SHIFTING SAVANNA STABILITY: ASSESSING SEMI-ARID GRASSLAND DYNAMICS VIA EXPERIMENTAL MANIPULATIONS OF PRECIPITATION, SOIL FERTILITY, FIRE DISTURBANCE, AND NON-NATIVE HERBIVORE IMPACTS

A Thesis

by

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ABSTRACT

Understanding how factors such as precipitation, nutrients, disturbances, and herbivory alter herbaceous cover in a savanna is imperative for conserving biological diversity and critical savanna ecosystem functions. This study investigates 1) how herbaceous plant productivity and community composition within a semi-arid savanna will respond to interactions of prescribed fire, drought, and nutrient addition (DroughtNet Experiment), and 2) varied levels of prescribed fire energy interact with mammalian wildlife herbivory to effect herbaceous plant productivity and community composition within a semi-arid savanna (Joint Fire Science Project). Separate experimental research projects were established at the Texas A&M AgriLife Research Station in Sonora, Texas on the Edward's Plateau in a semi-arid savanna ecosystem.

The objective of the DroughtNet experiment was to contribute to an international research network aimed at assessing how varied ecosystems respond to precipitation-limitations as predicted by future climate models. By constructing rainfall exclusion shelters, conducting prescribed fires, and adding nitrogen supplements full-factorial effects of each treatment on local vegetation were examined for a 2-year period. Fire had the most significant treatment effect on ANPP, drastically reducing standing biomass 1-year post burn, though above-ground biomass recovered within 2 years. All treatments had effects on diversity at different time-steps throughout the experiment. Drought had the most lasting impact on community composition even though higher than historically normal precipitation events occurred during the 3-year sampling period. It was expected that interactively drought, nutrient addition, and fire would be drivers of biomass loss, though that was not manifest in the data collected for this study. While this may be an artefact of unusual recent precipitation patterns, it may alternatively indicate the considerable resilience of semi-arid savanna vegetation to water-limitations and other natural disturbances.

In a separate study, I experimentally examined the effects of varying levels of prescribed fire energy interacting with mammalian wildlife herbivory on herbaceous plant productivity and community composition within a semi-arid savanna. Results indicated that high fire energy did not reduce vegetation diversity or productivity; however, combined grazing pressures of both native and non-native mammalian herbivores substantially reduced above-ground biomass.

These results will provide insight to how land managers can react to changing climate patterns and nutrient cycles, implement more effective burning regimes, and manage for native and non-native herbivores depending on their desired alternative outcomes.

DEDICATION

To my parents, thank you for your unwavering support and love. Dad, thank you for instilling in me a deep sense of pride and love for nature and our wonderful Texas. Mom, thank you for being my champion, you’ve taught me to be humble and determined in all that I do.

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TABLE OF CONTENTS

LIST OF FIGURES

Page

Chapter II

Chapter III

LIST OF TABLES

Page

Chapter II

Chapter III

CHAPTER I INTRODUCTION

Savannas are heterogeneous and dynamic systems representing 11% of earth's terrestrial land surface (LeVine and Crews 2019). Temperate savannas cover over 50 million ha of North America, making it a geographically extensive and socioeconomically important biome (Scholes and Archer 1997a). Degradation of this ecosystem would alter human-dependent ecosystem services such as nutrient cycling for agriculture (Sankaran et al. 2005), livestock grazing habitat (Hoogesteijn and Hoogesteijn 2010), and aquifer recharge zones (Ansley and Castellano 2006). These ecosystems are under threat due to altered fire regimes, woody encroachment (Bond and Keeley 2005), overutilization, and shifting weather patterns due to climate change (Fay et al. 2002).

Savanna vegetation structure can span a diversity of tree-grass ratio gradients ranging from open grasslands to dense woodlands (LeVine and Crews 2019). Simmons et al. (2003) define savannas as an ecosystem with discontinuous woody components and continuous herbaceous cover. Vegetation found in these ecosystems tends to be highly flammable and burns every 1-3 years (Biddulph and Kellman 1998). Alteration of disturbances, specifically reduced fire frequencies, increases the distribution and abundance of woody resprouters in grassland patches (Twidwell et al. 2016, Archer et al. 2017).

Savanna ecosystems developed nearly 8 million years ago and as indicated by changing atmospheric CO_2 levels and increased charcoal records (Metwally et al. 2014, Scott et al. 2014). This time was characterized by lower atmospheric CO_2 concentrations, which limited C_3 tree recruitment and allowed for the rapid expansion of C_4 grasses (Beerling 2006). Expansion of grasses established a grass-fire relationship that is classically considered to be the driver for endemic species distribution and abundance (Bond and Keeley 2005). Recurrent low intensity, surface fires are necessary for the establishment and co-dominance of grasses and forbs in woody pressured ecosystems, however, it is suggested this is not the sole ecosystem driver for savannas (Hairston et al. 1960, Rother et al. 2020).

It was determined by Polis (1999) that plant consumption by fire and herbivores, and water and nutrient availability are the most important factors for determining plant production and distribution. Top-down processes, such as disturbances, or bottom-up processes, such as resource availability, were long thought to be independently responsible for variations in vegetation structure (Scholes and Archer 1997a, Staver et al. 2017). Historic large-scale studies frequently lacked precision to isolate important variables driving system dynamics; in contrast, small-scale, site-specific studies generally focus on one determinant and fail to create a comprehensive model that encapsulates the diversity of savanna functionality (House et al. 2003, Sankaran et al. 2005). To understand the savanna tree-grass ratio, knowledge of how the contrasting life-forms interact with resource availability, disturbances, and their interactions is needed across multiple temporal and spatial scales (House et al. 2003).

Two primary theories attempt to explain the grass-tree co-dominance matrix: resource-based and/or disturbance-based hypotheses (Walter 1970, Bond and Van Wilgen 1996, Higgins et al. 2010, February et al. 2013). Walter (1970) proposed niche occupancy in soil profiles determines the resource allocation and competitive space for each life-form in savanna ecosystems. This theory hypothesizes that grasses have the over-all resource-based competitive advantage to woody species, but the deep-rooting habit of woody species provides access to resources unavailable to the more shallow-rooted grasses, providing a mechanism enabling co-dominance (February et al. 2013). Additionally, Walker and Noy-Meir’s two-layer soil-moisture competition model states that rainfall variability, soil-layer occupancy and dominance, and efficiency of nutrient uptake strongly influences the dominance ratio of grasses and woody plants (Walker and Noy-Meir 1982).

However, dissenting evidence suggests rooting niche differentiation is not always the primary driving factor determining grass-tree codominance (Scholes and Archer 1997a, Higgins et al. 2000). Seasonal water availability in semi-arid savannas could suggest, through these factors, the co-dominance structure of characteristic vegetation. Sankaran (2005) argued that in times of severe resource restrictions grasses and trees coexist because both are functioning at a survival state and are below critical density. When resources are abundant though, tree leaf area index increases and creates a facilitative feedback effect between light and soil resources that puts grasses at a competitive disadvantage (Siemann and Rogers 2003, Sankaran et al. 2005). Resource availability and allocation is significant to the growth structure of grasses and trees, but the theory that resources are the primary determinant of grass-tree dominance may not be adequate to explain the dynamics of savanna ecosystems (Higgins et al. 2007b).

Disturbance-based hypotheses have become more prevalent in current literature on savanna vegetation dynamics. Long term effects of life-history disturbance interactions, such as fire and drought, shape the complex grass-tree co-existence matrix of savannas (Higgins et al. 2010). Low-energy fires coupled with drought periods creates a grass-fire positive feedback loop that stimulates grass growth and limits recruitment rates of trees (Higgins et al. 2010, Bernardi et al. 2019). Variation in fire intensity is influenced by grass production, grazing pressures, and tree neighborhoods (Higgins et al. 2000). Temporal variability in fire energy and drought causes a fluctuation in tree recruitment (Gardner 2006). Frequent fire prevents juvenile trees from maturing and escaping the flame-zone and drought conditions hinder seed establishment and intensify competition with grasses in the upper soil layers (February et al. 2013). Drought conditions create a catalyst for fire, an important top-down determinant of woody recruitment and establishment (Scholes and Archer 1997a). Evidence also suggests that in times of drought, when woody regrowth potential is lowest, large browsing animals are instrumental in creating an open-canopy, grassland matrix (Axelrod 1985). Negative pressure on vegetation during stressful climactic events is seen to be exacerbated by local herbivores due to constraints on food supply, especially in times of drought (Axelrod 1985). Early persistent use of fire by man, lightning-caused fire, and large browser consumption/destruction all contributed to historic removal of relic tree stands in early-development savannas (Axelrod 1985, Bond and Van Wilgen 1996, Anderson 2006, Beerling 2006).

Defining what processes allow grass-tree codominance is the overarching theme of most savanna research. Climate theories attempt to explain this vegetation matrix simply by attributing composition and structure variability to climate fluctuations (Schimper 1898, Rodríguez-Iturbe et al. 1999). Climate and single factor explanations, such as resource-based and disturbance-based theories, cannot explain the distribution of savannas on a local or global scale (Murphy and Bowman 2012). New conceptual models, such as the alternate stable state model, are now trying to incorporate a large web of controls that intertwine to create distinct, novel savanna ecosystems (Walker and Noy-Meir 1982, Rodríguez-Iturbe et al. 1999, Hobbs and Suding 2009, Lloret et al. 2012, Murphy and Bowman 2012, Veldman et al. 2015). The alternative stable state model analyzes population stability and resilience to stress and ecosystem responses and changes (Holling 1973, Beisner et al. 2003). In savanna ecosystems it is thought that the equilibrium state is the definition composition of grasses and trees, while a disturbance or perturbation to the ecosystem could result in a compositional shifted to a more wooded or grassland type cover (Staver et al. 2011, Twidwell et al. 2013a).

Unmanaged woody encroachment, from fire suppression or herbivore exclusion, can convert savannas and grasslands to shrublands and woodlands (Archer et al. 2017). Fire suppression and human-induced fire seasons alterations allow woody seedlings and saplings to break free of the fire-trap phenomenon and establish dominance (Devine et al. 2017, Capozzelli et al. 2020). The fire-trap phenomenon is when frequent fires consume small tree above-ground biomass, limiting their resource use to resprouting rather than growing taller above the fire line (Freeman et al. 2017). Taylor et al. (2012) suggests high intensity, summer fires are needed to enact a firetrap and therefore control over-all, woody plant frequency and maintain semi-arid savanna community structure. Without deterrence by fire, tree and brush encroachment leads to decreases in forage production (Taylor et al. 2012a), alteration of local biogeochemistry (Zhou et al. 2018), and decreases landscape heterogeneity (Smit and Prins 2015).

Understanding how factors such as precipitation, nutrients, disturbances, and herbivory alter herbaceous cover in a savanna is imperative for conserving biological diversity and critical savanna ecosystem functions. Changing climates, disturbance regimes, and nutrient cycles could have major impacts in semi-arid savannas around the globe.

Literature review

Fire

Fire is an integral part of semi-arid savannas that has shaped system productivity and functionality since the Miocene (Nghalipo et al. 2019). Fire is necessary for removing litter layers, increasing light availability, stimulating grass growth, and destroying woody plant seedlings (Bond 2008, Archer et al. 2017, O'Connor et al. 2020). Season of burning, fire intensity, and frequency are important components of fire disturbances in most natural and managed systems (Glitzenstein et al. 1995). Environmental conditions, fire characteristics, and plant life stage determine community composition and productivity responses (Brockway et al. 2002, Russell et al. 2015, Bär et al. 2019).

Grassy understories and extended dry periods facilitate necessary recurring, low intensity fires (Grace et al. 2006). Dormant season burning significantly increases post-fire standing biomass of grass and forb species by preventing rigorous mid-story and top-story growth (Brockway and Lewis 1997). Seasonality of burning stimulates different phenology depending on dormancy at time of fire (Brockway and Lewis 1997). In many grasslands and savannas, burning in late-spring is practiced for greater biomass production for livestock consumption, woody species control, and control of dominant species proportion (Towne and Craine 2014). The season of burning in relation to growth cycle largely determines the increase or decrease of species type (Anderson et al. 1970, Towne and Craine 2014). At time of fire, active growing species are more likely to be injured or killed because new plant material is more sensitive to heat (Bond and Van Wilgen 1996). Injured plants then have to focus resource reserves on damaged parts, and it is unlikely they reach the reproduction cycle of growth (McMurphy and Anderson 1965, Anderson et al. 1970). Spring burning is preferred by range managers to stimulate warm season grasses, which are desired for livestock raising, and decrease occurrence of cool season undesirable species (Steuter 1987). This strategic burning can be used to lessen non-native graminoid species as well (Ruckman et al. 2012). Texas wintergrass (*Nassella leucotricha*, C_3) yield has been reported to increase two-fold after summer fires than winter fires. Early season wintergrass growth (February-June) allows full maturation and seeding by the summer fire season (June-August) but growth and germination were interrupted by winter fires (December-February) (Knapp et al. 2009). Altering historic lightning-ignited summer fires to prescribed spring fires has shifted species compositions to a greater proportion of warm season grasses (Howe 1994a, b, Knapp et al. 2009). Areas managed with summer burns have shown more species diversity and resilience to disturbances over-time possibly related to the "chaotic array" of historic fire occurrences (Howe 1994a, b, Knapp et al. 2009, Towne and Craine 2014). Overall, season of fire directly influences graminoid functional type dominance by inhibiting phenological advantages and management goals should consider type preference when implementing a prescription.

Fire frequency also influences physiological composition and competition between functional types. Clearing of shade-producing top-story vegetation by frequent fires allows for shade-intolerant, warm season C_4 species to dominate (Ripley et al. 2015). High productivity of C_4 species in arid ecosystems provides necessary fuel-loads for frequent fires, therefore, excluding fire-limited species such as shrubs and trees (Bond et al. 2003). Short fire return intervals benefit grass species that are more capable of exploiting increased resource availability after fire and precipitation (Benson et al. 2004). Fast regrowth of grasses after fire provides fine-fuels for short return-interval fire events creating a positive grass-fire feedback (Bernardi et al. 2019).

Fire intensity is a critical determinant of fires impact on vegetation regrowth capabilities and community composition (Govender et al. 2006). Intensity is controlled by environmental factors such as moisture content, fuel load, and weather conditions (Cheney et al. 1998, Laris et al. 2020). It is suggested that high-intensity burns coupled with dry conditions will have the most deleterious effect on woody individuals but not have a significant impact on grasses (Twidwell et al. 2016). High intensity crown fires that lead to destruction of regrowth organs and damage to hydraulic mechanisms means certain mortality for most trees (Bär et al. 2019). Reduced fire intensity, by either livestock fuel consumption or woody encroachment, would most likely lead to a reinforcing feedback loop perpetuating further woody encroachment (Smit and Prins 2015).

Fire prone species exhibit varying reproductive and regrowth responses based on above and below-ground resource allocation (Bond and Van Wilgen 1996, Ansley and Castellano 2006, Russell et al. 2015). In Central Texas, switchgrass (*Panicum virgatum),* sideoats grama (*Bouteloua curtipendula),* coastal live oak *(Quercus virginiana),* post oak *(Quercus stellata),* and vine mesquite (*Panicum obtusum)* are well adapted to fire-prone environments (Brockway et al. 2002, Ansley and Castellano 2006, Ansley et al. 2010). Above-ground fire-adapted and fire-related traits expressed by plants in these environments are fire-resistant tissues, insulated meristems, fire-stimulated flowering, serotiny/pyricence, thick outer bark, and deep root habitats (Pyke 2017, Lamont et al. 2019). Below-ground basal resprouting, seed incubation, and horizontal rhizome resprouting along with germination of soil-stored seeds ensures germination and regrowth after severe ground fires (Baskin and Baskin 1998, Lamont et al. 2019). Species such as Ashe juniper (*Juniperus asheii*), Eastern red cedar (*Juniperus virginiana),* and many non-native grasses (depending on fire season and severity) are highly flammable and typically vulnerable to fire-injury and mortality (Ortmann et al. 1998, Reemts et al. 2019). Fire presence reduces the likelihood of fire-vulnerable, non-native and undesirable species to become overly competitive and take over landscapes (Brockway et al. 2002, Reemts et al. 2019).

Burning in semi-arid savannas exerts strong structural control and is beneficial for the growth of herbaceous species and maintaining grass-tree codominance (Singh et al. 2018). Savannas are maintained by disturbances, such as fire, that depress early life-stages of woody plants, limiting establishment and allowing grass coverage of opened canopy and ground areas (Beckage et al. 2011). Fire suppression allows for the accumulation of woody vegetation cover, low nutrient cycling, and loss of land use potentials (LeVine and Crews 2019). In degraded savanna ecosystems, fire suppression programs and over-consumption of fine-fuel by livestock has nearly eliminated fire in disturbance-dependent savannas destabilizing essential ecosystem processes for co-dominance between grasses and trees (Brockway et al. 2002). Attempts to restore grasslands experiencing woody encroachment using prescribed fire typically show limited impact on many shrub species due to insufficient fire intensity, lack of fine fuel, and vigorous woody plant resprouting post-fire (Twidwell et al. 2016). Hesitation by land managers towards high intensity fires is creating a halting dialect based on unknowns and fear of reduced productivity (Twidwell et al. 2013b, Toledo et al. 2014, Wonkka et al. 2015, Twidwell et al. 2019). Concerns about varying fire intensity effect on herbaceous vegetation, soil health, and food web dynamics need to be addressed when determining optimal fire disturbance regimes to halt or reverse woody encroachment in grasslands.

Water

It is predicted that, due to climate change, precipitation patterns in semi-arid savanna ecosystems will shift to more extreme rain episodes followed by more severe droughts (Fay et al. 2002). More severe and frequent drought conditions could cause major vegetation mortality and shift community dynamics and composition to new functional states (Twidwell et al. 2014, Wonkka et al. 2016, Case et al. 2019). Individual species impact varies widely depending on plant adaptations and these outcomes are challenging to predict under various other ecosystem stressors (Allen et al. 2010). Water availability has been shown to be the primary factor affecting herbaceous vegetation and woody plant interactions while soil and fire disturbance factors are less influential (Sankaran et al. 2005, van der Waal et al. 2009). In savanna, woody cover typically increases with an increase in mean annual precipitation, therefore woody cover is expected to follow precipitation trends (Sankaran et al. 2008, van der Waal et al. 2009). Increases in precipitation variability will lead to prolonged droughts in many areas therefore woody plants are expected to experience an extreme die-off (Wonkka et al. 2016). Extreme drought events could potentially shift savanna grass-tree matrices to a grass dominated system or induce desertification and cause the ecosystem to collapse altogether (Kassas 1995, Ludwig and Tongway 1995, Bestelmeyer et al. 2013).

Net primary productivity (NPP) will likely drastically decline during drought events reducing carbon sequestration ability because of reduction of biomass accumulation (Ward et al. 1999). NPP is generally thought of as a proxy for ecosystem service value concentrating on plant growth and carbon sequestration ability (Liu et al. 2010). Drought is a prominent threat to NPP across the globe, but it is hypothesized that grasslands and savannas are the most susceptible to negative impacts (Raich and Tufekciogul 2000, Lei et al. 2020). Drought leads to net loss in carbon sequestration by declining photosynthetic rates and lowering ecosystem productivity (Zhang et al. 2019). Loss of productivity is seen to be more substantial when drought occurs in the early growing season as opposed to the end of the season. Reduced water availability in the early stages of vegetation growth is detrimental to a plants growth potential and therefore a successful seeding (Bates et al. 2006, Zhang et al. 2019). Contemporary research suggests that declining precipitation in savannas induces a linear reduction in ecosystem productivity, implying that future declines in precipitation could eventually lead to destabilized ecosystem functions (Ansley et al. 2013, Jin et al. 2018, Moore et al. 2018).

Ecosystems adapt to water constraints by different mechanisms (ie. reduction in plant growth, alterations in community structure) in order to reorganize ecosystem functions (Liu et al. 2018). Ecosystem resilience to drought occurs through two primary mechanisms: (1) compensatory functionality such that drought-tolerant plants increase due to drought-induced mortality of drought-intolerant plants (Gonzalez and Loreau 2009, Lloret et al. 2012, Moore et al. 2018), or (2) physiological compensation where all species in the community are drought-tolerant or recover fully (Connell and Ghedini 2015). Physiological differences between grass communities (C_3 and C_4 photosynthetic pathways) have been shown to significantly affect vegetation composition, succession, and productivity in grasslands (Reich et al. 2003). Grass community competition is facilitated by water availability and weather conditions. For instance, C_3 grasses (such as *Nassela pulchra)* are cool season grasses known to better compete in high water availability and lower temperatures. C_4 grasses (such as *Bouteloua curtipendula, Hilaria belangeri*) are warm season grasses adapted to outcompete C_3 grasses in lower water availability and hotter temperatures. High rates of net leaf photosynthesis at lower stomatal conductance allows C_4 grasses an advantage in predicted drought conditions (José et al. 2020).

Nitrogen

Nitrogen in soil is an essential nutrient for plant photosynthesis and growth (Boretti and Singarayer 2019). Inorganic nitrogen is often the most limiting nutrient for terrestrial plants, but the nitrogen cycle is being dramatically altered by increased anthropogenic inputs. Artificially-enhanced nitrogen depositions are predicted to globally increase by three-fold in semi-arid savannas (Scholes and Archer 1997b).

Increases in nitrogen deposition are primarily due to high rates of anthropogenic N emissions (Zhang et al. 2018). Increase of nitrogen deposition from anthropogenic activities is exposing ecosystems worldwide to unprecedented levels of N (Ibáñez et al. 2018). Anthropogenically-derived nutrient additions can alter the nutrient cycle drastically depending on proximity to emission sources (Vitousek 1994). Plant community composition can be altered from nitrogen supplementation (Tilman 1987). N addition to most ecosystems will elicit both positive and negative community responses across a wide ecosystem gradient (Ibáñez et al. 2018). An increase of N deposition in semi-arid systems could increase plant growth but this ultimately depends on seasonal rainfall patterns which could also lead to significant N leaching (Asner et al. 2001).

While precipitation dictates the timing of herbaceous plant growth, nitrogen determines the amount of ANPP in semi-arid savannas (Bennett and Adams 2001). Nutrient addition in semi-arid savannas increases plant biomass (Fay et al. 2015) while decreasing overall plant diversity (Smith et al. 2016). In nutrient limited ecosystems, plants have adapted to grow slowly and require fewer nutrients (Chapin 1991) causing these plants to be at higher risk of being out competed with projected higher nutrient deposition (Seabloom et al. 2015).

Higher levels of nitrogen are known to be favored by C_3 grasses and woody plants because of their ability to uptake nutrients more quickly than C_4 grasses (Zeng et al. 2010). C_4 nutrient use efficiency makes it competitive in nutrient limited environments by having conservative rates of nutrient uptake but higher rates of photosynthesis per unit of leaf N (Sage et al. 1987). Lower nutrient requirements in C_4 grasses decreases community resilience to nutrient supplementation and can reduce overall diversity in the landscape (Sage et al. 1987, Laidlaw et al. 1996).

Higher levels of N availability in savannas could destabilize ecosystem functions by shifting community composition. Not only does excess nitrogen availability alter functional group dominance but it also decreases ecosystem reliance to other stressors (van der Waal et al. 2009, Stevens et al. 2015). Combinations of nutrient overloading and uncharacteristic variations in precipitation leads to faster depletion of soil water which further exacerbates drought conditions (van der Waal et al. 2009). However, frequent fires volatilize N from plant tissues into the atmosphere instead of cycling it back into the soil. Fire frequency greatly effects cycling of N into the soil by combusting aboveground biomass and detritus hence removing available N from the system (Blair 1997). In frequently burned regions, plants exhibit many characteristics such as lower tissue N concentrations, higher nitrogen use efficiency, and greater productivity responses to nutrient additions in order to survive in nutrient limited ecosystems (Ojima et al. 1994, Blair 1997). Volatilization of N by fire would result in a reduction of plant productivity but in areas with increased anthropogenic N deposition those negative fire effects could be curbed (Coetsee et al. 2010).

Lowering of biodiversity due to nutrient addition could destabilize savanna systems especially in response to drought and altered fire regimes. Interactive effects of these disturbances could result in drastically different vegetation responses.

Herbivory

Savanna heterogeneity is influenced not only by abiotic factors such as fire, precipitation, and nutrients, but also by biotic factors like herbivory (Chikorowondo et al. 2017). Grazing animals have a profound impact on vegetation assembly and composition in savanna ecosystems (Stahlheber et al. 2017). Livestock grazing occurs on 51% of Earth's surface and is the most widespread human-land use globally (Heady 1999, Stahlheber et al. 2017). Grazing is present in every savanna ecosystem across the globe, but grazing effects on vegetation cover have been studied mostly at the ecosystem to regional scale (Scholes and Archer 1997a, Bond and Keeley 2005, Chikorowondo et al. 2017). Co-evolution of C_4 grasses and large herbivores played a major role in how savannas and grasslands are structured and modification of either variable will likely drive changes in grass community structure and composition (Hobbs 1996, Forrestel et al. 2015). Herbivores indirectly and directly influence vegetation structure by altering cover density, distributing seeds through manure, and mediating other disturbance factors (Fuhlendorf et al. 2009, Chikorowondo et al. 2017, Bernardi et al. 2019).

Large grazing animals, such as livestock or migratory species, alter plant distribution and diversity by spreading seeds of native and non-native species (Stahlheber et al. 2017). Consumption and movement of seeds by herbivores expands species spatial establishment and the type of plants taking establishment (Sullivan et al. 2016). Movement of grazing species in a rangeland or savanna is affected by forage quality, water access, and shade (Chapman et al. 2007). Graminoid nutritional value is seen to increase from open grass areas to tree under-stories resulting in increased grazing pressure surrounding and underneath woody patches (Treydte et al. 2007). Grazing under or on trees increases the possibility of seed consumption and later passing in a grass dominant area to potentially lead to woody establishment. Patches enriched by manure and urine have been reported to have higher productivity allowing establishment of consumed woody seeds or fertilization of grasses (Chikorowondo et al. 2017, Bernardi et al. 2019).

Grazing and fire are critical disturbances in determining community composition and productivity potential in savannas (Fuhlendorf et al. 2009). Consumption of grasses can mediate fire feedback mechanism shaping vegetation in an indirect way (Fuhlendorf and Engle 2004, Bernardi et al. 2019). Grazing driven by fire (pyric-herbivory) is a strong driving factor for the evolution of savannas and continue to be essential mechanisms in balancing grass-tree co-dominance (Fuhlendorf et al. 2009). Introduction of non-native species and alteration of fire regimes pushes most savannas to a state shift tipping point due to an imbalance of consumption from herbivores over fire (Hirota et al. 2011). Over consumption by herbivores reduces fine fuel loads, reducing the occurrence of necessary low energy surface fires, and allowing establishment and spread of woody species into grass patches (Fuhlendorf and Engle 2004, Bond and Keeley 2005, Fuhlendorf et al. 2009, Hirota et al. 2011). Depending on stocking rates and herbivore species, over consumption could lead to either a grass-dominated or tree-dominated matrix reducing savanna productivity.

Pyric herbivory is a combination of direct and indirect mechanisms of vegetation control by biotic and abiotic factors. Native species such as White-tailed deer (*Odocoileus virginianus)* display browsing trends influenced by seasonal fire trends and therefore benefitting from occurrence of fire instead of hindering fire (Meek et al. 2008). Fire as a regulator of herbivore range and site selection creates heterogeneity and patch contrast across a broad spectrum of environmental conditions (McGranahan et al. 2012).

In separate experimental field studies, I will investigate how 1) herbaceous plant productivity and community composition within a semi-arid savanna will respond to interactions of prescribed fire, drought, and nutrient addition (DroughtNet Experiment), and 2) varied levels of prescribed fire energy interact with mammalian wildlife herbivory to effect herbaceous plant productivity and community composition within a semi-arid savanna (Joint Fire Science Project).

Specifically, key predictions for the DroughtNet Experiment include:

1. Increase in cover of subdominant species through nutrient (N) addition.
    a) Nitrogen supplementation will increase C_3 grass dominance and increase overall biodiversity and species richness.
2. Drought treatments will favor only the most drought persistent perennial C_4 grasses, thus reducing diversity and limiting ANPP.
3. Fire combined with nitrogen treatments will stimulate herbaceous vegetation growth.
4. Fire combined with nitrogen will exhibit the greatest increases in ANPP.
    a) Greatest increase of ANPP in fire treated plots will be seen after a recovery period (2-3 years prior to initial treatment).
5. Drought will override potential increases in diversity and productivity conveyed by the other treatments to reduce herbaceous ANPP, re-sprouting ability, and survival, thereby indicating deleterious effects on the stability of the system.

Key Predictions for the Joint Fire Science Project sub-study include:

1. High fire energy treatments will cause mortality in mature resprouting woody plants (separately investigated) but will not deleteriously affect herbaceous production.
2. Moderate energy fire treatments are likely to enhance grass vegetation production and herbaceous plant cover.
3. Species richness and percent cover will be more variable after moderate fire energy treatments opposed to other treatments.

4. Exclusion of mammalian wildlife herbivores will positively affect plant species diversity and productivity, particularly in fire treatments that stimulated herbaceous productivity.

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CHAPTER II SHIFTING SAVANNA STABILITY: ASSESSING SEMI-ARID GRASSLAND DYNAMICS VIA EXPERIMENTAL MANIPULATIONS OF FIRE DISTURBANCE AND MAMMALIAN HERBIVORE IMPACTS

Introduction

Fire and herbivores play an important role in the establishment and maintenance of savanna ecosystems around the world (Bond and Keeley 2005, Fuhlendorf et al. 2009, Allred et al. 2011). Herbivores have been strong ecosystem drivers in savannas for thousands of decades, altering species diversity and richness, nutrient dispersion throughout the landscape, and reduction of tall statured vegetation (Fuhlendorf and Smeins 1999, Stahlheber et al. 2017, Bernardi et al. 2019). Fire disturbance is also an integral part of semi-arid savanna functionality and productivity (Scholes and Archer 1997a, Venter et al. 2017). Recent conceptual recognition of fire and herbivory as disturbances that have inherently coupled interactions has resulted in their being reconciled as a singular disturbance regime termed *pyric herbivory* (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009, Allred et al. 2011, Venter et al. 2017).

Pyric herbivory is an interactive phenomena driven by the constant consumption of vegetation by both fire and herbivores (Fuhlendorf et al. 2009). Though fire and herbivores affect ecosystem processes independently, the interaction between the two consumers is critically important for ecological complexity and resilience (van Langevelde et al. 2003, Allred et al. 2011). Extrinsic disturbance of fire, when combined with climate trends and soil fertility, facilitates a fire feedback essential in maintaining open grassland/canopy ecosystems (Archibald and Hempson 2016). Presence of mega-fauna throughout African savannas exhibit the same structural maintenance as fire, playing an important role in keeping these systems open canopied

(Lehmann et al. 2011, Archibald and Hempson 2016). Though both disturbances are fundamentally different, fire being a physicochemical process while herbivory is a biological process, they both influence and are influenced by local and regional vegetation patterns (Bowman et al. 2016). Fire affects grazing by altering forage patterns while grazers affect fire by altering fuel loads (Archibald et al. 2005). Changes in the rate of vegetation consumption by both herbivores and fire could throttle the grass-tree codominance and create an alternative stable-state (Noy-Meir 1975, van Langevelde et al. 2003).

Fire in savannas depends heavily on the density and flammability of available vegetation for fuel (Lehmann et al. 2011). Fire is the ultimate non-selective consumer, some of the only constraints it abides by is forage (fuel) moisture content and continuity (Veen et al. 2008). This selection variability is the defining consumer characteristic differentiating fire from mammalian herbivores. A continuous cover of grassy fine fuel permits frequent fires, which in turn creates and maintains an open canopy allowing ample sunlight to reach ground-level vegetation.

Herbivores are attracted to recently burned patches which offer quality regrowth for consumption (Fuhlendorf and Engle 2004, Koerner and Collins 2013, Burkepile et al. 2016). Recently burned areas attract grazing animals with nitrogen rich regrowth which is an important food source in the dry season (Yoganand and Owen-Smith 2014). Time since fire has been shown to be a primary factor for site selection by grazers and browsers and is seen to be more influential than slope or distance to water (Allred et al. 2011). Fire is an important influence on herbivore behavior and site selection creating shifting mosaics of vegetation patterns (Fuhlendorf and Engle 2004, Allred et al. 2011).

Savanna ecosystems maintained by pyric herbivory are under threat due to interference by human activity (Archibald et al. 2013). Archibald (2013) estimates that 20% of present-day fires occurring globally are controlled by humans and are often drastically different from ecosystem supported regimes (Archibald 2016). Alteration of fire regimes in savanna ecosystems has a negative effect on forage availability and quality for browsers and grazers (Veen et al. 2008, Archibald and Hempson 2016). Large, prescribed fires, where fire energy is generally uniform, create homogeneous grazing lawns lacking in diverse, quality forage (Fuhlendorf and Engle 2004, Bernardi et al. 2019). Application of varying fire energies and patch burning using historic return intervals will drive a more sustainable fire-grazer relationship and result in a more heterogeneous, and therefore resilient, savanna landscape.

Recurring fires strongly affect tree mortality and recruitment attempts, depending on the fire's intensity (Govender et al. 2006). Variation in fire intensity is possible during the same fire due to changing environmental conditions or fuel load continuity (Higgins et al. 2000, Govender et al. 2006). High intensity fires will top-kill most mid-tall tree species forcing regrowth from lower regions on the tree (Freeman et al. 2017, Bär et al. 2019). Under normal fire return intervals in savannas (3-6 years), these lower height regrowth areas will be consumed in future fires hindering their maturation (van Wilgen et al. 1990, Freeman et al. 2017). Extreme soil temperatures during fire events causes high mortality of tree seeds further reducing probability of woody establishment after high energy fires (Kennard et al. 2002). High intensity summer burns on the Edwards Plateau in Texas maintained the grass/tree codominance matrix while also reducing the presence of problematic species, such as cactus and small shrubs (Taylor et al. 2012a). Less intense treatments done by Taylor et al (2012) resulted in woody species overstory cover being generally maintained but the understory cover of woody species in the area increased over time therefore not halting woody encroachment. Grasses were generally less unaffected by fire intensity than by other environmental variables (weather, herbivores, legacy effects, etc.)

(Taylor et al. 2012a). Viability of savannas can be maintained by use of high intensity fire to reduce woody species encroachment while maintaining a continuous grass layer.

Maintaining disturbance regimes in semi-arid savannas is imperative for the persistence of these highly productive ecosystems. We experimentally assessed mammalian herbivore consumption and fire energy disturbance interactions and their impact on vegetation community composition. We examined the effects of varying levels of prescribed fire energy interacting with mammalian wildlife herbivory on herbaceous plant productivity and community composition within a semi-arid savanna. I hypothesized that: (1) high fire energy treatment will not deleteriously affect herbaceous production as evidenced by there being no reduction in ANPP at least 2 years after treatment implementation; (2) high fire energy treatments will show the greatest variation in community composition compared to other treatments as well due to the reduction of dominant tall-standing grasses (Collins et al. 1995); and (3) ; exclusion of mammalian wildlife herbivores will increase plant productivity using measures of above-ground biomass as a proxy for productivity.

Materials and methods

This study was conducted on the western Edwards Plateau at the Texas A&M Sonora Agrilife Research Station, (-100.574°, 30.251°). The average annual temperature ranges from 17 to 19°C. During the study duration minimum being -11°C and maximum being 41°C. This site is in a semi-arid savanna and receives between 533-711mm of precipitation per year. Yearly precipitation pattern is generally bimodal with peaks in spring and fall, though it is becoming more erratic. Precipitation patterns throughout the duration of the experiments were not uniform as shown in Figure 1. Average precipitation in the area is 556.3 mm, but this was exceeded in

2018 (586.5 mm), 2019 (558.8 mm), and 2020 (594.106). Pre-treatment year, 2017, experienced drought-like conditions only receiving 428.752 mm. Historic fire return intervals are between 1-12 years, being more common in late summer and late winter.

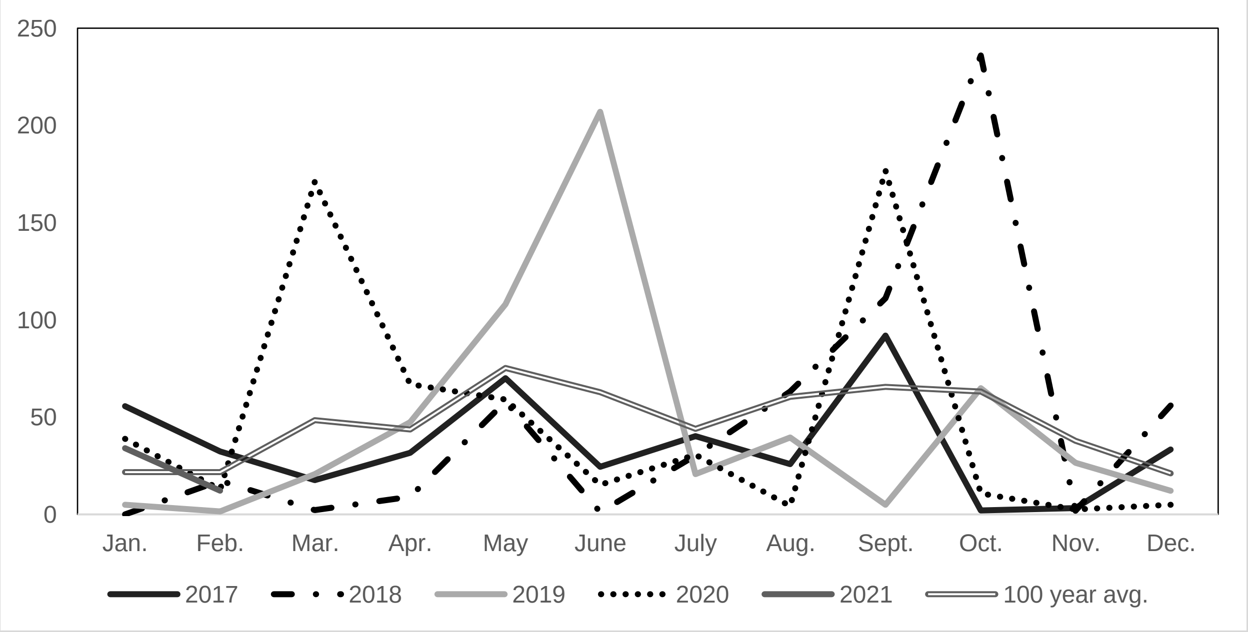

Figure 1 Monthly precipitation totals (mm) during years preceding and during the study

The soils are in the Tarrant soil series, characterizes as cobbly silty clay in the upper horizons. Exposed limestone bed and medium to large rocks are common in this area. The vegetation horizon is a continuous grass layer interspersed with large, long-lived trees and occasional shrubs and succulents. The dominant grass species are *Hilaria belangeri, Nassella leucotricha*, *Bouteloua curtipendula,* and *Aristida purpurea.* Dominant tree species are *Quercus spp., Juniperus spp.,* and *Prosopis glandulosa.*

Experimental design

Seventy-two 100m^2 plots were established centered on a mature (10+ year) *Prosopis* *glandulosa*. The seventy-two whole plots were then each divided into four ordinal subplots. Fire treatments were assigned to whole plots in a randomized design having three treatments (no fire, low fire energy, high fire energy), replicated 24 times. Herbivore exclusion treatment cages were assigned to subplots in a randomized design, a cage being assigned to two subplots within each whole plot and the remaining two plots served as control treatments. The study site was burned in August 2000 in a high intensity prescribed burn. Periodic, moderate grazing in the area by domesticated sheep and goats ceased in summer 2016, one growing season prior to the establishment of this project. Mammalian wildlife grazers and browsers such as native *Odocoileus virginianus (* white-tail deer) and *Lepus californicus* (black-tailed jackrabbit), and invasive *Axis axis* (axis deer) continued to freely access the area.

Areas surrounding the study site were burned in spring 2018 to consume naturally available fuel before prescriptions were carried out to improve safety for experimental burns. Each plot had a 5m wide firebreak cleared around the perimeter. Control plots received no further treatment. Low fire energy treatment plots received a layer of dry hay (61±1 kg) to achieve a continuous, low intensity fire. High fire energy treatment plots received a layer of dry hay (61±1 kg) mixed with dry juniper (201±1 kg) to achieve a continuous, high intensity fire. Plots were ignited using a drip torch using a fire ring method. Fires were set between July 30th and August 4th, 2018.

Table 1 Fuel additions and consumption at the plot level

	Mean±SE	**Maximum**	**Minimum**
Hay Addition (kg)	61 ± 1	96	47
Juniper Addition (kg)	201 ± 1	218	197
Fuel consumed (low-energy; kg)	55 ± 1	80	46
Fuel consumed (high-energy; kg)	259 ± 3	294	243

Four subplots were established within four quadrants of each of the 72 100m^2 plots. The subplots were randomly assigned mammalian herbivory treatments which consisted of a wildlife exclosure fence or were a no exclosure control. Exclosure plots consisted of a circular wire-mesh fence, 0.5m in diameter constructed of 1/2 in x 2.5 ft 19-gauge metal hardware cloth. Similar hardware cloth roofs were constructed and affixed on the top of the circular fences to ensure exclusion of vertebrate herbivory. Equivalent plots without a wire cage exclosure were permanently established to serve as controls.

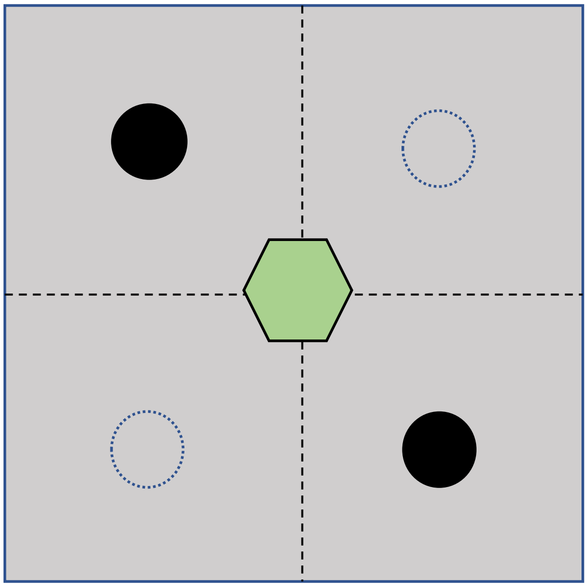

Figure 2 Visual representation of plot layout. Sizing not to scale. The green hexagon represents a mature mesquite tree at the center of all plots. The plot is divided into four subplots. The black circles represent the herbivory exclusion cages; dashed circles represent control sampling area.

Sampling

One year post experiment establishment (April 2019), one exclosure and one no-exclosure subplot were selected randomly for above-ground biomass harvesting. Exclosure cages were removed, and vegetation was hand-clipped to soil level, placed in paper bags and dried at 60°C for ~24hrs prior to weighing. No-exclosure, uncaged subplots were clipped in the same manner using a 0.5m diameter circular mold to mimic the caged area in adjacent subplots. This process was repeated in year 2 (August 2020) on the two unharvested plots.

Vegetation community composition was collected from each cage or uncaged per plot and recorded to the nearest 5% cover in winter 2018, spring 2019, and summer 2020. Cover percentages were later transformed into Daubenmire Classifications for computational modelling. Classifications were as follows:

Cover Classification	Percent Cover	Midpoint of Ranges
1	0-5%	2.5%
2	5-25%	15%
3	25-50%	37.5%
4	50-75%	62.5%
5	75-95%	85%
6	95 - 100%	97.5%

Statistical Analysis

Both 2019 and 2020 biomass data failed to meet assumptions of normality for analysis of variance models. I fit normal models for both years and assessed residual versus fitted models and quantile-quantile plots. Due to lack of fit to the normal model, histograms of 2019 data were again visually assessed, and it was determined a gamma regression would be a better fit. Residuals vs. fitted plot for the gamma distribution showed no pattern. Data from 2020 fit a normal distribution, checked by an Anderson-Darling test ($p<0.0001$). Our split-plot design, herbivory treatment nested as subplots within the fire treatment, applied at the whole plot level, required a mixed-effect model that allows for inclusion of “Plot” as a random effect to account for “within-subject” error (SAS Institute Inc. 2021). Data from 2019 was analyzed using R Studio (R Core Team 2021), using glmmADMB package to fit a generalized linear mixed model with gamma distribution, log link (Fournier et al. 2012). The model included biomass as the response variable, fire treatment, herbivory treatment, and their interaction as fixed effects and a unique identifier for 'plot' as a random effect. Biomass data from 2020 were analyzed with a mixed effect model with a Gaussian distribution using *Fit Model* in JMP Pro 15.0, personality 'mixed model'. The fixed effects were herbivory treatment, fire treatment, and their interaction as fixed effects, and a unique identifier for 'plot' as random effect (SAS Institute Inc. 2021). For all models, control treatments were used as reference variables.

Community composition data were assessed visually using non-metric multidimensional scaling. NMDS was chosen for ordination as it allows for the selection of dissimilarity measures appropriate for assessing plant community data and is based on sample rank (Zuur et al. 2007). It has been found to accurately represent dissimilarity among community composition within plots (find citation). I ran NMDS for each year of the study separately and visually assessed differences in community composition among fire treatments and between herbivory treatments. I statistically assessed plant community composition differences among treatments using permutational multivariate analysis of variance (PERMANOVA) with fire treatment, herbivory treatment, and their interaction included as terms in the model. I assessed homogeneity of variance separately for fire treatment and herbivory treatment using a multivariate analog of Levene's test. Ordination plots for both years were created using R Studio, using metaMDS from the vegan package with k=4, trymax=1000, distance= bray. PERMANOVA was run with 999 permutations, using Bray-Curtis distance as well (Oksanen et al. 2020). I used Betadisper to test for homogeneity and permutation multivariate analysis of variance (PERMANOVA) based on the Bray-Curtis dissimilarity was implemented on community composition data using vegan package function adonis (Oksanen et al. 2020). Three species were excluded from 2019 community composition data, *Oxalis stricta, Berberis trifoliolata,* and *Vine A,* for showing undue influence on ordination plots. They were found in so few plots that they completely defined a distinct axis and no other differences were able to be assessed. *Berberis trifoliolata*, and *Vine A* were only found in a single subplot and therefore it was excluded as well.

Results

Aboveground productivity response to treatments

Herbivory treatment was the only significant variable in models of biomass production in both 2019 and 2020 ($p<0.05$,

Table **2**). Mean difference between biomass collected in caged and uncaged plots in 2019 was about 75 g/m^2. The difference in biomass between caged and uncaged plots in 2020 was slightly less than in 2019, ~ 73 g/m^2. In 2019, holding all other variables constant, caged plots had 2.05 times more biomass than uncaged plots.

Though fire treatment did not have a significant effect on aboveground production of biomass, differences in biomass between 2019 and 2020 is notable. Mean biomass in 2019 for fire treatment plots was 112.6 g/m^2 for control, 99.5 g/m^2 for low energy, and 136.2 g/m^2 for high energy. Mean biomass in 2020 for fire treatment plots was 258.8 for control, 232.7 for low energy, and 185.0 for high energy. When differentiating biomass by functional group (forbs and grasses), 2020 had considerably skewed proportions compared to 2019. 2019 grass/forb proportions were relatively close to 50/50 for all treatments. High energy fire had the most different biomass proportion with 36% grass weight and 64% forb weight. 2020 biomass was relatively consistent across treatments as well with most grass/forb proportions being 90/10, (Figure 4Figure 5, Table 3). High energy treatment showed a drastic compositional proportion shift from 2019 to be comprised of 74% grass weight and 26% forb weight. High fire energy treatment plots had the highest recorded mean in year 1 samples and alternatively the lowest in year 2 sample plots (Figure 3).

When differentiating biomass by functional group (grasses and forbs), cage significantly affected both grasses and forbs in 2019 and 2020. Fire had significant effects on forbs in 2019 and grasses in 2020 (Table 4). No interactive effects of herbivory and fire treatments was shown for either functional group at either sampling time.

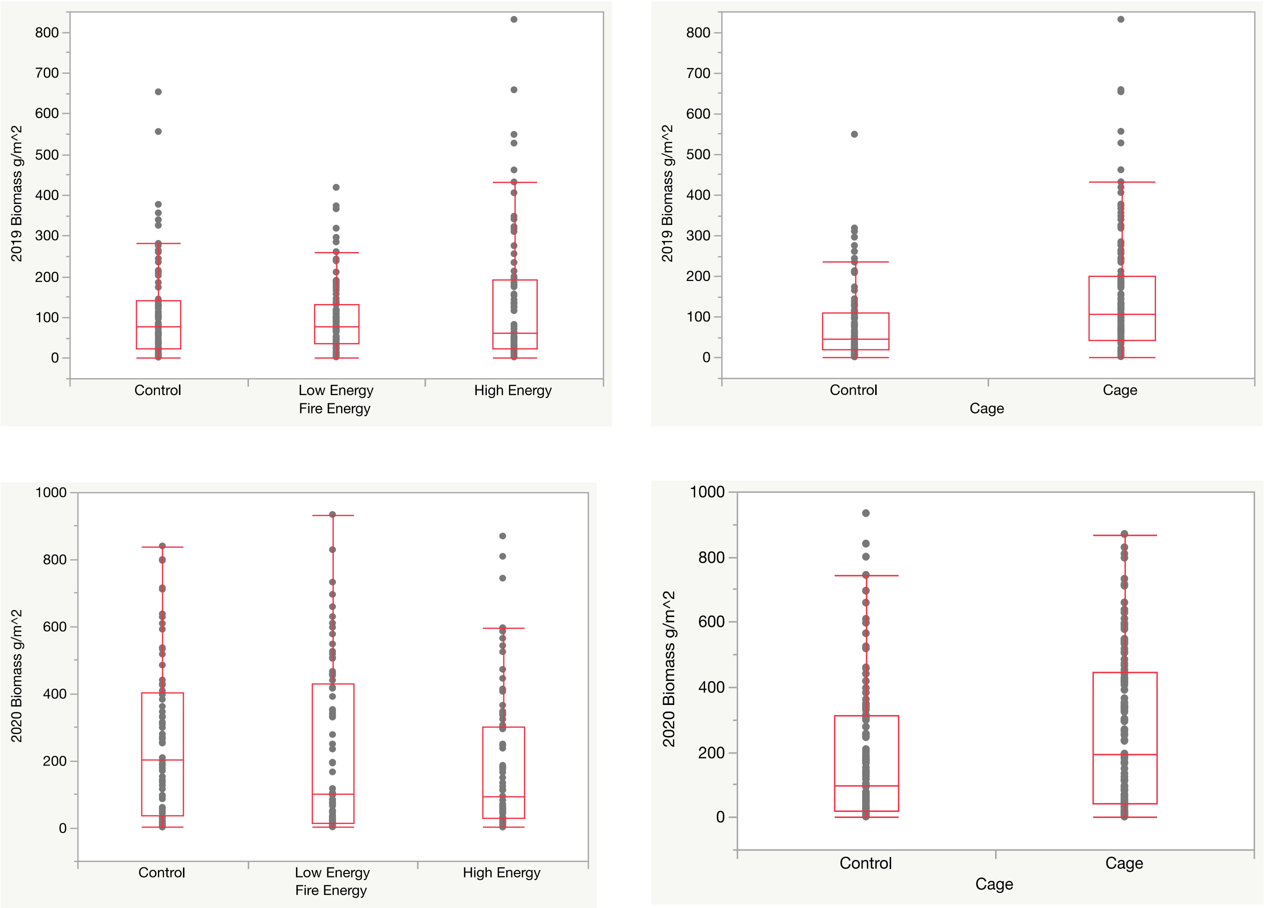

Figure 3 Boxplots for all individual treatments in year 1 (2019) and year 2 (2020)

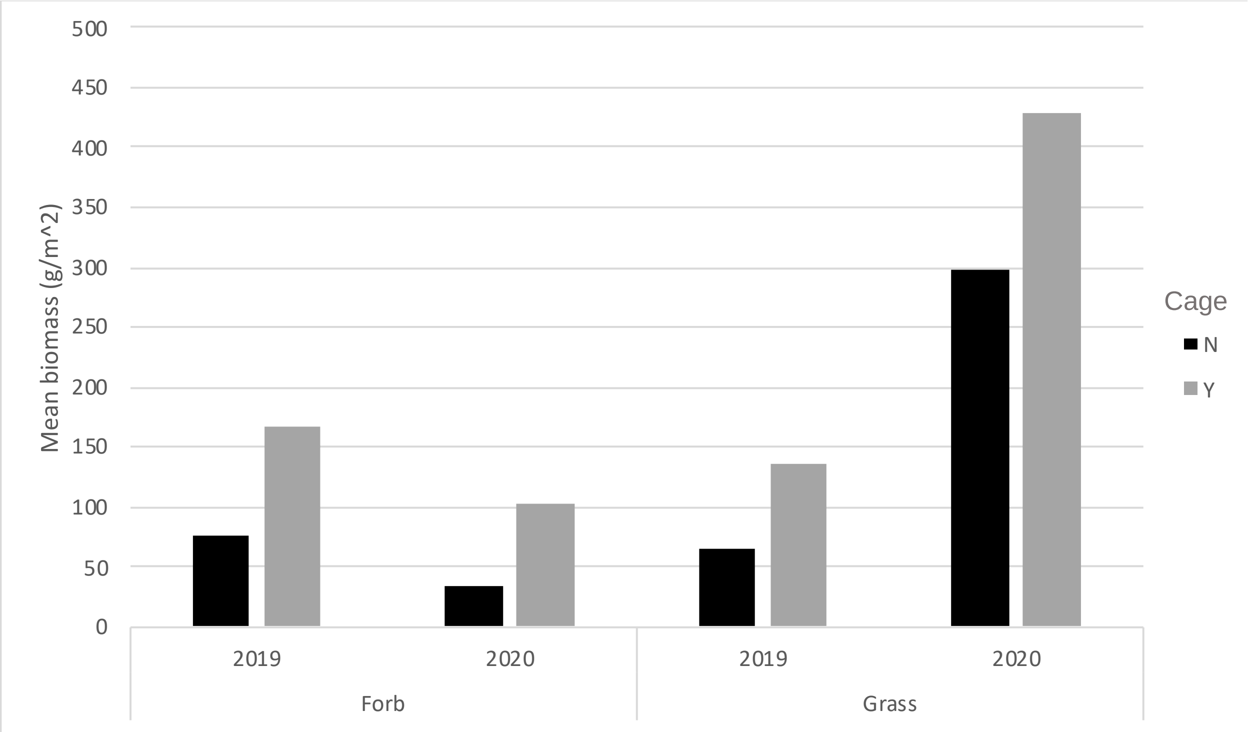

Figure 4 Mean biomass of year 1 (2019) and year 2 (2020) samples focused on herbivory exclusion/inclusion. "N" indicates no exclusion cage, "Y" indicates yes exclusion cage.

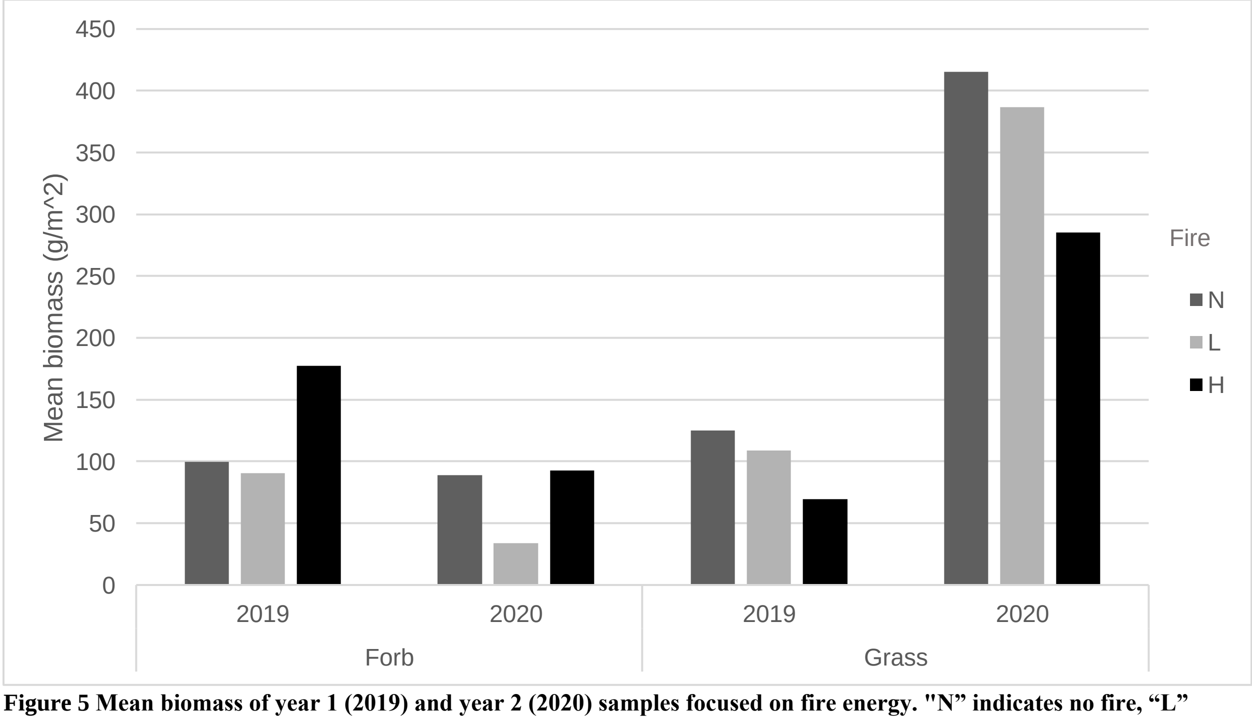

Figure 5 Mean biomass of year 1 (2019) and year 2 (2020) samples focused on fire energy. "N" indicates no fire, "L" indicates low fire energy, "H" indicates high fire energy.

Table 2 Coefficients table for 2019 gamma regression model. Reference variables were set as 'UNCAGED' for herbivory treatment and "CONTROL/UNBURNED' for fire treatment.

BIOMASS 2019				
PREDICTORS	*Estimates (odds-ratios)*	*Conf. Int (95%)*	*z-Value*	*p-Value*
(INTERCEPT)	147.31	106.83 – 203.14	30.45	**<0.001***
CAGE (YES)	2.05	1.30 – 3.22	3.09	**0.002***
FIRE ENERGY (LOW)	1.04	0.66 – 1.64	0.16	0.869
FIRE ENERGY (HIGH)	0.86	0.54 – 1.36	-0.65	0.518
CAGE (YES) * FIRE ENERGY (LOW)	0.78	0.41 – 1.49	-0.74	0.456
CAGE (YES) * FIRE ENERGY (HIGH)	1.42	0.74 – 2.70	1.06	0.289
OBSERVATIONS	144			

Table 3 Mean biomass of grasses and forbs in 2019 and 2020, biomass displayed in g/m^2

2019				
Treatment	**Mean Grass Biomass** (g/m^2)	**Std. Error**	**Mean Forb Biomass** (g/m^2)	**Std. Error**
Unburned / Control	124.8	17.0	99.5	19.8
Low Energy Fire	108.7	17.0	90.3	19.8
High Energy Fire	94.9	17.0	177.6	19.8
Uncaged / Control	73.7	13.9	79.0	16.2
Cage	146.6	13.9	157.4	16.2
2020				
Treatment	**Mean Grass Biomass** (g/m^2)	**Std. Error**	**Mean Forb Biomass** (g/m^2)	**Std. Error**
Unburned / Control	373.74	28.5	51.0	19.8
Low Energy Fire	386.9	27.2	33.6	16.5
High Energy Fire	267.6	29.9	92.5	16.3
Uncaged / Control	297.3	23.1	34.2	14.7
Cage	393.6	23,5	84.3	13.8

Table 4 ANOVA table for year 1 (2019) and year 2 (2020) biomass samples separated into functional groups (forbs and grass).

2019					
Forb					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Herbivory	1	1	299793.7	16.1732	<.0001*
Fire	2	2	220950.5	5.9599	0.0033*
Herbivory*Fire	2	2	87815.88	2.3687	0.0974
Grass					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Herbivory	1	1	181135.8	13.1749	0.0004*
Fire	2	2	78650.66	2.8603	0.0607
Herbivory*Fire	2	2	50589.46	1.8398	0.1627
2020					
Forb					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Herbivory	1	1	132689.2	7.0016	0.0096*
Fire	2	2	73762.7	1.9461	0.1486
Herbivory*Fire	2	2	32902.78	0.8681	0.4231
Grass					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Herbivory	1	1	628311.2	10.0467	0.0019*
Fire	2	2	437645.6	3.499	0.0331*
Herbivory*Fire	2	2	13985.58	0.1118	0.8943

Plant Community Composition

Vegetation samples were comprised mainly of grasses and forbs, though some succulents and woody material were present they were excluded from analysis because they were only present in a few subplots. Eighty species of plants were identified within the study plots, with the majority being natives. Most frequent native species recorded were: *Nassella leucotricha* (Texas wintergrass), *Hilaria belangeri* (curly mesquite grass), *Glandularia bipinnatifida* (prairie verbena), and *Cirsium Texanum* (Texas thistle). Introduced species included: *Bothriochloa ischaemum* (yellow bluestem)*, Erodium cicutarium* (redstem filaree)*, Medicago minima* (bur clover)*, and Sida abutifolia* (spreading fanpedals). Species with more than 10% mean canopy cover in winter 2018 include: *Hilaria belangeri*, *Nassella leucotricha*, *Tridens muticus,* and *Panicum obtusum*, in order of dominance. Species with more than 10% mean canopy cover in spring 2019 include: *Medicago minima, Nassella leucotricha, Hilaria belangeri,* and *Cirsium texanum*, in order of dominance. Species with more than 10% mean canopy cover in summer 2020 include: *Bouteloua hirsuta, Nassella leucotricha, Quercus fusiformis, and Glandularia bipinnatifida* in order of dominance.

Table 5 Species mean percentage canopy cover of listed observances in order of dominance in plots where they occurred.

Winter 2018		**Spring 2019**		**Summer 2020**	
Hilaria belangeri	28.7%	*Medicago minima*	36.5%	*Bouteloua hirsuta*	70.0%
Nassella leucotricha	24.0%	*Nassella leucotricha*	34.8%	*Nassella leucotricha*	44.2%
Bouteloua hirsuta	15.0%	*Cirsium texanum*	30.0%	*Quercus fusiformis*	35.0%
Tridens muticus	13.5%	*Hilaria belangeri*	29.0%	*Glandularia bipinnatifida*	34.2%
Bouteloua curtipendula	13.0%	*Glandularia bipinnatifida*	23.2%	*Bothriochloa ischaemum*	25.0%
Panicum obtusum	12.6%	*Panicum hallii*	20.3%	*Hilaria belangeri*	22.8%
Glandularia bipinnatifida	11.4%	*Eragrostis intermedia*	18.3%	*Bouteloua curtipendula*	21.3%
Aristida purpurea	11.1%	*Hordeum pusillum*	17.8%	*Digitaria cognata*	20.0%
Croton dioicus	10.8%	*Thymophylla pentachaeta*	16.8%	*Opuntia engelmannii*	18.8%
Engelmannia peristenia	10.6%	*Thelesperma filifolium*	16.6%	*Aristida purpurea*	16.3%

In 2019, multivariate Levene's tests indicated that there were differences in variability among fire treatments with high energy plots having the greatest among-plot variability and low energy having the least (Table 5 and Table 6). There was no heterogeneity of variance detected for the herbivory treatment in 2019 or any treatments in 2020.

Table 5 Results of Levene's test for homogeneity

		DF	SUMSQ	MEANSQ	F	PR(>F)
2019	Herbivory	1	0.007	0.007	0.367	0.545
	Fire	2	0.641	0.320	19.553	3.337e-08*
2020	Herbivory	1	0.034	0.034	1.190	0.277
	Fire	2	0.172	0.086	2.277	0.105

Table 6 Tukey multiple comparison test for 2019 fire samples

	DIFF	**LWR**	**UPR**	**P ADJ**
HIGH ENERGY-CONTROL	0.065	0.002	0.128	0.038
LOW ENERGY-CONTROL	-0.098	-0.160	-0.037	0.000
LOW ENERGY-HIGH ENERGY	-0.164	-0.227	-0.101	0.000

PERMANOVA detected statistically significant differences in community composition in 2019 and 2020 among fire energy treatments (

Table 7). Ordinations of subplots in species space are depicted in Figure 5. The centroids of each level of fire-energy treatment are labelled and each plot is connected to its centroid with line segments to show the range of plot spread over ordination spaces for each level (control, low, and high fire energy). Treatment centroids separated in ordination space from others signals a difference in community composition. In Figure 6A, high-energy fire plots separate from other treatments along the NMDS-2 axis along with several species, indicating that there are species that are associated more often with high energy plots than control or low-energy plots. 2020 data (Figure 6B) show the same trend, but to a lesser degree. There were no differences related to herbivory or the interaction of fire and herbivory. Ordinations showing species associated with the different levels of fire-energy treatment and herbivory treatments have been included in the appendix (Appendix A Figure 13 **NMDS species ordination 2019** and Figure 14).

Table 7 Permutational multivariate analysis of variance test for difference in group centroids within multivariate space based on canopy cover.

		DF	SUMSQ	MEANSQ	F.MODEL	R2	PR(>F)
2019	Fire Energy	2	2.890	1.444	4.406	0.060	0.001*
	Herbivory	1	0.343	0.343	1.046	0.007	0.377
	Fire*Herbivory	2	0.336	0.167	0.511	0.007	0.988
	Residuals	135	44.274	0.327		0.925	
	Total	140	47.843			1.000	
2020	Fire Energy	2	2.906	1.452	5.521	0.073	0.001*
	Herbivory	1	0.424	0.424	1.611	0.010	0.120
	Fire*Herbivory	2	0.421	0.210	0.800	0.010	0.610
	Residuals	136	35.786	0.263		0.905	
	Total	141	39.537			1.000	

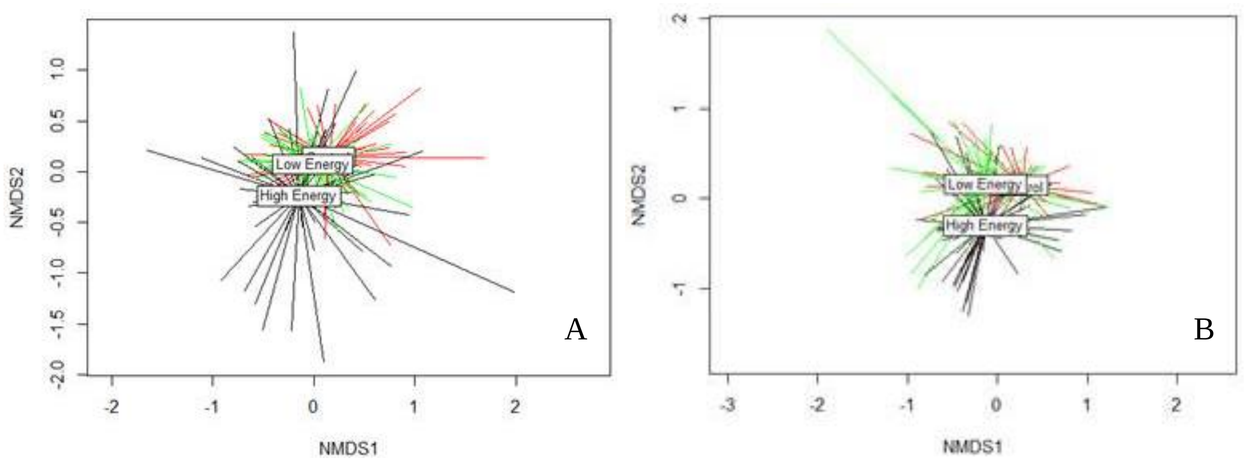

Figure 6 NMDS ordination plots of plant community composition. A) Four-dimensional ordination (stress=0.130) of 2019 samples B) Four-dimensional ordination (stress=0.120) of 2020 samples. Labels depict plot centroids in species space. The rays show the range of plots in species space for each fire treatment; black shows the range of high fire energy plots, green of low fire energy plots, and red of control plots

Discussion

Aboveground productivity response

Our evaluation of the interaction of fire energy and herbivory provides new insight to the influence of a combination of native and non-native grazers and browsers on vegetation regrowth after fire of varied energy levels. Our results indicate that, on a small temporal scale, high fire energy treatments do not deleteriously effect vegetation productivity either by directly reducing subsequent herbaceous production or indirectly by increasing herbivore attraction to burned areas. However, the combined grazing pressure of both native and non-native mammalian herbivores can substantially reduce savanna herbaceous biomass. In the first two years following treatments, 2019 and 2020, standing biomass only differed between herbivory treatments–

herbivore access versus exclusion. This result was expected given the large population of mammalian herbivores in the area, though these results merited further analysis because of the non-conventional absence of livestock herbivory in the region.

Introduction of exotics to the Edward's Plateau in the 1930's has caused a hierarchical shift in dominant ungulate species throughout the region (Henke et al. 1988). Fire occurrence influences the movement of these species by changing cover type and forage availability (Fuhlendorf et al. 2009, Cherry et al. 2018). White-tailed deer experience nutrient deficiencies when forced to consume only grasses, therefore they might be deterred from high energy burned areas where woody browsing material is removed (Henke et al. 1988, Karlin and Rankin 2016). Indian axis deer (*Axis axis)* have become increasingly more common because of their ability to shift browsing and grazing patterns depending on forage availability (Elliott and Barrett 1985). Increases in herbaceous material in high energy burned areas may simulate 'magnet effects' for axis deer while simultaneously deterring native white-tail deer (Archibald et al. 2005, Archibald and Hempson 2016). Grass biomass removal by herbivores limits the potential to conduct extreme fires needed to induce woody plant mortality (Higgins et al. 2007a). Though reduction of browsing may also have a negative effect on fire intensity potential by allowing more woody growth that hinders flammable herbaceous understories (Trollope 1982, van Langevelde et al. 2003). This ecological shift is prevalent in savannas that have experienced heavy livestock grazing which decimate fine fuel loads breaking the fire feedback loop allowing encroachment of woody plants in pasturelands (Roques et al. 2001). A shift in dominance from native browsers to non-native grazers in this savanna ecosystem could potentially uncouple the essential pyric herbivory interaction needed to maintain a grass-tree codominance.

Large herbivores can strongly impact plant regeneration and productivity not only by manual removal via consumption but also indirect effects on competition (Kurten 2013, Forbes et al. 2019). Exclusion of grazers and browsers has been shown to increase forb and woody species dominance due to released herbivore consumption pressure (Ritchie et al. 1998). Decreased grass coverage increases nutrient and light availability to forbs and reduces the chances of fire recurrence to suppress woody growth (Bond and Van Wilgen 1996, Archer et al. 2017, Bär et al. 2019). Herbivore exclusion in 2019 produced 2.05 times more biomass compared to uncaged plots when fire treatment was held constant. Mean grass biomass was higher in caged plots in both 2019 and 2020 compared to uncaged plots and forb biomass was also highest in caged plots in 2019 compared to uncaged plots. Fire treatments were not found to significantly influence amount of standing biomass one- or two-years post establishment, confirming our assumption that high fire energy treatment will not deleteriously affect herbaceous production. This finding is significant for land managers who have considered using high energy fires to control shrub and tree encroachment (Twidwell et al. 2016). This suggests that two years of herbivore exclusion could have a positive impact on standing biomass available for future grazing or fuel for subsequent fires.

The most abundant species found in caged and control plots was *N. leucotricha,* which is a preferred cool season grass by most browsers and grazers (Dillard et al. 2005). *N. leucotricha* was equally abundant after high energy fires as in control and low-energy plots. This is consistent with an assessment of grass-bud dynamics for this species. In a separate project associated with this experimental study, it was found that *N. leucotricha* experience minimal bud mortality in high-energy fire plots and recover within 8-months of treatment (Hiers et al. 2021). This suggests that high-energy fires do not have significantly negative repercussions for dominant graminoid species in this system and therefore could be an appropriate restoration approach for reducing resprouting woody plants without diminishing available forage for wildlife and/or livestock.

Plant community composition

Community composition was not influenced by the interaction of fire and herbivory, but the high-energy fire treatment plots did display a unique plant community composition relative to low-energy and control plots. *N. leucotricha (Texas wintergrass)* and *E. intermedia (* plains lovegrass*)* are seen to be the only indicator species for low energy and control plots in 2020. Our fire treatments were set in summer which has been found to be a favorable burn season for *N. leucotricha* (Ansley and Castellano 2007). Clearing of litter layers and recycling of plant material nutrients is essential for C_3 plants, like Texas wintergrass, and most forbs (Blair 1997, Ansley and Castellano 2007, Ansley et al. 2010).

High energy fire was the only treatment that displayed a community composition that was significantly different from the others. Species contributing to the community difference between high-energy plots and low-energy and control plots included *Verbena hastata, Solanum sp.,* and numerous unknown forbs. Annual forbs generally increase after high intensity summer fires because of the removal of litter which creates a more favorable seedbed and higher proliferation rates (Towne and Kemp 2008). High energy fires consume tall standing grasses which may allow for expansion of forb cover without allowing C_4-grasses to dominate (Kucera and Koelling 1964, Peterson et al. 2007). High light availability favors highly flammable C_4 grass species dominance initiating a positive feedback system between savanna vegetation and fire (Bond and Van Wilgen 1996, Beckage et al. 2009, Lehmann et al. 2011). Species found in both years include *Plantago rhodosperma, Croton capitatus, and Vicia lathyroides.* The species found in the plots in both years were not surprising as they are common in savanna ecosystems and adapted for high-light availability and are resilient to fire disturbances (Tester 1996, Peterson et al. 2007). High energy prescribed or wildfires shift plant communities towards more forb dominant while reducing overgrown woody species in the area, increasing forage quality for wildlife and maintaining an open canopied landscape.

Lack of compositional response to herbivore treatments could be the result of multiple factors. Small plot sizes could potentially not show impact of free moving grazers and browsers. Our study primarily focused on the exclusion of free-range, native and non-native deer species as opposed to some herbivory studies that focused on strictly cattle or caged bison (Koerner et al. 2014) and native and domesticated mammalian herbivores are known to have important differences in their vegetation consumption impacts (Hartnett et al. 1997). As discussed above, native white-tailed deer are predominant grazers while non-native axis deer are mixed feeders (Elliott and Barrett 1985, Meek et al. 2008). While no other consumer was identified or observed, grazing pressure was possibly too low due to only axis deer consumption and therefore community composition was not affected (Knapp et al. 2017).

Ultimately, this study has shown that high energy fires can be used for brush control with little to no negative effect on herbaceous regrowth (Hiers et al. 2021 and this study). Presence of non-native axis and native white-tailed deer substantially reduced standing biomass, decreasing grazing potential for livestock and fuel loads for subsequential fires. This will be useful to land managers whose goals are to reduce woody encroachment while preserving their pasturelands for livestock grazing or wildlife management. Continuation of exclosure experiments is needed to further investigate interactive effects of fire and herbivore on larger temporal and physical scales.

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CHAPTER III COMMUNITY RESPONSES TO PROLONGED DROUGHT, NITROGEN SUPPLEMENTATION, AND FIRE IN A SEMI-ARID SAVANNA

Introduction

Precipitation, nutrient availability, and fire are fundamental drivers of vegetation structure in semi-arid savannas (Scholes and Archer 1997a, Kraaij and Ward 2006). The historical dynamics of these processes are predicted to be altered in the near future due to changing climate patterns (Fay et al. 2002), increased anthropogenic nutrient deposition (Ibáñez et al. 2018), and continued interference of natural fire regimes (Bond and Keeley 2005). Human-induced disturbances put many vital ecosystem functions at risk such as forage and grazing sites for livestock, carbon sequestration potential, and maintenance of biodiversity (Ansley and Castellano 2006, Higgins et al. 2007b, Hoogesteijn and Hoogesteijn 2010). Understanding how factors such as precipitation, nutrients, and disturbances alter herbaceous cover in a savanna is imperative for conserving biological diversity and critical savanna ecosystem functions. Changing climates, disturbance regimes, and nutrient cycles could have major impacts on the maintenance and sustainability of semi-arid savannas around the globe.

Human activities have altered global atmospheric and hydrologic processes which are predicted to significantly modify precipitation and nutrient cycles in the near future (Karl and Knight 1998, Easterling et al. 2000). Global climate change models predict more concentrated precipitation events followed by prolonged drought conditions (Knapp et al. 2008, IPCC 2020). Semi-arid savannas are particularly sensitive to abnormal drought conditions resulting in significant reduction of above-ground net primary productivity and diversity (Prieto et al. 2009, Knapp et al. 2017, Lei et al. 2020). More severe and frequent drought conditions could cause major vegetation mortality and shift community dynamics and composition to new functional states (Twidwell et al. 2014, Wonkka et al. 2016, Case et al. 2019). Extreme drought events could potentially shift savanna grass-tree matrices to a grass dominated system or induce desertification and cause the ecosystem to collapse altogether (Kassas 1995, Ludwig and Tongway 1995, Bestelmeyer et al. 2013). Current savanna research suggests that net primary productivity, diversity, and therefore resilience have a linear relationship with precipitation rates and the uncertainty projected by future climate models could eventually lead to destabilization of ecosystem functions (Ansley et al. 2013, Jin et al. 2018, Moore et al. 2018).

Increases in atmospheric nitrogen deposition to terrestrial ecosystems are primarily due to high rates of anthropogenic sourced N emissions (Zhang et al. 2018) derived primarily from fossil fuel combustion and volatilization of N from fertilized croplands. Increased N deposition from anthropogenic activities is exposing ecosystems worldwide to unprecedented levels of N (Ibáñez et al. 2018). Nitrogen is a primary regulator of ANPP in semi-arid sites therefore it is expected with elevated N availability that ANPP will increase in these sites (Bennett and Adams 2001, Snyman 2002, Mbatha and Ward 2010). Though ANPP is anticipated to increase with increased N availability, diversity and species richness is found to decrease even with trace amounts of additional nitrogen (Clark and Tilman 2008, Zeng et al. 2010, Borer et al. 2014, Pellegrini 2016, Seabloom et al. 2021).

A decline in savanna heterogeneity can lead to degradation of ecosystem functioning, reduce capability to respond appropriately to disturbances, and increase dominance of undesirable species (Clark and Tilman 2008, Guo et al. 2018). In nutrient limited ecosystems, plants have adapted to grow slowly and require fewer nutrients causing these plants to be at higher risk of being out competed with projected higher nutrient deposition (Chapin 1991, Seabloom et al. 2015). A shift from C_4 grass dominance to C_3 grass and forb dominance is predicted in many savannas experiencing higher levels of N deposition (Sage et al. 1987, Avis et al. 2003, Reich et al. 2003).

Burning in semi-arid savannas exerts strong structural control and is beneficial for maintaining grass-tree codominance (Higgins et al. 2000, Singh et al. 2018). Fire in savannas is responsible for limiting establishment of woody plants helping maintain grass coverage of opened canopy and ground areas (Beckage et al. 2011, Twidwell et al. 2016). Human-induced fire suppression allows for the accumulation of woody vegetation cover, low nutrient cycling, loss of land use potentials, and decreases compositional heterogeneity (LeVine and Crews 2019, Meyer et al. 2019). Burning significantly increases post-fire ANPP and diversity by initially reducing dominant species allowing fire-stimulated and rare species to flourish (Brockway and Lewis 1997, Brockway et al. 2002, Towne and Craine 2014).

Fire, nutrients, and water availability are the most important factors determining plant production and distribution in every ecosystem, though their interactive effect in savannas is generally unknown (Polis 1999). As these key determinants of ecosystem functionality are anthropogenically altered, global implications are sure to follow. The objective of this study was to investigate how interactive ecosystem drivers' effect ANPP, diversity, and community composition over time. To answer these questions, I used rainout shelters, supplemental N additions, and prescribed fire treatments on an herbaceous-dominated site in a semi-arid savanna in West-Central Texas, USA. Predictions were that (H1) ANPP would be increased by nitrogen-addition treatment (Seabloom et al. 2021), but decreased by fire and drought treatments, (H2) diversity will be increased by fire treatments, but a decrease in diversity is predicted for drought and nitrogen treatments, (H3) fire combined with nitrogen treatments will stimulate herbaceous vegetation growth and show the greatest increase in ANPP, and (H4) drought treatment will override potential increases in diversity and productivity conveyed by the other treatments to reduce herbaceous ANPP, and negatively affect the re-sprouting ability and persistence of certain species, thereby having deleterious effects on the diversity and productivity of the system.

Methods and materials

Study site

The study site is located south of Sonora, Texas at the Texas A&M Agrilife Research Station (-100.574°, 30.251°). The site is located in a semi-arid savanna on the western portion of the Edwards Plateau. Mean annual precipitation is ~570 mm falling bimodally distributed with peaks occurring in May − June and September – October. Mean temperature in the area is 8°C in January and 26°C in July (SRS records). Precipitation throughout the study loosely followed a bimodal pattern, though there were times of uncharacteristic amounts of rain. Differentiating peak times of precipitation between sample years can be seen in 2018, 2019, and 2020 measurements (Figure 1).

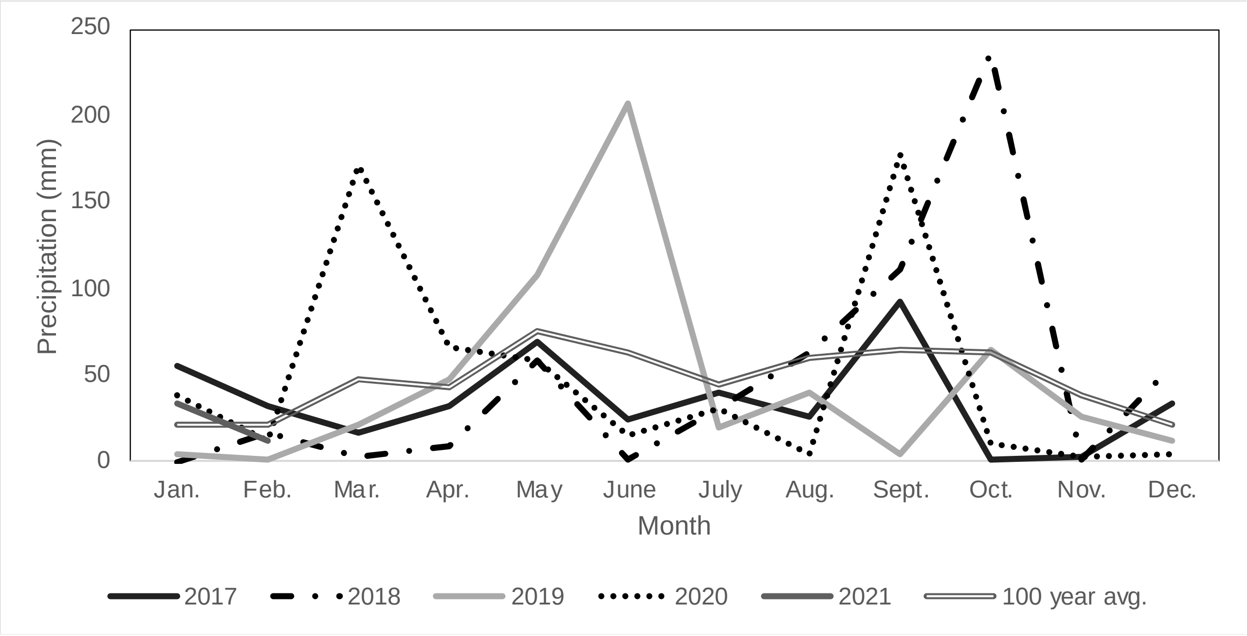

Figure 7 Monthly precipitation totals (mm) during years preceding and during the study

The major soil series is Valera clay which are derived from limestone and are moderately deep. Some plots in the southernmost part of the study area are Eckrant-Rock outcrop complex soil. Key vegetation includes live oak (*Quercus virginiana*), juniper species (*Juniperus spp*.), common curly mesquite (*Hilaria belangari*), Wright's threeawn (*Aristida wrightii*), King Ranch bluestem (*Bothriochloa ischaemum*), Texas cupgrass (*Eriochloa sericea*), sideoats grama (*Bouteloua curtipendula*), and Texas wintergrass (*Nassella leucotricha).*

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 0.33 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

Treatments were established in March 2018 and randomly assigned to 64 5x5 m plots in a 2 x 2 x 2 full factorial experimental design. The plots are situated on an herbaceous-dominated community in close proximity to each other, separated by 2 m alleyways. Fire treatments have been either prescribed ring fires or unburned control. Precipitation availability has been manipulated using rainout shelters on designated plots. Soil fertility treatments have been either ammonium nitrate addition (5g NH_4NO_3/m^2) or control. The sampling design of this study is in accordance with the International Drought Experiment protocol (www.drought-net.colstate.edu). The protocol states the site should be homogeneous, unaffected by any major disturbance within the last 3-5 years, and, but is not limited to, unmanaged ecosystems.

The study site is located on the Edwards Plateau characterized by limestone outcroppings and rolling terrain. Soils throughout the area are shallow, rocky, and heterogeneous in depth. Plant composition is predominantly herbaceous with a general absence of woody and succulent vegetation. The site is enclosed by a wildlife and livestock exclusion fence. Last occurrence of livestock grazing was more than 5 years ago, and the entire site was previously burned in 2008. No other disturbances or land management practices had been performed on the study area prior to construction of a 3m high perimeter fence in 2018 to exclude large mammalian wildlife herbivores such as deer.

Fires were conducted on 1 and 2 March 2018 using a propane vapor torch to allow for the ignition of the low fuel load. The fires were low-intensity and used to remove above-ground herbaceous biomass. Fire in dry savannas are typically low-intensity due to little small amounts of grass fuels (Kraaij and Ward 2006).

Rain-out structures were built on drought treatment plots using strips of clear polycarbonate roofing (8.28” strips) interspersed with open gaps. The roofing strips are affixed to a wooden frame/steel post structure approximately 1.5m above the soil surface. Rainout plots were trenched, and plastic barriers installed within the shelter border to a depth of 10-20” (up to ~0.5m) where permitted by rocky soil. The shelter simulates the 1st percentile drought scenario for the Sonora region. The shelter allowed 31% (175.65mm) of MAP within the plot (Hannusch et al. 2020).

Ammonium nitrate was distributed to selected plots using a broadcast spreader. We dispersed 5g NH_4NO_3/m^2 ammonium nitrate over the whole 5x5m plot area in late spring/early summer 2017, whereas 5g NH_4NO_3/m^2 was dispersed over only the center 4x4m of the plot area in late spring 2020. This change still administered the same amount of fertilizer per unit area as previous applications and took into account plot edge effects.

Sampling

Species Composition

Cover composition was evaluated in designated 1 m^2 quadrat for each plot pre-treatment and then 8, 12, 24, 30, and 36 months post treatments using a modified Daubenmire method (Daubenmire 1959). Pre-treatment sampling was at the end of the winter 2017 growing season (October) as grasses were beginning to senesce. Treatments were applied at the beginning of the spring growing season (March/April 2018) and 8- and 32-month post treatment sampling was done at the end of the winter growing season (November 2018 and 2020 respectively). Lastly, 12-, 24-, and 36-month samples were taken at the beginning of the spring growing season

(March 2019, 2020, and 2021 respectively). Vascular species representing >1% cover was recorded; individuals that did not meet this stipulation were regarded as uncommon and not recorded.

Aboveground Net Primary Productivity

A 0.25m^2 square quadrat was used for biomass clipping and collection. All 64 plots were clipped at a designated area in the northeastern section of the plot. Clipping was conducted at 4, 8, 12, and 32 months. Due to the impacts of the COVID-19 pandemic, other collections were not possible. All vegetation rooted within the quadrat was clipped to ground level then dried at 60°C for 48 hours. After drying, vegetation was separated between grasses and forb groups then weighed to the nearest 0.01g.

Statistical Analyses

Changes in community composition between treatments was assessed semi-parametrically as species cover and abundance are not normally distributed and zero-filled. This was performed using the vegan package (Oksanen et al. 2020) of RStudio (R Core Team 2021). Bray-Curtis dissimilarity index was calculated to quantify the similarity between community composition of plots using the function vegdist() for proportional canopy cover (function decostand(method=”total”)) in each plot.

Non-metric multi-dimensional scaling (NMDS) was used to visualize dissimilarities of study plot community composition using function metaMDS() and envfit(). NMDS was selected for ordination as it allows for the selection of an appropriate dissimilarity measure and is based on sample rank orders (Zuur et al. 2007). Species scored environmental fits were plotted using function wasscore() and envfit() on the NMDS plot with the standard error ellipses of treatment groups using function ordiellipse().

Treatment group dispersion was used as a metric of heterogeneity in the community as impacted by the treatments. To do this, we tested differences in group dispersion using the PERMDISP method (Anderson and Walsh 2013) implemented via the betadisper(method= “centroid”) and permutest(pairwise=TRUE) functions with 9999 permutations. We used post hoc, Tukey’s HSD in the “pairwise=TRUE” function of permutest.

Differences in ANPP between treatments over time were assessed parametrically. Biomass data was analyzed using R Studio (R Core Team 2021), using glmmADMB package to fit a generalized linear mixed model with gamma distribution, log link (Fournier et al. 2012). The model included biomass as the response variable, drought treatment, fire treatment, nitrogen treatment, sampling date, and their interaction as fixed effects and a unique identifier for ‘date’ as a random effect. Interactions that were not significant at $p<0.05$ were removed from the model. For all models, pre-treatment date and control treatments were used as reference variables.

Homogeneity of diversity was tested using Levene’s test, $p > 0.05$ (Zuur et al. 2007, van der Waal et al. 2009). Three-way factorial ANOVA was performed on Shannon diversity index values to test interactive effects of drought, nitrogen addition, and fire. Drought (shelter or control), Nitrogen (addition or control), and Fire (burned or control) were used as full factorial fixed effects using *Fit model*, standard least squares model in JMP Pro 15.0 (SAS Institute Inc. 2021).

Results

About 60 species of vascular plants were recorded through the sampling period, most being natives (Appendix Table 11). Common native species included *Eragrostis intermedia (ErIn), Nassella leucotricha (NaLe), Tridens albescens (TrAl), Plantago helleri (PlHe)*, and *Ratibida columnifera (RaCo).* Introduced species recorded include *Sida abutifolia (SiAb), Medicago polymorpha (MePo), Erigrostis superba (ErSu),* and *Erodium circutarium (ErCi).* The 10 most dominant plant species in all plots per sampling season are listed in Table 8. Species recorded in more than 5 sampling seasons are highlighted.

Table 8 Mean proportional canopy cover composition listed in descending order of dominance between pre-treatment (winter 2017) and 36 months post treatment (spring 2021). When abbreviated, plant names are given as the first two letters of the genus followed by the first two letters of the species (Appendix Table 11)

11.10.17		**11.3.2018**		**3.1.2019**		**3.12.2020**		**11.12.20**		**3.28.21**	
Species	Mean comp.	Species	Mean comp.	Species	Mean Comp.	Species	Mean Comp.	Species	Mean Comp.	Species	Mean Comp.
NaLe	56%	OxDr	27%	MePo	17%	NaLe	16%	OxSt	15%	PlMa	14%
HiBe	13%	GlBi	10%	LeGo	15%	HiBe	13%	HiBe	12%	NaLe	14%
ErIn	5%	HiBe	9%	GlBi	13%	SpCr	11%	NaLe	11%	OxSt	10%
BoCu	5%	BoCu	7%	AsNu	10%	BoCu	11%	MeMi	9%	HiBe	10%
ArWr	4%	PaHa	5%	NaLe	10%	ErIn	11%	PlMa	7%	MeMi	8%
OpPo	3%	MeOl	5%	RaCo	6%	ErPi	10%	PaCa	6%	BoCu	7%
SpCr	2%	NaLe	5%	OeTr	5%	DiAn	10%	LaPa	6%	TrAl	6%

CrDi	2%	annual forb	4%	HiBe	4%	OpEn	9%	BoCu	5%	ErTe	4%
VeCa	2%	CrMo	4%	PlRh	4%	LuTe	8%	CrMo	4%	EvPr	3%
DiCo	1%	AcPh	3%	ErCi	3%	OxSt	6%	annual grass	4%	VeHa	3%

Aboveground Net Primary Productivity (ANPP)

Biomass data did not fit a normal distribution and therefore was analyzed using a gamma distribution regression model. No independent treatments were significant in the biomass model. [Date3.19] and [Date11.20] are the only date samples significantly different from the pre-treatment sampling taken in Spring 2018. Large variations in mean biomass for both those samples are seen in Figure 8. Mean biomass steadily increases through the study duration for all treatments, though there was no independent influence from any variable on overall biomass (Appendix B Figure 18 and Figure 19).

Fire was the only variable to show a treatment*time interaction (p<0.001, Table 9). All other interactions were removed from the model to reduce statistical noise. The only reduction in biomass occurs after treatment implementation in Summer 2018 and then steadily recovers over time.

Table 9 Gamma distribution coefficients estimates table. (* indicates statistical significance, *: P <0.05, **: P <0.01, ***: P <0.001)

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	2.645	0.120	22	<0.001***
DroughtYes	-0.098	0.070	-1.41	0.159

NutrientYes	0.061	0.070	0.87	0.383
FireYes	0.079	0.156	0.5	0.613
Date7.18	-0.304	0.156	-1.95	0.051
Date11.18	0.136	0.156	0.87	0.382
Date3.19	0.797	0.156	5.12	<0.001***
Date11.20	1.315	0.156	8.44	<0.001***
FireYes:Date7.18	-0.773	0.220	-3.51	<0.001***
FireYes:Date11.18	-0.138	0.220	-0.63	0.531
FireYes:Date3.19	-0.274	0.220	-1.24	0.213
FireYes:Date11.20	-0.411	0.220	-1.87	0.062

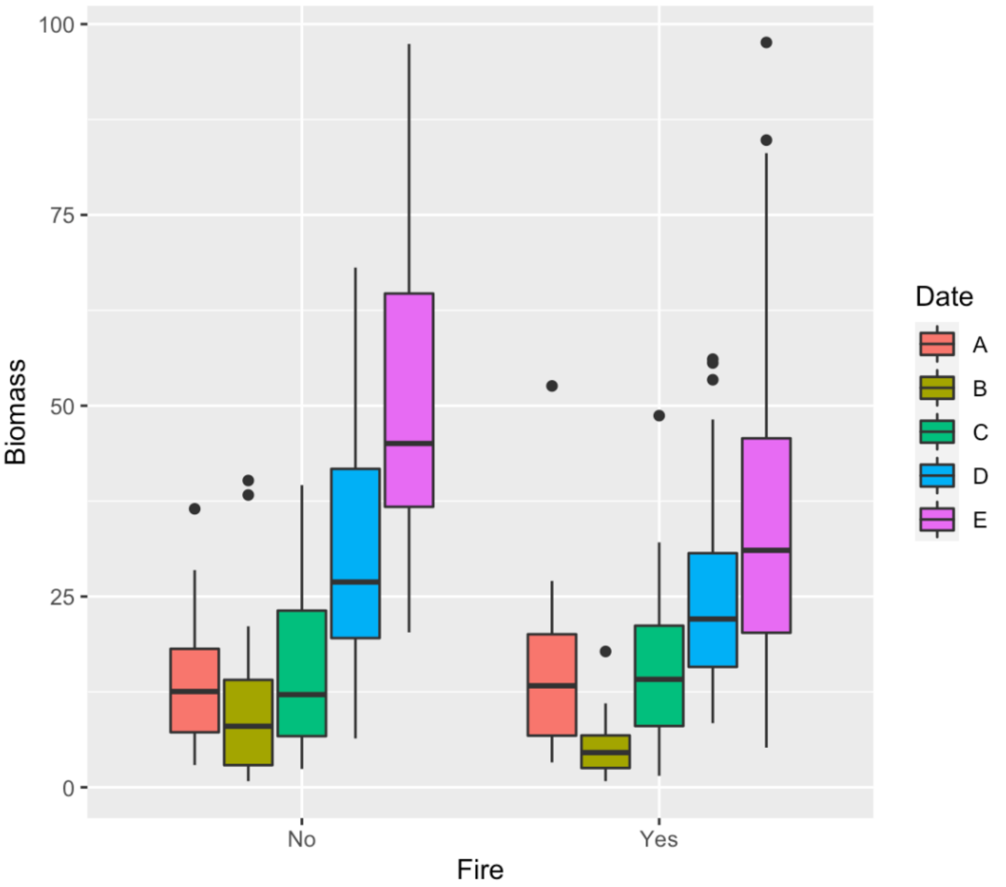

Figure 8 Overall mean biomass in fire plots over time. Date labels are as follows: A - Spring 2018, B - Summer 2018, C - Winter 2018, D - Spring 2019, E - Winter 2020. Biomass is in g/m^2.

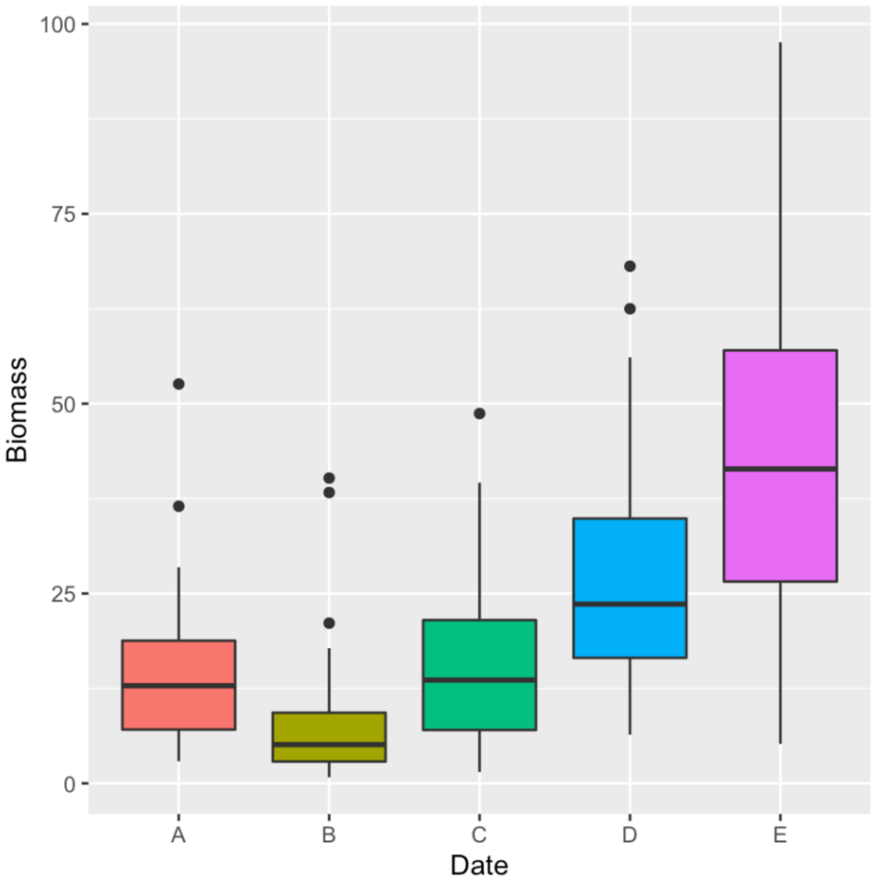

Figure 9 Overall mean biomass over time. Date labels are as follows: A - Spring 2018, B - Summer 2018, C - Winter 2018, D - Spring 2019, E - Winter 2020. Biomass is in g/m^2.

Community Composition and Diversity

The pre-treatment (winter 2017) community yielded a 2-dimensional ordination (stress=0.1235) which did not demonstrate plot groupings based on treatment groups. The winter 2018, spring 2019, spring 2020, winter 2020, and spring 2021 post-treatment samplings yielded 3-dimensional plots (winter 2018 stress=0.1742, spring 2019 stress=0.1614, spring 2020=0.1422, winter 2020=0.1393, spring 2021= 0.1512). 8 months post treatment herbaceous community composition was significantly affected by the Drought*Nitrogen*Fire interaction ($p<0.05$, Appendix B Table 12). No additional treatment effects were identified in the winter 2018 sampling. 12-month post-treatment had no significant effects on community composition in spring 2019. Drought and fire treatments had independent influence on community composition in spring 2020, 24 months post treatment ($p<0.05$). Significant differences in community composition in nitrogen and drought plots was detected for winter 2020 plots ($p<0.05$). Fire treatments influenced differences in community composition 36 months after prescription ($p<0.5$). No interactive effects of any treatment were significant to biodiversity after the winter 2018 sampling. To serve as a visual corroboration of PERMANOVA results in Table 12, NMDS plots show deviation of treatment effect on community composition (Figure 10). No individual or interactive effects of treatments significantly influenced community composition in spring 2020, winter 2020, or spring 2019. This is corroborated by the overlap of centroids (treatment labels) in the NMDS spider plots presented in Figure 11. Influential species responsible for certain treatment trends along axes are those closest to the end of treatment vectors.

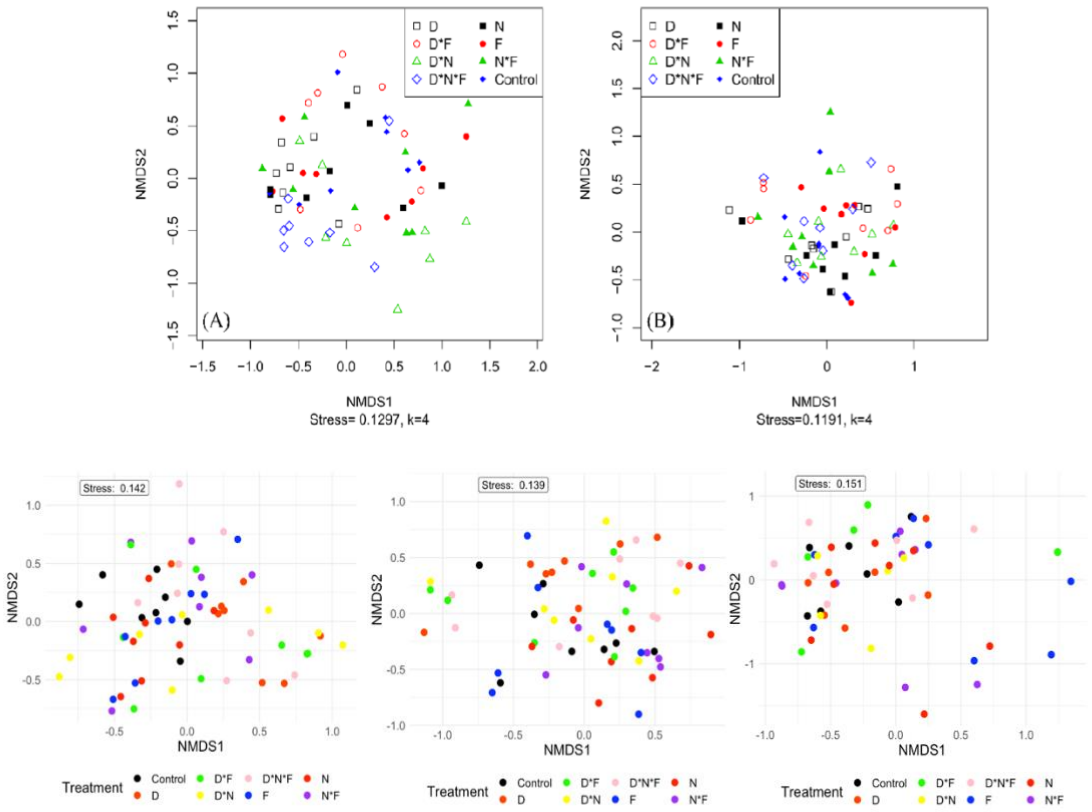

Figure 10 Non-metric multi-dimensional scaling (NMDS) ordination of plant community composition

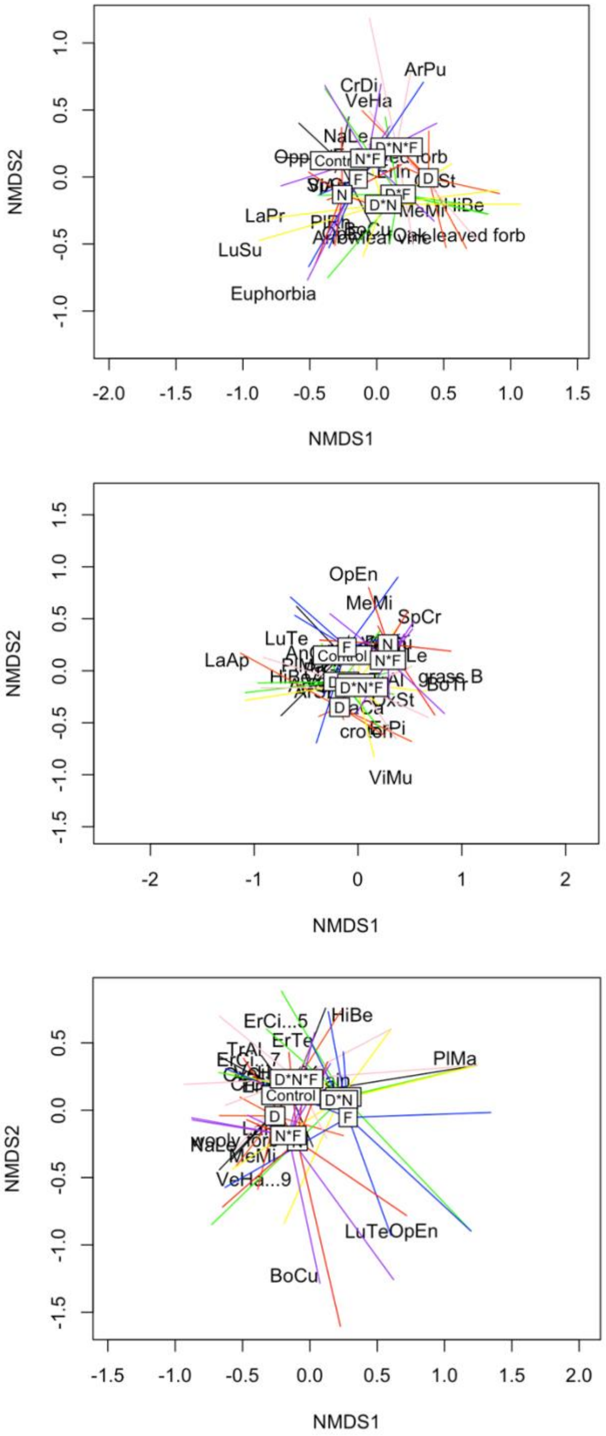

Figure 11 Species labelled NMDS plots. 3/20, 11/20, 3/21 respectively.

Nitrogen and Drought*Nitrogen plots had a significant difference between Summer 2017 and Winter 2018 ($p<0.05$). Drought significantly affected species diversity and richness between Spring 2020 and Winter 2020 ($p<0.05$). Magnitude of reduction of biodiversity was far greater in Drought[Yes] plots compared to Drought[No] plots (Table 14). Nitrogen and fire had significant effects on diversity change from Winter 2020 to Spring 2021 ($p<0.05$, Appendix B Table 13). Nitrogen[No]*Fire[No] and Nitrogen[Yes]*Fire[Yes] had less effects on reducing diversity as opposed to Nitrogen[No]*Fire[Yes] and Nitrogen [Yes]*Fire[No] (Appendix B Table 13 and Table 15 **LS means for significant Nitrogen*Fire interaction effects between Winter 2020 and Spring 2021**).

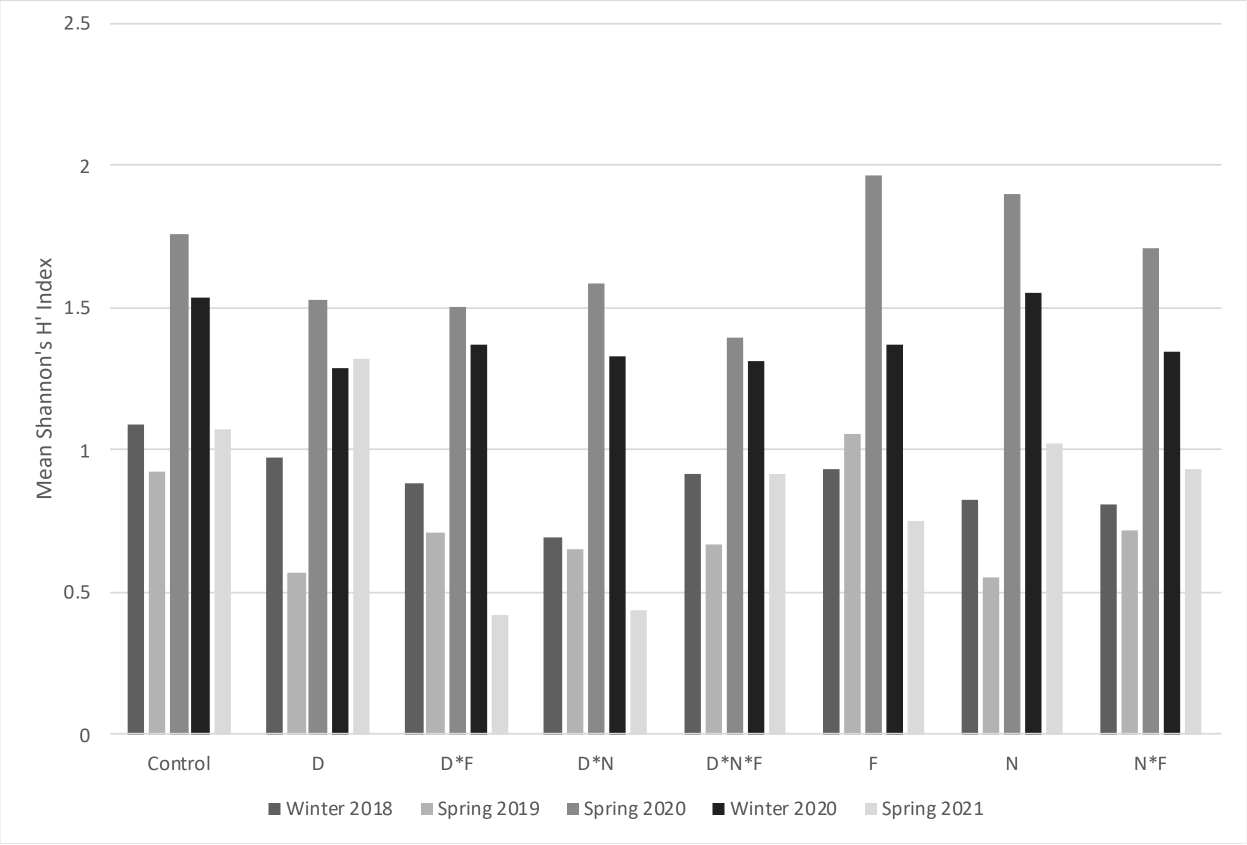

Figure 12 Mean Shannon's H'. Groups are identified with "D" signifying drought, "N" ammonium nitrate addition, and "F" that prescribed fires were conducted

Discussion

Aboveground Net Primary Productivity

Our evaluation of the interaction of drought, nutrient supplementation, and prescribed fire provides new insight to the influence of ecosystem drivers under future predicted changes. Our results indicate that fire had the most influence on ANPP while drought and nitrogen addition treatments were not significant. These muted effects of continuous drought conditions were possibly due to erratic precipitation patterns and/or presence of highly adapted drought tolerant species. While large precipitation periods in 2019 and 2020 may have overwhelmed the passive rainfall exclusion shelters and only created slight drought conditions, not to the severity of our hypothesized drought severity, there are reasons to assume this system exhibits considerable adaptation to low rainfall conditions. Numerous perennial grasses found in this study demonstrate remarkable resilience to periodic drought, including predominant species such as *Hilaria belangeri (HiBe)* and *Bouteloua curtipendula (BoCu)* (Hendrickson and Briske 1997, Evans et al. 2011). Both of these species, when present, are seen to be coupled with all drought treatments in the NMDS plots in (Figure 11 **Species labelled NMDS plots. 3/20, 11/20, 3/21 respectively.**). Evans et al. (2011) found *Bouteloua* species to be resilient to drought for at least 6 years of lowered precipitation rates. This study is within this time frame, therefore more significant effects of drought on native vegetation ANPP should be expected with the continuation of this experiment.

Fire occurrence caused a significant difference in biomass between sampling dates. Biomass collected in Summer 2018, 1-year post-establishment, was drastically lower in burned plots compared to unburned and significantly different from all other sampling dates. Immediate dieback from a fire event was to be expected but the implication of fire combined with nitrogen and drought was hypothesized to have a larger impact. This delayed effect of fire is similar to that found by Buis et al. (2009) study in South African and North American savanna grasslands where fire had no significant effect on ANPP up to 3-years post fire. Historic fire return intervals in savannas range from 3-7 years, therefore a drastic change in productivity after a single fire event is unlikely (Van Wilgen et al. 2004).

N addition had no independent or interactive effect on total ANPP across all samplings, failing to support our prediction that nitrogen supplementation will increase ANPP. Savanna soils tend to be highly deficient in many minerals, including N, resulting in native plants being efficient in nutrient use and having lower resource requirements (Chapin 1991, Pellegrini 2016). Nitrogen is frequently the most limiting mineral to plant growth and in abundant quantities can significantly stimulate biomass growth (Chapin et al. 1987, You et al. 2017). Response to nutrient addition could have also been curbed by water availability. There were extended periods of below average precipitation in 2018 and 2020 (based on 99 years SRS precipitation data). N uptake is constrained when plants are in a water-stressed state and therefore nutrient uptake and conversion to biomass may have been hindered (Freeman and Humphrey 1956, Zhang et al. 2018). Furthermore, our hypothesis that N*F interactions would cause an increase in ANPP was rejected suggesting that the aboveground productivity of this system is more water-limited than nitrogen-limited.

Overall mean ANPP progressively increased with each sampling, as seen in Figure 9, though no independent or interactive treatments were solely responsible. It was expected that interactively drought, nutrient addition, and fire would be drivers of biomass loss, though that was not manifest in the data collected for this study. The savannas of west-central Texas have been maintained historically by fire while under drought conditions, therefore suggesting an extreme resilience to perturbations as such (Walker and Noy-Meir 1982, Fuhlendorf et al. 1996). Many native savanna plants possess physiological characteristics that display moderate-extreme resilience to disturbances such as fire and drought (Schwinning and Sala Osvaldo 2004, Taylor et al. 2012a, Wilcox et al. 2020).

Community composition and diversity

Drought impacts, when they occurred, were minimal but had the most lasting effect on community composition. Differences in community structure was driven by drought independently in spring 2020 (24-months) and winter 2020 (32-months), while interactively with fire and nitrogen addition in winter 2018 (8-months). Overall diversity was found to be lower at times of water limitations, as seen with drought treatments, likely due to nutrient uptake constraints, changes in competitive advantages, and failure of drought-avoidance strategies (Chapin 1991, Sankaran 2019). Additionally, full treatment (D*F*N) effects on community composition in winter 2018 could indicate that shortly after all treatments were applied the community's ability to aptly respond to disturbance and resist community shifts failed but was able to recover shortly after.

Diversity was predicted to decrease with an increase in nutrient deposition especially coupled with drought conditions, though this was not found. Between winter samplings (2017-2018), above average winter precipitation likely played an important role in mitigating a negative community response to N addition ultimately causing no change to plant composition (Yang et al. 2011). After 32 months, nitrogen application induced a change in community composition despite diversity remaining unaffected. Nitrogen addition typically results in increased aboveground biomass, subsequently resulting in light reduction and changes in community composition due to competition for sunlight (Hautier et al. 2009, Avolio et al. 2014). Belowground nutrient allocations arising from nitrogen fertilization can also alter mycorrhizal symbiosis with C_4 grasses from mutualism to parasitism further causing drastic community shifts (Johnson et al. 1997).

In H3 we hypothesized that when fire occurs, nitrogen supplementation will decrease diversity; we found that fire and nitrogen interactions caused substantial decrease in diversity, thus supporting our hypothesis (Appendix Figure 17). A historic fire regime for the area is 4–7-year return interval consisting of low-moderate energy fires (Mayeux and Hamilton 1988, Taylor et al. 2012b). Addition of nutrients to soils by ash after fire in savannas is essential for nutrient cycling and availability (Soons et al. 2017). Increased N availability reduces diversity by favoring fast-growing species adapted to high nutrient availability therefore outcompeting less equipped species (Soons et al. 2017). A field experiment by Jensen et al. (2001) in southwestern Ethiopia found that low-severity fires in savannas cause long-term increases in inorganic N availability. Loss of climax species and reduced diversity from changes in soil nutrient levels by recycling after fire and deposition make savanna ecosystems more susceptible to state-changes (Snyman 2002). Supplementing nitrogen nutrients to recently burned areas could manifest a sort of nutrient magnification effect having detrimental reductions of diversity. With a consistent fire regimes and further nutrient addition by atmospheric deposition, savannas vegetation could become more homogeneous and less resilient to further disturbance (Blair 1997, Pellegrini et al. 2018).

Our findings suggest that prescribed fires in drought conditions with N supplementation does not evoke significant shifts in vegetation productivity or seemingly reduce ecosystem resilience to compositional change. Muted effects of drought conditions by large precipitation events demonstrates that ANPP may be able to withstand long drought periods following heavier rain events. Reduction of diversity by supplementation of N after prescribed fires should be noted by land managers interested in restoration or maintaining novel savannas. Potential impacts of N addition and fire appeared to be dependent on drought conditions, therefore management in wet or dry seasons is imperative to alternative outcomes.

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CHAPTER IV CONCLUSION

Savanna ecosystems are under threat due to altered fire regimes, woody encroachment, overutilization, and shifting weather patterns due to climate change. Shifts of important disturbance regimes could have substantial negative impacts on the economics productivity, biodiversity, ecosystem services, and historic importance of south Texas savannas. Determining impacts of key ecosystem drivers such as drought, nutrient loading, herbivore pressure, and fire on community productivity and composition is necessary to equip land managers with useful tools to combat shifting ecosystem states and maintain diverse and resilient savannas across Texas.

Burning in semi-arid savannas exerts strong structural control and is beneficial for the growth of herbaceous species and maintaining grass-tree codominance (Singh et al. 2018). Savannas are maintained by disturbances, such as fire, that depress early life-stages of woody plants, limiting establishment and allowing grass coverage of opened canopy and ground areas (Beckage et al. 2011). Fire suppression by land managers and alteration of historic fire regimes has allowed advancement of woody encroachment throughout savannas across the globe. Implementation of high energy fires to halt woody encroachment has been seen to be an effective land management strategy in this semi-arid savanna (Twidwell et al. 2016). Opposed to previous suspicion by land managers, high energy prescribed fires will reduce woody plant dominance and not negatively affect herbaceous vegetation. My study found that after high energy fire, there was no significant effect of the treatment on standing biomass 1- or 2-years post fire. There were also no effects when coupled with herbivory treatments. Though, presence of non-native axis and native white-tailed deer substantially reduced standing biomass, decreasing grazing potential for livestock and fuel loads for subsequential fires. This will be useful to land managers whose goals are to reduce woody encroachment while preserving their pasturelands for livestock grazing or wildlife management.

Our evaluation of the interaction of drought, nutrient supplementation, and prescribed fire provides new insight to the influence of ecosystem drivers under future predicted changes. More severe and frequent drought conditions, excessive nutrient deposition from burning fossil fuels and agricultural practices and suppressed or altered fire regimes could cause major vegetation mortality and shift community dynamics and composition to new functional states (Twidwell et al. 2014, Wonkka et al. 2016, Case et al. 2019). Findings suggest that prescribed fires in drought conditions with N supplementation show insignificant effects on overall savanna community composition and diversity. Individual drivers show characteristic effects through time, though interactions may manifest differently on a larger time scale. This stability could be credited to well-adapted native species who exhibit extreme tolerance to drought, nutrient supplementation, and altered fire regimes.

Overall, understanding how factors such as precipitation, nutrients, disturbances, and herbivory alter herbaceous cover in a savanna is imperative for conserving biological diversity and critical savanna ecosystem functions. These results provide insight to how resilient and stable savannas are to changing climate patterns and nutrient cycles, uncharacteristic burning regimes, and pressure of native and non-native herbivores. Short term effects of changing ecosystem drivers in this savanna were relatively insignificant, though further studies into the influence of altered ecosystem functions on a larger temporal and physical scale could give valuable insight to the larger state shift threat facing many savannas across the globe.

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APPENDIX A

Table 10 Coefficient table for 2020 mixed model

BIOMASS 2020			
PREDICTORS	*Estimates (g/m^2)*	*Conf. Int (95%)*	*p-Value*
(INTERCEPT)	221.62	193.51 - 249.72	**<0.001***
CAGE (YES)	36.97	6.81 - 67.13	**0.0166***
FIRE ENERGY (LOW)	6.56	(-32.23) - 45.36	0.733
FIRE ENERGY (HIGH)	-38.12	(-77.91) – 1.66	0.0599
CAGE (YES) * FIRE ENERGY (LOW)	2.04	(-39.77) – 43.86	0.9231
CAGE (YES) * FIRE ENERGY (HIGH)	12.23	(-30.39) – 54.84	0.5719
OBSERVATIONS	166		

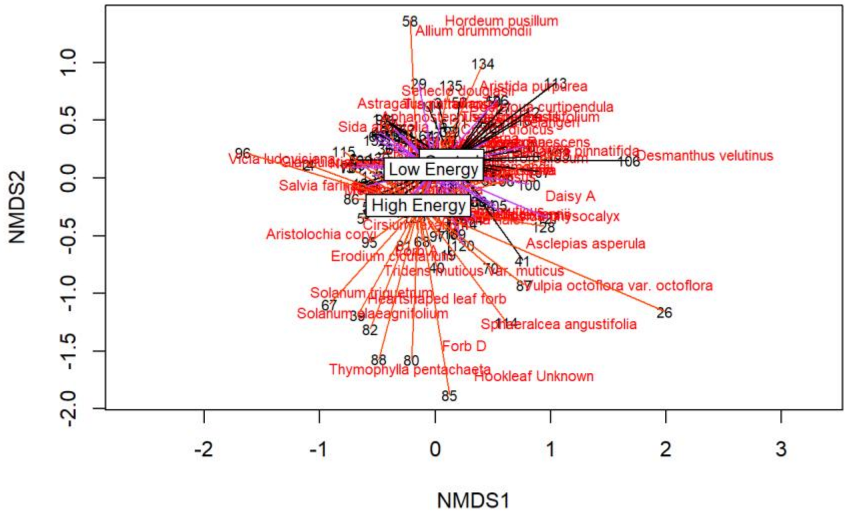

Figure 13 NMDS species ordination 2019

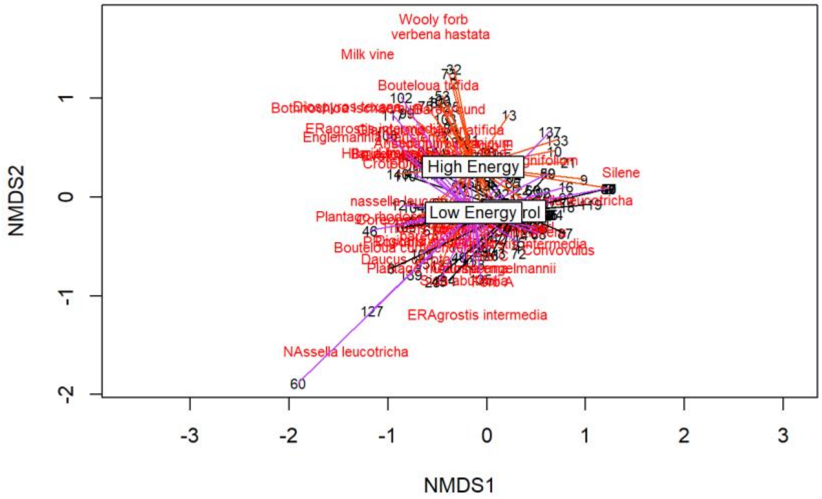

Figure 14 NMDS species ordination 2020.

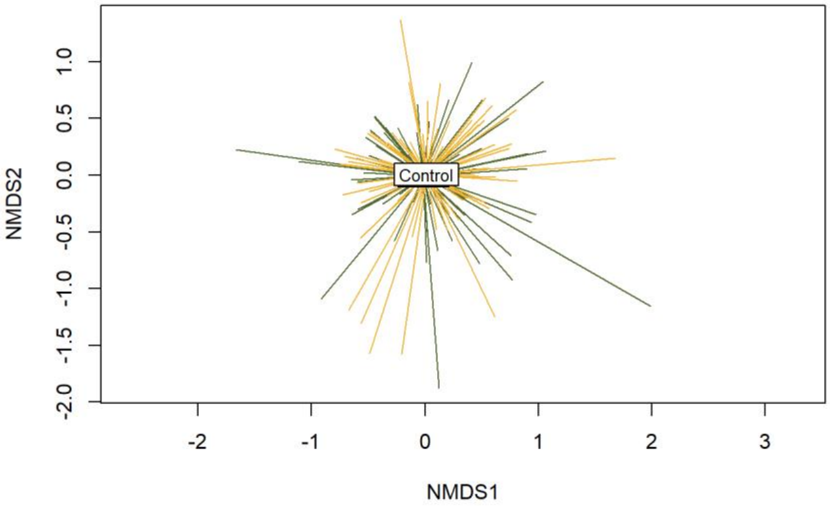

Figure 15 2019 NDMS ordination plot for herbivory treatment

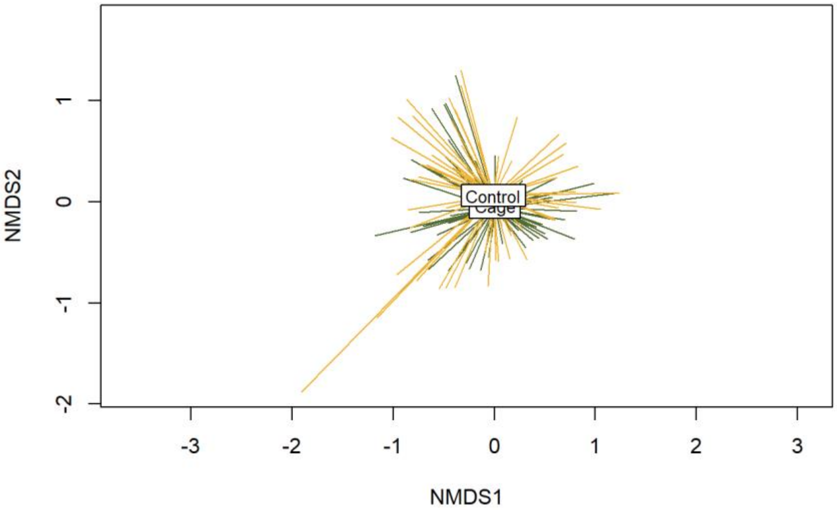

Figure 16 2020 NDMS ordination plot for herbivory treatment

APPENDIX B

Table 11 Observed species list

Taxa		**Common Name**	**Group**	**Life term**	**Provenance**
Abutilon fruticosum Guill. & Perr.	AbFr	Indian mallow	forb	perennial	native
Acalypha phleoides Cav.	AcPh	Lindheimers copperleaf			
Anemone berlandieri Pritz.	AnBe	Tenpetal anenome	forb	perennial	native
Aristida purpurea Nutt.	ArPu	Purple threeawn	grass	perennial	native
Aristida purpurea var. wrightii	ArWr	Wrights threeawn	grass	perennial	Native
Aristolochia coryi I.M. Johnst.	ArCo	Dutchman's pipe	forb	perennial	native
Astragalus mollissimus Torr.	AsMo	Wooly locoweed	forb	perennial	native
Astragalus nuttallianus DC.	AsNu	Nuttal milkvecth	forb	annual	native
Bothriochloa ischaemum var. songarica (L.) Keng	BoIs	K.R. bluestem	grass	perennial	introduced
Bothriochloa laguroides spp. Torreyana	BoLa	Silver bluestem	grass	perennial	native
Bouteloua curtipendula (Michx.) Torr.	BoCu	Sideoats grama	grass	perennial	Native
Bouteloua dactyloides (Nutt.) J.T. Columbus	BoDa	Buffalograss	grass	perennial	native
Bouteloua trifida Thurb.	BoTr	Red grama	grass	perennial	native
Bromus catharticus Vahl	BrCa	Rescuegrass	grass	annual	introduced
Centaurea melitensis	CeMe	Malta Starthistle	forb	annual	introduced

Cirsium texanum Buckl	OnAc	Texas thistle	forb	annual	native
Croton dioicus	CrDi	Grassland croton	forb	perennial	native
Croton monanthogynus Michx.	CrMo	One-seed croton	forb	annual	native
Digitaria cognata (Schult.) Pilg.	DiCo	Fall witch	grass	perennial	native
Ditaxis humilis	DiHu	Low wild mercury	forb	perennial	native
Engelmannia peristenia (Raf.) Goodman & C.A. Lawson	EnPe	Englemann's daisy	forb	perennial	native
Eragrostis intermedia Hitchc.	ErIn	Plains lovegrass	grass	perennial	native
Eragrostis superba Peyr.	ErSu	Wilman's lovegrass	grass	perennial	introduced
Eriochloa sericea (Scheele) Munro ex Vasey	ErSe	TX cupgrass	grass	perennial	native
Erioneuron pilosum (Buckley) Nash	ErPi	Hairy tridens	grass	perennial	native
Erodium cicutarium (L.) L'Hér. ex Aiton	ErCi	California filaree	forb	annual or biennial	introduced
Erodium texanum A. Gray	ErTe	Texas filaree	forb	annual	native
Glandularia bipinnatifida (Nutt.) Nutt.	GlBi	Prairie verbena	forb	perennial	native
Glandularia pumila (Rydb.) Umber	GlPu	Pink vervain	forb	annual	native
Gutierrezia sarothrae (Pursh) Britton & Rusby	GuSa	Broom snakeweed	subshrub	perennial	native
Hilaria belangeri (Steud.) Nash	HiBe	Curlymesquite	grass	perennial	native

Hymenoxys odorata DC.	HyOd	Western bitterweed	forb	annual	native
Lesquerella gordonii	LeGo	Gordon's bladderpod	forb	annual	native
Lupinus texensis Hook.	LuTe	Bluebonnet	forb	annual	native
Medicago polymorpha L.	MePo	Bur clover	forb	annual	introduced
Mentzelia oligosperma Nutt. ex Sims	MeOl	Stickleaf	shrub	perennial	native
Nassella leucotricha (Trin. & Rupr.) Pohl	NaLe	Tx wintergrass	grass	perennial	Native
Oenothera triloba Nutt.	OeTr	Stemless evening primrose	forb	annual	native
Opuntia engelmannii Salm-Dyck ex Engelm. var. lindheimeri (Engelm.) Parfitt & Pinkava	OpEn	Prickly Pear	cactus	perennial	native
Oxalis drummondii A. Gray	OxDr	Drummond's oxalis	herb	perennial	native
Panicum hallii Vasey	PaHa	Hall panicum	grass	perennial	native
Panicum obtusum Kunth	PaOb	Vine Mesquite	grass	perennial	native
Panicum virgatum L.	PaVi	Switchgrass	grass	perennial	native
Phemeranthus aurantiacus (Engelm.) Kiger	PhAu	Orange Flameflower	forb	perennial	native
Plantago helleri Small	PlHe	Heller's plantain	forb	annual	native
Plantago rhodosperma Decne.	PlRh	Red-seed plantain	forb	annual	native
Prosopis glandulosa Torr.	PrGl	Mesquite	woody	perennial	native
Ratibida columnifera (Nutt.) Woot. & Standl.	RaCo	Mexican hat	forb	perennial	native

Salvia reflexa	SaRe	Lance-leaf sage	forb	annual	native
Scutellaria drummondii Benth.	ScDr	Drummond's skullcap	forb	annual	native
Setaria reverchonii (Vasey) Pilg.	SeRe	Reverchon's Bristlegrass	grass	perennial	native
Sida abutifolia Mill.	SiAb	Spreading sida (potentially Sida abutifolia)	forb	perennial	native
Solanum elaeagnifolium Cav.	SoEl	Silverleaf nightshade	forb	perennial	native
Sporobolus cryptandrus (Torr.) A. Gray	SpCr	Sand dropseed	grass	perennial	native
Tridens albescens (Vasey) Woot. & Standl.	TrAl	White tridens	grass	perennial	native
Tridens muticus (Torr.) Nash	TrMu	Slim tridens	grass	perennial	native
Verbena canescens Kunth	VeCa	Gray vervain	forb	annual	native

Table 12 Permutational multivariate analysis of variance test for differences in group centroids within multivariate space based on canopy cover.

	Df	**SumOfSqs**	**R2**	**F**	**Pr(>F)**
Winter 2017					
Drought	1	0.152	0.011	0.669	0.607
Nitrogen	1	0.645	0.045	2.843	0.0280*
Fire	1	0.068	0.005	0.299	0.929
Drought:Nitrogen	1	0.412	0.029	1.817	0.118

Drought:Fire	1	0.108	0.008	0.475	0.792
Nitrogen:Fire	1	0.170	0.012	0.749	0.546
Drought:Nitrogen:Fire	1	0.046	0.003	0.203	0.971
Residual	56	12.702	0.888	*NA*	*NA*
Total	63	14.303	1.000	*NA*	*NA*
Winter 2018					
Drought	1	0.451	0.022	1.420	0.168
Nitrogen	1	0.558	0.027	1.758	0.064
Fire	1	0.145	0.007	0.458	0.920
Drought:Nitrogen	1	0.381	0.018	1.199	0.284
Drought:Fire	1	0.226	0.011	0.713	0.711
Nitrogen:Fire	1	0.385	0.019	1.213	0.270
Drought:Nitrogen:Fire	1	0.670	0.033	2.109	0.0275*
Residual	56	17.781	0.863	*NA*	*NA*
Total	63	20.597	1.000	*NA*	*NA*
Spring 2019					
Drought	1	0.328	0.024	1.503	0.143
Nitrogen	1	0.126	0.009	0.577	0.819
Fire	1	0.287	0.021	1.315	0.222
Drought:Nitrogen	1	0.093	0.007	0.428	0.924
Drought:Fire	1	0.175	0.013	0.800	0.611

Nitrogen:Fire	1	0.240	0.018	1.099	0.353
Drought:Nitrogen:Fire	1	0.067	0.005	0.307	0.974
Residual	56	12.230	0.903	*NA*	*NA*
Total	63	13.547	1.000	*NA*	*NA*
Spring 2020					
Drought	1	0.741	0.050	3.414	0.002**
Nitrogen	1	0.368	0.025	1.693	0.100
Fire	1	0.614	0.041	2.827	0.006*
Drought:Nitrogen	1	0.208	0.014	0.956	0.457
Drought:Fire	1	0.210	0.014	0.966	0.443
Nitrogen:Fire	1	0.340	0.023	1.568	0.121
Drought:Nitrogen:Fire	1	0.178	0.012	0.821	0.592
Residual	56	12.160	0.821	*NA*	*NA*
Total	63	14.819	1.000	*NA*	*NA*
Winter 2020					
Drought	1	0.815	0.042	2.747	0.009*
Nitrogen	1	0.637	0.033	2.147	0.017*
Fire	1	0.248	0.013	0.834	0.571
Drought:Nitrogen	1	0.172	0.009	0.581	0.841
Drought:Fire	1	0.321	0.016	1.080	0.363
Nitrogen:Fire	1	0.371	0.019	1.249	0.216

Drought:Nitrogen:Fire	1	0.292	0.015	0.985	0.441
Residual	56	16.620	0.853	*NA*	*NA*
Total	63	19.476	1.000	*NA*	*NA*
Spring 2021					
Drought	1	0.417	0.018	1.097	0.347
Nitrogen	1	0.557	0.024	1.466	0.118
Fire	1	0.724	0.031	1.907	0.019*
Drought:Nitrogen	1	0.348	0.015	0.916	0.522
Drought:Fire	1	0.189	0.008	0.496	0.936
Nitrogen:Fire	1	0.606	0.026	1.595	0.076
Drought:Nitrogen:Fire	1	0.252	0.011	0.663	0.804
Residual	54	20.517	0.869	*NA*	*NA*
Total	61	23.610	1.000	*NA*	*NA*

Table 13 Full-factorial ANOVA of the change in Shannon's H' between sampling dates (*Indicates statistical significance, *:P<0.05, **:P<0.01, ***:P<0.001)

		WINTER 2018 - SUMMER 2017			SPRING 2019 - WINTER 2018			SPRING 2020 - SPRING 2019			WINTER 2020 - SPRING 2020			SPRING 2021 - WINTER 2020		
Source	DF	Sum of Sqs	F Ratio	Prob > F	Sum of Sqs	F Ratio	Prob > F	Sum of Sqs	F Ratio	Prob > F	Sum of Sqs	F Ratio	Prob > F	Sum of Sqs	F Ratio	Prob > F
D	1	0.176	0.671	0.415	0.008	0.044	0.834	0.448	1.950	0.168	0.660	4.286	0.043*	0.029	0.071	0.789
N	1	1.399	5.333	0.024*	0.516	2.737	0.103	0.267	1.163	0.285	0.017	0.116	0.733	0.051	0.127	0.722
D*N	1	1.060	4.043	0.049*	0.030	0.161	0.689	0.461	2.006	0.162	0.007	0.047	0.828	0.270	0.665	0.418
F	1	0.092	0.353	0.554	0.012	0.065	0.798	0.431	1.876	0.176	0.010	0.071	0.790	0.274	0.674	0.415
D*F	1	0.000	0.000	0.989	0.013	0.073	0.787	0.008	0.035	0.850	0.452	2.936	0.092	0.194	0.478	0.491
N*F	1	0.036	0.137	0.712	0.063	0.338	0.563	0.217	0.944	0.335	0.173	1.128	0.292	3.116	7.662	0.007*
D*N*F	1	0.008	0.031	0.860	0.053	0.285	0.595	0.139	0.606	0.439	0.080	0.520	0.473	1.446	3.557	0.064

Table 14 LS means for significant Drought effects between Spring 2020 and Winter 2020

Level	Least Sq Mean	Std Error	Mean
No	-0.3825745	0.06938575	-0.38257
Yes	-0.1794235	0.06938575	-0.17942

Table 15 LS means for significant Nitrogen*Fire interaction effects between Winter 2020 and Spring 2021

Level	Least Sq Mean	Std Error
No,No	-0.2132523	0.15943941
No,Yes	-0.7855461	0.15943941
Yes,No	-0.7114695	0.15943941
Yes,Yes	-0.4010568	0.15943941

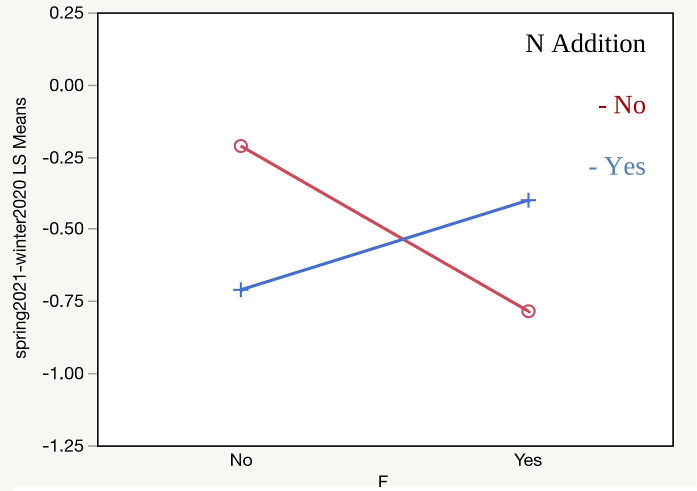

Figure 17 Spring 2021 – Winter 2020 N*F least square means plot

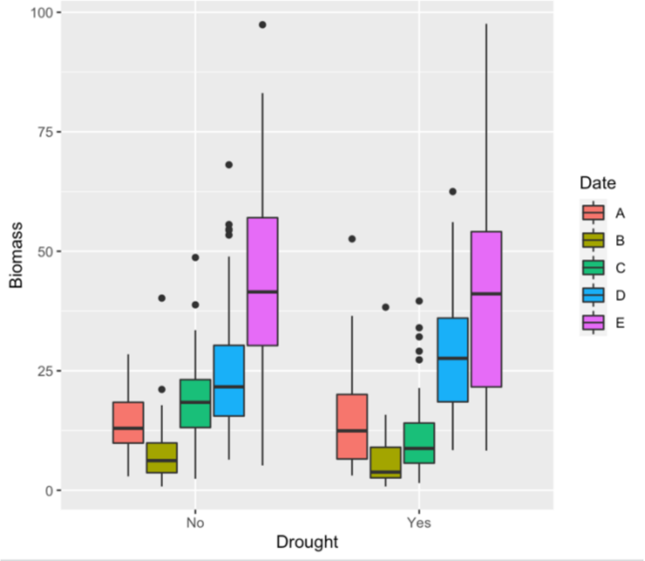

Figure 18 Overall biomass in drought plots over time.

Date labels are as follows: A - Spring 2018, B - Summer 2018,

C - Winter 2018, D - Spring 2019, E - Winter 2020. Biomass is in g/m^2

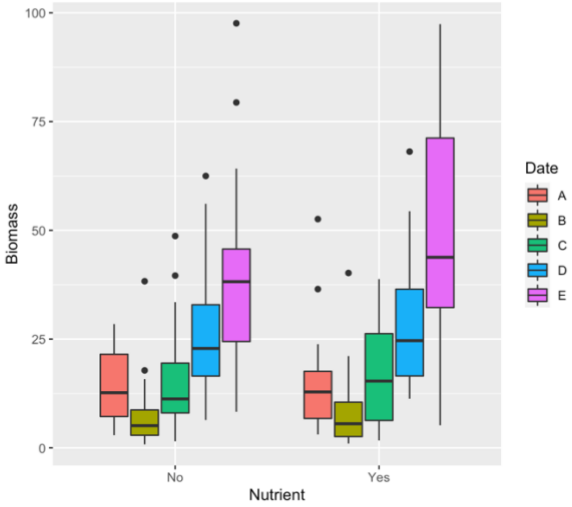

Figure 19 Overall biomass in nutrient plots over time.

Date labels are as follows: A - Spring 2018, B - Summer 2018,

C - Winter 2018, D - Spring 2019, E - Winter 2020. Biomass is in g/m