fire frequency and resource conditions in a savanna

In addition to structural heterogeneity, savannas also hold tremendous biogeochemical heterogeneity. Nutrient and moisture concentrations are greater beneath the canopy of woody plants due to shading and litterfall (Schlesinger et al. 1996, Tessema and Belay 2017). Conversely, infiltration can be greater beneath continuous grass cover in deep soils with tallgrasses (Walker et al. 1981). Blackburn (1975) suggests that the surface morphology of bare ground spaces largely controls infiltration in semi-arid rangelands. Therefore, deterioration of the heterogeneous structure of savannas may trigger an alteration of ecosystem services including aquifer recharge and nutrient cycling (Olenick et al. 2005, Ansley and Castellano 2006).

Both the vegetation and biogeochemical cycling within savannas are dependent on resource conditions and disturbance regimes (February et al. 2013). According to Kraaij and Ward (2006), moisture, nutrients, and fire are all integral factors which govern cover ratios in savannas. However, climate trends predict altered biogeochemical cycles via increased drought intervals (IPCC 2013) and nitrogen deposition fertilizing native systems (Galloway 2004, Fowler et al. 2013). Burke at al. (2006) even predicts a doubling in severe drought frequency in savanna regions. Under such unprecedented resource conditions, much uncertainty exists as to how savanna processes and structure will respond.

Sankaran et al. (2005) and others (Higgins et al. 2000, Van Der Waal et al. 2009) propose that arid and semi-arid savannas with MAP of less than 650 mm are stable, climatically-determined savannas. They point out that woody encroachment is regulated and encroachment prevented when precipitation is inadequate for seedling establishment. If true, prescribed fires may have minimal impact in these ecosystems, especially under a regime of increasingly intense droughts (Snyman 2003). Precipitation in arid and semi-arid regions is highly variable and often occurs in small events which may be insufficient to reach the deep, woody plant rooting zone (i.e. Mesquite) (Noy-Meir 1973, Sala and Lauenroth 1982, Knapp et al. 2008). Additionally, the season of precipitation is crucial as seedling establishment only needs soil moisture at a specific period of time. Evaluating the herbaceous and soil responses to the interactions between fire, drought, and deposition will be crucial to prudent management options for these semi-arid savannas under altered climatic conditions.

Fire

Grasses are resilient to prescribed fires, even high-intensity growing season fires (Lemon 1949, Rideout-Hanzak et al. 2011, Taylor et al. 2012). Many grasses co-adapted with recurring fires and thus possess traits enabling them to persist through fires. For example, voluminous seed production, rhizomes, basal and intercalary meristems, and belowground axillary bud banks enable individuals to replenish tissue which is combusted in fires (Lemon 1949, Russell et al. 2015). However, the season/frequency of burn, environmental conditions, and plant growth stage determine specific composition and production responses (Ewing and Engle 1988, Silva and Castro 1989, Thonicke et al. 2001, Collins and Calabrese 2012, Russell et al. 2015). Generally, burning stimulates either C3 (cool season) or C4 (warm season) grasses depending on which group is dormant at the time of a fire (Brockway and Lewis 1997, Brockway et al. 2002). Plants undergoing active growth during fires may be inhibited as their resources are concentrated above-ground where they are combusted and lost (Ruckman et al. 2012). Those plants must then invest more carbon into restoring those losses.

In mesic, productive systems, plants are limited by competition for light and space (Grime 1973). Consequently, when a dominant group is suppressed via fire in a mesic system, subdominant species often become more competitive resulting in increased diversity (Brockway and Lewis 1997, Collins and Calabrese 2012). Fire can also be necessary to maintaining diversity in savannas (Savadogo et al. 2008). In arid and semi-arid communities which are constrained by resource stress, however, subdominant species demonstrate a limited competitive response to alterations in space allocation (Valone 2003). Even so, fires have been found to help maintain the abundance of grass individuals in a semi-arid ecosystem, especially during droughts (Bock et al. 1995).

Even among the same life form and region, different species can demonstrate opposing responses to fire. For example, Wink and Wright (1973) found that fires reduced or had no impact on C4 grass *Bouteloua curtipendula var. curtipendula* (rhizomatous), while *Panicum obtusum* (stoloniferous), a similarly-sized C4 grass was stimulated by the same fires. While some studies have exhibited reductions in *Bouteloua curtipendula* (Wink and Wright 1973, Wright 1974, Ansley et al. 2006a), other studies have observed stimulation or null response of *Bouteloua curtipendula* following fires (Dix and Butler 1954, Ansley and Castellano 2007, Castellano and Ansley 2007). Wright (1974) suggests that this opposing response may be explained by the differential persistence of the rhizamatous variety, *curtipendula* versus the caespitose variety, *caespitosa.* Opposing growth forms can exhibit variable fire responses based on the amount of meristematic protection (e.g. above- versus below-ground) and fuel concentration around the plant crown which translates into heat intensity.

Under more abundant resource conditions, aboveground net primary production (ANPP) is stimulated by fire for multiple reasons. In the absence of fire, the accumulation of litter and senescent vegetation can shade out photosynthetically active radiation and thus reduce growth (Knapp and Seastedt 1986). Growth conditions can be further stimulated by post-fire enhancement of soil nutrients in deposited ash (Solbrig et al. 1996, Blair 1997, Smith et al. 2016). The post-fire soil warming and nitrogen-depleted conditions benefit microbe-dependent and nutrient use efficient C4 grasses (Wink and Wright 1973, Seastedt et al. 1991, Castellano and Ansley 2007).

Fires tend to exacerbate drought stress leading to increased rates of mortality and damage (Wink and Wright 1973, Snyman 2003). In arid and semi-arid conditions, therefore, recovery from fires has been more variable than in mesic systems. In a semi-arid region of South Africa, Snyman (2003), observed a decrease in grass cover and density along with decreased water use efficiency (WUE) following fires. Taylor et al. (2012), on the other hand, observed minimal changes in C4 grass communities following even high intensity fires in a semi-arid system within Texas. Wink and Wright (1973) exhibited opposing results in post-fire grass cover of an Ashe juniper community in Texas depending on whether the fires were conducted in an above- or below- average precipitation year.

In order to avoid such seemingly unpredictable (and potentially detrimental) recovery results, it is crucial to understand interactions between fire recovery and resource conditions at a local scale (Solbrig et al. 1996). Future savanna management via prescribed fire requires careful planning. The forecasted novel environmental conditions have the potential to alter the benefits sought by prescribed fires.

Drought

A drought is considered “prolonged dry weather, generally when precipitation is less than three-quarters of the average annual amount” (Kothmann 1974). Many climate change models (including the IPCC 2013) predict increasingly intense precipitation events followed by prolonged drought periods in the southwestern United States (Trenberth et al. 2003, Knapp et al. 2008, Dai 2013). These changes will have inevitable consequences for savannas as precipitation pulses and timing influence plant species persistence, biomass production, and soil properties. Species’ varying ability to persist during extreme drought may lead to widespread species mortality and shifts in ecosystem boundaries (Smith 2011a).

Water is crucial for plant processes and is considered the most limiting resource to net primary production and ecosystem processes in arid and semi-arid systems (Weltzin and McPherson 2000, Cherwin and Knapp 2012). ANPP is highly correlated with annual precipitation (Knapp and Smith 2001). Inadequate soil moisture following disturbance constrains recovery and can cause mortality in new shoots (Skarpe 1992, Solbrig et al. 1996, Drewa and Havstad 2001).

The timing and size of precipitation events can be as influential as the amount (Fay et al. 2002, Van Der Waal et al. 2009). A regime of less frequent, but larger and more concentrated precipitation events is likely to reduce the amount of precipitation lost to soil water evaporation (Schwinning and Sala 2004, Knapp et al. 2008). A possible result would be greater soil water availability and a pulse of biomass exceeding the biomass produced by an equitable amount of precipitation spread across several smaller events (Knapp et al. 2008). ANPP data indicate that large precipitation events are the most important variable explaining inter-annual fluctuations in ANPP as biological soil activity is regulated by precipitation events (Heisler-White et al. 2009). Variability in precipitation timing alone can reduce ANPP to the same extent as a reduction in amount of precipitation (Fay et al. 2003). The timing of precipitation also differentially affects various functional groups. Woody plants, forbs, or grasses can be preferentially favored by precipitation timing depending on life history stage (Noy-Meir 1973, Brown et al. 1997, Weltzin and McPherson 2000).

Soil moisture deficit induces a cascade of responses: a decrease in plant water potential, decreases in cell water, reduced metabolism, reduced photosynthesis, and reduced growth; plant stress responses are then triggered (Porporato et al. 2001). Alam (1999) defines water stress as occurring when the water exiting the plant is greater than the water entering the plant. Plant water stress is further exacerbated by a decreased diffusion potential of roots and transport via transpiration (Alam 1999). General stress responses include reductions in tillering and altered carbohydrate allocation (Fernández and Reynolds 2000). Microbial abundance and activity within the soil is also reduced by drought, resulting in decreased litter decomposition and slowed nutrient turnover (Alster et al. 2013). When resources are limited, plants allocate carbohydrates to root storage rather than above-ground growth (Fay et al. 2002, Dukes et al. 2005). Consequently, biomass and ground cover decline (Herbel et al. 1972, Gibbens and Beck 1988). The loss of herbaceous cover and increase in bare ground has the potential to cause desertification (Wonkka et al. 2016). These effects enhance the risk of wind and water erosion.

Annual plants escape drought by producing seeds that can withstand resource shortages; although, those seeds also require specific conditions for germination and are thus still constrained by shortages (Noy-Meir 1973, Chesson et al. 2004). Perennial plants in general are more tolerant of dehydration than annual plants (Volaire et al. 2009). Greater total root length and size in grasses has also been correlated to a stronger drought resistance and more access to soil water (Chamrad and Box 1965, Box 1967, Yoder et al. 1995).

C4 plants have greater WUE due to their higher CO_2 affinity and superior stomatal efficiency (Ward et al. 1999). As a result, C4 plants can maintain higher (and more stable) levels of stomatal conductance during droughts (Fernández and Reynolds 2000, Taylor et al. 2011). C4 species exhibit better leaf area and biomass recovery following periods of drought (Ward et al. 1999). Water-deficit adapted plants typically cope with drought either by delaying dehydration (via increased water uptake or reduction of water loss), tolerating dehydration, or summer dormancy (Volaire et al. 2009). In the Edwards Plateau of Texas, C4 grasses regularly undergo a bimodal growth pattern which incorporates a mid-summer growth dormancy (Ewing et al. 2005). During dormancy, those grasses are able to reduce leaf production, senesce mature foliage, and utilize below-ground carbohydrate/water reserves (Volaire and Norton 2006). These below-ground storage reserves, characteristic of perennial ephemeroids, not only protect meristematic tissue, but also enable the rapid biomass recovery following the return of rainfall (Noy-Meir 1973, Fuhlendorf and Smeins 1997).

Water availability also regulates the nutrient use efficiency (NUE) of plants (Snyman 2000, 2002a). Nutrient uptake and transport in plants is usually in soluble forms transported via water into the roots and pulled through the plant via transpiration (Scholes 2003). Without soil water, nutrient transport becomes limited. In times of scarcity, nitrogen from the leaves is translocated to below-ground parts for protection (Heckathorn and DeLucia 1994). This response combined with reduced nutrient uptake leads to aboveground tissue with high C/N ratio, and thus, low quality litter (Sardans and Peñuelas 2012, He and Dijkstra 2014). Litter quality is low as much of the nitrogen must be retained by the microbes during decomposition rather than being returned to the soil for plant uptake (Vitousek 1982).

Within the soil, extractable soil organic carbon and nitrogen tend to accumulate under drought conditions (White 1986, Knapp et al. 2008, Schaeffer et al. 2017). This phenomenon can be explained by increased detritus availability, the ongoing extracellular enzyme activity and decline in microbial uptake during drought conditions (Sala et al. 2012, Schaeffer et al. 2017). Nutrient accumulation during drought can cause significant resource pulses in the intense rainfall events predicted to follow prolonged droughts of the future (Moretto et al. 2001, Knapp et al. 2008).

Nitrogen deposition

Soil nitrogen availability plays an integral role in plant growth and tissue replacement (Yahdjian et al. 2011). Aside from water, it is considered one of the most limiting resources in semi-arid ecosystems (Mbatha and Ward 2010, Fay et al. 2015). Bennett and Adams (2001) suggest that while precipitation may regulate the *timing* of herbaceous production, nitrogen regulated the *amount* of ANPP at a semi-arid site. Chlorophyll (the green pigment for photosynthesis) and photosynthesizing enzymes are composed of nitrogen. Thus, the concentration of nitrogen in leaves is among the most important traits which determine photosynthetic capture and accumulation of carbon for growth and storage (Vitousek and Howarth 1991, Sardans et al. 2008b).

Due to the high rates of nitrogen emissions from anthropogenic sources, wet and dry nitrogen deposition rates are expected to alter natural systems (Vitousek 1994, Zhang et al. 2012). In fact, anthropogenic nitrogen fixation doubles global nitrogen cycling by contributing 210Tg N/yr while biological fixation contributes 203Tg N/yr (Fowler et al. 2013). Depending on a region's proximity to emission sources, deposition rates vary spatially (Zhang et al. 2012). Reactive nitrogen is typically deposited in the forms of NH_x and NO_y of which Zhang et al. (2012) estimates that 2.3 Tg N and 4.2 Tg N, respectively, are deposited over the contiguous U.S each year. The National Atmospheric Deposition Program (NADP) has sites across the U.S. which monitor the chemistry of precipitation and track nitrogen deposition ("National Atmospheric Deposition Program (NRSP-3)" 2018). The ORNL DAAC Global Maps of Nitrogen Deposition use emissions estimates and forecasted trends to provide spatial predictions of inorganic nitrogen deposition across the U.S. in 2050 (Dentener 2006). These deposition rates can be extreme enough to induce fertilization responses in uncultivated systems (Vitousek et al. 1997, Matson et al. 2002, Yahdjian et al. 2011).

Fires also alter the nitrogen cycle. Intense prescribed fires can volatilize nitrogen, leaving recently or frequently-burned areas depleted (Blair 1997, Dukes et al. 2005). Nutrient losses from fire volatilization are especially costly in arid regimes (Joubert et al. 2012). Stimulated growth following fires is often temporary and declines as the reduced soil nutrient reserves are exhausted (Blair 1997).

The addition of nitrogen has been observed to increase aboveground net primary productivity (ANPP) (Dukes et al. 2005, Mbatha and Ward 2010, Yahdjian et al. 2011, Borer et al. 2014b, Fay et al. 2015). The availability of nitrogen furnishes the compounds needed for photosynthetic acquisition of carbohydrates for growth. Particularly shoot growth is stimulated by nitrogen (Dukes et al. 2005). With respect to fires, subsequent fertilization results in a prolonged production increase compared to non-fertilized areas (Seastedt et al. 1991, Briggs and Knapp 1995, Buis et al. 2009).

Nitrogen supplementation also influences community composition (Collins et al. 2008). Differential nitrogen use efficiencies and uptake capabilities between species lead to unique species responses (Vitousek 1994, Snyman 2002a). Plants adapted to grow in resource-limited environments grow slowly and have low nutrient requirements (Chapin 1991). These plants have traits to maximize nutrient retention rather than nutrient acquisition. As a result, the cover and diversity of locally-adapted native species are particularly at risk (Seabloom et al. 2015). Busso et al. (2001) further demonstrated this trade-off between nutrient acquisition versus preservation in determining that while the highest rates of nitrogen uptake were seen in the species with the lowest grazing resistance, the lowest rate of nitrogen uptake was seen in the most grazing tolerant species within a semi-arid savanna.

Species diversity and richness commonly decline with N addition (Snyman 2002a, Stevens et al. 2004, Zeng et al. 2010, Yahdjian et al. 2011, Borer et al. 2014b, Smith et al. 2016). In a mesic system, Tilman (1987) found that high nitrogen levels induced a dominance shift toward longer-lived, taller plants relatively independent of initial abundance. Even low levels of nitrogen supplementation can trigger a dramatic loss of species diversity (Clark and Tilman 2008). Following nitrogen addition, shifts from C4 to C3 dominance have been observed as C3 grasses exhibit the highest nutrient uptake (Wedin and Tilman 1997, Reich et al. 2001, Zeng et al. 2010). C4 grasses are more NUE and can be competitive in nitrogen-limited environments but exhibit slow rates of nutrient uptake (Christie 1981, Sage et al. 1987). In addition to differential NUEs, a reduction in diversity can result from dominant plants simply having more tissue with which to respond to nitrogen availability (La Pierre et al. 2016). Less diversity within the community can result in lower resistance to and recovery from drought (Tilman and Downing 1994, Van Ruijven and Berendse 2010).

Studies have found that nitrogen fertilization alters soil chemistry via acidification and increasing nitrogen and carbon pools (Zeng et al. 2010, Khalili et al. 2016). Addition of nitrogen, particularly in dry lands, tends to reduce soil moisture and make systems more sensitive to drought (Snyman 2002a, Van Der Waal et al. 2009). The combination of predicted increases in drought length and nitrogen deposition could therefore have additive effects of decreasing the stability of arid and semi-arid savannas.

Drought-Net

As climatic extremes become more common globally, the need arises for widely coordinated environmental data (Fraser et al. 2012). Extreme Climate Events (ECE) are defined as " an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability" (Smith 2011a). In order to cope with a global issue that causes locally unique responses, future policy, management, and ecological stewardship should be focused on identifying meaningful trends in ecosystem responses across systems.

Past understandings of climate extremes was based largely on data collected from opportunistic studies. Opportunistic studies assess the influence of naturally occurring conditions and can cover large temporal and spatial scales (Smith 2011a). While valuable, these non-experimental studies lack proper replication and have no capability to control for covariates. Experimental studies assessing climatic extreme-induced responses are on the rise in response to this need for scientifically sound data.

Meta-analysis studies have been widely used in an attempt to isolate meaningful results across studies. However, meta-analysis are only as robust as their individual studies (Fraser et al. 2012). If scientifically weak studies are included, they can skew the derived results. Furthermore, even subtle differences in methodology and/or scale can render inter-study comparisons fallacious. For these reasons, intentionally coordinated research networks are needed to provide data which varies in spatial and temporal scale but holds other variables as constant as possible (Weltzin et al. 2003, Fraser et al. 2012).

Challenges to understanding ecological responses to climate extremes include establishing a climatic baseline (off of which to determine change,) possessing a sufficient knowledge of systems, and identifying drivers of change (Smith 2011b). Coordinated research networks seek to overcome those challenges by requiring participating studies to 1) be hypothesis-driven, 2) be geographically diverse, 3) utilize a standardized research design, 4) standardize data management, and 5) share resulting data (Fraser et al. 2012). Inclusion of each of these attributes ensures that resulting data is comparable and robust. Borer et al. (2014a) further emphasize the need for clear goals, simplicity of design, and affordability in global experiments. Those characteristics encourage wide participation, thus adding validity and insight to the results.

Additionally, ecological studies are commonly conducted from a focused perspective. Too narrow a focus can lead to important results being overlooked. When data is shared and standardized via coordinated experiments, collaboration is encouraged (Weltzin et al. 2003). This unique promotion of interdisciplinary communication holds potential to piece together broad, but significant ecological interactions.

Drought-Net, or the Integrated Drought Experiment (IDE) Network is one of many coordinated, ecological research initiatives. The goal of Drought-Net is "to determine how and why terrestrial ecosystems may differ in their sensitivity to extreme drought" (www.drought-net.org). The core treatment of the study is through passive rainout shelters which intersect a unique amount of natural rainfall using clear roofing strips (Yahdjian and Sala 2002). The amount of precipitation excluded by the shelters is based on a site-specific extreme drought rather than a standard amount across all studies (www.drought-net.org.) Knapp et al. (2017) found this method to be appropriate and effective to comparably evaluate precipitation variability and extremes across ecosystems. Standardized protocols are provided for treatment establishment, experimental design, and sampling procedures. In mesic systems, the precipitation manipulations have caused reductions in both C4 grasses and C3 forbs, but increases in diversity and rapid post-drought recovery (Knapp et al. 2002, Hoover et al. 2018). A stronger response in subdominant than dominant species has further been identified (Fay et al. 2003). The majority of those studies within the network, however, are in temperate systems (Knapp et al. 2017). Arid grasslands, however, appear to be more sensitive to droughts (Knapp et al. 2015a). Breshears et al. (2016) point out the potential for a state shift in savannas during droughts. This introduces an integral knowledge gap in the drought sensitivity of arid and semi-arid savannas which exhibit more extreme deviation from average annual precipitation (Knapp et al. 2015b).

Objectives and Hypothesis

The variable interactions between fire, drought, and soil fertility will become increasingly relevant under the irrepressible effects of lengthened droughts and nitrogen deposition combined with ongoing management actions. Understanding how those factors interact is essential to avoiding ecological degradation such as increased erosion (Wink and Wright 1973), decreased forage production (Wink and Wright 1973), monoculture development (Harrison et al. 2003), and exotic invasions (Balogianni et al. 2014). As previously mentioned, changes in functional diversity can reduce system stability and resilience (Tilman et al. 1997). The interactions between fire, precipitation, and soil fertility are the cornerstones of semi-arid savanna conservation under changing environmental conditions.

This study will investigate 1) how an herbaceous community within a semi-arid savanna will respond to drought, N deposition, and prescribed fire *in terms of production, composition, species diversity, and vegetation and soil chemistry* and 2) how these factors will interact to alter those responses.

Key predictions are that:

1. Spring fires will temporarily reduce the cover of C3 Texas wintergrass, *Nassella leucotricha*, increasing the cover of subdominant species through nutrient release and thus increasing diversity (Brockway et al. 2002, Lebbink et al. 2018). Fires were also expected to stimulate ANPP after a recovery period (Ansley et al. 2006a, 2006b).
2. Drought treatments will favor only the most drought-persistent perennial C4 grasses, thus reducing diversity, limit ANPP, and accumulate SOC and nitrogen (Ward et al. 1999, Volaire et al. 2009, Schaeffer et al. 2017).
3. Nitrogen addition will increase the dominance of C3 plants, leading to a reduction in diversity, increase in ANPP, and acidification of the soil (Zeng et al. 2010).
4. Fire combined with nitrogen treatments will exhibit the greatest increases in ANPP (Buis et al. 2009).

5. When combined with any other treatments, drought will override the other treatments to reduce ANPP and re-sprouting ability, indicating deleterious effects on the stability of the system (Weltzin and McPherson 2000).

CHAPTER II

COMMUNITY CHANGES

Introduction

Savannas are defined as having mostly continuous grassy cover with patches of trees (Scholes and Archer 1997). This heterogeneous community structure provides a unique set of valuable ecosystem services such as aquifer recharge, forage grazing, and nutrient cycling (Young and Solbrig 1992, Olenick et al. 2005). The herbaceous layer of savannas influences woody encroachment both directly through resource partitioning of rooting layers and indirectly by serving as the fuel load for fires (Weaver 1935, Walter 1939, Scholes and Archer 1997). Therefore, community composition, biomass production, and diversity of the herbaceous layer is key to sustainable savanna management.

According to Kraaij and Ward (2006), moisture, nutrients, and fire are all integral factors which govern vegetation cover ratios in savannas. Unfortunately, both the ecological services and biodiversity of savannas are being threatened by woody encroachment, overgrazing, fire suppression, drought, and soil erosion. Using historical aerial photographs (Archer et al. 1988), isotope analysis (Boutton et al. 1998), and long-term vegetation plots (Fuhlendorf et al. 1996), a trend of increasing woody plant density has been documented in savannas and grasslands worldwide including those in Australia (Fensham et al. 2005) and South Africa (Kraaij and Ward 2006). Fire suppression has been identified as a leading cause for this phenomenon (Van Auken 2009). Climate trends also predict altered biogeochemical cycles via increased drought intervals (IPCC

2013) and nitrogen (N) deposition fertilizing native systems (Galloway 2004, Fowler et al. 2013). Under such unprecedented resource conditions, much uncertainty exists as to how savanna processes and vegetative composition will respond.

While many savanna grasses can persist even in high-intensity fires, the season/frequency of burn, post-fire environmental conditions, and plant growth stage determine specific composition and production responses (Lemon 1949, Ewing and Engle 1988, Thonicke et al. 2001, Rideout-Hanzak et al. 2011, Russell et al. 2015). Nutrient Use Efficient (NUE) C4 grasses are often favored by fires as the post-fire soil conditions may be depleted of N, but microbially-stimulated and warmed (Wink and Wright 1973, Seastedt et al. 1991, Castellano and Ansley 2007). Differential responses to fire within the same functional groups can be attributed to differences in growth form (i.e. caespitose versus rhizomatous species and varieties) (Wright 1974). Lebbink et al. (2018) confirms that fire enhances understory diversity in semi-arid savannas, demonstrating an additional benefit of fires in semi-arid savannas.

Due to the unpredictability of the climate, however, prescribed fires have produced highly variable results in arid and semi-arid environments (Wink and Wright 1973, Knapp and Seastedt 1986, Blair 1997, Smith et al. 2016). Decreased plant cover and increased erosion are both potential risks associated with conducting prescribed fires in semi-arid and arid regions (Snyman 2003, Ludwig et al. 2005). Fires can also exacerbate the drought stress commonly experienced in these regions by decreasing water use efficiency (WUE) and soil moisture (Wink and Wright 1973, Snyman 2002b).

A drought is loosely considered “a deficit of water relative to normal conditions” (Sheffield and Wood 2012). Many climate change models (including the IPCC 2013) predict increasingly intense precipitation events followed by prolonged drought periods in the southwestern United States (Trenberth et al. 2003, Knapp et al. 2008, Dai 2013). ANPP growth and recovery is highly tied to yearly precipitation (Knapp and Smith 2001) and thus, these changes will have inevitable consequences for savannas in terms of composition, biomass production, and soil properties. A regime of less frequent, more intense precipitation events is, however, likely to reduce the amount of precipitation lost to soil water evaporation and slightly reduce periods of soil water deficit in those regions (Schwinning and Sala 2004, Knapp et al. 2008). Furthermore, soil nutrient uptake which occurs via soluble forms entering plant roots is constrained when soil water is lacking (Snyman 2000, Scholes 2003).

Soil moisture deficit induces a cascade of plant responses: decline in nutrient use efficiency (NUE), a decrease in root absorption potential, decreases in cell water, reduced metabolism, and reduced photosynthesis; stress responses are then triggered (Alam 1999, Porporato et al. 2001). General stress responses include reductions in tillering and carbohydrate allocation to underground parts (Fernández and Reynolds 2000, Fay et al. 2002, Dukes et al. 2005). Consequently, biomass and ground cover decline (Herbel et al. 1972, Gibbens and Beck 1988). The loss of herbaceous cover and increase in bare ground has the potential to cause desertification (Wonkka et al. 2016). Water-deficit adapted plants cope with drought through dormancy, reduced growth, and below-ground carbohydrate/water reserves (Volaire and Norton 2006, Volaire et al.

2009). Perennial plants in general are more tolerant of dehydration than annual plants (Volaire et al. 2009). C4 plants have greater WUE than C3 plants due to their higher CO_2 affinity and superior stomatal efficiency (Ward et al. 1999). As a result, C4 plants can maintain higher (and more stable) levels of stomatal conductance during droughts and have better leaf area and biomass recovery following drought (Ward et al. 1999, Fernández and Reynolds 2000, Taylor et al. 2011).

The recent increases in atmospheric N deposition are also likely to induce changes in the vegetative communities of semi-arid savannas as N addition alters community composition and biomass production (Collins et al. 2008). Bennett and Adams (2001) suggest that although the *timing* of herbaceous production is regulated by precipitation, the *amount* of ANPP is regulated by N availability at a semi-arid site. Thus, water and N availability respectively are commonly the most and second-most limiting factors in arid and semi-arid ecosystems (Chapin et al. 1987, Yahdjian and Sala 2010).

While N addition generally increases ANPP, it generally decreases species diversity and richness (Snyman 2002a, Stevens et al. 2004, Zeng et al. 2010, Mbatha and Ward 2010, Yahdjian et al. 2011, Borer et al. 2014b). Even low levels of N supplementation can trigger a dramatic loss of species diversity (Clark and Tilman 2008). Plants adapted to grow in resource-limited environments grow slowly and have low nutrient requirements and uptake (Chapin 1991, Hobbie 1992). These plants have traits to maximize nutrient retention rather than nutrient acquisition. Shifts from C4 to C3 dominance have commonly been observed following N addition as C4 grasses are more nutrient use efficient and C3 grasses generally exhibit greater nutrient uptake (Christie 1981, Sage et al. 1987, Wedin and Tilman 1997, Reich et al. 2001). In addition to differential NUEs, a reduction in diversity can result from dominant plants simply having more tissue with which to respond to N availability (La Pierre et al. 2016).

Less diversity within the community can result in lower resistance to and recovery from drought (Tilman and Downing 1994, Van Ruijven and Berendse 2010). Changes in soil fertility can thus increase a system's vulnerability to drought. Snyman (2002a) found that semi-arid climax grasses experienced increasing drought sensitivity with increasing amounts of N application. Furthermore, N uptake is dependent on soil water availability for transport to roots (Scholes 2003).

As demonstrated, fire, drought, and N can all independently and interactively play a strong role in altering the community composition of semi-arid plant communities. The ecological implications of fire, drought, and N addition will become increasingly significant under the predicted, but irrepressible, effects of lengthened droughts and N deposition combined with ongoing savanna management actions. While each of these factors has been studied somewhat extensively both independently and interactively in mesic environments (Knapp 1985, Collins 1987, Tilman 1987, Fay et al. 2002), much less is known about their effects in the climatically erratic arid and semi-arid regions. This knowledge gap is of particular concern as arid grasslands have been found to be more sensitive to drought than other grassland systems (Knapp et al. 2015a). Furthermore, savannas may be at risk of state shifts under changing climatic conditions (Breshears et al. 2016). Changes in the functional diversity of savannas can reduce system stability and resilience (Tilman et al. 1997). Ecologists and managers alike should seek a holistic understanding of these altered disturbance and resource conditions in order to avoid increased erosion (Wink and Wright 1973), decreased forage production (Wink and Wright 1973), monoculture development (Harrison et al. 2003), and exotic invasions (Balogianni et al. 2014). The interactions between fire, precipitation, and soil fertility are the cornerstones of semi-arid savanna conservation under changing environmental conditions.

The objective of this study was to investigate 1) how an herbaceous community within a semi-arid savanna will respond to Drought, N deposition, and Prescribed Fire *in terms of ANPP, diversity, and community composition,* and 2) how these factors will interact to alter those responses. To investigate this, rainout shelters were deployed, ammonium nitrate was applied, and prescribed ring fires were conducted on herbaceous-dominated plots in a semi-arid savanna system located in central Texas, USA. Predictions were that H1) ANPP would be stimulated by the N treatment and Fire treatment (after a period of recovery), but would be reduced by the Drought treatment; H2) diversity would be enhanced by the Fire treatments, but that Drought and N treatments would cause diversity to decline due to increasing dominance in either C4 grasses or C3 plants, respectively; H3) interactively, Fire and N addition was predicted to exhibit the greatest increases in ANPP and H4) interactions including Drought were predicted to demonstrate constrained responses to Fire and N addition.

Methods

Study site

This study took place at the Texas A&M Agrilife Sonora Research Station (SRS) located 56 km south of Sonora, Texas (30°16'N, 100°33'W). Located on the western edge of the Edwards Plateau, the site is a semi-arid savanna system. According to Guyette et al. (2012), the western Edward's Plateau historically lies within a 4-8-year fire return interval. Mean annual precipitation on the site is 567.88 mm falling in a bimodal, spring/fall pattern. However, variation from the mean is the norm (Figure 2). The average growing season at the station is 240 days with the mean January temperature of 8 °C and the mean July temperature of 26 °C (SRS records and Fuhlendorf et al. 2001).

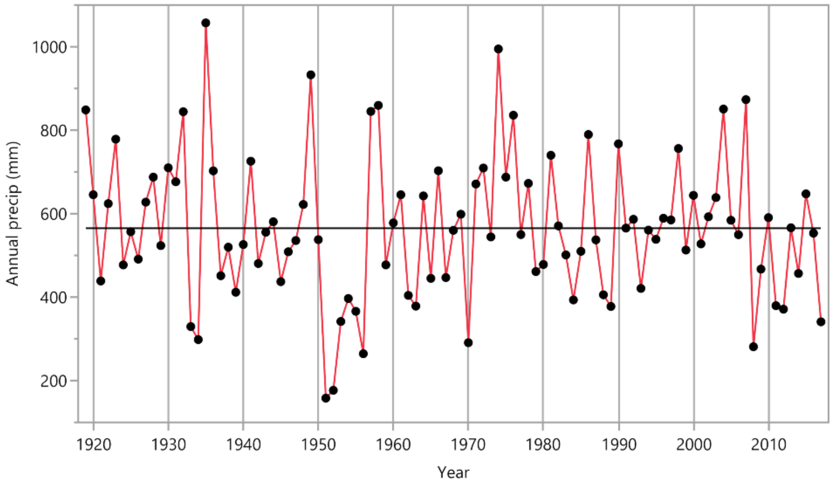

Figure 2. Time series of historic annual rainfall at Sonora Research Station from 1919-2018

The soil type is a Valera clay with a petrocalcic layer 51-102 cm below the surface on 1-3% slopes (Garbiel and Loomis 2017). Some plots at the southern end of the study area are Eckrant-Rock outcrop complex soils. Soils throughout the region are shallow, rocky, and heterogeneous in depth. Characteristic vegetation includes live oak (*Quercus virginiana*), juniper species (*Juniperus spp*., especially *Juniperus pinchotii*), Texas wintergrass (*Nassella leucotricha*), common curlymesquite (*Hilaria belangeri*), Wright's threeawn (*Aristida wrightii*), King Ranch bluestem (*Bothriochloa ischaemum*), Texas cupgrass (*Eriochloa sericea*), sideoats grama (*Bouteloua curtipendula*), and prairie verbena (*Glandularia bipinnatifida*).

The SRS has been a National Trends Network monitoring station (TX16) for the National Atmospheric Deposition Program (NADP) since 1984. The NADP (http://nadp.slh.wisc.edu/NTN/) data shows that the site is currently receiving 0.2 g/m^2 of total N deposition. Based on predictions from NASA's ORNL Distributed Active Archive Center (https://daac.ornl.gov/), this amount could increase to 1.7 g/m^2 as soon as the year 2050 in the region.

Study design

Sixty-four 5 x 5 m plots separated by 2 m alleyways were established in an herbaceous-dominated area enclosed by a wildlife and livestock-exclusion fence. The area had been excluded from livestock grazing for more than five years, but axis deer commonly grazed the site prior to fence construction. Woody communities were not assessed in this study. The soil beneath the plots are moderately alkaline clay loam. Treatments were Drought (rainout shelter or ambient,) N deposition (N) (N addition or control,) and Fire (prescribed ring fires or control). The eight treatment combinations were randomly assigned to plots using a 2 x 2 x 2 full factorial design resulting in eight replicates of each treatment combination.

Rainout shelters were constructed to cover an area of 3 x 3 m with clear polycarbonate roofing strips affixed to PVC frames and installed on March 3, 2018. The strips covered approximately 69% and diverted that precipitation away from the plots to simulate 1st percentile extreme drought for the site (175.65 mm/year) according to the Drought-Net protocol (www.drought-net.colstate.edu). Drought-Net has similar sites established around the world where a site-specific intense drought is simulated by calculating the 1st percentile extreme drought record for each site. Site-specific precipitation records from 1919-2013 were utilized. The size of the shelter was sufficient to cover a core sampling area of 2 x 2 m in addition to a 50 cm buffer, exceeding the 20 cm edge effect noted by Yahdjian and Sala (2002). Shelter roofs were ca. 1.4 m tall. A 25-38 cm trench was dug surrounding drought plots for the instillation of 6 mil. sheet plastic which also protruded 7-12 cm above the ground level as in Figure 3. The depth trenched was dependent on the depth of limestone below. Precipitation trapped by the roofing strips drains beyond the plastic barriers and trenches.

Figure 3. Rainout shelter (3 x 3m) in field

Ring fires were conducted on March 1 and 2, 2018. This season was selected in order to precede the first expected peak in precipitation. A propane vapor torch, or "prickly pear torch" was used in order to compensate for the low fuel loads and high humidity. Mean wind speed was 4.4 mph on March 1 and 2.6 on March 2. Mean relative humidity was 34.7% on March 1 and 62.1% on March 2. Mean air temperature was 19.67 ºC on March 1 and 16.17 ºC on March 2.

A Scotts Wizz hand-held spreader was used to evenly dispense ammonium nitrate (NH_4NO_3: 34% N) to plots assigned to the N treatment on April 18, 2018 preceding rains. It was applied at a rate of 5 g N/m^2 in a dry granular (prill) form.

Sampling

Aboveground Net Primary Productivity

A 0.25 m^2 square quadrat was used for destructive biomass sampling in each of the 64 plots pre-treatment, at 4, 8, and 12 months post-treatment. All vegetation rooted within the quadrat was clipped to the ground level. Quadrat location was modified at each sampling date to avoid any compensatory growth effects. Biomass was then sorted to live and dead vegetation which was further sorted to grass, forb, and woody groups. These groups were separated as they have broad implications for grazing value, carbon storage, and potential for fires. When possible, dead vegetation was further sorted to previous and current year's dead growth. All samples were then dried in an oven at 60°C for 48 hours. After drying, each of the categories was weighed separately and recorded on a per-plot basis to the nearest 0.01 g.

Species composition

Cover composition was evaluated in a designated $1m^2$ quadrat for each plot pre-treatment and 4, 8, and 12 months post-treatments. A modified Daubenmire (Daubenmire 1959) method was used as cover values per species were noted to the nearest percent. Species representing >1% cover were recorded. The density of those species in each quadrat was also recorded. In the fall of 2018, unknown annual forb seedlings were classified into an "annual forb" group.

Statistical analysis

Differences in Shannon's diversity (H') and biomass between treatments were assessed parametrically. To meet the assumptions of parametric tests, $\log_{10}$

transformations were applied as needed to achieve normality and homogeneity of variance. While normality was evaluated visually as suggested by Zuur et al. (2010), homogeneity of variance was tested using the Levene's test (Van Der Waal et al. 2009). Three-way, factorial ANOVAs were performed to test the interactive effects of Drought, N, and Fire on ANPP (biomass) and Shannon's diversity with function *Fit Model* in JMP Pro 13.0 (SAS Institute Inc., Cary, NC USA).

Changes in the overall community composition between the treatments were assessed semi-parametrically as species cover and abundance data is non-normally distributed and zero-filled. In order to quantify the similarity between the community composition of the plots, the Bray-Curtis dissimilarity index which ignores double absences was calculated using function vegdist() for proportional canopy cover (function decostand(method=”total”)) in each plot. Because it ignores double absences, the index is particularly well-suited for composition datasets and has often been used to assess plant communities (Clarke 1993).

Permutational multivariate analysis of variance (PERMANOVA) based on the Bray-Curtis dissimilarity index was then used to statistically assess differences in the overall plant community. A semi-parametric test, the PERMANOVA was designed for ecological studies and geometrically partitions multivariate variance in the space of a desired dissimilarity index and obtains p-values based on permutation techniques (Anderson 2017). In contrast to traditional analysis of variance (ANOVA) tests, the PERMONOVA does not assume normal distribution of residuals or homogeneity of variance and is well-suited to assess multivariate ecological responses (Anderson 2001, 2017). The PERMANOVA was also confirmed to be robust to differences in dispersion and strictly test the null hypothesis that there are no differences in multi-dimensional centroids between groups for balanced designs such as this one (Anderson and Walsh 2013). PERMANOVA tests were conducted with function adonis2() with 9,999 permutations.

Results of the PERMANOVA are visualized using non-metric multi-dimensional scaling (NMDS) (function metaMDS()) based on the Bray-Curtis index as in Jones et al. (2016), Prevéy et al. (2010), and Tredennick et al. (2018). NMDS was selected for ordination as it allows the selection of an appropriate dissimilarity measure and is based on the sample rank orders (Minchin 1987, Clarke 1993, Zuur et al. 2007). The species scores (function wascores()) were also plotted on the NMDS with the standard error ellipses of treatment groups (plotted using functions orditorp() and ordihull()). Differences in group dispersion were tested using the PERMDISP method (Anderson and Walsh 2013) implemented via the betadisper(method= “centroid”) and permutest(pairwise=TRUE) functions with 9,999 permutations. This method was selected as it is considered to be a more specific test of group differences in multivariate dispersion than other alternatives such as ANOSIM (Anderson and Walsh 2013).

Unless otherwise noted, analyses were performed using the vegan package (Okasanen et al. 2018) of RStudio (RStudio Team 2018)

Results

Fifty-seven species of vascular plants were recorded with the majority being natives and only seven considered introduced species (See Appendix 1). Introduced species were: Spreading sida- SiAb (*Sida abutifolia*), California filaree- ErCi (*Erodium cicutarium*), Malta Starthistle- CeMe (*Centaurea melitensis*), Bur clover- MePo (*Medicago polymorpha*), Wilman's lovegrass- ErSu (*Eragrostis superba*), K.R. bluestem- BoIs (*Bothriochloa ischaemum var. songarica*), and Rescuegrass- BrCa (*Bromus catharticus*). The species comprising at least 5% mean canopy cover in the winter of 2017, winter of 2018, or spring 2019 were: *Nassella leucotricha, Hilaria belangeri, Bouteloua curtipendula, Eragrostis intermedia, Oxalis drummondii, Panicum hallii, Glandularia bipinnatifida, Medicago polymorpha, Lesquerella gordonii, Astragalus nuttallianus,* and *Ratibida columnifera.* Species composition changed dramatically in response to precipitation and seasonal phenology.

Throughout the duration of study, the precipitation pattern was particularly erratic as shown in Figure 4. Precipitation was slightly above-average in 2017 at 586.49 mm accumulated. The large disparity in the amount of fall precipitation preceding the pre- and 8 month post-treatment samplings contributed to the differences in dominance shown in Table 1 in which only the species common to the top ten dominance at all dates are highlighted. One of the most notable changes in average proportional cover across all plots is in *Nassella leucotricha* which went from the overwhelmingly most dominant species pre-treatment in the winter of 2017 (µ =0.56) to a low mean proportional cover in the winter of 2018 (µ=0.05) with an increase to µ=0.10 in spring 2019. In the spring of 2019, the mean canopy cover by annual plants was 61% compared to 11% in the winter of 2018, perhaps helping to explain the decline in cover by *Nassella leucotricha*.

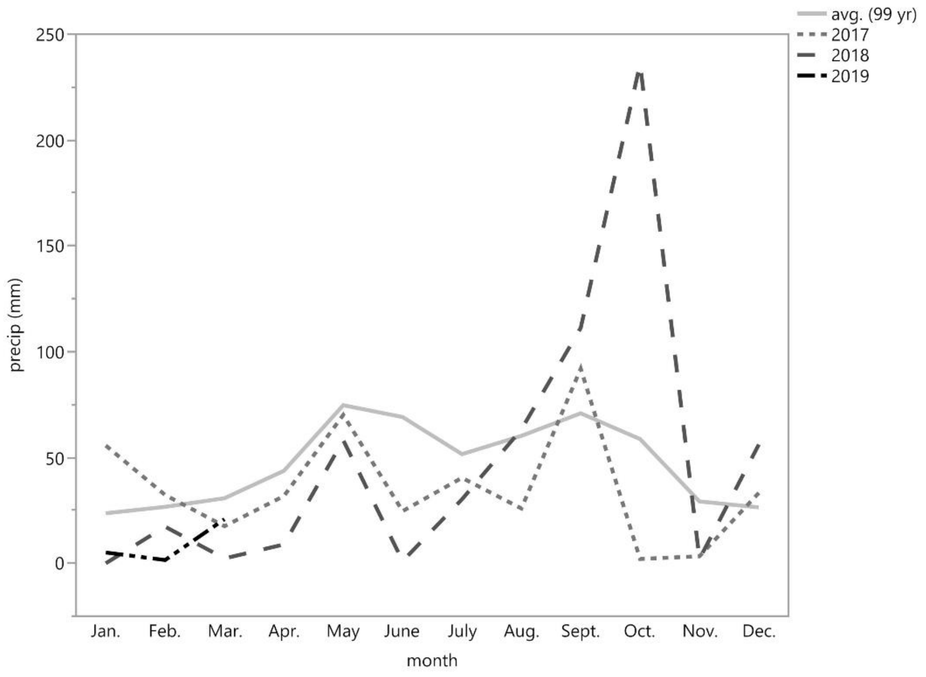

Figure 4. Monthly precipitation totals (mm) during years preceding and during the study with the 99-year average precipitation for this site

Table 1. Mean proportional canopy cover composition listed in descending order of dominance between pre-treatment (winter 2017), 8 months post-treatment (winter 2018), and 12 months post-treatment (spring 2019). When abbreviated, plant names are given as the first two letter of the genus followed by the first two letters of the species name (i.e. GeSp, See Data Appendix 1.)

11.10.2017		11.3.2018		3.1.2019	
Species	**Mean comp.**	**Species**	**Mean comp.**	**Species**	**Mean Comp.**
NaLe	0.557337	OxDr	0.274475	MePo	0.169334694
HiBe	0.153984	GlBi	0.100771	LeGo	0.149644
ErIn	0.05364	HiBe	0.092084	GlBi	0.132248268
BoCu	0.048237	BoCu	0.067728	AsNu	0.100079046
ArWr	0.036846	PaHa	0.053785	NaLe	0.09615927
OpPo	0.025881	MeOl	0.049476	RaCo	0.057608738
SpCr	0.019901	NaLe	0.047447	OeTr	0.048979818
CrDi	0.018725	annual forbs	0.038758	HiBe	0.042846963
VeCa	0.015439	CrMo	0.036748	PlRh	0.035080674
DiCo	0.013686	AcPh	0.026611	ErCi	0.026907846

Aboveground Net Primary Productivity (ANPP)

In the full-factorial ANOVA of transformed total ANPP, no differences were detected between groups in the spring 2018 (pre-treatment) data (P>0.05, Data Appendix 1). A summer ANPP sampling revealed that 4 months after treatment, a significant reduction in $\log_{10}$-transformed, total ANPP by Fire was present (p<0.05, Data Appendix 1). This indicates that ANPP was unable to recover from the prescribed fires within 4 months of application during a time of drought. The ANOVAs for total ANPP in the winter 2018 and spring 2019 are shown in Table 2. After 8 months of treatment implementation, Drought caused a significant reduction (p<0.01) in total ANPP and no significant difference was attributed to the Fire treatment (p>0.05). Large, concentrated events of precipitation during the fall of 2018 caused the Drought treatment to produce the expected decrease in ANPP, but also facilitated the full recovery from the Fire treatment. In the spring 2019 (12 months after treatment initiation), no differences in overall ANPP were detected as a result of the treatments either independently or interactively.

Table 2. Full factorial ANOVA of $\log_{10}$-transformed ANPP in the winter of 2018 (8 months post-treatment) and spring of 2019 (12 months post-treatment) (indicates statistical significance, *: P <0.05, **: P <0.01, ***: P <0.001)*

		WINTER 2018			**SPRING 2019**		
Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**	**Sum of Squares**	**F Ratio**	**Prob > F**
Drought	1	1.1385037	10.5578	0.0020*	0.09069084	1.6376	0.2059
Nitrogen	1	0.0296077	0.2746	0.6024	0.02297714	0.4149	0.5221
Drought*Nitrogen	1	0.0411770	0.3819	0.5391	0.00768655	0.1388	0.7109
Fire	1	0.0165549	0.1535	0.6967	0.12101444	2.1852	0.1449
Drought*Fire	1	0.0353212	0.3275	0.5694	0.00783082	0.1414	0.7083
Nitrogen*Fire	1	0.0182458	0.1692	0.6824	0.05523731	0.9974	0.3222
Drought*Nitrogen*Fire	1	0.1365022	1.2658	0.2653	0.00844323	0.1525	0.6977

In the spring of 2018 (pre-treatment), the back-transformed mean ANPP was 47.62 g/m^2 or 424.86 lbs/acre. In the summer of 2018, four months post-treatment, the back-transformed mean ANPP was 21.01 g/m^2 or 187.54 lbs/acre. The winter of 2018 (8 months post-treatment) back-transformed mean was 47.78 g/m^2 or 426.28 lbs/ac. The ANPP in the spring of 2019 was significantly higher than other sampling dates (Kruskal Wallis Rank Sums Test, $p<0.05$, Data Appendix 1) with a back-transformed mean ANPP of 97.14 g/m^2 or 866.69 lbs/acre.

Full-factorial ANOVAs were conducted on growth form ANPP groups to understand more specific responses within live grass and forb functional groups. No distinction was made within the groups between annual and perennial species. Live grass ANPP was significantly reduced by the Drought treatment after 8 months ($p<0.05$, Data Appendix 1) in the winter 2018 sampling. In the spring of 2019, the live grass ANPP failed to achieve normality and homogeneity of variance, so only the live forb group was assessed. The winter 2018 sampling ANOVA (Table 3) showed that live forb ANPP was increased by the N treatment ($p<0.01$). The spring 2019 transformed live forb group was significantly increased by Drought ($p<0.05$) and significantly reduced by Fire ($p<0.01$). LS Means for the live forb group are shown in Figure 5. Post-treatment ANPP by treatment group (TRT) is shown in Figure 6.

*Table 3. Full-factorial ANOVA of $\log_{10}$-transformed live forb ANPP 8 months post-treatment (winter of 2018) and 12 months post-treatment (spring of 2019) (*Indicates statistical significance, *:$P<0.05$, **:$P<0.01$, ***:$P<0.001$)*

		WINTER 2018			**SPRING 2019**		
Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**	**Sum of Squares**	**F Ratio**	**Prob > F**
Drought	1	0.4692077	2.4558	0.1227	0.66079642	5.4603	0.0231*
Nitrogen	1	1.4299322	7.4841	0.0083**	0.12182093	1.0066	0.3200
Drought*Nitrogen	1	0.0022702	0.0119	0.9136	0.00064993	0.0054	0.9418
Fire	1	0.1007227	0.5272	0.4708	0.96555813	7.9786	0.0065**
Drought*Fire	1	0.0294415	0.1541	0.6961	0.03077473	0.2543	0.6160
Nitrogen*Fire	1	0.0082762	0.0433	0.8359	0.03127855	0.2585	0.6132
Drought*Nitrogen*Fire	1	0.0051990	0.0272	0.8696	0.06682124	0.5522	0.4605

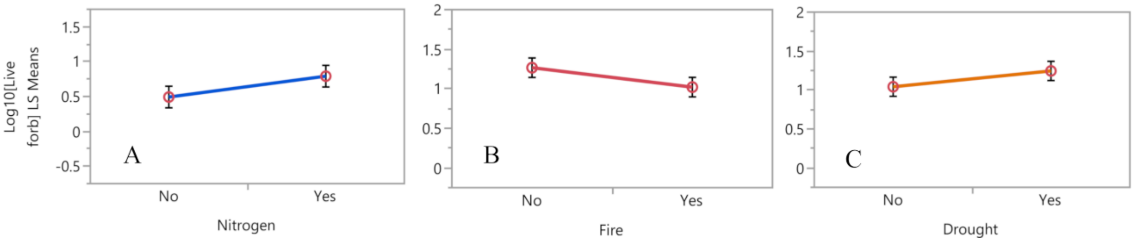

Figure 5. LS Means of live forb ANPP in the winter of 2018 (A) and spring of 2019 (B and C)

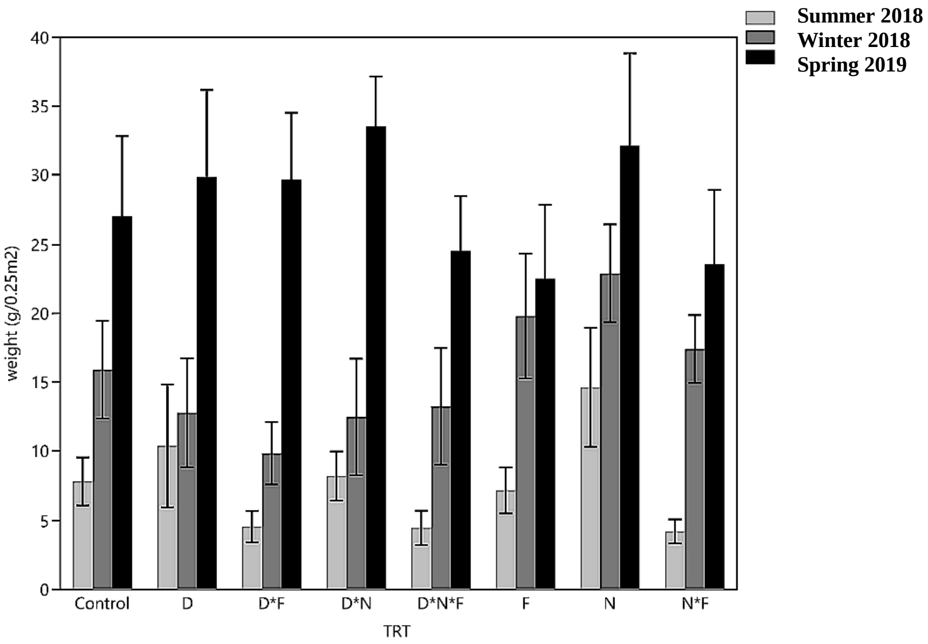

Figure 6. Mean overall ANPP for three post-treatment ANPP samplings. Note that groups are identified with "D" for drought shelters, "N" for application of ammonium nitrate, and "F" for prescribed fires

*Table 4. Full-factorial ANOVA of the change in Shannon's H' from pre-treatment to 8 months post-treatment (winter 2018-winter 2017) (*Indicates statistical significance, *:P<0.05, **:P<0.01, ***:P<0.001)*

		WINTER 2018-WINTER 2017			**SPRING 2019-WINTER 2018**		
Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**	**Sum of Squares**	**F Ratio**	**Prob > F**
Drought	1	0.1762692	0.6719	0.4159	0.00831255	0.0441	0.8345
Nitrogen	1	1.3993364	5.3338	0.0247*	0.51609028	2.7372	0.1036
Drought*Nitrogen	1	1.0607538	4.0432	0.0493*	0.03045806	0.1615	0.6893
Fire	1	0.0926893	0.3533	0.5547	0.01234933	0.0655	0.7989
Drought*Fire	1	0.0000463	0.0002	0.9895	0.01377806	0.0731	0.7879
Nitrogen*Fire	1	0.0361273	0.1377	0.7120	0.06374286	0.3381	0.5633
Drought*Nitrogen*Fire	1	0.0081826	0.0312	0.8605	0.05384033	0.2856	0.5952

Vegetation diversity

The effect of each treatment on the magnitude of change in diversity from the winter of 2017 to the winter of 2018 and winter 2018 to spring 2019 was analyzed using a full-factorial ANOVA on the change in Shannon's diversity (H'). This method was used in order to attain data normality as well as to assess how the treatments *induced change in* diversity of the vegetative community. The N treatment significantly affected the magnitude of change in diversity ($p<0.05$) after 8 months of treatment (Table 4) with the addition of N inducing change of greater magnitude from the winter of 2017 to the winter of 2018 (Shannon's H' LS Means, Data Appendix 1- No: 0.2178, Yes: 0.5161).

The Drought*N interaction was also significant ($p<0.05$) after 8 months with the plant community experiencing more change in diversity following the addition of N only when the plots were not experiencing Drought (Shannon's H' LS Means, Data Appendix 1- No, No: 0.0349, No, Yes: 0.5930). Figure 7 additionally shows that the control and fire treatment groups experienced less mean change in diversity 8 months after treatment application compared to other groups. Diversity was higher overall in the winter of 2018 compared to the winter of 2017 and highest in spring 2019 (Kruskal-Wallace rank sum test, Data Appendix 1, z<0.001). Twelve months after the fires were conducted and shelters were installed (spring 2019), there were no significant effects of treatments either on Shannon's H' or on the change in Shannon's H' between spring 2019 and winter 2018 as shown in Table 5 and the Data Appendix 1.

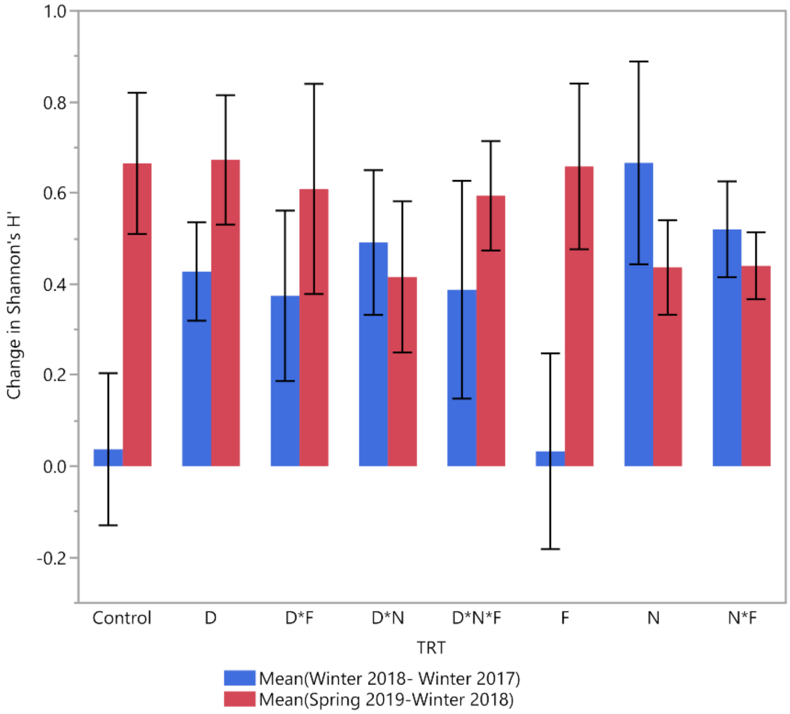

Figure 7. Change in Shannon's H' (Winter 2018 -Winter 2017) between the eight treatment groups where "D" signifies drought, "N" ammonium nitrate addition, and "F" that prescribed fires were conducted

Vegetation community composition

The PERMANOVA detected pre-treatment statistical significance of the N treatment ($p < 0.05$) because the community composition of our plots was heterogeneous even prior to treatment application (Table 5). Additionally, after only 8 months of treatments, the herbaceous community composition was significantly affected by the interaction ($p<0.05$) of the full combination of treatments (Drought*N*Fire) which went from having the least significance in winter 2017 to being the most significant in winter 2018. This indicates that the full combination of treatments caused a community shift in multivariate space. No additional treatment effects on community composition were identified in the winter of 2018 ($p>0.05$). When percent bare ground was included in the winter 2018 PERMANOVA, Drought independently effected community composition significantly ($p<0.001$, Data Appendix 1). The spring 2019 sampling indicated no treatment effects on the community (after 12 months of treatment implementation) ($p>0.05$) when based on canopy cover. It should, however, be noted that Drought caused a significant shift in community composition ($p<0.05$, Data Appendix 1) when Bray-Curtis was based on the density of plant individuals rather than canopy cover.

*Table 5. Permutational multivariate analysis of variance test for differences in group centroids within multivariate space based on canopy cover. adonis under reduced model (formula = comm.BC1 ~ Shelter * Nitrogen * Fire, data = community, permutations = 9999, method = "bray") (*Indicates statistical significance, *:P<0.05, **:P<0.01, ***:P<0.001)*

		Df	SumOfSqs	R2	F	Pr(>F)
Winter 2017	Drought	1	0.15169971	0.010606515	0.6688058	0.6066
	Nitrogen	1	0.64493097	0.045092178	2.8433383	0.0280*
	Fire	1	0.06786587	0.004745035	0.2992035	0.9293
	Drought:Nitrogen	1	0.41219153	0.028819540	1.8172487	0.1177
	Drought:Fire	1	0.10780523	0.007537509	0.4752861	0.7917
	Nitrogen:Fire	1	0.16990239	0.011879208	0.7490569	0.5462
	Drought:Nitrogen:Fire	1	0.04608825	0.003222391	0.2031915	0.9713
	Residual	56	12.70201817	0.888097626	*NA*	*NA*
	Total	63	14.30250212	1.000000000	*NA*	*NA*
Winter 2018	Drought	1	0.4507632	0.021884697	1.4196563	0.1675
	Nitrogen	1	0.5582050	0.027101027	1.7580387	0.0642
	Fire	1	0.1453697	0.007057743	0.4578345	0.9198
	Drought:Nitrogen	1	0.3807183	0.018483995	1.1990534	0.2842
	Drought:Fire	1	0.2264636	0.010994881	0.7132359	0.7113
	Nitrogen:Fire	1	0.3852062	0.018701881	1.2131876	0.2698
	Drought:Nitrogen:Fire	1	0.6695808	0.032508358	2.1088113	0.0275*
	Residual	56	17.7808822	0.863267418	*NA*	*NA*
	Total	63	20.5971890	1.000000000	*NA*	*NA*
Spring 2019	Drought	1	0.32835624	0.024237771	1.5034601	0.1432
	Nitrogen	1	0.12593844	0.009296206	0.5766403	0.8191
	Fire	1	0.28710862	0.021193058	1.3145977	0.2216
	Drought:Nitrogen	1	0.09349424	0.006901322	0.4280865	0.9242
	Drought:Fire	1	0.17476271	0.012900192	0.8001942	0.6107
	Nitrogen:Fire	1	0.24011259	0.017724024	1.0994148	0.3526
	Drought:Nitrogen:Fire	1	0.06710183	0.004953153	0.3072423	0.9744
	Residual	56	12.23042045	0.902794273	*NA*	*NA*
	Total	63	13.54729512	1.000000000	*NA*	*NA*

To serve as a visual corroboration of the PERMANOVA, the NMDS (Figure 8) shows treatment group clustering in the winter 2018 sampling (A), but not the spring 2019 (B) sampling. The pre-treatment (winter 2017) community yielded a three-dimensional ordination (stress=0.0727, Data Appendix 1) which did not demonstrate plot groupings based on treatments. The winter 2018 post-treatment sampling (winter 2018) yielded a four-dimensional ordination (stress=0.1297) as did the spring 2019 sampling (stress=0.1191). In the winter 2018 sampling, the full combination of treatments group (D*N*F – open diamonds) attained some distinction as is evidenced by the proximity of those plots to one another in the ordination. The group receiving only the Drought treatment (D – open squares) also demonstrates some grouping in the winter of 2018.

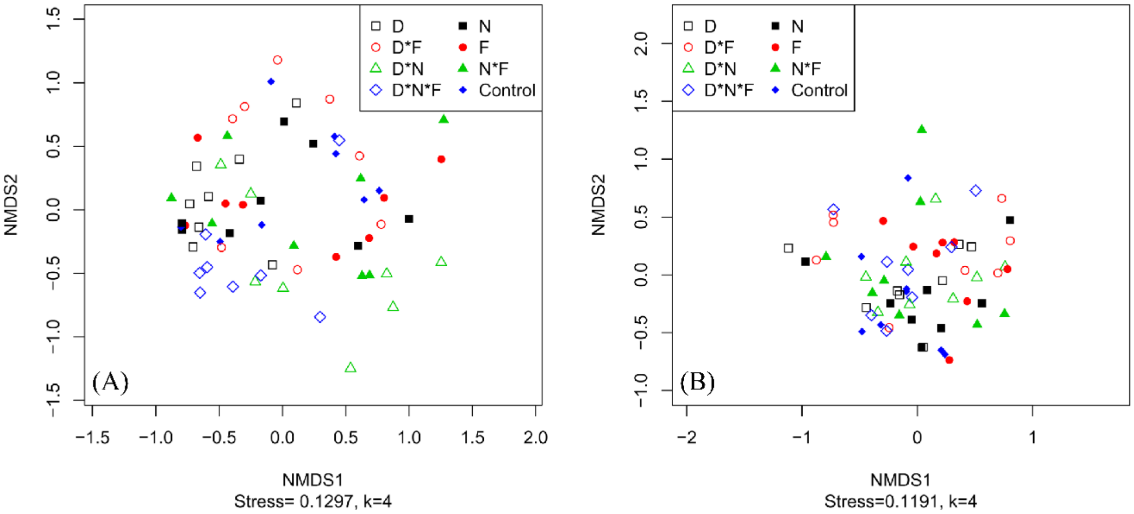

Figure 8. Non-metric multi-dimensional scaling (NMDS) ordination of plant community composition for a) four-dimmensional ordination (stress=0.1297) of 8 months post-treatment and b) four-dimmensional ordination (stress=0.1191) of 12 months post-treatment of the full set of Bray-Curtis dissimilarity indices based on the post-treatment canopy cover of each plot.

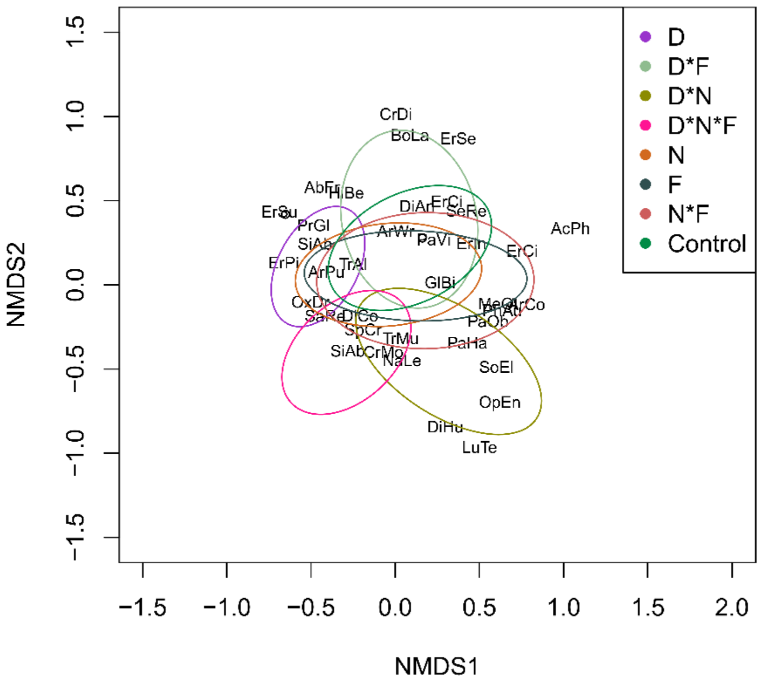

Figure 9. Four-dimensional winter 2018 NMDS species scores plotted with standard error ellipses (conf=0.95) of the treatment groups. When abbreviated, plant names are given as the first two letter of the genus followed by the first two letters of the species name (eg. GeSp), see Appendix 1 for taxa list. Some species were automatically removed by the algorithm for visual spacing.

Additionally, the winter 2018 treatment group 95% confidence interval standard error ellipses can be ordinated with the species which constitute that community composition (Figure 9). *Hilaria belangeri* (NMDS1: -0.2900, NMDS2: 0.5473), *Aristida purpurea* (NMDS1: -0.4087, NMDS2: 0.0778), and *Erioneuron pilosum* (NMDS1: -0.6630, NMDS2: 0.1320) all ordinate in close proximity to the Drought group. As was indicated by the PERMANOVA, the spring 2019 community lacked community groupings based on treatment group or species associations.

The heterogeneity of grassland ecosystems is crucial to their functioning. Therefore, an assessment of how the treatments affect community heterogeneity is equally important as analysis of shifts in species composition. The winter 2018 (8 months post-treatment) increased clustering in the NMDS of the D and D*N*F groups is quantitatively corroborated by the results of the PERMDISP analysis for homogeneity of dispersions. PERMDISP analysis results indicated that there were no significant differences in group dispersions prior to treatment application (p>0.05, Data Appendix 1) but that group dispersions were significantly different after 8 months of treatments in the winter of 2018 (p<0.01, Table 6). During the spring of 2019, however, no differences in dispersion were identified (p>0.05).

*Table 6. Permutation test for homogeneity of multivariate dispersions based on canopy cover (PERMDISP:9999 PERM). (*Indicates statistical significance, *: p<0.05, **: p<0.01, ***: p<0.001).*

		WINTER 2018				**SPRING 2019**			
	Df	Sum Sq	Mean Sq	F	Pr(>F)	Sum Sq	Mean Sq	F	Pr(>F)
Groups	7	0.24562	0.03509	3.1069	0.0084 **	0.09601	0.013715	1.1161	0.3708
Residuals	56	0.63246	0.01129	NA	NA	0.68814	0.012288	NA	NA

Median distances to group centroids pre-treatment, 8, and 12 months post-treatment are compared in Figure 10. It is evident that the Drought treatment caused a reduction in distance to group centroid especially 8 months post-treatment, but also after 12 months; post-treatment, the D group consistently has the lowest median.

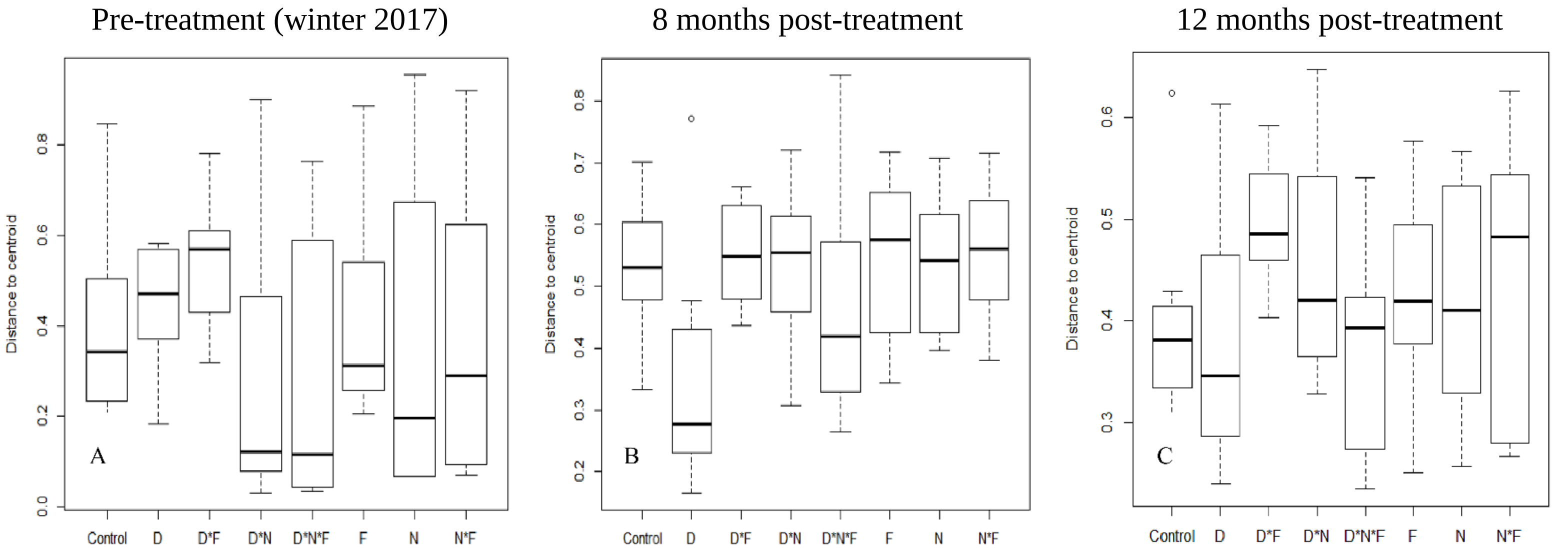

Figure 10. Mean distance to the group centroids pre-treatment (winter 2017, A), 8 months post-treatment (winter 2018, B), and 12 months post-treatment (spring 2019, C). Groups are identified with "D" for drought shelters, "N" for application of ammonium nitrate, and "F" for prescribed fires.

Post-hoc Tukey's HSD tests for differences in group dispersion also found no differences in pairwise group comparisons pre-treatment (winter 2017) or in the spring of 2019 (p adj.>0.05, Data Appendix 1). After 8 months of treatment, however, the post-hoc tests indicate that the Control-D, N-D, D*N-D, F-D, D*F-D, N*F-D, and Control-D*N*F pairs all had statistically different dispersions about their centroids (p adj.<0.05, Data Appendix 1.) The Drought group thus had a significantly lower dispersion than did any of the other treatment groups with the exception of the full combination of treatments. These differences can be observed in Figure 10.

Discussion

Even in a relatively short time frame, a potential for significant changes in herbaceous community composition and production was identified under a regime of increasingly altered precipitation patterns, N deposition, and prescribed fire. Perennial species dominance led to more pronounced responses to alterations than did annual dominance. While some of the broad hypotheses were supported by these findings, some surprising patterns were also evident.

Above-ground net primary productivity responses

As predicted in H1, ANPP was reduced by the Drought treatment after 8 months of implementation (Hoover et al. 2014, Koerner and Collins 2014). Mixed effects of Drought on ANPP were found in this semi-arid savanna, however, as no reduction in ANPP was identified 4 months later in the spring of 2019. It is likely that this was due to a lag in response to the large precipitation events occurring during the fall of 2018. Cherwin and Knapp (2012) identified a similar lack of drought-induced ANPP sensitivity in a semi-arid grassland and suggest that reductions in *precipitation amount* may be over-ridden by *the size of precipitation events* occurring naturally. These more concentrated, larger precipitation events lead to higher amounts of ANPP and may be the most important variable to explain inter-annual ANPP fluctuations (Heisler-White et al. 2008).

Also in keeping with H1, ANPP experienced a reduction from the Fire treatment for a short period of time (4 months after Fires) but then recovered by 8 months following the Fire, indicating no deleterious effect of fire on this system's productivity, although no significant increases in ANPP from fire were observed either (Taylor et al. 2012). It may be that a longer duration of fire implementation is required for enhanced ANPP in response to fire to become manifest (Buis et al. 2009).

Failing to support H1, no increase in overall ANPP was observed in response to the N treatment at any of the samplings. In light of the common findings of increased production in other studies, this result is surprising (Snyman 2002a, M̃batha and Ward 2010, Yahdjian et al. 2011, Borer et al. 2014b). Chapin et al. (1987) states that N is the mineral nutrient most often required by plants. However, plants which live in low-resource environments have adapted to grow slowly, conserve resources, and have low resource requirements (Chapin 1991); these characteristics may have limited the native, predominantly C4 species' response to N supplementation. This concept is corroborated by the findings of Ladwig et al. (2012) who also found no response of ANPP to N in four out of six years of a study in the arid Chihuahuan desert. Furthermore, there was an extended period of below-average precipitation during the study (January-July of 2018 based on 99 years of SRS precipitation records). The lack of production response may be due to constrained uptake by plants during that reduced precipitation and consequently, a lack of N limitation in this system, contrasting with what was found by Freeman and Humphrey (1956), Hamilton et al. (1998), Yahdjin and Sala (2011), and others. White et al. (2004), however, found that N was not co-limiting in ANPP with precipitation immediately following drought such as was the case during this study. Consequently, this system could have still been experiencing recovery from water limitation at the time of N supplementation and for the duration of its availability (Snyman 2002a). Additionally, the lack of ANPP response to N can be attributed to a trade-off between increased N uptake with decreased plant NUE (Lü et al. 2015). Furthermore, H3 was not supported by these results as no significance was identified for the interaction between N*Fire. These findings reinforce that the overall ANPP of this system is water-limited, rather than N-limited.

An analysis of ANPP by functional groups lent itself to understanding production responses in this system which may have broader implications compared to the species-specific compositional responses discussed later. In the winter of 2018, the live forb functional group ANPP was significantly increased by the application of N. This is in partial support of H2 which predicted that plants possessing the C3 photosynthetic pathway (such as forbs) would increase in dominance in response to N addition (Reich et al. 2001). These findings support that shifts from C4 to C3 groups (or production) can occur following N addition due to the inferior NUE and more rapid N uptake by C3 plants compared to C4 plants (Chapin et al. 1987, Seastedt et al. 1991, Wedin and

Tilman 1997, Zeng et al. 2010). These results of N effects on only the forb group provide support for the growth/defense trade-off; while grasses with basal-meristems are slow-growing and uptake less nutrients, forbs have high Specific Leaf Areas, apical meristems, and grow more rapidly but would be less defended from herbivores (Lind et al. 2013). Biogeochemical analysis in Chapter III demonstrate that supplemented N was exhausted by the spring 2019 as the enhanced forb ANPP faded; soil N failed to exhibit elevated N levels in the winter of 2018 and C3 grass tissue N content was only elevated in early spring 2019 when accompanied by the Fire treatment. The reduction of live grass ANPP in the fall of 2019 supports H1 and alludes to the water limitation on grass ANPP.

The increase in forb ANPP in plots receiving Drought treatment in the spring 2019 results from differences in growth form and precipitation seasonality. While forbs are stimulated by winter precipitation in a semi-arid environment, long-lived native grasses are more responsive to summer precipitation which was lacking during this experimental period (Clarke et al. 2005). Rather than being directly increased by the presence of the Drought shelters, the increased forb production was an incidental consequence of perennial grass mortality under the combined ambient and experimental drought. Briggs and Knapp (1995) observed this phenomenon in a mesic grassland as grass production was limited by water stress and forb density was able to increase due to competitive release. Annuals were similarly found to capitalize on the drought-induced openings in cover during the historic droughts of the late 1940’s near this research site in southwest Texas (Osborn 1950). On a larger scale of management, this increase in forb production would further alter the grazeability by cattle and potential for effective fires following droughts.

The timing of prescribed fires determines the responses of growth forms as has been discussed. If removed during a period of reproduction or active growth, forb mortality can occur (Brockway et al. 2002). The decline in forb production due to fire in the spring of 2019 can be interpreted as an indication of prescribed fire-induced winter forb mortality the previous year. Because burns occurred during the spring, many of these cool-season forbs were actively growing or producing seeds. Growing season fires can cause forb morality (Brockway et al. 2002) and their removal by fire limited the regrowth of that functional group the following year.

Vegetation diversity

The significantly increased magnitude of change in diversity between the winter of 2017 and winter of 2018 by the addition of N fails to support H2. These results resemble those of Ladwig et al. (2012) who also found an increase in Shannon's H' as a result of fertilization during one year of study in an arid grassland, but in contrast to the findings of decreased diversity by others (Clark and Tilman 2008, Yahdjian et al. 2011). The beneficial effects on diversity of the heavy rains which preceded the winter 2018 sampling were likely enhanced by the increased availability of nutrients in the N addition plots because diversity is positively associated with growing season precipitation (Prieto et al. 2009). Thus, the plots' diversity was likely constrained more by ambient environmental conditions than by competitive interactions which would have limited diversity in plots experiencing increased growth from N addition (Grime 1973, Valone 2003). Competition in these ecosystems is dependent upon environmental conditions and species assemblages (Auken 2000). Because the rate of change induced by fertilization is highly dependent on the level of application and environmental conditions (Wedin and Tilman 1997, Snyman 2002a, Xu et al. 2014, Zhou et al. 2018), expected results may have been obscured by the short length of study or N volatilization prior to uptake. A lack of observable response in diversity or magnitude of diversity change in the spring of 2019 is attributable to the high proportion of annual species canopy cover (61%) which apparently didn't express diversity responses to treatments. Moreover, plots of differing treatments in this study had limited time which could eventually enable observable differences in colonization by annual propagules from remote seedbanks. These results contrast the decline in even annual richness and diversity in response to N both in the short- and long-term (Borer et al. 2014b). It is likely that the unexpected diversity responses throughout this study were the result of uncharacteristic precipitation (below- and then above-average) regimes overriding other disturbance responses (McPherson 1994) in addition to the small-scale nature of this study. We expect that the enhanced diversity was due to increases in both evenness and richness as the N expanded the range of nutrient availability enabling more species to grow.

The implementation of the Drought treatment had a significant effect on the system's response to the level of N treatment at 8 months of treatments as seen through the significant Drought*N interaction. The N treatment only increased (the magnitude of change in) diversity when the Drought treatment was not applied. This asserts H4 whence interactions including drought were predicted to demonstrate constrained responses to the other factors; the magnitude of change in diversity was lower when both N and Drought were applied versus when N was applied and Drought was not. As predicted, water availability and drought alters the vegetation response to N availability (Scholes 2003, Huang et al. 2018). Because nutrient uptake requires water for solubility and use, changes to diversity via deposition impacts may be lessened by the concurrent effects of drought (Scholes and Archer 1997, Alam 1999, Van Der Waal et al. 2009). Conversely, this interaction may intuit the risks of N deposition combined with increased drought intervals in this system as both diversity N supplementation have been found to decrease drought resistance in vegetative communities (Van Ruijven and Berendse 2010, Xu et al. 2014). However, care should be taken with this interpretation as overall diversity was found to be lower at times of lower precipitation and these results are considered preliminary (Prieto et al. 2009).

Vegetative community composition

Variation between these study plots was naturally high. This heterogeneity shouldn't be disregarded as a statistical inconvenience, however, as the soil and vegetation heterogeneity (functional diversity) enhances ecosystem functioning and vegetation patterns in savannas (Guo et al. 2018). The drastic change in C3 perennial species, *Nassella leucotricha* (Texas wintergrass), mean proportional cover (and dominance) is the result of a dieback following the severe ambient drought which occurred during the summer of 2018 (see Figure 3). Because it is a cool-season grass, its fall green-up following summer dormancy was likely inhibited and delayed by the limited precipitation. The other graminoid species which were dominant at both winter samplings possessed the C4 photosynthetic pathway (*Hilaria belangeri and Bouteloua curtipendula)* and experienced less change in overall mean proportional cover composition. The greater losses of cover in the C3 grass can be attributed to less overall leaf reduction, superior leaf area recovery, and superior water and NUE by C4 grasses during and following drought (Ward et al. 1999, Taylor et al. 2011). This seasonal comparison allows us to understand the differential canopy cover maintenance between C3 and C4 grasses during drought.

Following the heavy rains in the fall of 2018, *Nassella leucotricha* exhibited some recovery in average proportional canopy cover at the spring 2019 sampling though not to the levels of winter 2017. Additionally, the spring 2019 sampling displayed a high proportion of annual plant canopy cover (61%- majority forbs) due to the high precipitation of the preceding fall. The prevalence of this seasonally-responsive functional group which utilizes an escape strategy (Volaire et al. 2009) serves to explain why treatment responses were so different from the previous sampling only four months prior. Following the winter rainfalls, annuals (especially forbs) still dominated prior to the onset of perennial active growth in the early spring of 2019. The annuals which were able to escape the drought of the first half of the year were then able to occupy the open space left by perennial thinning from the ambiently-occurring drought (Osborn 1950). At the same study site, Nicolai et al. (2008) also identified the dependence of annual forbs on precipitation.

The lack of compositional response to the independent prescribed fire treatments could be the result of two things. Firstly, the fires were low-intensity as they were conducted during the spring with low temperatures, low fuel, and high humidity; these factors decreased the effectivity of the fires. Low-intensity fires, however, are the norm in dry savannas where grass fuels are low (Skarpe 1992, Higgins et al. 2000, Kraaij and Ward 2006). Secondly, as previously discussed, the system is adapted to fires which historically occurred every 4-8 years and even high-intensity fires can fail to cause significant native graminoid alterations (Mayeux and Hamilton 1988, Taylor et al. 2012, Guyette et al. 2012). This single burn period did not establish a frequency or intensity sufficient to induce change.

The interaction of the full combination of treatments (Drought*N*Fire) induced a significant shift in the overall herbaceous community composition only 8 months after treatment application. As other independent factors and interactions failed to induce a shift in community composition, the system appears to be resistant to canopy cover change in the short-term until Drought, N, and Fire all occur together and interact. Drought limits systems’ ability to respond to N (Scholes 2003, Huang et al. 2018), N makes communities more susceptible to drought (Snyman 2002a, Xu et al. 2014, Vourlitis 2017), and fires tend to increase drought stress (Wink and Wright 1973, Snyman 2003). Those factor interactions significantly altered the positions of community composition after 8 months, indicating that the full combination of treatments surpassed the community’s ability to resist compositional change.

In the spring of 2019, no shifts in community composition were observed based on canopy cover, but Drought did significantly alter the community when based on the density of individuals. This demonstrates that the canopy cover was more stable to treatment effects than was the number of individuals during this season. The density of those individuals may be more sensitive to changing conditions and disturbance due to the regulation of seed production and consequent germination by preceding disturbance influencing the previous generation's capacity to re-seed (Briske and Noy-Meir 1998). Additionally, the high amounts of precipitation in the winter of 2018 could have expedited the recovery from the single, low-intensity fires to baseline conditions in annual species which have exhibited positive responses to fires in dry systems (Valone and Kelt 1999, Killgore et al. 2009). The timing of treatments is imperative in determining their effects on annuals; if seed production is not interrupted, the annuals will be much less responsive (Briske and Noy-Meir 1998). A final explanation for the minimal responses in the spring 2019 community composition is simply that the community had recovered from initial perturbations, exhibiting rapid adaptation to novel conditions, particularly to drought (Franks 2011).

Non-metric multi-dimensional scaling of the winter 2018 species composition visually demonstrated the community divergence of the Drought*N* Fire treatment combination group and also of the group receiving the Drought treatment alone but not of treatment groups in the spring of 2019. Overlaying the winter 2018 treatment group centroids with an ordination of the species scores reveals which species within community composition had resulted in observed dissimilarity of plots. This demonstrated some notable associations, particularly in the Drought group. The perennial species closely associated with the scaled location of the D*N*F group centroid are SpCr (*Sporobolus cryptandrus*), DiCo (*Digitaria cognata*), CrMo (*Croton monanthogynus*), TrMu (*Tridens muticus*), and NaLe (*Nassella leucotricha*). Characteristics correlating these species to one another and the full combination treatment group are difficult to identify at this point in the study, but may be the early stages of a shift towards sub-climax vegetation (Snyman 2002a). The perennial species closely associated with the D group centroid are ErPi (*Erioneuron pilosum*), ErSu (*Eragrostis superba*), SiAb (*Sida abutifolia*), ArPu (*Aristida purpurea*), and HiBe (*Hilaria belangeri*) ordinates just beyond the 95% C.I. centroid ellipse. *Hilaria belangeri* and *Erioneuron pilosum* are two of the most dominant C4 shortgrass species at the site; their close association with the Drought group alludes to the increased drought tolerance of short grasses at semi-arid sites and enhanced WUE of the C4 photosynthetic pathway (Taylor et al. 2011). *Hilaria belangeri*'s remarkable drought persistence may be further attributable to its stoloniferous growth strategy. Furthermore, the association of these C4 graminoid species with the Drought group corroborates the observational findings that dominant C4 gaminoids experienced less loss of cover dominance than did a C3 graminoid following an ambient drought. Small plants with low Specific Leaf Area (SLA) have been long-observed to demonstrate superior performance in drought conditions (Westoby et al. 2002, Nogueira et al. 2018). This phenomenon reinforces findings by an early, local study of ambient drought by Osborn (1950) which also found *Hilaria belangeri* to be notably resilient to drought.

The mean dispersions in multivariate space being non-equivalent among the treatment groups in the winter of 2018 indicates that the treatment groups had varying levels of community heterogeneity. The Control group was different in dispersion from the D*N*F group, presumably because the Control group received no treatments and the D*N*F group received all treatments which induced a change in the plant community and a decrease in post-treatment heterogeneity. More notably, the Drought group dispersion which was significantly lower than each of the other groups except the D*N*F group demonstrates that Drought alone treatment caused a decline in the heterogeneity so characteristic of this semi-arid savanna, producing a lowest mean distance to centroid (type of multivariate average). As droughts have been found to cause the loss of rare and annual species, this homogenization could be the result of similar species losses in all plots receiving the Drought treatment alone (Prieto et al. 2009). This Drought-induced homogenization may have deleterious impacts on functional diversity and ultimately, the heterogeneous mosaic of processes within savannas (Guo et al. 2018). These results further allude to the fact that Drought has a more rapid effect on the plant community than the other treatments, providing further support for H4. While the other treatment groups exhibit similarly high dissimilarity from their centroids, the Drought group has experienced a change in which plots receiving the Drought treatment alone became more similar to one another in their overall plant communities and thus achieved lower within-group beta diversity. This response was obscured by dominance by annuals in early spring which exhibited a lack of treatment grouping in the NMDS and similar group dispersions in the 12-month sampling.

Notes on interpretation

The interpretation of these results should be approached with acknowledgement of the scope of this study. Firstly, the site experienced particularly erratic precipitation patterns the first year of the study. Low levels of precipitation were received for much of the experimental period until late summer and fall of 2018 when precipitation fell in high volumes. Because the typical, bi-modal Spring/Fall pattern was interrupted during this study, plants may have exhibited exaggerated responses to a combination of treatments and climate.

Secondly, the small scale of this study should be taken into consideration. Fuhlendorf and Smeins (1996) found that variation *between units* at this site is highest at a smaller scale while variation *within units* is higher at a larger scale. Additionally, they suggest that trends can be more difficult to disentangle from small-scale assessments. Therefore, the application and interpretation of these results should be founded on the processes observed rather than assuming direct translation to larger scales.

Conclusions

Savannas together with grasslands account for between 30 and 35% of terrestrial primary productivity worldwide (Field et al. 1998). Therefore, understanding how climatic and disturbance interactions may impact their herbaceous communities can have implications for the global carbon budget (Archibald and Scholes 2007, Zhao and Running 2010) and management alike (Young and Solbrig 1992). With functional group dominance being largely determined by resource and disturbance conditions (Van Der Waal et al. 2009), predicted alterations to resource conditions through droughts and N deposition shed uncertainty on herbaceous community responses in semi-arid savannas. While this study did not assess the effects of fire on brush, many studies have found that these grass fires can deter woody seedling establishment (Higgins et al. 2000, Peterson and Reich 2001, Bond 2008). In this study, low-intensity spring prescribed fire did reduce the production of forbs the following year. The diversity of the system appears to be more resource-limited and seasonal than it is competition-limited as it was higher overall in response to increased precipitation and as a result of N supplementation. This study demonstrated that semi-arid savannas are resistant to overall community change up to a point, but that when the full combination of factors interact in the short-term, the system may experience a significant change from the natural composition in a short amount of time. Additionally, drought alone may induce a shift in the community towards the dominant warm-season short-grasses and an overall homogenization of the community composition. When dominated by annuals, however, the site was much less responsive to perturbations. Practitioners may observe an increase in forb production under increased N deposition and following a drought, a reduction in grass production during droughts, and an overall shift in community composition under the occurrence of all three factors. Future studies should be conducted in order to understand these mechanisms at a larger scale and longer timeframe in order to identify trends within the community.

CHAPTER III

BIOGEOCHEMICAL RESPONSES

Introduction

The heterogeneous nature of vegetative cover within dryland ecosystems and savannas creates a mosaic of biogeochemical cycling (Srikanthasamy et al. 2018). Nutrient and moisture concentrations are greater beneath the canopy of woody plants due to shading and litterfall (Belsky and Canham 1994, Schlesinger et al. 1996, Tessema and Belay 2017). Conversely, water infiltration can be greater beneath continuous grass cover, but only under tallgrasses in deep soils (Walker et al. 1981). Soil physical characteristics and morphology can play a larger role than litter and vegetation in the infiltration of semi-arid rangelands (Blackburn 1975). Water availability, soil nutrients, and fire regime are key determinants influencing savanna vegetation composition and cover ratios (Scholes and Walker 1993, Sankaran et al. 2004). Unfortunately, savannas worldwide are threatened by degradation via woody encroachment, overgrazing, and anthropogenically altered fire return intervals (Fuhlendorf et al. 1996, Fuhlendorf and Smeins 1997, Fensham et al. 2005, Kraaij and Ward 2006). The consequential deterioration of savannas' diverse, heterogeneous structure triggers an alteration of ecosystem services such as pollinator and wildlife conservation, hydrological functionality and aquifer recharge, and nutrient cycling and soil erosion prevention (Olenick et al. 2005, Ansley and Castellano 2006).

Both the resource conditions and disturbance regimes of semi-arid savannas are being altered by human activity. Fire suppression, which is considered a leading cause of brush encroachment, is already common (Van Auken 2009). Drought intervals are predicted to lengthen in the southwestern U.S., perhaps doubling in savanna regions (Burke et al. 2006, IPCC 2013). Additionally, nitrogen (N) deposition is fertilizing native rangelands in the forms of NH_x and NO_y which are estimated to be deposited over the U.S. at rates of 2.3 Tg N and 4.2 Tg N respectively every year (Galloway 2004, Zhang et al. 2012, Fowler et al. 2013). These alterations to disturbance and resource regimes will inevitably impact not only the plant communities, but also the biogeochemical processing within semi-arid savannas. Although water availability is the primary limiting factor of dry ecosystems (Yahdjian and Sala 2010, Sala et al. 2012), past studies have found that the biogeochemical properties within the soil and vegetation also respond to above-ground disturbance and nutrient conditions which consequently impacts plant growth and savanna structure (Solbrig et al. 1996, White et al. 2004, Sardans et al. 2008b, Zeng et al. 2010).

Intense fires have been observed to reduce soil nitrogen (SN) via volatilization (Vitousek 1982, Solbrig et al. 1996, Blair 1997, Dukes et al. 2005). However, low-intensity fires which stimulate mineralization are the norm in the herbaceous layer of dry savannas where fuel loads are low (Skarpe 1992, Kraaij and Ward 2006). Fires also serve as an important component of decomposition to release nutrients into useable forms within those arid and semi-arid regions (Frost 1986, Davies et al. 2013). The nutrients and pH of deposited ash are largely dependent on the quality and quantity of fuel, although low-intensity fires tend to temporarily mobilize nutrients and increase pH (Raison 1979, Solbrig et al. 1996, Materechera et al. 1998). Grasses which re-sprout following fire often exhibit temporary, stimulated growth which declines as the nutrients mobilized in the ash are exhausted (Blair 1997). Drought stress has been enhanced by fires which decrease water use efficiency (WUE) and soil moisture (Wink and Wright 1973, Snyman 2002b).

Although drought is difficult to define, consensus has emerged around the loose definition of “a deficit of water relative to normal conditions”(Sheffield and Wood 2012). The IPCC 2013 and other climate models forecast prolonged droughts followed by intense precipitation events in the southwestern United States (Trenberth et al. 2003, Knapp et al. 2008, Dai 2013). Because above-ground net primary productivity (ANPP) and functional group persistence are tied to annual precipitation (Knapp and Smith 2001), an altered precipitation regime will inevitably impact savanna species composition, biomass production, and consequently, soil properties. Furthermore, precipitation events that occur less frequently but in greater volume are likely to reduce the amount of water lost to evaporation and reduce the soil water deficit in those regions (Schwinning and Sala 2004, Knapp et al. 2008).

Nutrient use efficiency (NUE), root absorption potential, protein synthesis, and other plant processes decline with water limitation (Alam 1999, Snyman 2000, 2002b). Nutrient uptake and transport in plants, including that of inorganic N, is usually in soluble forms transported via water into the roots and pulled through the plant via transpiration (Chapin et al. 1987, Scholes 2003). Consequently, without adequate soil water, nutrient transport becomes limited. In times of scarcity, N from the leaves is translocated to stems or below-ground parts for preservation (Heckathorn and DeLucia

1994). This response combined with reduced nutrient uptake leads to aboveground tissue with high C/N ratio during droughts, and thus, low quality forage and litter which requires longer to decompose (Moretto et al. 2001, Sardans and Peñuelas 2012, He and Dijkstra 2014). Microbial abundance and activity within the soil are reduced by drought, resulting in further decreased litter decomposition and constrained nutrient turnover (Alster et al. 2013).

Due to the high rates of N emissions from anthropogenic sources, wet and dry N deposition rates are expected to alter natural systems (Vitousek 1994, Galloway 2004, Zhang et al. 2012). In most cases, the addition of N increases ANPP but decreases diversity (Dukes et al. 2005, Mbatha and Ward 2010, Yahdjian et al. 2011, Borer et al. 2014b, Fay et al. 2015). Shoot growth is readily stimulated by N (Dukes et al. 2005). Nitrogen fertilization alters soil chemistry via acidification and increasing N and C pools (Zeng et al. 2010, Khalili et al. 2016). Addition of N, particularly in drylands, tends to reduce soil moisture and make systems more sensitive to drought (Snyman 2002b, Van Der Waal et al. 2009). The predicted combination of increases in drought length and N deposition could therefore have interactive effects to decrease the stability of arid and semi-arid savannas.

Nitrogen and water are considered the two most limiting resources in semi-arid regimes (Vitousek and Howarth 1991, Mbatha and Ward 2010, Fay et al. 2015). The biogeochemical cycling of N within semi-arid savannas is dictated by water availability and disturbance regimes (February et al. 2013). Bennett and Adams (2001) found that precipitation regulates the *timing* of herbaceous production, but N regulates the *amount* of ANPP at a semi-arid site. Scholes (1990) further suggests that moisture controls *the duration of plant growth* and nutrients regulate *the rate of plant growth*. The concentration of N in leaves is one of the most important traits which determines the photosynthetic capture and accumulation of carbon for growth and storage (Vitousek and Howarth 1991, Sardans et al. 2008b). Furthermore, foliar N is responsive to environmental conditions and resource availability (Frost 1986).

Within the soil, extractable soil organic carbon (SOC) and SN tend to accumulate under drought conditions (White 1986, Knapp et al. 2008, Schaeffer et al. 2017). This phenomenon can be explained by increased detritus availability from vegetation mortality, ongoing extracellular enzyme activity, and a decline in microbial uptake during drought conditions (Sala et al. 2012, Schaeffer et al. 2017). Nutrient accumulation during drought may cause significant resource pulses in the intense rainfall events predicted to follow prolonged droughts of the future (Moretto et al. 2001, Knapp et al. 2008). Denitrification and leaching may also occur more intensely in precipitation events following droughty periods in which N uptake is lower than N mineralization (Bernhard-Reversat 1982).

As disturbance regimes and resource conditions are anthropogenically altered in savannas, their biogeochemistry is expected to be both directly and indirectly affected. While the effects of fires, drought, and simulated N deposition have been assessed both independently and interactively in mesic environments (Knapp 1985, Collins 1987, Tilman 1987, Fay et al. 2002), their effects are less understood in arid and semi-arid regions where the climate tends to be more erratic. Because arid grasslands have demonstrated more drought sensitivity than other grassland systems, it is crucial to fill this knowledge gap (Knapp et al. 2015a). Additionally, changing climatic conditions pose the risk of state shifts in savannas (Breshears et al. 2016). Undesirable changes in functional diversity can reduce system stability and resilience (Tilman et al. 1997). Savanna biogeochemistry is both a determinant and a product of the heterogeneous community structure; as such, it is foundational to the integrity of savannas.

The purpose of this study was to investigate 1) how the biogeochemistry of the herbaceous layer within a semi-arid savanna will respond to prescribed fire, drought, and simulated N deposition in terms of soil and vegetation chemical properties and 2) how these factors will interact to alter those responses. Prescribed ring fires were conducted, shelters constructed, and ammonium nitrate applied in order to assess the effects of these factors both independently and interactively. Predictions were that H1) low-intensity spring fires would temporarily increase SOC, SN, and pH within the soil due to stimulated decomposition and the deposition of ash; H2) drought treatments were expected to accumulate SOC and SN within the soil while reducing the N concentration in vegetative tissues; H3) the addition of N was expected to increase SN and vegetation N but reduce soil pH; H4) drought was predicted to be the overriding factor when combined with other treatments to reduce general ANPP and increase the potential for SOC and SN accumulation.

Methods

Study site

This study was conducted at the Texas A&M Agrilife Sonora Research Station (SRS) located 56 km south of Sonora, Texas (30°16'N, 100°33'W). Located on the western edge of the Edwards Plateau, the site is a semi-arid savanna system. According to Guyette et al. (2012), the western Edward's Plateau historically lies within a 4-8-year fire return interval. Mean annual precipitation on the site is 567.88 mm occurring in a bimodal, spring/fall pattern. However, annual precipitation at the site is highly variable (Figure 11). The average growing season at the station is 240 days with the mean January temperature of 8 °C and the mean July temperature of 26 °C (SRS records and Fuhlendorf et al. 2001).

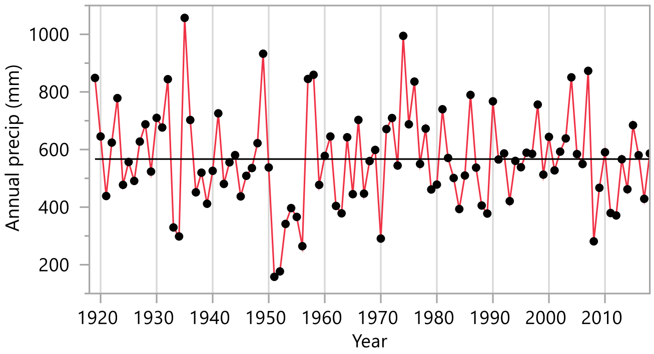

Figure 11. Annual precipitation totals 1919-2018 (mm) at the Sonora Agrilife Station

The primary topography is 1-3% slopes with Valera clay soils and the petrocalcic layer lying 51-102 cm below the surface (Garbiel and Loomis 2017). The southernmost plots of the study area lie on Eckrant-Rock outcrop complex soils. Soils are generally shallow, rocky, and heterogeneous in depth. Characteristic vegetation includes Texas wintergrass (*Nassella leucotricha*), common curlymesquite (*Hilaria belangari*), Wright's threeawn (*Aristida wrightii*), King Ranch bluestem (*Bothriochloa ischaemum*), Texas cupgrass (*Eriochloa sericea*), sideoats grama (*Bouteloua curtipendula*), prairie verbena (*Glandularia bipinnatifida*), juniper species (*Juniperus spp.),* and oak species (*Quercus spp.*).

The SRS has been a National Trends Network monitoring station (TX16) for the National Atmospheric Deposition Program (NADP: http://nadp.slh.wisc.edu/NTN/) since 1984. This data indicates that the site currently receives 0.2 g/m^2 of total N deposition. NASA's ORNL Distributed Active Archive Center (https://daac.ornl.gov/) predictive map indicates that the area could receive up to 1.7 g/m^2 as soon as the year 2050.

Study design

On March 2, 2018, sixty-four close-proximity 5 x 5 m plots were set up separated by 2 m alleyways in a primarily herbaceous area that was enclosed within a livestock and wildlife-exclusion fence. The plots lie on a moderately alkaline clay loam soil. The eight treatment combinations were randomly assigned to the plots based on a 2 x 2 x 2 full factorial design with eight replicates of each treatment combination. Treatments were Drought (rainout shelter or ambient), N deposition (N) (N addition or control), and Fire (prescribed ring fires or control).

Rainout shelters covered 3 x 3 meters diverting 69% of precipitation with clear polycarbonate roofing strips alternating with open spaces affixed to PVC frames at ca. 1.4 m high. The shelters simulate the 1st percentile extreme drought for the site (175.65 mm/year) according to the Drought-Net protocol (www.drought-net.colstate.edu). Site-specific precipitation records from 1919-2013 were utilized. The size of the shelter was designed to preserve a core sampling area of 2 x 2 m with approximately a 50 cm buffer to exceed the 20 cm edge effect identified by Yahdjian and Sala (2002). Designated drought plots were also trenched to 25-38 cm, depending on the depth of the underlying limestone layer. Sheet plastic (6 mil.) was inserted into the trenches in such a way that 7-12 cm of plastic protruded above the ground level. Runoff from the roofing strips falls outside of the plastic barriers of the trenches as seen in Figure 12.

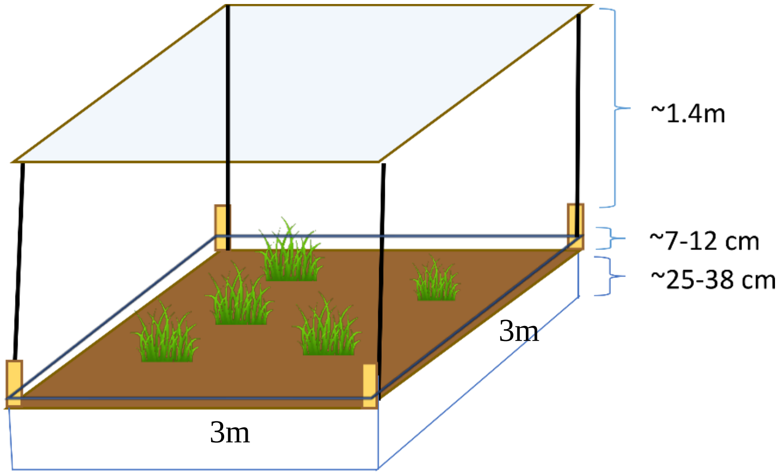

Figure 12. Schematic of rainout shelter design

Ammonium nitrate (NH_4NO_3: 34% N) was applied evenly in assigned plots using a Scotts Wizz hand-held spreader in mid-April 2018 preceding rains. The application rate was 5 g N/m2 in a dry granular (prill) form.

Ring fires were conducted on March 1 and 2, 2018. Due to the low fuel loads, a propane vapor torch, or “prickly pear torch” was used. Wind speed averaged 4.4 mph on the March 1 and 2.6 on March 2. Relative humidity averaged 34.7% on March 1 and 62.1% on March 2. Air temperature averaged 19.67 ºC on March 1 and 16.17 ºC on March 2.

Sampling

Soils collection

Three soil cores (10-15 cm deep by 2 cm diameter) were taken and combined in each plot in the fall of 2017 and fall of 2018. Samples were sieved through a #20 sieve to ensure the removal of roots as in Lugo et al. 1990, Naeth et al. 1991, and Hua et al. 2018. Soils were then dried in an oven for 48hrs at 60°C. A ball mill was used to grind the samples to a fine, powder-like consistency.

Soil pH

The pH analysis was performed for each soil sample using a Fischer Scientific pH meter in a 1:2 soil: 0.01M $CaCl_2$ solution. Calcium chloride was chosen as it is less sensitive to electrolyte and seasonal fluctuations, thus providing more consistent results (Minasny et al. 2011).

Soil conditions

A metal probe was inserted four times along the border of each plot to get an average soil depth (*sensu* Fuhlendorf and Smeins 1998). The depth of soil penetrated by the probe was measured in cm. A soil thermometer was inserted to a depth of 12-18 cm in each plot to determine soil temperature in November 2018. Soil moisture was quantified in each plot at a depth of 12-18 cm using an EXTECH MO750 Soil Moisture Meter in November 2018 at post-treatment soil sampling. Three soil moisture readings were taken in each plot to obtain an average per plot.

Vegetation blade collection

Green blades were collected from Texas wintergrass (*Nassella leucotricha*) in each plot in February 2018 and 2019. *Nassella leucotricha*, a C3 grass, was chosen as the dominant species pre-treatment and based on the expectation that its low NUE would make it responsive to treatments. Blades were taken from a minimum of two separate plants, depending on prevalence and availability of those individuals. Pre-treatment data was only analyzed from 63 plots as *Nassella leucotricha* was unavailable in plot #7. Leaf blades were washed in deionized water and then dried at 60° C for 48 hours. A ball mill was then used to grind the vegetation for analysis.

Elemental analysis

Elemental analysis for both vegetation and soils was conducted using a Costech Elemental Combustion System coupled to a Thermo Conflo IV and a Thermo Scientific Delta V Advantage Stable Isotope Mass Spectrometer in continuous flow (He) mode. %N and %C were derived based on NIST plant standard Apple1515.

Statistical Analysis

Biogeochemical values between treatments were assessed parametrically. To meet the assumptions of parametric tests, $\log_{10}$ transformations were applied as needed to achieve normality and homogeneity of variance. While normality was evaluated visually as suggested by Zuur et al. (2010), homogeneity of variance was tested using the Levene's test (Van Der Waal et al. 2009). Three-way, factorial ANOVAs were performed to test the fixed, interactive effects of Drought, N, and Fire on soil pH, SOC, SN, soil depth, and vegetation N with function *Fit Model* in JMP Pro 13.0 (SAS Institute Inc., Cary NC USA). When data was non-normal or failed to meet homogeneity of variance, a Wilcoxon Rank Sum non-parametric pairwise analysis was conducted using *Fit Y by X* in JMP Pro 13.0 (SAS Institute Inc., Cary NC USA).

The change in pH between the two samplings was assessed with a three-way, factorial ANOVA on differences in the magnitude of change. This approach lent itself to identifying treatment impacts on pH despite site heterogeneity.

The percentages of SOC, SN, and vegetation N were assessed using a three-way factorial ANOVA. Both pre-treatment and post-treatment results are shown in order to isolate treatment-induced effects. Soil temperature and moisture conditions were assessed non-parametrically using a Pairwise Wilcoxon test for differences between treatment groups using function *Fit Y by X* in JMP Pro 13.0 (SAS Institute Inc., Cary NC USA).

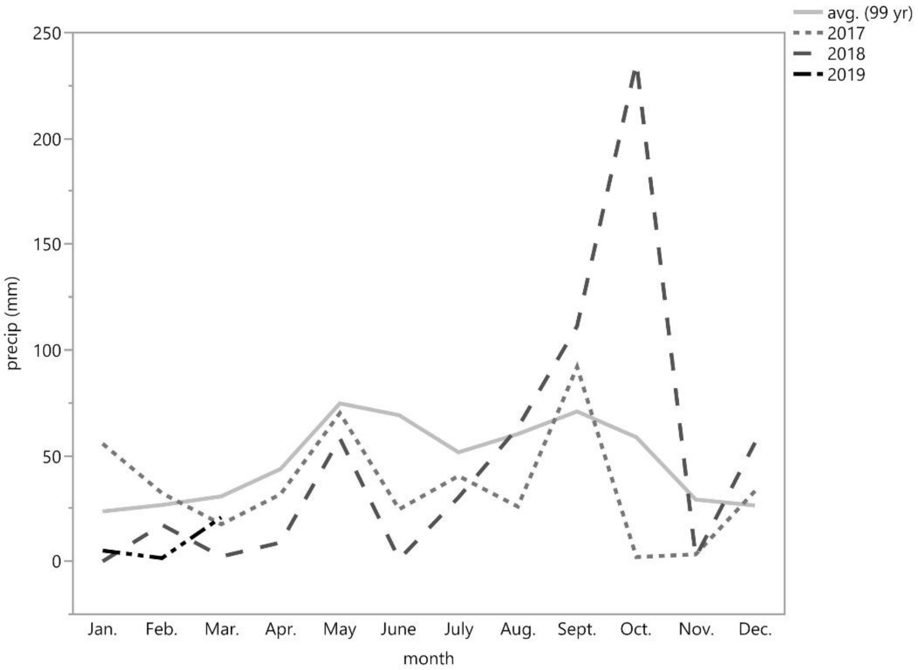

Figure 13. Cumulative monthly precipitation (in mm) for the years preceding and during the study period with the 99-year average

Results

The research site experienced markedly erratic precipitation during the year of the study as shown in Figure 13. As shown, the first six months experienced low precipitation amounts, but was high for the last part of the year. Precipitation accumulated in 2017 was 428.75 mm and in 2018 it was 586.49 mm.

Soils

pH

Soil pH was not significantly affected by the treatments during the duration of the study period. Although the Drought*Fire interaction was significant in the full-factorial analysis of variance on the change in pH between pre- and post-treatment sampling, this significant interaction echoed an existing significant pre-treatment interaction (Winter 2017 full-factorial ANOVA, Data Appendix 2). This indicates that treatment differences occurred due to site heterogeneity rather than treatment effects (results shown in Data Appendix 2). Pre-treatment, the minimum pH was 7.5 and the maximum pH was 7.75 with a median value of 7.63. Eight months after implementation, the minimum pH was 7.45, the maximum pH was 7.58 and the median was 7.51.

Soil organic C responses

Analysis of variance indicates that the soil organic carbon content was unchanged by treatments during the period of the study (Table 7). Overall pre-treatment (winter 2017) %SOC back-transformed mean was 3.28% and 8 months post-treatment, the soil %TOC mean was 3.41%.

The ANOVA and graph of treatment means (Figure 14) detected heterogeneity as pre- and post-treatment statistical significance was identified. Because the statistical significance existed in pre-treatment data, this is the result of soil heterogeneity at the site rather than true treatment effects. No treatment effects on organic carbon concentration were identified.

*Table 7. Pre-treatment (Winter 2017) and 8 months post-treatment (Winter 2018) analysis of variance in soil %OC (*Indicates statistical significance, *:P<0.05, **:P<0.01, ***:P<0.001)*

	LOG$_{10}$[WINTER 2017]				**WINTER 2018**			
Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Drought	1	0.00225871	0.4461	0.5069	1	0.24626406	0.7765	0.3820
Drought*Fire	1	0.00325974	0.6438	0.4257	1	0.04785156	0.1509	0.6992
Drought*Nitrogen	1	0.00006251	0.0123	0.9119	1	0.01182656	0.0373	0.8476
Drought*Nitrogen*Fire	1	0.00024034	0.0475	0.8283	1	0.00878906	0.0277	0.8684
Fire	1	0.00419126	0.8277	0.3668	1	0.82128906	2.5897	0.1132
Nitrogen	1	0.03792762	7.4905	0.0083**	1	1.46712656	4.6261	0.0358*
Nitrogen*Fire	1	0.00030545	0.0603	0.8069	1	0.47437656	1.4958	0.2264

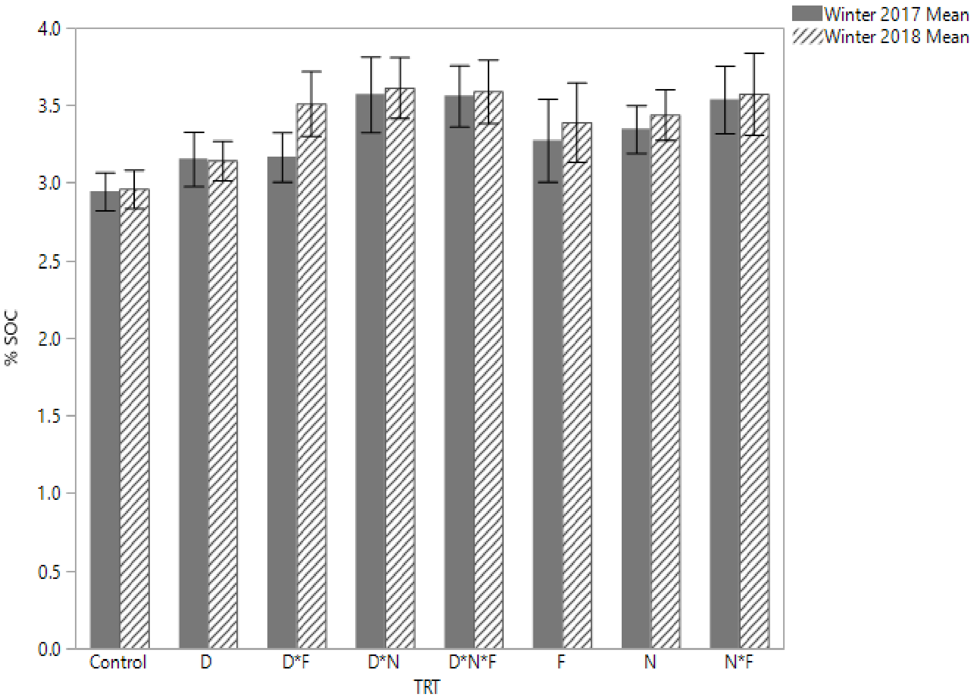

Figure 14. Pre-treatment (Winter 2017) and 8 months post-treatment (Winter 2018) soil % OC by treatment group where "D" identifies drought, "N" ammonium nitrate addition, and "F" that prescribed fires were conducted

Soil N responses

No effects of the treatments or their interactions were identified on the SN within the study period (Table 8). The overall mean %N pre-treatment (winter 2017) was

0.32% (SE= 0.0065) and post-treatment (winter 2018) the mean %N was 0.33% (SE= 0.0058). As with the soil %SOC, the plots randomly assigned to the N treatment contained pre-treatment, elevated levels of soil N regardless of treatment effects.

This heterogeneity is reflected in both pre- and post-treatment “Nitrogen” statistical significance. Examination of the ANOVA results and graph of treatment group means (Figure 15) demonstrates that no significant *changes* in soil N levels occurred as the result of treatment application.

*Table 8. Pre-treatment (Winter 2017) and 8 months post-treatment (Winter 2018) analysis of variance in soil %TN (*Indicates statistical significance, *:P<0.05, **:P<0.01, ***:P<0.001)*

	WINTER 2017				**WINTER 2018**			
Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Drought	1	0.00082656	0.3572	0.5525	1	0.00040000	0.1975	0.6585
Drought*Fire	1	0.00581406	2.5125	0.1186	1	0.00140625	0.6943	0.4082
Drought*Nitrogen	1	0.00045156	0.1951	0.6604	1	0.00000625	0.0031	0.9559
Drought*Nitrogen*Fire	1	0.00026406	0.1141	0.7368	1	0.00022500	0.1111	0.7402
Fire	1	0.00543906	2.3504	0.1309	1	0.00275625	1.3608	0.2483
Nitrogen	1	0.02600156	11.2363	0.0014 **	1	0.01625625	8.0260	0.0064 **
Nitrogen*Fire	1	0.00056406	0.2438	0.6234	1	0.00202500	0.9998	0.3217

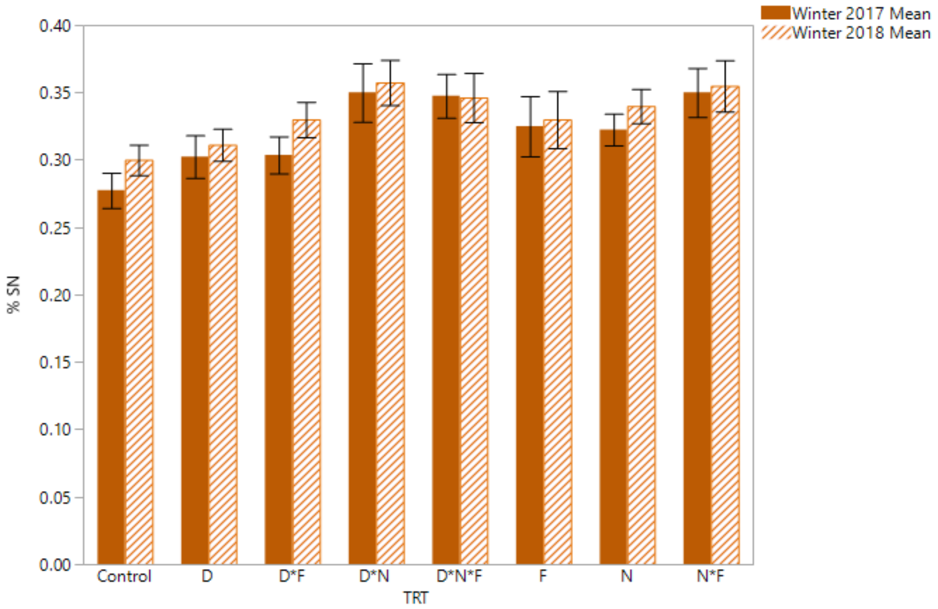

Figure 15. Pre-treatment (Winter 2017) and 8 months post-treatment (Winter 2018) soil %N by treatment group where "D" identifies drought, "N" ammonium nitrate addition, and "F" that prescribed fires were conducted

Soil conditions

During the winter 2018 sampling, soil temperature and moisture data was non-normal, so differences between groups were assessed based on ranks using the Wilcoxon Rank Sum test and non-parametric pairwise comparisons. Soil temperature was significantly higher in the Drought*N than Control ($p<0.01$), Drought than Control ($p<0.05$), Drought*N compared to N ($p<0.05$), and the Drought*N compared to N*Fire ($p<0.01$) treatment groups in November 2018 (Wilcoxon Rank Sum Test, Data Appendix 2). Additionally, the Drought*N percent moisture was significantly higher than the Drought group ($p<0.05$) and likewise the Drought*N significantly higher than the N*Fire ($p<0.05$) group (Data Appendix 2).

At the final vegetative community sampling (spring 2019), soil temperature was significantly increased by the Drought treatment ($p<0.05$, Data Appendix 2). Soil moisture was non-normal and was compared between groups using the Wilcoxon Rank Sum test which indicated that the N group had a significantly higher percent moisture than the control group ($p<0.05$, Data Appendix 2).

Soil depth was found to be heterogeneous in that differences between treatments were detected in a significant Drought*Fire interaction ($p<0.05$, Data Appendix 2). No other differences (independent or interactive treatment effects) were exemplified. As the Drought*Fire interaction was not significant in other analysis, this difference in soil depth doesn't appear to have had an impact on other observations.

Nassella leucotricha %N

Pre-treatment, the mean %N was 2.35% (SE=0.04) and post-treatment it was 2.88% (SE=0.04). Prior to treatment application, no differences were detected in *Nassella leucotricha* %N as shown in Table 9. Post-treatment (approximately 11 months of treatment implementation), the N*Fire interaction was significantly ($p<0.01$) altering the N content in the grass blades.

*Table 9. Pre-treatment (February 2018) and post-treatment (February 2019) analysis of variance in vegetation %N (*Indicates statistical significance, *:P<0.05, **:P<0.01, ***:P<0.001)*

		February 2018			February 2019		
Source	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**	**Sum of Squares**	**F Ratio**	**Prob > F**
Drought	1	0.00131657	0.0165	0.8983	0.22562500	2.3613	0.1300
Nitrogen	1	0.01116570	0.1400	0.7098	0.02560000	0.2679	0.6068
Drought*Nitrogen	1	0.00083236	0.0104	0.9190	0.00855625	0.0895	0.7659
Fire	1	0.00079201	0.0099	0.9210	0.19802500	2.0725	0.1555
Drought*Fire	1	0.08789552	1.1017	0.2985	0.29430625	3.0801	0.0847
Nitrogen*Fire	1	0.17671131	2.2149	0.1424	0.81450625	8.5243	0.0050 **
Drought*Nitrogen*Fire	1	0.00006920	0.0009	0.9766	0.03422500	0.3582	0.5519

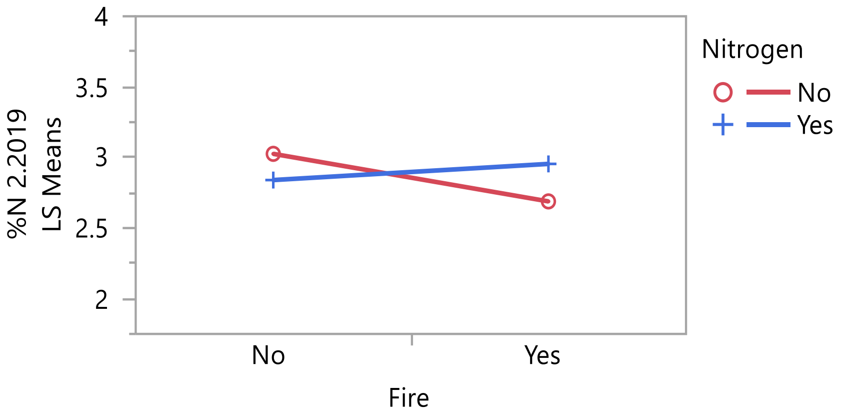

*Figure 16. Least Squares Means plot showing the Nitrogen*Fire interactive effects on grass blade %N*

As seen in Figure 16, the N content in the blades was higher following a fire with the addition of N (LS Means: 2.95 compared to 2.69 respectively, Data Appendix 2) relative to the application of N alone (LS Means: 2.84 compared to 3.03, respectively, Data Appendix 2). Furthermore, a Wilcoxon test indicates that N content in blades was significantly higher on average in the post-treatment compared to the pre-treatment sampling (p<0.001) and these results are reflected in Figure 17.

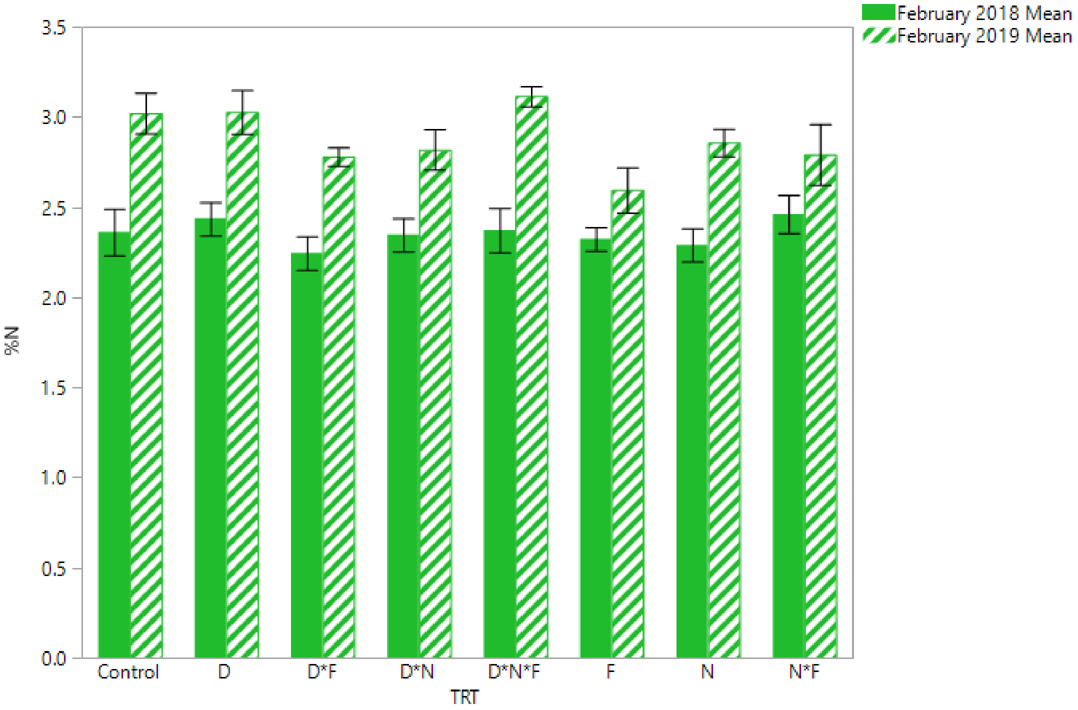

Figure 17. Pre-treatment (February 2018) and post-treatment (February 2019)) vegetation blade %N by treatment group where "D" identifies drought, "N" ammonium nitrate addition, and "F" that prescribed fires were conducted

Discussion

Rainout shelters, N supplementation, and prescribed fires were used to assess how semi-arid savanna biogeochemistry may respond to future resource and disturbance regimes. These results indicate that the soil biogeochemistry of these systems is considerably resistant to change in the short term. The concentration of N in the blades of the dominant C3 grass, *Nassella leucotricha*, experienced a significant interaction between prescribed fire and N addition. The short duration, small scale, and atypical ambient precipitation of this study should be taken into account when interpreting these results and drawing implications for different systems.

Soil heterogeneity

In statistical tests of all soil chemistry parameters, pre-existing heterogeneity was detected. Further analysis and interpretations were conducted in such a way to account for this heterogeneity. The ambient significant differences in SOC, SN, and pH were not surprising as resource islands are common in semi-arid and savanna ecosystems and occur as a result of the patchy vegetation structure (Bernhard-Reversat 1982, Schlesinger et al. 1996, Huang et al. 2015, Tessema and Belay 2017). The distribution, quantity, and quality of below-ground organic matter is dependent on the chemistry of above-ground vegetation (Klemmedson 1989). Soil depth was also confirmed to be heterogeneous among treatment combinations. Especially at a small scale, variation is high in this semi-arid savanna (Fuhlendorf and Smeins 1996). This soil heterogeneity is also key to the structural heterogeneity so valuable in savannas.

The Drought treatment expressed higher soil temperature than other treatment combinations; the fact that differences were identified in the winter may suggest that this increased temperature is presumably due to the progressive loss of ground cover and vegetation height rather than shelter effects which have been found to be minimal (English et al. 2005). Reducing the quantity of precipitation had minimal effects on soil moisture as was found by Fay et al.(2000). Differences in moisture between treatments may have been obscured in November 2018 as the soils were inundated and the moisture meter maxed out with 43/64 of the plots having soil moisture of 50% or greater (235.97mm precipitation the previous month).

The effects of prescribed fire on soil chemistry

In arid and semi-arid ecosystems, fires play an integral role in the nutrient turnover process through decomposition, stimulated mineralization, and can temporarily boost available nutrients such as SOC (Solbrig et al. 1996, Van de Vijver et al. 1999, Stavi et al. 2017). Carbon reserves are important energy stores for plants to be able to capture N for growth (Vitousek 1982, Chapin et al. 1987). Prescribed fires in this study did not increase SOC, SN, and soil pH, failing to support H1. Each of those parameters remained unchanged by the application of low-intensity fire or its interaction with any other treatments likely attributable to its low intensity and single occurrence. Although high-intensity fires can volatilize N, low-intensity fires have been found to temporarily stimulate N mineralization, boosting plant-available N and plant growth (White 1986, Overby and Perry 1996, Stavi et al. 2017). Similar to these findings, however, Savadogo et al. (2008) found no differences in savanna soil pH between burned and unburned treatments even after a 12-year study of fires that would be expected to deposit base-rich ash and increase the pH. Consequently, rather than being an insufficient amount of time for fire impacts to become expressed, Raison (1979) concludes that changes in soil chemistry caused by fire are short-lived and may disappear completely within one year. Accordingly, any effects which these low-intensity fires may have had on the biogeochemistry were likely exhausted and had returned to ambient levels at the time of sampling eight months after treatments. Thus, infrequent, low intensity prescribed fires are unlikely to alter the soil chemistry of the herbaceous patches of semi-arid savannas.

The effects of drought on soil chemistry

SOC and SN concentrations within samples were unaffected by the presence of the Drought treatment, failing to support H2. Although results have been conflicting (Khalili et al. 2016), extractable SOC and N tend to accumulate during droughts due to continued activity of extracellular enzymes combined with the reduced uptake by soil microbes and plants (White et al. 2004, Schaeffer et al. 2017). Variable results were also found by Sardans et al. (2008a) who detected increases in SOC pools but no changes in SN due to drought after five years of treatment implementation in a shrubland. In this case, it is likely that the experimental period was of insufficient length for the Droughts to induce changes in the TOC and SN pools along with pH as changes in soil chemistry are the result of nutrient turnover which would be further constrained by the lack of precipitation (Sanaullah et al. 2011, Alster et al. 2013). Because decomposition rate is positively correlated with annual precipitation, arid and semi-arid regions experience slower decomposition than areas with higher MAP thus limiting the movement of SOC and SN through soils and plants (Yahdjian et al. 2006, Austin and Vivanco 2006, Davies et al. 2013). Additionally, the low initial biomass at the site resulted in less carbon available for break-down.

Accumulation of soil nutrients during drought would have significant implications for the pattern of future rainfall patterns; nutrients which accumulate during the prolonged drought periods can create enhanced flushes of productivity in the intense precipitation episodes predicted to follow those droughts (Khalili et al. 2016). The lack of nutrient accumulation during simulated Drought suggests that this system may pose less risk of drastic nutrient pulses upon rewetting following short-duration Drought as in this study (Knapp et al. 2008, Borken and Matzner 2009).

The effects of N deposition on soil chemistry

The addition of N did not increase SN or acidify soil pH as predicted in H3. This demonstrates the buffering effects of the highly basic soil as well as the short-lived nature of surface-applied N in this ecosystem. In both cultivated and native systems, SN is the nutrient most limiting to plant growth (Chapin et al. 1987), the most important factor to grass nutritional quality (Mbatha and Ward 2010), and one of the most limiting resources in arid ecosystems (Yahdjian et al. 2011, Sala et al. 2012). Alterations to its availability could produce pronounced changes in community composition and structure (Vitousek and Howarth 1991, Sardans et al. 2008b, Yahdjian and Sala 2010). Not surprisingly, others have found N supplementation to boost SN concentration (Huang et al. 2015, Khalili et al. 2016). However, in a semi-arid study, Zeng et al. (2010), applied high rates of N deposition for a lengthened study period (5 years) and neither SOC nor SN expressed response. Even after 30 years of N and P fertilization in a hay-production veld by Donaldson et al (1984) and 2 ½ years of N fertilization by Huang et al. (2015), minimal impact has been observed on SC. These studies and ours converge around their dryland study systems; their lack of fertilization impact on SN and SC implies that more arid soils may be less able to accumulate nutrients from deposition, at least not in the short-term. Because N mineralization and mobilization depend on water and movement into the soil can be limited by the number of days which the soil is wet, N deposited may be lost in these arid and semi-arid ecosystems (Bernhard-Reversat 1982).

Acidification of soil pH could have dramatic impacts on the processing of other nutrients. The soil pH plays an important role in biogeochemical processes as it determines the availability of elements for soil solution buffering and microbial diversity (Matson et al. 2002, Zhang et al. 2018). Additionally, soil C and N concentrations are regulated by pH (Jiao et al. 2016). While pH has been commonly reduced by N additions, this process requires extended periods of time (Donaldson et al. 1984, Vitousek et al. 1997, Matson et al. 2002, Zeng et al. 2010, Vourlitis 2017). The eight-month experimental period of this study is shorter than the study periods exhibiting soil acidification; four years in the case of Vourlitis (2017) and five years in Zeng et al. (2010). Furthermore, as is characteristic of dry ecosystems, the soils of this study site were basic. These basic, limestone-rich soils buffered N additions, preventing soil acidification.

Patterns observed in pH

Arid regions typically have a higher, or more basic pH than areas with higher levels of precipitation where the soil pH is more acidic (Jiao et al. 2016). In this study, an overall decrease in soil pH post-treatment (compared to pre-treatment) was observed. This change can be attributed to the high levels of precipitation which preceded post-treatment sampling and could have leached nutrients and basic cations causing the observed decline in pH across all treatments (Rengel 2011, McCauley et al. 2017). Especially because the community was recovering from drought, the soil was vulnerable to the heavy precipitation and at-risk of leaching (Bernhard-Reversat 1982).

Responses observed in Nassella leucotricha %N

The concentration of N in leaves is an indicator of photosynthetic capacity, grass quality, and ultimately, decomposition rates (Chapin et al. 1987, Sardans et al. 2008b, Ramoelo et al. 2013). Nitrogen application and fire significantly interacted meaning that the addition of N affected how the blade N concentration responded to prescribed fires. In this C3 grass, the addition of N only enhanced leaf N concentration when the blades were new growth after removal by fire. This indicates that mature growth of this C3 grass does not respond to N deposition with increased blade N concentration. Both prescribed fires and the addition of N have been found to increase vegetative N concentration (Van de Vijver et al. 1999, Reich et al. 2001, Saneoka et al. 2004, Rau et al. 2008, Zeng et al. 2010); when applied together, young grass blades had more N available with which to rebuild. Independently, N deposition failed to increase the concentration of foliar N contrasting the findings of others (He and Dijkstra 2014, Kou et al. 2018) and previous expectations (H3). It is possible that the ammonium nitrate which was applied to treatment plots experienced volatilization before precipitation mobilized it into the soils and enabled plant uptake (application: 4/18/2018 and 8.13mm precipitation: 4/25/2018). It could also be that this resource-limitation adapted species which grows slowly and conserves energy for survival (Chapin 1991) is unable to rapidly respond to novel soil nutrient conditions unless constructing new growth as in the case of the N*Fire interaction. While at a small scale and of short duration, these findings indicate that N deposition and prescribed fire may interact to yield vegetation with higher concentrations of N compared to the independent effects of either factor.

This could create areas of more nutritious forage for grazing animals and more rapid nutrient turnover.

Surprisingly, foliar N did not decline in response to Drought as predicted in H2. This could be due to an overall increased growth response to the high precipitation levels at the post-treatment sampling. Otherwise, it could be a physiological difference as studies which have found that decline in %N have largely considered C4 grasses (Heckathorn and DeLucia 1994) or shrubs (Sardans et al. 2008b) while here a C3 grass was assessed which was largely senescent at the time of N application.

The higher N overall in *Nassella leucotricha* blades in February 2019 compared to 2018 can be attributed to the large efflux of precipitation which the site received in the fall and winter of 2018 (299.21mm received in October-January prior to post-treatment sampling compared to 38.61mm of rainfall prior to the February 2018 sampling). Though sampled at the same time of year, the high 2018 precipitation compared to 2017 likely resulted in vegetation undergoing more active growth in post-treatment sampling. As the N concentration of leaves is indicative of photosynthetic capacity (Chapin et al. 1987), precipitation-induced new growth was reflected in this increased N concentration. In fact, new leaves tend to grow in response to rain in semi-arid regions and have higher concentrations of N (Tolsma et al. 1987) which then declines with maturity. N concentration in vegetation blades has even been found to increase in response to the experimental addition of water (Lü et al. 2015). These results corroborate the emergence of new C3 grass growth in response to rainfall; new plant tissue growth is high in N due to active growth. Available N is also abundant following precipitation (largely due to microbial activity) but then declines over time. Additionally, these results serve to exemplify the inter-annual variation which occurs in plant chemistry (Tolsma et al. 1987, Lü et al. 2015).

Conclusions

Because savannas hold 15-20% of global SOC (Dintwe and Okin 2018), it is crucial that an understanding is gained as to how savanna biogeochemical processes and concentrations may respond to future conditions. Furthermore, changes in semi-arid soil chemistry distribution can impact the plant community dramatically, serving as an index of desertification (Schlesinger et al. 1996). These findings demonstrate that the soil chemistry in this semi-arid savanna is highly heterogeneous and recalcitrant to changes caused by prescribed fire, drought, N deposition, and their interactions in the short-term. The ambient low precipitation likely constrains the rate of biogeochemical processes and consequently, reduces the soil chemistry's sensitivity to altered conditions. The significant interaction between low-intensity prescribed fire and N deposition on the N concentration of C3 grass blades illustrates that their predicted future interactions may have the potential to perturb grazing selection and decomposition rates in this dominant C3 grass. Additionally, these results show the relationship between precipitation patterns and C3 foliar N concentration as related to growth stage. More research is needed on the long-term effects of prescribed fire, drought, and N deposition on biogeochemical parameters in semi-arid savannas as these factor interactions are expected to become a long-term condition in the future.

CHAPTER IV

CONCLUSIONS

Because savannas are both economically and ecologically significant, it is imperative that their response to future alterations be investigated. Savannas worldwide serve a crucial role in wildlife habitat, grazing lands, nutrient processing, and even for habitation by humans. Beyond their local services, savannas hold global significance in terms of their primary productivity and carbon stores, particularly in the soil (Field et al. 1998, Dintwe and Okin 2018). Additionally, functional group composition within savannas is largely determined by resource and disturbance conditions (Kraaij and Ward 2006, Van Der Waal et al. 2009).

Prescribed fires are a common management practice used to maintain savanna integrity. They are crucial for enhancing nutrient cycling and preventing savannas from degradation (Thonicke et al. 2001, Ansley and Castellano 2006). Solbrig et al. (1996) suggests that the conditions which exist during the burn recovery period determine the community composition responses to the fire. Altered climate conditions of intensified precipitation regimes and/or N deposition may introduce the risk of a compositional shift (Breshears et al. 2016). Perturbations to savanna structure, production, or sequestration will have local, regional, and global implications. Both the global carbon budget (Archibald and Scholes 2007, Zhao and Running 2010) and management efficacy (Young and Solbrig 1992) may be effected by anthropogenic changes in the herbaceous layer of semi-arid savannas. This semi-arid savanna's herbaceous layer responded most to simulated N deposition, drought, and fires in terms of ANPP, multivariate dispersions, and diversity with the exception of the full combination of treatments inducing a significant shift in community composition. Results indicate that properties of the vegetative community are more sensitive to alteration than are the biogeochemical components of the herbaceous layer of this semi-arid savanna.

The soils and consequently, vegetation, of this semi-arid savanna were found to be highly heterogeneous. The patchy nature of dryland vegetation creates a mosaic of biogeochemical cycling which is the cornerstone to ecological processes and structure within savannas (Srikanthasamy et al. 2018, Guo et al. 2018).

During dominance by perennial species, extreme drought appears to reduce the vegetative heterogeneity. This reduction in heterogeneity may have negative implications on the community's recovery following drought (Van Ruijven and Berendse 2010) and on more general ecosystem functioning (Guo et al. 2018). Additionally, the ecosystem was highly seasonal and responsive to precipitation levels in components of both biogeochemistry and vegetative community.

Overall ANPP, a key element of the global C budget, was reduced by Drought treatment but not when trumped by the occurrence of ambient, large precipitation events. In savannas, droughts have also been found to cause woody mortality which would have further implications on sequestration and the C budget of these systems (Fensham et al. 2009). Forb ANPP, on the other hand, was increased by N deposition and following droughts, thereby reducing grazeability and economic profitability for landowners.

Community composition was most impacted by the Drought treatment alone and the full combination of N deposition, Drought, and Fire when perennials were dominant.

Therefore, the interaction of these effects surpasses the community's ability to resist change and because Drought independently has the strongest effect on the community in the short-term.

Diversity responses exhibited more resource and season-limitation than competition-limited (Ladwig et al. 2012). This contrasts the reduction in diversity observed in studies with the application of N (Zeng et al. 2010, Yahdjian et al. 2011) perhaps due to differences in space limitation and competition. Lessened responses to fertilization within dry ecosystems such as this one could be the result of low yield potentials of the plants or limited soil water for uptake (Tainton 1999, Snyman 2002a).

In terms of biogeochemistry, the slow nutrient cycling of this dry ecosystem limited the responses observed during this short time-frame (Davies et al. 2013). The distribution, quantity, and quality of below-ground organic matter is dependent on the chemistry of above-ground vegetation which must respond to perturbations before transferring those nutrient changes to the soil (Klemmedson 1989). Like the findings of Mbatha and Ward (2010), the addition of N interacted with fire to increase the quality of grass blades. The blade N concentration of *Nassella leucotricha*, is more responsive to simulated N deposition when it is new growth following removal by fire. This interaction may be additive to increase grazing selection and the rate of nutrient cycling on recently burned areas undergoing increased N deposition compared to unburned areas. Changes in semi-arid soil chemistry distribution can impact the plant community dramatically and serve as an index of desertification (Schlesinger et al. 1996). These findings, however, revealed soil biogeochemical recalcitrance under short-term changes to disturbance and resource conditions in the herbaceous layer of this semi-arid savanna.

This study has expanded the understanding of how semi-arid savannas may respond to future changes in both vegetative community and biogeochemical parameters. Although this study occurred at a small scale and for a short duration, these findings serve as a useful foundation for continued savanna research. Future studies should further disentangle the interactions between anthropogenically-induced climate change and management actions at a larger scale and over prolonged periods of time.

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APPENDIX 1

CHAPTER II DATA SUPPLEMENT

ANPP

Spring 2018 (Pre-treatment)

Spring 2018 (Pre-treatment)ANOVA log10[overall ANPP] Parameter estimates

Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**
Intercept	1.0756994	0.03473	30.97	<.0001*
Drought[No]	0.0121135	0.03473	0.35	0.7286
Nitrogen[No]	0.0187287	0.03473	0.54	0.5918
Drought[No]*Nitrogen[No]	0.0248202	0.03473	0.71	0.4778
Fire[No]	-0.01566	0.03473	-0.45	0.6538
Drought[No]*Fire[No]	0.0354821	0.03473	1.02	0.3113
Nitrogen[No]*Fire[No]	-0.022703	0.03473	-0.65	0.5160
Drought[No]*Nitrogen[No]*Fire[No]	-0.061515	0.03473	-1.77	0.0820

Spring 2018 (Pre-treatment)ANOVA log10[overall ANPP] Effects test

SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	0.00939116	0.1217	0.7286
Nitrogen	1	1	0.02244888	0.2908	0.5918
Drought*Nitrogen	1	1	0.03942679	0.5107	0.4778
Fire	1	1	0.01569470	0.2033	0.6538
Drought*Fire	1	1	0.08057479	1.0438	0.3113
Nitrogen*Fire	1	1	0.03298601	0.4273	0.5160
Drought*Nitrogen*Fire	1	1	0.24218311	3.1372	0.0820

Summer 2018 (4 months post-treatment)

ANOVA log10[overall ANPP] Parameter estimates

TERM	ESTIMATE	STD ERROR	T RATIO	PROB>|T|
Intercept	0.7203446	0.046974	15.33	<.0001*
Drought[No]	0.0575294	0.046974	1.22	0.2258
Nitrogen[No]	-0.002259	0.046974	-0.05	0.9618
Drought[No]*Nitrogen[No]	0.0036548	0.046974	0.08	0.9383
Fire[No]	0.1218814	0.046974	2.59	0.0121*
Drought[No]*Fire[No]	-0.011252	0.046974	-0.24	0.8116
Nitrogen[No]*Fire[No]	-0.066865	0.046974	-1.42	0.1602
Drought[No]*Nitrogen[No]*Fire[No]	-0.053376	0.046974	-1.14	0.2607

ANOVA log10[overall ANPP]Effect test

SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	0.21181636	1.4999	0.2258
Nitrogen	1	1	0.00032662	0.0023	0.9618
Drought*Nitrogen	1	1	0.00085490	0.0061	0.9383
Fire	1	1	0.95072418	6.7322	0.0121*
Drought*Fire	1	1	0.00810274	0.0574	0.8116
Nitrogen*Fire	1	1	0.28614342	2.0262	0.1602
Drought*Nitrogen*Fire	1	1	0.18233300	1.2911	0.2607

Wilcoxon test / Kruskal-Wallis Tests (Rank Sums)

Mean ANPP ranks between sampling dates

(All four dates (2.9.2018, 7/24/2018, 11/3/2018, 3/1/2019))

ChiSquare: 91.0726, **DF:** 3, **Prob>ChiSq:** <.0001*

LEVEL	COUNT	SCORE SUM	EXPECTED SCORE	SCORE MEAN	(MEAN-MEAN0)/STD0
02/09/2018	64	8021.50	8224.00	125.336	-0.394
03/01/2019	64	12298.0	8224.00	192.156	7.941
07/24/2018	64	4310.50	8224.00	67.352	-7.628
11/03/2018	64	8266.00	8224.00	129.156	0.081

Nonparametric Comparisons For Each Pair Using Wilcoxon Method

LEVEL	- LEVEL	SCORE MEAN DIFFERENCE	STD ERR DIF	Z	P-VALUE	HODGES-LEHMANN	LOWER CL	UPPER CL
03/01/2019	02/09/2018	38.2813	6.557401	5.83787	<.0001*	11.1800	7.8800	15.3900
11/03/2018	07/24/2018	32.6250	6.557054	4.97556	<.0001*	6.5000	3.9000	9.7000
11/03/2018	02/09/2018	2.2031	6.557392	0.33598	0.7369	0.4900	-2.4200	3.6400
11/03/2018	03/01/2019	-33.5313	6.557204	-5.11365	<.0001*	-10.7500	-14.9000	-6.9000
07/24/2018	02/09/2018	-34.1719	6.557288	-5.21128	<.0001*	-6.1400	-8.7400	-3.9800
07/24/2018	03/01/2019	-55.4531	6.557176	-8.45686	<.0001*	-17.5000	-21.2000	-14.1000

Winter 2018 (8 months post-treatment)

ANOVA log10[Live grass ANPP] Parameter Estimates

TERM	ESTIMATE	STD ERROR	T RATIO	PROB>|T|
Intercept	0.5486435	0.075055	7.31	<.0001*
Drought[No]	0.1554446	0.075055	2.07	0.0430*
Nitrogen[No]	0.0776456	0.075055	1.03	0.3053
Drought[No]*Nitrogen[No]	-0.061938	0.075055	-0.83	0.4127
Fire[No]	-0.08922	0.075055	-1.19	0.2396
Drought[No]*Fire[No]	-0.050508	0.075055	-0.67	0.5038
Nitrogen[No]*Fire[No]	-0.048855	0.075055	-0.65	0.5178
Drought[No]*Nitrogen[No]*Fire[No]	-0.058308	0.075055	-0.78	0.4405

ANOVA log10[Live grass ANPP] Effect Tests

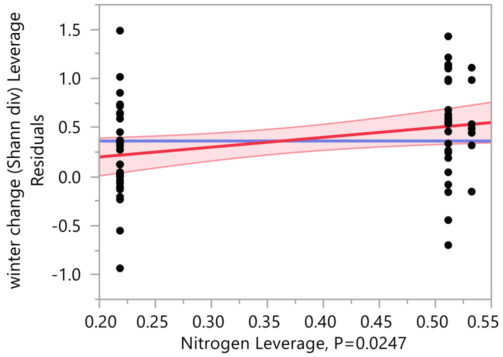
SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	1.5464335	4.2893	0.0430*
Nitrogen	1	1	0.3858461	1.0702	0.3053
Drought*Nitrogen	1	1	0.2455260	0.6810	0.4127
Fire	1	1	0.5094487	1.4131	0.2396
Drought*Fire	1	1	0.1632652	0.4528	0.5038
Nitrogen*Fire	1	1	0.1527575	0.4237	0.5178
Drought*Nitrogen*Fire	1	1	0.2175867	0.6035	0.4405

Diversity

Least Squares Means for Winter Change in H’

Nitrogen

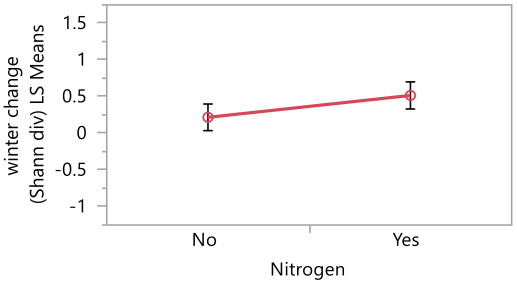
Leverage Plot



Nitrogen Least Squares Means Table

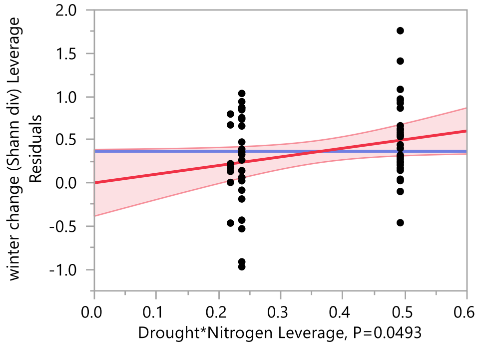
LEVEL	LEAST SQ MEAN	STD ERROR	MEAN
No	0.21775418	0.09054556	0.217754
Yes	0.51611685	0.09214827	0.516927

LS Means Plot



Drought*Nitrogen

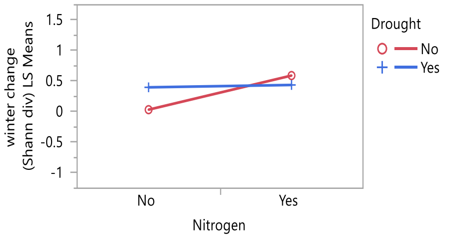
Leverage Plot



Drought*Nitrogen Least Squares Means Table

LEVEL	LEAST SQ MEAN	STD ERROR
No,No	0.03492163	0.12805077
No,Yes	0.59305534	0.12805077
Yes,No	0.40058673	0.12805077
Yes,Yes	0.43917837	0.13254514

LS Means Plot



Wilcoxon non-parametric test to determine if mean Shannon’s H’ rank differs by sampling date

ChiSquare: 105.7861 DF: 2 Prob>ChiSq: <.0001*

LEVEL	COUNT	SCORE SUM	EXPECTED SCORE	SCORE MEAN	(MEAN-MEAN0)/STD0
11/10/2017	63	3282.00	6048.00	52.095	-7.699
11/03/2018	64	5395.00	6144.00	84.297	-2.076
03/01/2019	64	9659.00	6144.00	150.922	9.746

Nonparametric Comparisons For Each Pair Using Wilcoxon Method

LEVEL	- LEVEL	SCORE MEAN DIFFERENCE	STD ERR DIF	Z	P-VALUE	HODGES-LEHMANN	LOWER CL	UPPER CL
03/01/2019	11/10/2017	59.51550	6.531324	9.112319	<.0001*	0.9346436	0.7665446	1.109368
03/01/2019	11/03/2018	50.76563	6.557429	7.741696	<.0001*	0.5750092	0.4613216	0.684662
11/03/2018	11/10/2017	27.57651	6.531295	4.222212	<.0001*	0.3805239	0.1999497	0.543982

Spring 2019 Shannon’s H’ ANOVA

Parameter Estimates

TERM	ESTIMATE	STD ERROR	T RATIO	PROB>|T|
Intercept	1.6766618	0.027123	61.82	<.0001*
Drought[No]	0.0004461	0.027123	0.02	0.9869
Nitrogen[No]	0.0085664	0.027123	0.32	0.7533
Drought[No]*Nitrogen[No]	0.0029844	0.027123	0.11	0.9128
Fire[No]	-0.016887	0.027123	-0.62	0.5361
Drought[No]*Fire[No]	-0.020202	0.027123	-0.74	0.4595
Nitrogen[No]*Fire[No]	-0.021025	0.027123	-0.78	0.4415
Drought[No]*Nitrogen[No]*Fire[No]	-0.005635	0.027123	-0.21	0.8362

Effect Tests

SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	0.00001274	0.0003	0.9869
Nitrogen	1	1	0.00469650	0.0998	0.7533
Drought*Nitrogen	1	1	0.00057002	0.0121	0.9128
Fire	1	1	0.01825093	0.3876	0.5361
Drought*Fire	1	1	0.02612102	0.5548	0.4595
Nitrogen*Fire	1	1	0.02829141	0.6009	0.4415
Drought*Nitrogen*Fire	1	1	0.00203189	0.0432	0.8362

PERMANOVA

Winter 2018 with bare ground included

Permutation test for adonis under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 9999
Call: adonis2(formula = comm.BC2long ~ Drought * Nitrogen * Fire, data = longcommunity2, permutations = 9999, method = "bray")

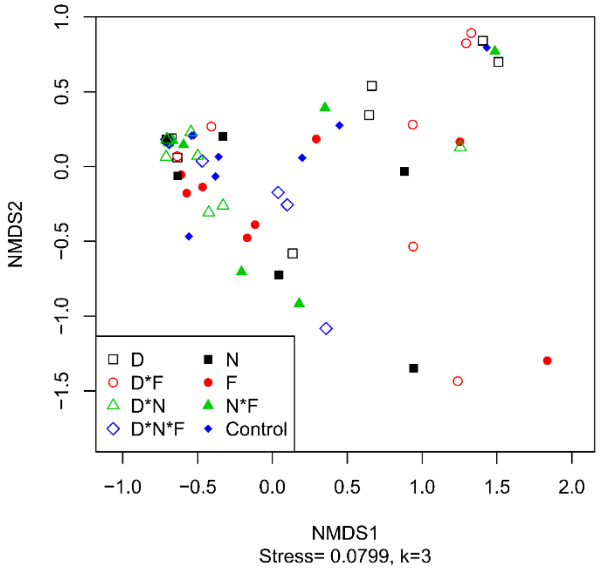
11.3.2018 W/BARE	DF	SUMOFSQS	R2	F	PR(>F)
Drought	1	1.2294030	0.081349194	5.4585481	0.0003
Nitrogen	1	0.1661608	0.010994803	0.7377536	0.6418
Fire	1	0.1138140	0.007531037	0.5053342	0.8592
Drought:Nitrogen	1	0.2944303	0.019482360	1.3072705	0.2175
Drought:Fire	1	0.1520173	0.010058933	0.6749565	0.7040
Nitrogen:Fire	1	0.1129243	0.007472161	0.5013836	0.8720
Drought:Nitrogen:Fire	1	0.4312985	0.028538879	1.9149648	0.0640
Residual	56	12.6126153	0.834572633	*NA*	*NA*
Total	63	15.1126635	1.000000000	*NA*	*NA*

Spring 2019 based on abundance/density

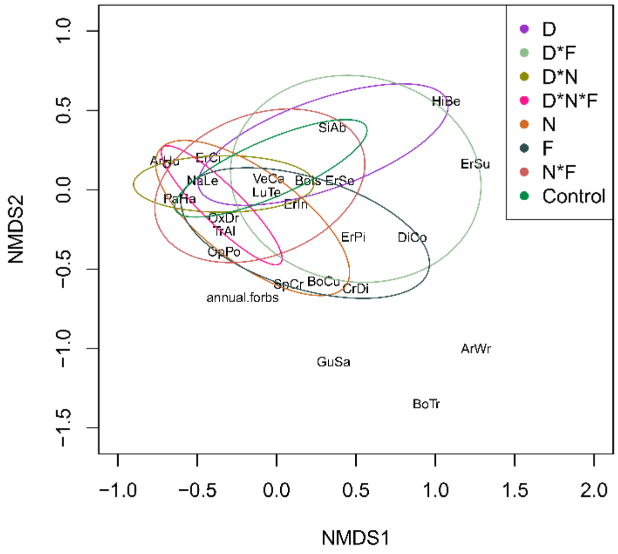
Permutation test for adonis under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 9999

3.1.2019	DF	SUMOFSQS	R2	F	PR(>F)
Drought	1	0.4599453	0.03702275	2.3761794	0.0227
Nitrogen	1	0.1388197	0.01117413	0.7171735	0.6630
Fire	1	0.2635297	0.02121251	1.3614529	0.2200
Drought:Nitrogen	1	0.1282854	0.01032618	0.6627509	0.7211
Drought:Fire	1	0.2271065	0.01828067	1.1732827	0.3158
Nitrogen:Fire	1	0.2208215	0.01777477	1.1408131	0.3324
Drought:Nitrogen:Fire	1	0.1451637	0.01168478	0.7499479	0.6354
Residual	56	10.8396428	0.87252421	*NA*	*NA*
Total	63	12.4233147	1.00000000	*NA*	*NA*

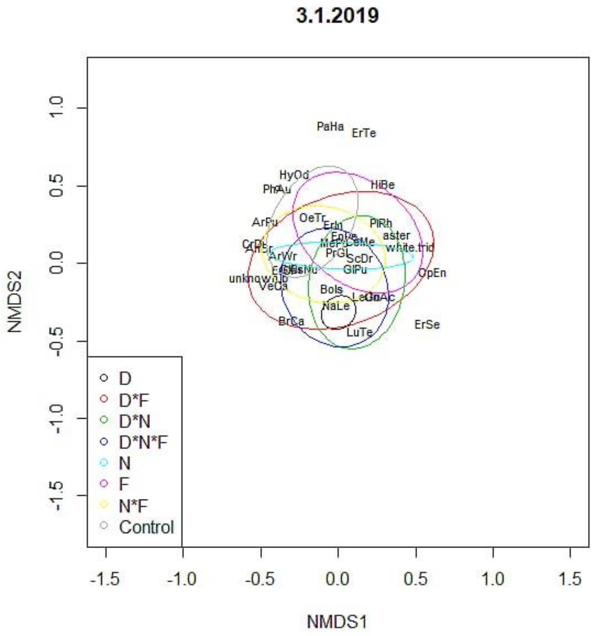
NMDS
Winter 2017 (Pre-treatment)



Winter 2017 (Pre-treatment) treatment group centroids



Spring 2019 based on density treatment group centroids



PERMDISP

Winter 2017 homogeneity of dispersions

Call: Permtestcentr1<-permutest(disp1centr,permutations=9999,pairwise = TRUE)

	DF	SUM SQ	MEAN SQ	F	N.PERM	PR(>F)
Groups	7	0.2853992	0.04077131	1.433575	9999	0.2053
Residuals	56	1.5926572	0.02844031	NA	NA	NA

Tukey multiple comparisons of means (11.10.2017, centroid)

```
95% family-wise confidence level
 factor levels have been ordered

 Fit: aov(formula = distances ~ group, data = df)

 $`group`
                      diff         lwr       upr     p adj
 D*N-D*N*F     0.0003537885 -0.26511341 0.2658210 1.0000000
 N-D*N*F       0.0784957169 -0.18697149 0.3439629 0.9816399
 Control-D*N*F 0.0892979430 -0.17616926 0.3547651 0.9625316
 N*F-D*N*F     0.0924037145 -0.17306349 0.3578709 0.9550805
 F-D*N*F       0.1085324834 -0.15693472 0.3739997 0.8998303
 D-D*N*F       0.1304698664 -0.13499734 0.3959371 0.7784810
 D*F-D*N*F     0.2219805385 -0.04348666 0.4874477 0.1661927
 N-D*N         0.0781419283 -0.18732527 0.3436091 0.9821068
 Control-D*N   0.0889441544 -0.17652305 0.3544114 0.9633207
 N*F-D*N       0.0920499259 -0.17341728 0.3575171 0.9559776
 F-D*N         0.1081786949 -0.15728851 0.3736459 0.9013563
 D-D*N         0.1301160779 -0.13535113 0.3955833 0.7808175
 D*F-D*N       0.2216267500 -0.04384045 0.4870940 0.1676461
 Control-N     0.0108022261 -0.25466498 0.2762694 1.0000000
 N*F-N         0.0139079976 -0.25155921 0.2793752 0.9999998
 F-N           0.0300367666 -0.23543044 0.2955040 0.9999607
 D-N           0.0519741496 -0.21349305 0.3174414 0.9985097
 D*F-N         0.1434848217 -0.12198238 0.4089520 0.6861368
 N*F-Control   0.0031057715 -0.26236143 0.2685730 1.0000000
 F-Control     0.0192345404 -0.24623266 0.2847017 0.9999982
 D-Control     0.0411719234 -0.22429528 0.3066391 0.9996736
 D*F-Control   0.1326825955 -0.13278461 0.3981498 0.7636315
 F-N*F         0.0161287690 -0.24933843 0.2815960 0.9999995
 D-N*F         0.0380661520 -0.22740105 0.3035334 0.9998062
 D*F-N*F       0.1295768241 -0.13589038 0.3950440 0.7843581
 D-F           0.0219373830 -0.24352982 0.2874046 0.9999954
 D*F-F         0.1134480551 -0.15201915 0.3789153 0.8771469
 D*F-D         0.0915106721 -0.17395653 0.3569779 0.9573209
```

Winter 2018 (11.3.2018) homogeneity of dispersions Tukey multiple comparisons of means (centroid)

95% family-wise confidence level
factor levels have been ordered
Fit: aov(formula = distances ~ group, data = df)

	diff	lwr	upr	p adj
D*N*F-D	0.114224009	-0.053064404	0.2815124	0.3972482
Control-D	0.172619366	0.005330953	0.3399078	0.0385166
N-D	0.174065315	0.006776902	0.3413537	0.0358356
D*N-D	0.175851732	0.008563318	0.3431401	0.0327539
F-D	0.187127379	0.019838966	0.3544158	0.0182165
D*F-D	0.190753016	0.023464602	0.3580414	0.0149849
N*F-D	0.196250386	0.028961972	0.3635388	0.0110804
Control-D*N*F	0.058395357	-0.108893057	0.2256838	0.9544055
N-D*N*F	0.059841306	-0.107447107	0.2271297	0.9482135
D*N-D*N*F	0.061627722	-0.105660691	0.2289161	0.9397967
F-D*N*F	0.072903370	-0.094385043	0.2401918	0.8658974
D*F-D*N*F	0.076529006	-0.090759407	0.2438174	0.8344976
N*F-D*N*F	0.082026376	-0.085262037	0.2493148	0.7804865
N-Control	0.001445949	-0.165842464	0.1687344	1.0000000
D*N-Control	0.003232366	-0.164056048	0.1705208	1.0000000
F-Control	0.014508013	-0.152780400	0.1817964	0.9999936
D*F-Control	0.018133649	-0.149154764	0.1854221	0.9999707
N*F-Control	0.023631020	-0.143657394	0.1909194	0.9998246
D*N-N	0.001786417	-0.165501997	0.1690748	1.0000000
F-N	0.013062064	-0.154226349	0.1803505	0.9999969
D*F-N	0.016687700	-0.150600713	0.1839761	0.9999834
N*F-N	0.022185071	-0.145103343	0.1894735	0.9998851
F-D*N	0.011275647	-0.156012766	0.1785641	0.9999989
D*F-D*N	0.014901284	-0.152387129	0.1821897	0.9999923
N*F-D*N	0.020398654	-0.146889759	0.1876871	0.9999348
D*F-F	0.003625636	-0.163662777	0.1709140	1.0000000
N*F-F	0.009123007	-0.158165407	0.1764114	0.9999997
N*F-D*F	0.005497370	-0.161791043	0.1727858	1.0000000

Spring 2019 (3.1.2019 cover) homogeneity of group dispersions Tukey multiple comparisons of means

```
    95% family-wise confidence level
    factor levels have been ordered

Fit: aov(formula = distances ~ group, data = df)
                      diff         lwr       upr     p adj
D-D*N*F        0.011982148 -0.16251504 0.1864793 0.9999987
Control-D*N*F  0.028199802 -0.14629738 0.2026970 0.9995717
N-D*N*F        0.051815298 -0.12268189 0.2263125 0.9811931
F-D*N*F        0.057119976 -0.11737721 0.2316172 0.9676530
N*F-D*N*F      0.069158080 -0.10533910 0.2436553 0.9135880
D*N-D*N*F      0.084603462 -0.08989372 0.2591006 0.7899995
D*F-D*N*F      0.127980007 -0.04651718 0.3024772 0.3071687
Control-D      0.016217654 -0.15827953 0.1907148 0.9999898
N-D            0.039833150 -0.13466403 0.2143303 0.9960778
F-D            0.045137828 -0.12935936 0.2196350 0.9915983
N*F-D          0.057175931 -0.11732125 0.2316731 0.9674805
D*N-D          0.072621314 -0.10187587 0.2471185 0.8911697
D*F-D          0.115997859 -0.05849932 0.2904950 0.4320289
N-Control      0.023615496 -0.15088169 0.1981127 0.9998684
F-Control      0.028920175 -0.14557701 0.2034174 0.9994944
N*F-Control    0.040958278 -0.13353891 0.2154555 0.9953417
D*N-Control    0.056403660 -0.11809352 0.2309008 0.9698036
D*F-Control    0.099780206 -0.07471698 0.2742774 0.6225338
F-N            0.005304678 -0.16919251 0.1798019 1.0000000
N*F-N          0.017342781 -0.15715440 0.1918400 0.9999838
D*N-N          0.032788163 -0.14170902 0.2072853 0.9988555
D*F-N          0.076164709 -0.09833247 0.2506619 0.8649580
N*F-F          0.012038103 -0.16245908 0.1865353 0.9999987
D*N-F          0.027483485 -0.14701370 0.2019807 0.9996385
D*F-F          0.070860031 -0.10363715 0.2453572 0.9029686
D*N-N*F        0.015445382 -0.15905180 0.1899426 0.9999927
D*F-N*F        0.058821928 -0.11567526 0.2333191 0.9621042
D*F-D*N        0.043376546 -0.13112064 0.2178737 0.9933883
```

Taxa

taxa	code	common_name	lifeform	lifespan	provenance
Eragrostis intermedia Hitchc.	ErIn	Plains lovegrass	grass	perennial	native
Nassella leucotricha (Trin. & Rupr.) Pohl	NaLe	Tx wintergrass	grass	perennial	native
Aristida purpurea Nutt. var. wrightii (Nash) Allred	ArWr	Wrights threeawn	grass	perennial	native
Digitaria cognata (Schult.) Pilg.	DiCo	Fall witch	grass	perennial	native
Sporobolus cryptandrus (Torr.) A. Gray	SpCr	Sand dropseed	grass	perennial	native
Hilaria belangeri (Steud.) Nash	HiBe	Curlymesquite	grass	perennial	native
Bouteloua curtipendula (Michx.) Torr.	BoCu	Sideoats grama	grass	perennial	native
Erioneuron pilosum (Buckley) Nash	ErPi	Hairy tridens	grass	perennial	native
Bouteloua trifida Thurb.	BoTr	Red grama	grass	perennial	native
Eragrostis superba Peyr.	ErSu	Wilman's lovegrass	grass	perennial	introduced
Panicum hallii Vasey	PaHa	Hall panicum	grass	perennial	native
Tridens albescens (Vasey) Woot. & Standl.	TrAl	White tridens	grass	perennial	native
Eriochloa sericea (Scheele) Munro ex Vasey	ErSe	TX cupgrass	grass	perennial	native
Bothriochloa ischaemum var. songarica (L.) Keng	BoIs	K.R. bluestem	grass	perennial	introduced
Bothriochloa laguroides (DC.) Herter ssp. torreyana (Steud.) Allred & Gould	BoLa	Silver bluestem	grass	perennial	native
Croton dioicus Cav.	CrDi	Grassland croton	forb	perennial	native
Oxalis drummondii A. Gray	OxDr	Drummond's oxalis	herb	perennial	native
Sida abutifolia Mill.	SiAb	Spreading sida	forb	perennial	introduced
Verbena canescens Kunth	VeCa	Gray vervain	forb	annual	native
Gutierrezia sarothrae (Pursh) Britton & Rusby	GuSa	Broom snakeweed	subshrub	perennial	native
Erodium cicutarium (L.) L'Hér. ex Aiton	ErCi	California filaree	forb	annual or biennial	introduced

Lupinus texensis Hook.	LuTe	Bluebonnet	forb	annual	native
Opuntia engelmannii Salm-Dyck ex Engelm. var. lindheimeri (Engelm.) Parfitt & Pinkava	OpEn	Prickly Pear	cactus	perennial	native
Argythamnia humilis (Engelm. & A. Gray) Müll. Arg. var. humilis	DiHu	Low wild mercury	forb	perennial	native
Panicum obtusum Kunth	PaOb	Vine Mesquite	grass	perennial	native
Erodium texanum A. Gray	ErTe	Texas filaree	forb	annual	native
Bouteloua dactyloides (Nutt.) J.T. Columbus	BoDa	Buffalograss	grass	perennial	native
Croton monanthogynus Michx.	CrMo	One-seed croton	forb	annual	native
Aristida purpurea Nutt.	ArPu	Purple threeawn	grass	perennial	native
Solanum elaeagnifolium Cav.	SoEl	Silverleaf nightshade	forb	perennial	native
Mentzelia oligosperma Nutt. ex Sims	MeOl	Stickleaf	shrub	perennial	native
Prosopis glandulosa Torr.	PrGl	Mesquite	woody	perennial	native
Tridens muticus (Torr.) Nash	TrMu	Slim tridens	grass	perennial	native
Glandularia bipinnatifida (Nutt.) Nutt.	GlBi	Prairie verbena	forb	perennial	native
Setaria reverchonii (Vasey) Pilg.	SeRe	Reverchon's Bristlegrass	grass	perennial	native
Panicum virgatum L.	PaVi	Switchgrass	grass	perennial	native
Phemeranthus aurantiacus (Engelm.) Kiger	PhAu	Orange Flameflower	forb	perennial	native
Aristolochia coryi I.M. Johnst.	ArCo	Dutchman's pipe	forb	perennial	native
Acalypha phleoides Cav.	AcPh	Shrubby copperleaf	forb	perennial	native
Salvia reflexa Hornem.	SaRe	Lance-leaf sage	forb	annual	native
Abutilon fruticosum Guill. & Perr.	AbFr	Indian mallow	forb	perennial	native
Anemone berlandieri Pritz.	AnBe	Tenpetal anenome	forb	perennial	native
Astragalus mollissimus Torr.	AsMo	Wooly locoweed	forb	perennial	native

Oenothera triloba Nutt.	OeTr	Stemless evening primrose	forb	annual	native
Centaurea melitensis L.	CeMe	Malta Starthistle	forb	annual	introduced
Medicago polymorpha L.	MePo	Bur clover	forb	annual	introduced
Astragalus nuttallianus DC.	AsNu	Nuttal milkvetch	forb	annual	native
Plantago rhodosperma Decne.	PlRh	Red-seed plantain	forb	annual	native
Bromus catharticus Vahl	BrCa	Rescuegrass	grass	annual	introduced
Glandularia pumila (Rydb.) Umber	GlPu	Pink vervain	forb	annual	native
Cirsium texanum Buckley	OnAc	Texas thistle	forb	annual	native
Lesquerella gordonii (A. Gray) S. Watson	LeGo	Gordon's bladderpod	forb	annual	native
Engelmannia peristenia (Raf.) Goodman & C.A. Lawson	EnPe	Englemann's daisy	forb	perennial	native
Scutellaria drummondii Benth. var. drummondii	ScDr	Drummond's skullcap	forb	annual	native
Hymenoxys odorata DC.	HyOd	Western bitterweed	forb	annual	native
Plantago helleri Small	PlHe	Heller's plantain	forb	annual	native
Ratibida columnifera (Nutt.) Woot. & Standl.	RaCo	Mexican hat	forb	perennial	native

APPENDIX 2

CHAPTER III DATA SUPPLEMENT

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pH

The Winter 2017 full-factorial ANOVA of soil pH

Parameter Estimates

TERM	ESTIMATE	STD ERROR	T RATIO	PROB>|T|
Intercept	7.63375	0.004959	1539.5	<.0001*
Drought[No]	0.0040625	0.004959	0.82	0.4161
Nitrogen[No]	0.0090625	0.004959	1.83	0.0729
Drought[No]*Nitrogen[No]	-0.004375	0.004959	-0.88	0.3814
Fire[No]	0.0040625	0.004959	0.82	0.4161
Drought[No]*Fire[No]	0.01125	0.004959	2.27	0.0272*
Nitrogen[No]*Fire[No]	0.009375	0.004959	1.89	0.0639
Drought[No]*Nitrogen[No]*Fire[No]	-0.000938	0.004959	-0.19	0.8507

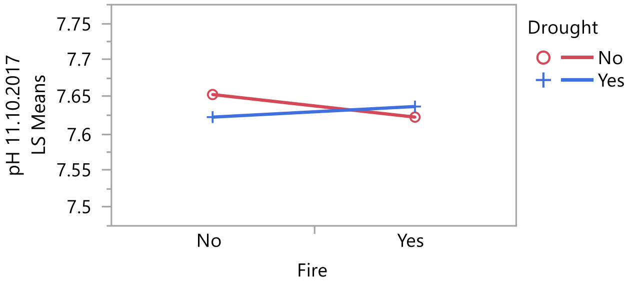
Effect test

SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	0.00105625	0.6712	0.4161
Nitrogen	1	1	0.00525625	3.3401	0.0729
Drought*Nitrogen	1	1	0.00122500	0.7784	0.3814
Fire	1	1	0.00105625	0.6712	0.4161
Drought*Fire	1	1	0.00810000	5.1472	0.0272*
Nitrogen*Fire	1	1	0.00562500	3.5745	0.0639
Drought*Nitrogen*Fire	1	1	0.00005625	0.0357	0.8507

D*F Least Squares Means Table

LEVEL	LEAST SQ MEAN	STD ERROR
No,No	7.6531250	0.00991735
No,Yes	7.6225000	0.00991735
Yes,No	7.6225000	0.00991735
Yes,Yes	7.6368750	0.00991735

Pre-treatment pH D*F LS Means Plot



The difference in pH (Winter 2018- Winter 2017) full-factorial ANOVA of soil pH

Winter 2018- Winter 2017ANOVA Parameter Estimates

TERM	ESTIMATE	STD ERROR	T RATIO	PROB>|T|
Intercept	-0.117813	0.005966	-19.75	<.0001*
Drought[No]	-0.005625	0.005966	-0.94	0.3498
Nitrogen[No]	-0.001562	0.005966	-0.26	0.7944
Drought[No]*Nitrogen[No]	1.388e-17	0.005966	0.00	1.0000
Fire[No]	-0.001875	0.005966	-0.31	0.7545
Drought[No]*Fire[No]	-0.012812	0.005966	-2.15	0.0361*
Nitrogen[No]*Fire[No]	-0.00625	0.005966	-1.05	0.2993
Drought[No]*Nitrogen[No]*Fire[No]	0.0021875	0.005966	0.37	0.7153

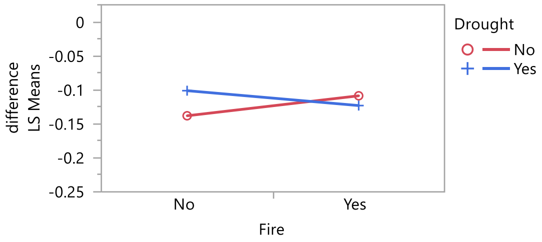
Winter 2018- Winter 2017ANOVA Effect test

SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	0.00202500	0.8889	0.3498
Nitrogen	1	1	0.00015625	0.0686	0.7944
Drought*Nitrogen	1	1	1.2326e-32	0.0000	1.0000
Fire	1	1	0.00022500	0.0988	0.7545
Drought*Fire	1	1	0.01050625	4.6118	0.0361*
Nitrogen*Fire	1	1	0.00250000	1.0974	0.2993
Drought*Nitrogen*Fire	1	1	0.00030625	0.1344	0.7153

pH Difference D*F Least Squares Means Table

LEVEL	LEAST SQ MEAN	STD ERROR
No,No	-0.1381250	0.01193243
No,Yes	-0.1087500	0.01193243
Yes,No	-0.1012500	0.01193243
Yes,Yes	-0.1231250	0.01193243

pH Difference LS Means Plot



Soil conditions

Winter 2018 temperature

Winter 2018 Temperature non-parametric comparisons for each pair using Wilcoxon method

LEVEL	- LEVEL	SCORE MEAN DIFFERENCE	STD ERR DIF	Z	P-VALUE	LOWER CL	UPPER CL
D*N	Control	6.25000	2.354074	2.65497	0.0079*	0.66667	4.00000
D	Control	4.62500	2.352304	1.96616	0.0493*	0.00000	3.33333
D*F	Control	4.37500	2.369951	1.84603	0.0649	-0.33333	3.66667
D*N*F	Control	4.12500	2.357612	1.74965	0.0802	-0.33333	3.33333
D*N	D	3.50000	2.355844	1.48567	0.1374	-0.33333	1.33333
N	Control	2.75000	2.368192	1.16122	0.2456	-0.33333	3.33333
F	Control	2.37500	2.357612	1.00738	0.3138	-1.00000	3.00000
D*N	D*F	2.00000	2.361144	0.84705	0.3970	-0.66667	1.33333
N*F	Control	1.12500	2.352304	0.47825	0.6325	-1.00000	2.66667
N	F	0.87500	2.364671	0.37003	0.7114	-1.00000	1.33333
D*F	D	0.62500	2.350532	0.26590	0.7903	-1.00000	1.33333
D*N*F	D	-0.25000	2.341652	-0.10676	0.9150	-1.00000	0.66667
D*N*F	D*F	-0.87500	2.362908	-0.37031	0.7112	-1.33333	1.00000
N*F	F	-1.12500	2.350532	-0.47862	0.6322	-1.66667	1.00000
N	D	-1.50000	2.346984	-0.63912	0.5227	-1.33333	0.66667
N	D*N*F	-1.62500	2.350532	-0.69133	0.4894	-1.00000	0.66667
N	D*F	-1.75000	2.352304	-0.74395	0.4569	-1.66667	0.66667
F	D*N*F	-1.87500	2.350532	-0.79769	0.4250	-1.33333	0.66667
N*F	N	-2.50000	2.296737	-1.08850	0.2764	-1.66667	0.66667
F	D	-2.62500	2.336308	-1.12357	0.2612	-1.33333	0.66667
F	D*F	-2.87500	2.362908	-1.21672	0.2237	-2.00000	0.66667
D*N*F	D*N	-3.75000	2.338090	-1.60387	0.1087	-1.66667	0.33333
N*F	D*F	-4.12500	2.345208	-1.75891	0.0786	-2.00000	0.33333
F	D*N	-4.37500	2.362908	-1.85153	0.0641	-2.00000	0.33333
N*F	D*N*F	-4.37500	2.350532	-1.86128	0.0627	-1.66667	0.33333
N*F	D	-4.50000	2.309401	-1.94856	0.0513	-1.66667	0.00000
N	D*N	-4.75000	2.346984	-2.02387	0.0430*	-1.66667	0.00000
N*F	D*N	-7.12500	2.357612	-3.02213	0.0025*	-2.33333	-0.33333

Winter 2018 Moisture

Winter 2018 Moisture non-parametric comparisons for each pair using Wilcoxon method

LEVEL	- LEVEL	SCORE MEAN DIFFERENCE	STD ERR DIF	Z	P-VALUE	LOWER CL	UPPER CL
D*N	D	4.87500	1.957890	2.48993	0.0128*	0.0000	20.30000
D*F	D	3.25000	2.071634	1.56881	0.1167	0.0000	20.30000
D*N	Control	2.87500	1.622755	1.77168	0.0764	0.0000	25.73333
N	D	2.87500	2.160247	1.33087	0.1832	0.0000	20.30000
D*N*F	D	2.00000	2.228602	0.89742	0.3695	-4.5000	20.20000
D*F	Control	1.75000	1.811997	0.96579	0.3342	0.0000	25.73333
F	D	1.75000	2.228602	0.78525	0.4323	-3.0000	19.23333
N	Control	1.12500	1.957890	0.57460	0.5656	-6.6333	25.73333
D*N	D*F	0.87500	1.000000	0.87500	0.3816	0.0000	0.00000
N	D*N*F	0.87500	1.957890	0.44691	0.6549	-6.9000	8.20000
N	F	0.62500	1.957890	0.31922	0.7496	-6.9000	6.70000
N*F	D	0.62500	2.280351	0.27408	0.7840	-10.7667	13.46667
D*N*F	Control	0.25000	2.071634	0.12068	0.9039	-7.9333	25.63333
F	Control	0.00000	2.071634	0.00000	1.0000	-6.4333	24.66667

F	D*N*F	0.00000	2.071634	0.00000	1.0000	-6.7000	8.20000
N*F	Control	-0.37500	2.160247	-0.17359	0.8622	-11.5333	19.10000
N	D*F	-0.62500	1.622755	-0.38515	0.7001	-6.9000	0.00000
N*F	F	-0.87500	2.160247	-0.40505	0.6854	-11.8000	5.90000
D	Control	-1.12500	2.226732	-0.50522	0.6134	-20.0333	17.20000
N*F	D*N*F	-1.12500	2.160247	-0.52077	0.6025	-11.8000	7.40000
D*N*F	D*F	-1.75000	1.811997	-0.96579	0.3342	-8.2000	0.00000
F	D*F	-1.75000	1.811997	-0.96579	0.3342	-6.7000	0.00000
N	D*N	-1.87500	1.369306	-1.36931	0.1709	-6.9000	0.00000
N*F	N	-1.87500	2.071634	-0.90508	0.3654	-11.8000	6.10000
N*F	D*F	-2.37500	1.957890	-1.21304	0.2251	-11.8000	0.00000
D*N*F	D*N	-2.87500	1.622755	-1.77168	0.0764	-8.2000	0.00000
F	D*N	-2.87500	1.622755	-1.77168	0.0764	-6.7000	0.00000
N*F	D*N	-3.87500	1.811997	-2.13852	0.0325*	-11.8000	0.00000

Spring 2019 temperature

Parametric, full-factorial ANOVA

Spring 2019 Temperature ANOVA Parameter Estimates

TERM	ESTIMATE	STD ERROR	T RATIO	PROB>|T|
Intercept	61.140625	0.133877	456.69	<.0001*
Drought[No]	-0.338542	0.133877	-2.53	0.0143*
Nitrogen[No]	0.0677083	0.133877	0.51	0.6150
Drought[No]*Nitrogen[No]	0.1927083	0.133877	1.44	0.1556
Fire[No]	-0.088542	0.133877	-0.66	0.5111
Drought[No]*Fire[No]	-0.005208	0.133877	-0.04	0.9691
Nitrogen[No]*Fire[No]	0.0260417	0.133877	0.19	0.8465
Drought[No]*Nitrogen[No]*Fire[No]	0.0885417	0.133877	0.66	0.5111

Spring 2019 Temperature ANOVA Effect Tests

SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	7.3350695	6.3946	0.0143*
Nitrogen	1	1	0.2934028	0.2558	0.6150
Drought*Nitrogen	1	1	2.3767361	2.0720	0.1556
Fire	1	1	0.5017361	0.4374	0.5111
Drought*Fire	1	1	0.0017361	0.0015	0.9691
Nitrogen*Fire	1	1	0.0434028	0.0378	0.8465
Drought*Nitrogen*Fire	1	1	0.5017361	0.4374	0.5111

Spring 2019 moisture

Nonparametric Comparisons For Each Pair Using Wilcoxon Method

Q*	ALPHA
1.95996	0.05

LEVEL	- LEVEL	SCORE MEAN DIFFERENCE	STD ERR DIF	Z	P-VALUE	LOWER CL	UPPER CL
N	Control	5.37500	2.378725	2.25961	0.0238*	0.1000	15.40000
F	Control	4.37500	2.378725	1.83922	0.0659	-0.2333	10.33333
N*F	Control	4.37500	2.378725	1.83922	0.0659	-0.6667	10.73333
D*N	Control	3.87500	2.378725	1.62902	0.1033	-1.4000	6.20000
N	D	3.75000	2.378725	1.57647	0.1149	-1.5000	15.16667
F	D	3.37500	2.380476	1.41778	0.1563	-2.0667	10.16667
D*N	D	2.87500	2.380476	1.20774	0.2271	-2.6000	6.60000
N	D*F	2.87500	2.380476	1.20774	0.2271	-2.2000	14.40000
N*F	D	2.87500	2.380476	1.20774	0.2271	-2.2667	9.63333
N	D*N*F	2.62500	2.380476	1.10272	0.2701	-2.5333	12.40000
F	D*N*F	2.37500	2.380476	0.99770	0.3184	-2.4000	9.10000
F	D*F	2.25000	2.378725	0.94588	0.3442	-3.4667	9.83333
D*N*F	Control	2.12500	2.378725	0.89334	0.3717	-1.6333	5.36667
N	D*N	2.00000	2.378725	0.84079	0.4005	-3.4333	12.33333
N*F	D*F	1.87500	2.380476	0.78766	0.4309	-4.5667	10.50000
D*N*F	D	1.62500	2.380476	0.68264	0.4948	-3.3667	5.60000
F	D*N	1.62500	2.380476	0.68264	0.4948	-4.0000	9.36667
D*N	D*F	1.37500	2.380476	0.57762	0.5635	-4.0667	5.60000
D*F	Control	1.12500	2.378725	0.47294	0.6363	-2.8000	8.56667
N*F	D*N*F	1.12500	2.380476	0.47259	0.6365	-3.4333	9.73333
D*F	D	0.75000	2.378725	0.31529	0.7525	-4.5000	7.46667
D*N*F	D*F	0.62500	2.380476	0.26255	0.7929	-5.6333	5.26667
N	F	0.12500	2.380476	0.05251	0.9581	-7.3667	8.96667
D	Control	0.00000	2.378725	0.00000	1.0000	-2.7000	3.33333
N*F	D*N	0.00000	2.378725	0.00000	1.0000	-4.4000	6.86667
N*F	F	-0.62500	2.380476	-0.26255	0.7929	-7.9667	6.80000
D*N*F	D*N	-0.87500	2.380476	-0.36757	0.7132	-5.3000	3.13333
N*F	N	-0.87500	2.380476	-0.36757	0.7132	-12.2667	8.30000

Soil depth

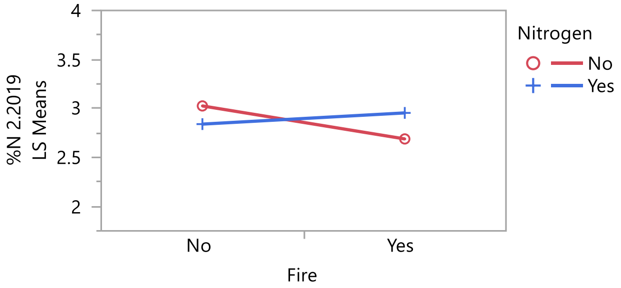
Full-factorial ANOVA for soil depth in cm

SOURCE	NPARM	DF	SUM OF SQUARES	F RATIO	PROB > F
Drought	1	1	21.74619	0.6622	0.4192
Nitrogen	1	1	41.59242	1.2665	0.2652
Drought*Nitrogen	1	1	0.04765	0.0015	0.9698
Fire	1	1	4.01689	0.1223	0.7278
Drought*Fire	1	1	193.50114	5.8922	0.0184*
Nitrogen*Fire	1	1	0.53908	0.0164	0.8985
Drought*Nitrogen*Fire	1	1	3.70502	0.1128	0.7382

C3 grass blade %N

February 2019 C3 grass blade %N: N*F Least Squares Means Table

LEVEL	LEAST SQ MEAN	STD ERROR
No,No	3.0256250	0.07727827
No,Yes	2.6887500	0.07727827
Yes,No	2.8400000	0.07727827
Yes,Yes	2.9543750	0.07727827



Pre- and post-treatment C3 grass blade %N comparison:

Wilcoxon / Kruskal-Wallis Tests (Rank Sums) comparison of pre- and post-treatment

LEVEL	COUNT	SCORE SUM	EXPECTED SCORE	SCORE MEAN	(MEAN-MEAN0)/STD0
2.2018	63	2471.50	4032.00	39.2302	-7.523
2.2019	64	5656.50	4096.00	88.3828	7.523

1-Way Test, ChiSquare Approximation

CHISQUARE	DF	PROB>CHISQ
56.6352	1	<.0001***