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THE IMPORTANCE OF SOIL CARBON IN LARGE-SCALE SHRUB REMOVAL PRACTICES IN THE CHIHUAHUAN DESERT

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Dedication

I would like to dedicate this work to my mom, brothers, and grandfather whose love and support made it possible for me to go to graduate school. I would also like to thank my advisor Dr. Jennie McLaren who has been a constant advocate for me and is truly the best mentor a person could have. I also want to thank my fellow lab members and graduate student peers who have been an amazing source of strength and knowledge for me during my time at UTEP. As well as my awesome committee members, whose perspectives have provided invaluable guidance both for me and this project. Additional thanks to the numerous undergraduate students and assistants whose help in the field and in the lab made it possible for me to make it to this point (you all are the best!).

Lastly, I am grateful for all my pets who have helped me stay positive (or "paw-sitive") throughout this journey.

THE IMPORTANCE OF SOIL CARBON IN LARGE-SCALE SHRUB REMOVAL PRACTICES IN THE CHIHUAHUAN DESERT

by

KATHLEEN E. SCHAEFFER, B.S. BIOLOGICAL SCIENCES

DISSERTATION

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Abstract

Shrub encroachment is a worldwide phenomenon that affects multiple biomes at different ecological and anthropogenic levels. In dryland ecosystems, shrub encroachment is a noted concern amongst land managers, as it can lead to a loss of soil resources and biodiversity. To mitigate the negative effects of shrub encroachment in Drylands, land managers can implement large-scale shrub removal practices. These land restoration practices can shift landscapes to novel ecosystems, where resulting plant communities can vary following treatments. Grass recovery or increasing herbaceous cover is often a primary goal of these treatments, however predicting which sites may show higher grass responses to treatments is challenging. There is also still much unknown on how these shrub removal practices will affect valuable soil resources such as soil carbon, or whether these effects will vary with the age of treatment. The overarching goal of this dissertation is to address these gaps in knowledge by exploring the importance of soil properties and resources (like soil carbon) in large-scale shrub removal practices in the Chihuahuan Desert of southwestern New Mexico. Our aims are to explore if soil and site-level properties can help support desert grassland restoration planning, as well as determine how these large-scale shrub removal practices affect soil resources like soil carbon. We present here three chapters that address each of these research aims. In Chapter 2, we identify accessible site-level and soil properties that can be used to help select ideal areas for desert grassland restoration (via shrub removal). In Chapter 3, we determine if large-scale shrub removal practices affect soil organic and inorganic carbon (8 years after shrubs were removed). In Chapter 4, we explore whether the effects of large-scale shrub removal on soil carbon vary at different time points (ages) of restoration. This dissertation furthers our understanding on how soil carbon (inorganic and organic) could change with shrub removal (at different time points of restoration) and identifies site and soil properties that could provide support for future desert grassland restoration planning.

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Chapter 1: Introduction to shrub encroachment and grassland restoration in Drylands

The encroachment of shrubs into grasslands or other ecosystems has been widely observed over the last few centuries in dryland regions throughout the world (Eldridge et al., 2011; Van Auken, 2000). These large-scale shifts in plant communities have been a concern among land managers and stakeholders, particularly in cases where shrub encroachment leads to a loss of ecosystem services and function (Sharp et al., 2012). In Drylands, when shrub encroachment is persistent, it is thought that these ecosystems may eventually reach a completely degraded state (e.g., desertification) (Safriel, 2009). However, there is still much debate on whether shrub encroachment necessarily equates to degradation due to the variety of observed effects (i.e., positive, negative, null) that shrub encroachment can have on different ecosystem properties (Chandregowda et al., 2018; Eldridge et al., 2011; Maestre et al., 2016). Nevertheless, shrub encroachment is still often diagnosed as a negative land transition, particularly because it can displace other plant species along with the organisms that depend on them (Drake et al., 2016; Saintilan & Rogers, 2015; Van Auken, 2009). To mitigate any negative effects of shrub encroachment, dryland managers frequently turn to various restoration tactics that aim to reduce shrub species and increase grasses or other native species (Bestelmeyer et al., 2019; Copeland et al., 2018).

CAUSES AND CONSEQUENCES OF DRYLAND SHRUB ENCROACHMENT

Below I will discuss the leading causes of shrub encroachment in dryland grasslands, specifically patterns of heavy livestock grazing and factors arising from environmental and climate change. I will also discuss ecosystem factors that enable shrubs to continually encroach upon desert grasslands and briefly describe how shrub encroachment affects wildlife, and resources that people depend on from these environments.

Causes

Although each occurrence of dryland shrub encroachment is caused by factors unique to that environment, encroachment is frequently attributed to historical (or sometimes contemporary) overgrazing of livestock; shifts in fire and drought cycles; and climate or environmental changes (Archer et al., 2017). These factors (or catalysts) can occur simultaneously or sequentially, making it difficult to single out a dominant cause of dryland shrub encroachment. However, the recurring theme in the literature is that factors that lead to the loss of soil structure and protection (i.e., erosion) tend to be the significant drivers of shrub encroachment in Drylands (Archer et al., 2017; Li et al., 2022). Below I will summarize these common drivers of encroachment while describing how each of them influence soil structure and erosional processes.

1.1 Historical Overgrazing

Historically, the use of Drylands as foraging grounds for commercial and pastoral livestock has presented many challenges (Reynolds et al., 2007; Weber & Horst, 2011). Relative to other biomes, deserts have hotter annual temperatures and low intermittent rainfall patterns - which typically leads to low levels of primary productivity (White & Nackoney, 2003). And while endemic desert plants (e.g., desert grasses) have evolved to survive and reproduce under these conditions, they are vulnerable to disturbances like overgrazing (Van Auken, 2009). In dryland case studies, overgrazing by herbivores is often attributed to non-native domesticated animals (e.g., sheep, cattle, pigs) that are introduced to the system for human use (Hempson et al., 2017)

There have been cases where native herbivores have been identified as the cause of overgrazing in some Drylands; however, these instances were heavily linked to predator removals (e.g., human removal of larger mammal predators in Australia led to overgrazing by native herbivores like Kangaroos) (Mills et al., 2020). Direct comparisons of native versus non-native herbivory rates can also be challenging to piece together from herbivore removal experiments, as many studies focus on one non-native herbivore type or make comparisons between multiple non-native herbivores (i.e., sheep vs. cattle) (Filazzola et al., 2020). Despite these uncertainties, it has been consistently found that non-native herbivores (i.e., livestock) are a leading cause of overgrazing in Drylands (Mirzabaev et al., 2019).

Grazing livestock does not always have negative effects on dryland ecosystems (Jordan et al., 2022; Stavi et al., 2021); however, the presence of livestock imposes additional environmental pressures that should be actively accounted for (Maestre et al., 2022). Firstly, cattle are generally larger than native herbivores found in Drylands, and their herbivory rates of palatable grass species are markedly higher than those of native herbivores (e.g., cattle diet is composed of ~58% of grasses compared to 22% consumed by native lagomorphs in the Chihuahuan Desert) (Alipayou et al., 1993). Herbivory is not the only mechanism by which cattle can affect vegetation, as their large size and behavior (e.g., trampling) can also lead to the physical destruction of vegetation as well as soil structure (e.g., via compaction or erosion) (Dunne et al., 2011). Cattle have also acted as significant dispersal agents in more recent encroachments of mesquite shrubs in the Chihuahuan Desert (e.g., mesquite seeds are consumed and passed by cows along cattle trails) (Archer et al., 2017). Overall, the mere presence of livestock can have profound effects on dryland ecosystems, meaning selected range areas require sufficient time to recover between grazing events (Valone et al., 2002).

Preventing overgrazing also requires strategic planning around the seasonal and environmental requirements of desert grass species (Archer et al., 2017). For instance, heavy grazing during a grass species' growing season can damage its reproductive structures (e.g., destruction of grass seedheads) and negatively affect fecundity (Trlica, 2013). Historically, this type of high intensity grazing during inappropriate times is noted as the cause of much of the diminishment of desert grassland habitats (Abdelsalam, 2021). Overall, this historical overgrazing of livestock has helped facilitate the encroachment of shrubs by 1) decreasing competition from grasses (via herbivory and physical destruction), 2) altering soil structure (via compaction and erosion), 3) and livestock acting as dispersal agents for select shrub species (i.e., honey mesquite).

1.2 Climate and Environmental Change

Contemporary global warming and the increase in atmospheric gases like CO_2 have also been identified as overarching drivers of shrub encroachment (Morgan et al., 2007). Perennial desert grass species (e.g., *Bouteloua* spp.) are thought to have evolved under cooler and wetter climate conditions, which likely played a role in their diminishment - as shrub species are notably more drought tolerant (Pockman & Sperry, 1996). Similarly, the increase of atmospheric CO_2 may have disproportionately benefitted shrubs, whose C_3 photosynthetic pathways may have optimized the excess CO_2 to accelerate their growth (Archer et al., 2017) (e.g., an influx in atmospheric CO_2 increased N_2 fixation in honey mesquite shrubs) (Polley et al., 1997). Contemporary increases in temperature may also have contributed to higher rates of evapotranspiration in soils, which, in turn, could have led to grass reduction over time in specific desert regions (Kidron & Gutschick, 2017). Temperature increases could also have restricted shrub seed establishment; however, shrubs that were at least at the sapling life stage were likely more resilient to these climate changes (Archer et al., 2017). Together, overgrazing and climate drivers can also affect fire regimes in dryland regions such as the Chihuahuan Desert (i.e., decreases in grass spp. equates to less fuel for natural fires, which in turn benefits shrub seedlings) (Brooks & Chambers, 2011). Even grass species themselves may have provided optimal shelter for shrub seed banks through different pathways (e.g., provision of shade and soil moisture retention in upper soil layers protects shrub seeds from deterioration) (De Dios et al., 2014). Overall, shrub encroachment was optimized by the timing and degree of these combined factors.

Consequences

Our collective understanding of how shrub encroachment affects ecosystems is still growing, and findings are often variable. Studies continue to identify that there can be negative, positive, or negligible effects on habitats, depending on the characteristics of shrub species that are encroaching, land use history, and the degree and rate of shrub encroachment (Bestelmeyer et al., 2019). In some cases of shrub encroachment, a lack of historical data on land use and disturbance can further complicate evaluating the effects on the ecosystem (Barger et al., 2011). Additionally, the goals and needs of land managers often shape the underlying perspectives from which shrub mediated effects are considered harmful or beneficial by policymakers and the public (Davies, 2017).

For instance, in metanalyses on the effects of shrub encroachment across multiple Drylands (~273 case studies) (Eldridge et al., 2011), it was found that encroachment often led to increases in aboveground carbon and soil carbon and nitrogen; and decreases in other variables (e.g., soil pH). These differences in effects were attributed to variations in climate (i.e., aridity) as well as the individual traits of encroaching shrubs (Eldridge et al., 2011). In general, the effects of shrub encroachment are considered harmful when the regime shift leads to an unproductive or highly disturbed state that passes an environmental threshold.

1.3 Going past points of return - State change theory and concepts

Several paradigms have been used to explain large-scale ecosystem change (regime shifts) that account for both linear and non-linear dynamics in ecosystems (Peters et al., 2015). These include concepts such as alternative stable states and ecosystem tipping points (Table 1.1). A common theme among state change concepts is that a single ecosystem can exist under different sets (parameters) of biotic conditions. Individual parameters can be viewed as stages of ecosystem succession; however, the perception of whether a stage is degraded or not has often depended on anthropocentric ideals of ecosystem productivity (i.e., what ecosystem services are being provided?) (Beisner et al., 2003; Bestelmeyer et al., 2003). More recently, combinations of these state change concepts have been restructured to explain state change from both anthropocentric and biocentric (e.g., animals and plants) perspectives within the context of relevant time and spatial scales (Peters et al., 2015). These emerging paradigms are essential for understanding state change in Drylands (i.e., shrub encroachment) and identifying where and when restoration practices may be the most effective (e.g., are some areas already too degraded to restore?).

Table 1.1: Common theories and terminology used to describe ecosystem state change that is catalyzed by disturbance or other environmental factors.

TERMS	DESCRIPTION
Alternative Stable States	The idea that an ecosystem can exist within multiple states – where each state occurs within the same physical environment but is characterized by unique biotic attributes (Beisner et al., 2003).
Cross Scale Interactions	When drivers of state change and their effects on ecosystems may occur or interact at different spatial and temporal scales. (Soranno et al., 2014).
Scaled/Nested Hierarchies	A hierarchal system that divides ecosystems into discrete levels, layers, or scales (ex. Regional, landscape, habitat, individual). Each level is defined by its most significant attributes (physical, chemical, socioeconomic, etc.), and ecosystem processes or services are designated to these attributes. (Zhang et al., 2013). Comparisons are then made on how specific disturbances affect each level or attribute (Lancaster & Belyea, 1997).
Regime Shifts	The term used to describe the actual transition that an ecosystem makes when crossing an ecological threshold (tipping point). Usually caused by a gradual or abrupt disturbance to the system (Scheffer & Carpenter, 2003).
Disturbance and Feedbacks	A disturbance is any element or factor introduced to an ecosystem that disrupts ecosystem processes and services or changes the functionality of that ecosystem at any level (ex., organism level or community level). Feedbacks are processes or factors that reinforce (or less frequently mitigate or lessen) the effects of disturbances (Battisti et al., 2016).
Tipping Points	A point when land cover change or disturbance causes an ecosystem to go past an ecological threshold, and that ecosystem is no longer able to revert to its previous condition (Dakos et al., 2019).
Hysteresis	The variation in the amount of energy an ecosystem needs to expend to return to previous alternate states after that system has crossed a critical threshold (tipping point). i.e., a return to some previous states would require significant changes/energy from that ecosystem (Scheffer et al., 2001).
Resilience	An ecosystem's ability to resist disturbances and the time it takes for that ecosystem to recover from any negative or harmful effects caused by those disturbances (Holling, 1973).

SHRUB ENCROACHMENT IN THE CHIHUAHUAN DESERT

The Chihuahuan Desert is the largest desert in North America and is estimated to be approximately 9,000 years old (a relatively young desert) (Havstad et al., 2006). Studies also suggest that this desert has likely gone through at least three land cover transitions during its existence, altering between grassland and woody plant dominated states (trees or shrubs) (Van Devender & McClaran, 1995). The earlier shifts in land cover have been widely attributed to glacial retreat (Milstead, 1960; Neilson, 1986; Van Devender & Spaulding, 1979). In contrast, the most recent land cover shift of perennial desert grasslands to shrublands began in the mid-1800s and has been heavily linked to anthropogenic drivers (e.g., historical overgrazing) (Havstad et al., 2006).

2.1 Drivers of shrub encroachment in the Chihuahuan Desert

Before the 16th century, perennial grasslands covered much of the Chihuahuan Desert. These grasslands were made up of species such as tobosa grass (*Pleuraphis mutica*), black grama (*Bouteloua eriopoda*), and bush muhly (*Muhlenbergia porteri*) (Humphrey, 1953; Shantz & Zon, 1924; Smith, 1899). During the early 1500s, European settlers introduced cattle into the Mexican and (what is now) the southern New Mexican Chihuahuan Desert regions. Initially, cattle grazing was limited to southern areas that were adjacent to naturally available water sources like the Rio Grande Valley (Merlan, 2008). Following the Homestead Act in 1862, an influx of people migrated into New Mexico, bringing with them infrastructure and irrigation networks that would allow cattle stocks to be brought further north (McNaughton, 1993). Similar to the Dryland ecosystems in general discussed earlier, historical and recent studies have concurred that the subsequent heavy grazing and land usage greatly reduced perennial grasslands in the Chihuahuan Desert (Havstad et al., 2006; Smith, 1899; Wooton, 1908). Following this release from interspecific competition, shrub species like creosote bush (*Larrea tridentata*) and honey mesquite (*Prosopis glandulosa*) that had existed in lower abundance were then able to encroach and displace perennial desert grasslands (Archer, 2009; Buffington & Herbel, 1965; Grover & Musick, 1990).

2.2 Effects of shrub encroachment on ecosystem function in the Chihuahuan Desert

In the Chihuahuan Desert, shrub encroachment has led to a decrease or alteration in biodiversity via the displacement of grasses and other plant species (Baez & Collins, 2008). Several prey species (e.g., lizards, birds, lagomorphs) have declined with shrub encroachment due to the loss of food, habitat, and refuge. For example, through the creation of mounds, ecosystem engineers in grasslands such as the banner-tailed kangaroo rat (*Dipodomys spectabilis*), provide significant refuge from predators to species like the desert cottontail (*Sylvilagus audubonii*). Since it has been found that shrub encroachment leads to declines in kangaroo rats (Cosentino et al., 2013), species such as the cottontail have also been negatively affected by a loss of refuge space (Wagnon et al., 2020). This lack of habitat for grass-specific organisms has also led to changes in predator dynamics. For instance, in shrublands, smaller predators like kit foxes (*Vulpes macrotis*) have less cover from predators like coyotes (*Canis latrans*), who they also must compete against for prey (rodents and lagomorphs) (Wagnon et al., 2020). Shrub encroachment has also negatively affected livestock and recreational services (e.g., a decrease in game birds like scaled quail (*Callipepla squamata*)) (Coffman et al., 2014).

The overall distribution of soil resources has also changed as shrub species typically concentrate nutrients (e.g., leaf or branch litter) beneath their subcanopies – known as the island of fertility effect (Walker et al., 2001). This generally leads to the capture and storage of organic rich materials under shrub canopies, with eroded materials depositing (via wind or rain runoff) in interspaces between shrubs (Bolling & Walker, 2002). This change in soil and vegetation has had notable effects on hydrology – where an increase in unvegetated interspace can promote groundwater recharge (Schreiner-McGraw et al., 2020). However, this positive relationship is not always found, which may adversely affect establishing plants (i.e., reinforce unvegetated interspace patches) (Ochoa et al., 2023).

RESTORATION OF GRASSLANDS THROUGH SHRUB REMOVAL - "RESTORE NEW MEXICO"

To mitigate the negative effects of shrub encroachment, the New Mexico Bureau of Land Management (BLM) began extensively treating shrub encroached areas with aerially applied herbicide in the 1980s to reduce shrub cover - in the anticipation that perennial and herbaceous cover would subsequently increase. In 2005, the BLM initiated the Restore New Mexico program (RNM) to expand on their restoration efforts. In 2007, the BLM partnered with the USDA Agricultural Research Service Jornada Experimental Range (JER) to apply rigorous experimental monitoring of the effects of RNM treatments (e.g., effects on plant cover, hydrology, and biodiversity), which had not been done previously (Bestelmeyer et al., 2019). The RNM program has since grown into an intensive collaboration between federal and state government agencies, livestock suppliers, and conservation organizations.

RELATIONSHIP BETWEEN SHRUB REMOVAL PRACTICES WITH SOIL CARBON

In Drylands, the transition of perennial desert grasslands to shrub-dominated landscapes is considered a regime shift - where shrubs have established in the same physical environment that grass communities previously existed in (Peters et al., 2015). This physical environment includes ecosystem resources like soil nutrients and carbon (Xiao et al., 1995). After regime shifts occur, these physical properties can be altered by the new ecosystem state (i.e., encroaching shrubs) (Havstad et al., 2006). Thus, the dynamics of soil carbon in an altered ecosystem can be a reference point for the current state of an ecosystem. For example, when shrublands displace grasslands, the proportion of interspace increases, which results in patch scale variations in soil resources (i.e., organic matter concentrates under shrub canopies and much lower in interspaces) (Throop et al., 2013). When shrubs are removed through desert restoration practices (e.g., herbicide) an additional regime shift occurs, where novel plant communities emerge (described below). However, it is not well known how this additional regime shift will affect soil carbon, which is both an indicator of ecosystem state - as well as an essential resource in Drylands.

4.1 Importance of soil carbon in Drylands

In Drylands, soil carbon fuels microbial nutrient cycling (Costantini et al., 2016; Throop et al., 2013) that provides plants with nutrients that are limited in these regions, such as nitrogen (Lajtha & Schlesinger, 1986). Collectively, global Drylands contribute significantly to the inter-annual variability of the terrestrial global carbon cycle (Lal, 2019; Poulter et al., 2014). Recent reports estimate that Drylands make up roughly 27-33% of the global organic carbon stocks and up to 97% percent of global inorganic soil carbon stocks (Plaza et al., 2018; Safriel, 2005). There is also emerging evidence that Drylands play a key role in sequestering and storing carbon long-term, which may aid in future CO_2 sequestration (Lal, 2004; Poulter et al., 2014). Along with being significant to the global carbon cycle, dryland carbon pools tend to be extremely vulnerable to carbon loss and redistribution, especially in semi-arid regions like the Chihuahuan Desert (Brazier et al., 2014). Predicting soil carbon vulnerability is challenging in this region, as these areas are also undergoing multiple environmental changes, including those from large-scale shrub removal practices. It is imperative that researchers assess how these essential (yet highly vulnerable) soil carbon stocks are being impacted by shrub removal practices.

4.2 Effects of shrub encroachment on soil carbon

When these habitats shift from perennial desert grasslands to shrub encroached areas, the distribution of organic matter inputs into the soil also changes. Even including annual or weedy plant species that occur sparsely and seasonally in shrublands, shrubs are the most significant contributors of organic matter to soil (Havstad et al., 2006). Between these shrubs exist large stretches of unvegetated interspace that are exposed to erosional processes by wind and rain. This difference in patch scale variation and exposure (i.e., protection) of soils has led to much uncertainty on how soil carbon will persist as a resource in these regions. Recent studies have found that soil organic carbon varies by ground cover type in shrublands (live shrub vs. interspace), with shrubs holding twice the amount that interspace patches do (Throop et al., 2013). Additionally, Throop et al., 2013 found that shrubs like creosote had less soil inorganic carbon present than interspace patches – which they attributed to erosional loss of soils in interspace patches. In a study that took place in the northern part of the Chihuahuan Desert, it was found that across ca.4-year period (with notably dry conditions), shrublands sequestered carbon at an average rate of 49 g C m^{-2} yr^{-1}, and in contrast, adjacent grasslands were a source of carbon – with an average rate of 31 g C m^{-2} yr^{-1} (i.e., grasslands lost carbon as CO_2 due to higher microbial respiration) (Petrie et al., 2015). Additionally, findings from other shrub-dominated deserts, like the Sonoran, show that shrub encroachment may stabilize (i.e., sequester) soil organic carbon over large timescales (Demarco et al., 2016). These findings indicate that shrublands, although functionally different from previously existing grasslands, do still play a role in soil carbon storage, and their removal may lead to changes in dryland soil carbon.

4.3 Predicted effects of shrub removal on soil carbon

When shrubs are removed, the effects on the plant community can be highly variable, resulting in variations of novel plant communities (Archer et al., 2011; Bestelmeyer et al., 2018). In the Restore New Mexico restoration efforts, a successful shrub removal treatment has been defined as one that leads to the increase of perennial grass and herbaceous cover – that subsequently helps restore biodiversity and soil conditions (i.e., shrub removal lowers the proportion of bare ground - retaining more soil, water, nutrients) (Bestelmeyer et al., 2019). The positive effects would ideally radiate up the food chain, as the livestock and grass-specific wildlife would benefit (Unnasch, 2017).

A second possible scenario would be a "moderately" restored area that still has 'undesirable' shrubs but also includes increased amounts of desirable vegetation (forbs and grasses). This would still provide services to wildlife and cattle but on a lesser scale than shrub removals that resulted in the formation of intact grasslands. Finally, a shrub removal treatment that is defined as unsuccessful would be one where no non-shrub vegetation becomes established in the treated area. This landscape change could result in a significant loss of soil due to erosion, and it would provide significantly fewer services to wildlife and cattle (Maliva et al., 2012; Zeng & Yoon, 2009). This variation in the emerging plant communities that follow shrub removal indicates that shrub removal treatments may lead to variations in soil carbon inputs as well.

However, there are still significant gaps in our knowledge as to how this shift to novel plant communities will affect soil carbon relative to the two previous landscape regimes (i.e., grassland vs. shrubland). Below we propose two scenarios describing how soil carbon may be affected by these different types of vegetation changes after shrub removal.

Scenario 1: An increase in grass/herbaceous cover following successful shrub removal treatments will lead to increases in soil moisture, carbon, and nutrient retention, as well as decreases in soil loss via erosion.

If shrub removal treatments are successful, and there is a subsequent increase in herbaceous species following shrub removal, this would likely change the organic matter turnover rates in the uppermost soil layers. Grass root systems would increase soil moisture and nutrient retention in the top horizon of the soil (De Dios et al., 2014). Additionally, if shrub removal treatments are successful, there would, in theory, be less unvegetated interspace (relative to shrub encroached areas). This would equate to more soil protection from erosional processes. Less unvegetated space may also lead to more connectivity of microbial communities that, in turn, may enhance limited nutrients such as nitrogen (Darrouzet-Nardi et al., 2023; Gao et al., 2022).

Scenario 2: No increase in grass/herbaceous cover following successful shrub removal treatments will lead to decreases in soil moisture, carbon, and nutrient retention; as well as increases in soil loss via erosion.

If shrub removal treatments are successful, but grasses or herbaceous species do not recover, this could lead to significant, and arguably negative, changes in soil carbon. In this case, dead shrub skeletons and ephemerally occurring species (e.g., weeds) would likely be the primary contributors of plant-derived soil organic matter, which may correlate to lower rates of microbial activity and ultimately lower moisture and nutrient retention (Gao et al., 2022). Additionally, soils would be highly susceptible to losses via erosion due to both the lack of vegetation and the increase in interspace (i.e., the proportion of interspace may eventually increase as dead shrubs gradually decay and reduce into the soils). As more soil organic carbon is typically found in the uppermost soil horizons of desert regions (Wang et al., 2010), this increase in erosion would equate to decreases in soil organic carbon.

OPPORTUNITIES TO EXPLORE EFFECTS OF SHRUB REMOVAL ON SOIL CARBON

5.1 Restore New Mexico Study Region

Our study was conducted in the Chihuahuan Desert of southwestern New Mexico, at 39 Restore New Mexico (RNM) shrub removal sites and one reference grassland (Figure 1.1). We divided the 39 RNM sites into three groups: older experimental, newer experimental, and historic site groups (described below). The elevations of these study sites range from 1260m to 1750m.

The average annual rainfall ranged from 200-350 mm. The dominant vegetation varied between sites. The most prevalent shrub species present at these sites are creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), and tarbush (*Flourensia cernua*). The dominant grass species present are short-lived perennials, fluffgrass (*Dasyochloa pulchella*), and perennial grasses like bush muhly (*Muhlenbergia porteri*). Soils in this region are typically classified as gravelly to loamy (Cosentino et al., 2013). The primary land use in this region has been for livestock and recreation.

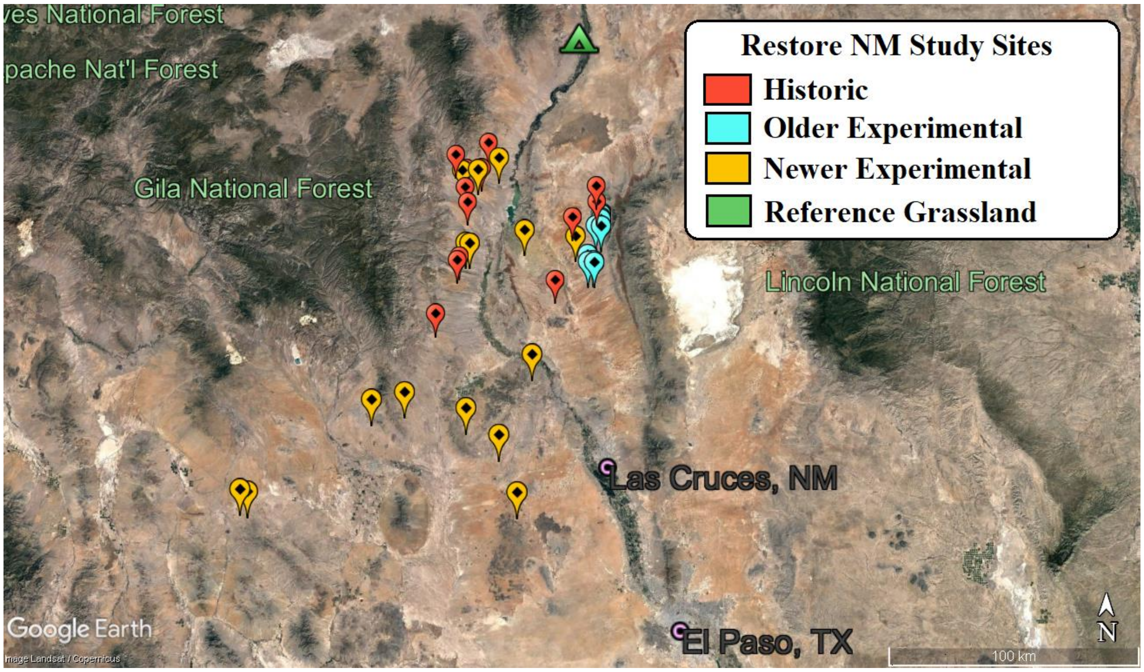

Figure 1.1 Map showing 39 study sites that were part of a shrub removal experiment ("Restore New Mexico") in the Chihuahuan Desert of southwestern New Mexico. Twenty-five of the study sites (Newer and Older Experimental sites) received one-time shrub removal treatments in 2007 or 2009. The remaining 14 Historic sites received one-time shrub removal treatments at different time points from 1982 – 2002. One reference grassland (at the Bosque del Apache Wildlife Refuge) was also included to represent pre-shrub encroachment conditions. (Map credit: generated using Google Earth, downloaded May 2023)

5.2 RNM Shrub Removal Treatments

All RNM shrub removal treatment sites (historic, older, and newer experimental) were treated using the same herbicide application (described below). However, the timing of treatment application and the selection process for treated sites varied by group. The details on application times and selection methods are described separately below for each group of sites. For all treatment sites, once selected, shrub removal areas underwent treatment by aerially applied tebuthiuron (N-[5-(1-1-dimethylethyl)-1,3,4thiadiazol-2-yl]-N, N'-dimethylurea (tebuthiuron pellets) at an application rate of 0.56 – 0.84 kg-ha (Coffman et al., 2014). The application times varied by year but always took place in the fall or winter seasons. The temporary removal of cattle from the treated areas was implemented following treatment application.

5.2.1 RNM Older and Newer Experimental Sites

In 2007, the BLM and the JER launched a pilot study of 10 experimental treatment pairs (referred to here as *Older experimental sites*). Using ArcGIS, the JER allocated leave-out areas (polygons to leave out from aerial herbicide application). After treatment application, treatment pairs were established by matching an untreated control area (CTL) from within the leave-out area with a nearby treated area (TRT) of a similar landform, soil, ecological state, and plant community. These paired areas became the designated experimental treatment sites. The final selection of TRT areas was based on successful shrub removal treatment (defined as ~75% or more of shrub mortality). Before treatments occurred, three 20-m transects were established in each CTL and TRT area (200x200 m area) by the JER to monitor vegetation changes over 5-year interval benchmarks (*Note: These experimental sites were used in Chapter 2*).

Beginning in 2009, BLM LCDO and JER created a second set of experimental treatment pairs (referred to here as *Newer experimental sites*). At multiple sites, the JER stratified the area by ecological site and vegetation state and then selected two 9-ha (300m x 300m) squares in the dominant strata. One square was randomly assigned to TRT, and the other was assigned to CTL, which was left out from herbicide application. Within each square, two 50-meter transects were established by the JER on the ground post-treatment in both the TRT and the CTL, ensuring matching local soil and vegetation between the TRT and CTL transects. In our study, we sampled 15 of these newer experimental sites. (*Note: These experimental sites were used in Chapters 2 and 3*)

5.2.2 Historic RNM Sites and Reference Grassland

From the 1980s to the early 2000s, the BLM aerially applied herbicide to large shrub encroached areas at different time points (i.e., different years). In a previous study, these treated areas were retroactively paired with nearby untreated shrub-dominated areas that had similar pedologic and ecological baseline features (Coffman et al., 2014). In our study, we used 14 of these historic sites to represent a chronosequence of shrub removal treatments ranging from 1982-2002 (referred to here as *RNM chronosequence*). Additionally, we sampled one reference grassland site at the Bosque Del Apache Wildlife Refuge to represent “pre-shrub encroachment” conditions. (*Note: These shrub removal sites were used in Chapter 4*)

DISSERTATION: THE IMPORTANCE OF SOIL CARBON IN LARGE-SCALE SHRUB REMOVAL PRACTICES IN THE CHIHUAHUAN DESERT

Large-scale shrub removal in Drylands is a land restoration practice that has been found to shift landscapes to novel ecosystems, where resulting plant communities can vary following treatments (Bestelmeyer et al., 2019). Grass recovery or increasing herbaceous cover is often a primary goal of these treatments; however, predicting which sites may show higher grass responses to treatments is challenging. Additionally, there is still much unknown on how these shrub removal practices will affect valuable soil resources such as soil carbon or whether these effects will vary with the age of treatment. To address these uncertainties in large scale shrub removal research, we have identified the following research aims:

Research Aims:

1) Identifying accessible site and soil properties that can be used to help select ideal areas for desert grassland restoration (via shrub removal)
2) Determining if large-scale shrub removal practices affect soil organic and inorganic carbon
3) Exploring whether the effects of large-scale shrub removal on soil carbon vary at different time points (ages) of restoration

DISSERTATION SUMMARY

Below I will discuss how each of the following chapters will address these research aims and further our understanding of how soil and site properties both influence and are influenced by large-scale shrub removal practices in the Chihuahuan Desert – with a particular focus on soil carbon.

In Chapter 2, we explore relationships between site and soil properties and grass response following shrub removal to determine if these properties can be used as indicator variables for desert grassland restoration potential. Desert grassland restoration outcomes are challenging to predict, and successes and failures are often attributed to inherent site properties (e.g., soils, topography) or overarching factors such as climate (Brudvig et al., 2017; Gremer et al., 2015). In recent restoration ecology, there has been a consistent call to incorporate these inherent soil and site properties both in the planning and assessment of restoration success (Gann et al., 2019; Stanturf et al., 2021). In our study, we identify six site and soil variables to test as potential indicators for grass response following grass restoration treatments (via shrub removal) in the Chihuahuan Desert. These variables were selected based on their accessibility (i.e., ease of measurement) as well as for their correlation to grass growth (Costantini et al., 2016; Jackson et al., 2017). For this study, we used the 25 experimental shrub removal sites across the Chihuahuan Desert of southwest New Mexico established by the Restore New Mexico Program in 2007 and 2009 (*older and newer experimental sites described above*). We sampled soils from non-shrub removal control areas, which served as a proxy for pre-shrub removal conditions. A grass response was calculated as the relative gain of grass percent cover between the non-shrub removal and shrub removal areas. We analyzed control soils for soil organic carbon, bulk density, and soil pH and included these as our potential soil indicators. Elevation and rainfall were used as our potential site indicators. We then used linear and multiple linear regression analyses to identify which of these indicator variables had relationships with grass response.

In Chapter 3, we examine the effects of Chihuahuan Desert large-scale shrub removal practices on soil carbon (organic and inorganic) ~8 years after shrubs were removed. Soil organic carbon is an essential resource in the Chihuahuan Desert, as it provides soil structure, nutrient, and water retention, as well as provides resources to microbes that drive nutrient cycling for plants (Lal, 2019; Wheeler et al., 2007). Similarly, soil inorganic carbon (e.g., calcium carbonates) is important for these ecosystems, as it sequesters and promotes long-term storage of carbon (Monger, 2014; Monger & Martinez-Rios, 2000). While there is a working knowledge of how shrub encroachment affects these soil carbon resources (Havstad & Herrick, 2003), less is known about how these resources will be affected by large-scale shrub removal practices. In our study, we test the effects that these restoration practices have had on soil carbon. We used 15 experimental shrub removal sites established by the Restore New Mexico program in ca. 2009 in the Chihuahuan Desert of southwestern New Mexico (*newer experimental sites described above*). We sampled soils at paired non-shrub removal control areas and shrub removal treatment areas. We then analyzed soils for organic and inorganic carbon, as well as for soil texture, pH, and bulk density. We then calculated plot-level soil carbon, using the relative cover of different vegetation and ground cover types and their specific soil carbon content, to determine if soil carbon has changed with the removal of shrubs.

In Chapter 4, we tested for relationships between the time since a shrub removal treatment occurred and relative plot-level soil carbon to determine whether the effects of large-scale shrub removal practices on soil carbon vary at different time points (ages) of restoration. In restoration ecology, the temporal variation of ecosystem factors that co-occur along with the effects of restoration treatments, can make it difficult to account for the temporal dynamics in site response to treatments. To account for these temporal differences, chronosequences can be used to estimate the trajectory of ecosystem and plant community succession (Johnson & Miyanishi, 2008). We used a chronosequence of 14 shrub removal sites with varying restoration ages that were established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico (Coffman et al., 2014) (*historic shrub removal sites described above).* We sampled soils at paired non-shrub removal control areas and shrub removal treatment areas. We analyzed soils for organic and inorganic carbon and bulk density. We measured vegetation and ground cover at both treatment areas to calculate a relative percent cover difference. We then calculated relative vegetation cover and plot-level soil carbon (organic and inorganic) (described above) and explored relationships with time since shrub removal treatment (e.g., with ages of treatments ranging from 16 to 36 years old).

In Chapter 5, we provide a summary of our findings and discuss how soil carbon and other soil properties are affected by large-scale shrub removal practices in the Chihuahuan Desert – as well as how these soil variables can provide support for desert grassland restoration planning.

Chapter 2: Soil carbon and elevation as indicators for grassland restoration potential in the Chihuahuan Desert

ABSTRACT

Over the past century, shrub encroachment has led to the displacement of perennial grasslands in many arid rangeland systems. To mitigate the negative effects that accompany shrub encroachment, land managers have concentrated their efforts toward removing shrubs to restore grasslands. Predicting the outcomes of large-scale shrub removal practices is challenging for desert grassland restoration. We set out to determine if soil and site-level (i.e., rainfall and elevation) properties that have previously been associated with grass growth, could act as indicator variables for grass response following shrub removal in the Chihuahuan Desert. Our study took place in southwest New Mexico at experimental shrub removal sites across multiple elevations that were established by a collaborative restoration program - Restore New Mexico (RNM). We sampled soils from each site and analyzed them for soil organic carbon (SOC), texture (% sand, silt, and clay), pH, and bulk density. Site level grass % cover data from before and after shrub removal was used to calculate grass response (GGS) to shrub removal treatment. GGS was positively related to SOC, with a stronger relationship for soils from under shrub canopies than interspace soils. GGS was not strongly related to soil texture, except for a negative relationship with % sand at some sites. Across all sites, GGS was not related to average annual rainfall. GGS was positively correlated with elevation; and elevation was also related to SOC, soil texture (% sand and silt), soil pH, and average annual rainfall. Our results indicate that measuring SOC and elevation could support grassland restoration planning in Drylands such as the Chihuahuan Desert.

INTRODUCTION

Over the past century, many arid regions have gone through grassland to shrubland state transitions (Van Auken, 2000), in which historically semi-arid perennial grasslands are replaced by shrub-dominated plant communities. Shrub-dominated communities previously either existed separate from, but adjacent to grasslands, or shrubs co-existed with grasses in low abundance (Archer et al., 2017). Landscape level transitions are caused by co-occurring factors that include, but are not limited to, excessive livestock grazing, prolonged or intense droughts, and shifts in fire cycles (D’Odorico et al., 2012; Eldridge et al., 2011). These factors have also been affected by contemporary global warming and land use pressures (García Criado et al., 2020). Collectively, these conditions have provided opportunities for shrub species to regularly outcompete other plants and encroach upon desert grasslands (Bestelmeyer et al., 2018; Cao et al., 2019; D’Odorico et al., 2012).

In the Chihuahuan Desert of North America, a grassland to shrubland state transition has been ongoing since the mid-nineteenth century (Buffington & Herbel, 1965; Smith, 1899). Perennial grasslands that existed prior to the 1800s were gradually replaced by communities dominated by shrubs including creosote bush (*Larrea tridentata*) and honey mesquite (*Prosopis glandulosa*) (Gao & Reynolds, 2003). Shrub encroachment has regularly been acknowledged as an undesirable transition, as it displaces grasses and grass-dependent organisms, altering biodiversity (Branscomb, 1956; Peters et al., 2013). With shrub encroachment comes an increase in bare (unvegetated) soils between shrubs, which are subject to lower water and nutrient retention and higher rates of erosion (D’Odorico et al., 2012). Although recent studies have shown that not all instances of shrub encroachment led to land degradation (Hering et al., 2019), it is still considered to be a form of desertification in regions where soil erosion accelerates because of grass loss (Chappell et al., 2019; Prince & Podwojewski, 2020).

In the Chihuahuan Desert, land managers have attempted to counteract the negative impacts of shrub encroachment by removing shrubs through different methods such as prescribed burning, mechanical removal, and targeted herbicide application (Bestelmeyer et al., 2021; Herbel et al., 1985; Lister et al., 2012; Wilson et al., 2001). Each method alone has its limitations (e.g., a lack of fine fuels in shrublands may negate the benefits of prescribed burns); however, combinations of these methods can be effective, albeit expensive or labor-intensive. Over the last few decades, land managers have used targeted herbicide application as a more cost-effective option for grassland restoration (Invasive Species Management on Federal Lands, 2013). In the 1980s, the Bureau of Land Management (BLM) in New Mexico began extensively treating shrub encroached areas with aerially applied herbicide. In 2005, the BLM initiated "Restore New Mexico (RNM)", a collaborative restoration program, to expand their shrub removal efforts, and in 2007 the BLM Las Cruces District Office (BLM LCDO) partnered with the USDA Agricultural Research Service Jornada Experimental Range (JER) to establish experimental monitoring of the effects of RNM herbicide treatments (Bestelmeyer et al., 2019). It is estimated that approximately 300,000 ha of land in the south of New Mexico has received shrub removal treatments since the BLM initially began applying herbicide in the 1980s (Bestelmeyer et al., 2019; Schooley et al., 2021).

The financial costs, time, and personnel that restoration efforts require are often significant, yet estimating the outcomes of these efforts is challenging for many reasons. Part of the challenge is due to there being comparatively more research on the effects that shrub encroachment has on ecosystems rather than the effects that restoration practices may have on those same systems

(Suding, 2011). Restoration practices can also yield results that are highly variable, meaning individual sites grouped within the same study can react to the treatments very differently (i.e., can have positive, negative, or no effects) (Bestelmeyer et al., 2019). Variation in the results of restoration treatments is often attributed to site scale differences like soil texture, topography, and differences in weather experienced by individual sites (Brudvig et al., 2017). Although “restoration failures” have sometimes been attributed to underlying soil degradation or soil properties, there is still a need for research that explores whether ecological processes (e.g., nutrient cycling) and soil attributes can serve as an index for restoration potential (Costantini et al., 2016; Suding, 2011; Wortley et al., 2013).

The goal of our study was to determine if local site and soil properties were related to post treatment grass cover responses in areas where shrubs have been removed and, ultimately, if any of these properties could act as indicator variables of desert grassland restoration potential. We examined soil organic carbon, texture (proportions sand, silt, clay), bulk density, and pH as potential indicator variables for grass response after shrub removal treatment. We chose these variables because they are often used in restoration studies as indicators of overall soil function (Costantini et al., 2016), and are associated with properties that promote grass growth (e.g., soil moisture, infiltration, nutrient turnover) (Jackson et al., 2017). We also included site elevation and average annual rainfall as potential indicators for grass response, as previous studies have shown that desert perennial grass growth is related to precipitation (Khumalo & Holechek, 2005) and may be positively correlated with altitude (Desmond & Montoya, 2006). Relationships between site elevation and indicator variables were also explored, as soil properties and microclimate (rainfall) have been known to vary along altitudinal gradients (Roukos et al., 2017; Wheeler et al.,2007)

METHODS

Study Area

We conducted this study in the Chihuahuan Desert of southwestern New Mexico at 25 experimental sites that were established by the JER in collaboration with the BLM LCDO in 2007 or 2009 (site descriptions below). The elevations of our study sites range from 1340 to 1740 m, and the average annual rainfalls range from 200-300 mm. The dominant vegetation varies across the study sites, and the most prevalent shrub species present across these sites are creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), and tarbush (*Flourensia cernua*). The dominant grass species present are short-lived perennials, fluffgrass (*Dasyochloa pulchella*), and perennial grasses like bush muhly (*Muhlenbergia porteri*). The soils within this region are classified as gravelly to loamy. Historically, the two primary uses of land in this region are livestock production and recreation (Merlan, 2008; Unnasch, 2017; Vincent, 2019).

Restore New Mexico Experimental Site Design

Our study included two sets of experimental sites established by the JER and BLM LCDO. Both sets have experimental treatment plot pairs, consisting of an untreated control area (leave out area) and a corresponding area where shrubs were removed by the aerial application of herbicide (treated area) (*see* Supplemental Figure 2.4 for example photo). Herbicide (tebuthiuron (N-[5-(1-1-dimethylethyl)-1,3,4 thiadiazol-2-yl]-N, N'-dimethylurea) application occurred once at each site, in the fall or winter, with the year of application differing between sets of sites. The herbicide was applied to remove creosote bush at a rate ranging from 0.56 kg-ha to 0.84 kg-ha. The two sets are described separately below, but they will be collectively referred to as "RNM experimental sites". Growing season deferment (subsequent removal of cattle) was implemented for two to five years following treatment.

The first set of sites are 10 experimental treatment pairs that were established across three BLM allotments in 2007, hereafter called the “2007 sites”. Three tebuthiuron herbicide treatments were applied in 2007 in areas ranging from 2254-7751 ha. “Leave-out areas” (demarcated by digitized map “polygons”) were excluded from these herbicide applications and range in size from 13.6-32.1 ha. After herbicide application, 0.04 ha (20 x 20 m) treatment plot pairs were established by matching an untreated control area (CTL) from within the leave-out area with a nearby treated area (TRT) of similar landform, soil, ecological site and state, and plant community. The final selection of TRT areas was based on successful shrub removal treatment (defined as ~75% or more of shrubs defoliated).

The second set of sites are 15 treatment plot pairs established among thirteen allotments in 2009 and 2010, hereafter referred to as “2009 sites”. In 2009 JER stratified treatment polygons by ecological site and vegetation state and selected 9 ha (300 m x 300 m) ‘twins’ in the dominant strata. These visually identical squares were randomly selected to comprise a pair of experimental plots, and one of each pair was randomly assigned to be the CTL plot (leave-out area). The leave-out areas were excluded from BLM herbicide application, which occurred in 2009 and 2010 when thirteen tebuthiuron herbicide treatments were applied in areas ranging from 168 – 10,292 ha.

Vegetation Sampling

Permanently located transects were established by the JER in each CTL and TRT after herbicide was applied. For the 2007 sites, three 20 m transects were established in each area 10 m apart, and the 2009 sites had two 50 m transects established in each, separated by 20 m. 20 m transects were sampled at 20 cm intervals, and 50 m transects were sampled at 25 cm intervals, creating 300 points per plot. Vegetation data was collected using the line-point intercept method (Herrick et al., 2005). We used data collected in 2015 and 2016 for our analyses, as well as initial baseline vegetation data from each of the sets of sites. Baseline data at the 2007 sites was collected in 2007, and 2011 & 2012 for the 2009 sites.

Index for differences in grass cover between CTL and TRT areas

We calculated an index of grass cover difference between CTL and TRT using only perennial grass (graminoid) cover. Initial perennial grass cover between CTL and TRT plot pairs across all RNM experimental sites was not significantly different (t (47) = - 0.29, p = 0.77).

Our index included the initial baseline vegetation data from the CTL and TRT plot pairs to calculate a "Grass Gain Score" based on the relative change in grass cover over time at each respective plot.

$$\textit{Grass Gain Score} = (\textit{Final- Initial \% Grass cover at TRT}) - (\textit{Final- Initial \% Grass cover at CTL}) \quad \textbf{[1]}$$

A positive Grass Gain Score (GGS) could result from 1) an increase in grass cover at the TRT areas and a decrease in grass cover at the CTL areas; or 2) an increase in grass cover at the TRT areas that is greater than the increase in grass cover at CTL areas; or 3) a decrease in grass cover at the TRT areas that is less than the decrease in grass cover at the CTL areas.

Soil Sampling

We collected soil from CTL areas only, to serve as a proxy for site-level soil properties and pre-treatment conditions. Sampling under shrubs was consistently done at the dripline (canopy edge) at all RNM sites (2007 & 2009). Soil from the ten 2007 sites was sampled in June - August 2016. We sampled soil to 5 cm depth at each site from 10 to 15 haphazardly selected locations from each of two microsites – under living creosote shrub canopies (subcanopy) and from interspace between shrubs (interspace). Samples were spatially separated by a minimum of 10 m and at least 10 m from the JER vegetation transects to avoid disturbing long-term measurements. For bulk density, a single sample was taken from each CTL area.

Soil from the fifteen 2009 sites was sampled in June - November 2017. At the center of the CTL plot, we established two parallel 50 m transects approximately 25 m apart that were at least 10 m away from JER vegetation transects. Soils were collected along each of these 50-meter transects to 5 cm depth from nine haphazardly selected patches from each of the microsite types (subcanopy and interspace patches), ensuring the samples were evenly distributed across both transects. We then pooled these nine individual samples to form three combined samples for each subcanopy and interspace soil sample. For bulk density, we used three separate soil samples from interspace soils to yield a plot-level bulk density for each CTL area.

Average Annual Rainfall Data

Site level rainfall data was queried from PRISM climate data (PRISM Climate Group, 2017). All RNM sites' average annual rainfall was calculated from 10 years of data ranging from 2008-2017.

Soil Analyses

***Soil Carbon**:* Prior to soil carbon (C) analysis, soils were sieved at 2 mm, dried at 60 ℃ for a minimum of 72 hours, and then ground into a fine powder (less than 150 µm grain size). For samples from the 2007 sites, we analyzed soils for soil organic carbon (SOC) only using a dry combustion C analyzer (ElementarPyrocube®) after acid fumigation of soils to remove carbonates (Harris et al., 2001). For samples from the 2009 sites, we analyzed samples for both total soil carbon (TC) and soil organic carbon (SOC). TC was measured using a LECO SC632 carbon and sulfur determinator (LECO CO., St. Joseph, MI), and SOC was measured following the same procedure after leaching inorganic carbon (inorganic carbonates) from the soil with 10 ml of 10% HCL. For both TC and SOC analysis, pure calcium carbonate (12% Carbon), ore tailings (0.50% Carbon), and LECO Soil (0.926 % Carbon) were used as calibration standards, and synthetic carbon (5.03% Carbon) used as a check standard. An additional check standard of pure calcium carbonate (12% Carbon) leached with 10 ml of 10% HCL was used in the SOC analysis to ensure that the leaching process removed all inorganic carbon.

Soil Texture (Particle Size): We mixed a known weight (30-50 grams) of soil with 100 mL of DI water, breaking up larger soil aggregates manually. Soil was placed in an ultrasonic bath for 10 minutes to further break up larger aggregates and then stirred to break up residual aggregates. We then passed the solution through a 63µm mesh sieve, collecting the sand on the sieve, and the clay/silt suspension that passed through was centrifuged at 750 rpm for 7 minutes, resulting in a silt pellet with the clay suspended in liquid. Sand and silt components were dried (60℃ for at least 72hrs) and weighed, and the clay portion was determined by subtracting the silt and sand weights from the initial weight.

Soil pH and Bulk Density: We measured soil pH on 15 grams of soil in a 1:2 slurry of soil to DI water, which was left to stand for 30 minutes after stirring to equilibrate to the ambient atmospheric CO2. We calculated soil bulk density as the dry weight of the soil samples (dried at 60 ℃ for 72 hours) divided by its measured field volume. Soil volume at the 2007 sites was determined using a soil ring (corer) method (the soil ring yielded an approximate volume of 250cm^3). Soil volume measurement at the 2009 sites consisted of using trowels and rulers to measure and excavate soil as an approximately 5x5x5cm cube - two times, yielding an approximate volume of 250cm^3, and actual excavated volume was recorded.

Statistical Analyses

For all analyses, we first averaged soil variables by microsite type (subcanopy or interspace) within each plot, with each plot/site acting as a single replicate. We used linear regressions to test for correlations between our potential soil indicator variables and Grass Gain Score (GGS), analyzing subcanopy and interspace soils separately. We also used linear regressions to explore relationships between GGS and site-level variables (plot bulk density, elevation, and rainfall), as well as the relationship between site elevation and our other site and soil variables. Due to the two-year difference in time since shrub removal between the two site groups (2007 vs. 2009), we ran a series of ANCOVAs to determine if any of our regression model slopes differed by site group. In cases where the slopes of the site groups were significantly different, we separated the analyses by site group – when slopes were not different, both site groups' data remained pooled together for the regression model.

We used multiple linear regressions to determine the extent that our indicator variables could be related to grass response by testing if more than one of our variables could simultaneously be predictors for GGS. We separated multiple linear regression analyses by site group (2007 vs. 2009) but included both microsite types (subcanopy and interspace), equaling two data points per site. For multiple linear regressions, we used scatterplots with correlation coefficients to eliminate any indicator variables that did not have a significant correlation coefficient ($\alpha \geq 0.2$) with Grass Gain Score. We then used the backwards selection method to eliminate non-significant relationships (*p-value* ≥ 0.05) between the remaining indicator variables and Grass Gain Score. We ensured that the adjusted R^2 did not decrease from the initial to final fit models and that the VIF (Variance Inflation Factor) for each relationship was less than $\alpha = 2$ in the final models. Additionally, we plotted the residuals of each model and used a Shapiro-Wilk test to ensure that the residuals of the models were normally distributed (p-$value > 0.05$). For all regression analyses, a two-sided p-value was reported. For single predictor linear regression models, an R^2 value was reported, and for multiple linear regression analyses, an adjusted R^2 was reported. All analyses were conducted using RStudio Version 1.3.1093. R package ggplot2 was used for graphing (Wickham, 2009), as well as JMP® Version 17.0.0.

RESULTS

There was no significant difference in Grass Gain Score (GGS) between the 2007 and 2009 RNM site groups ($F_{1,24} = 0.58, p = 0.46$). GGS ranged from -4.3 to 42.3% and on average was 13.3% (*see* Supplemental Figures 2.1 and 2.2; Supplemental Table 2.1). There was a significant difference in the slope of the regression between site groups (2007 and 2009) for the relationship between GGS and soil organic carbon (Subcanopy). Thus, those relationships were analyzed separately by site group. GGS was positively correlated to soil organic carbon in interspace patches across all RNM sites, but we caution that this relationship was driven by two points with relatively high soil carbon values ($R^2 = 0.15, p = 0.05$) (Figure 2.1a). GGS was also positively correlated with soil organic carbon for soil from under subcanopy in both the 2007 ($R^2 = 0.70, p = 0.002$) and 2009 site groups ($R^2 = 0.49, p = 0.004$) (Figure 2.1b).

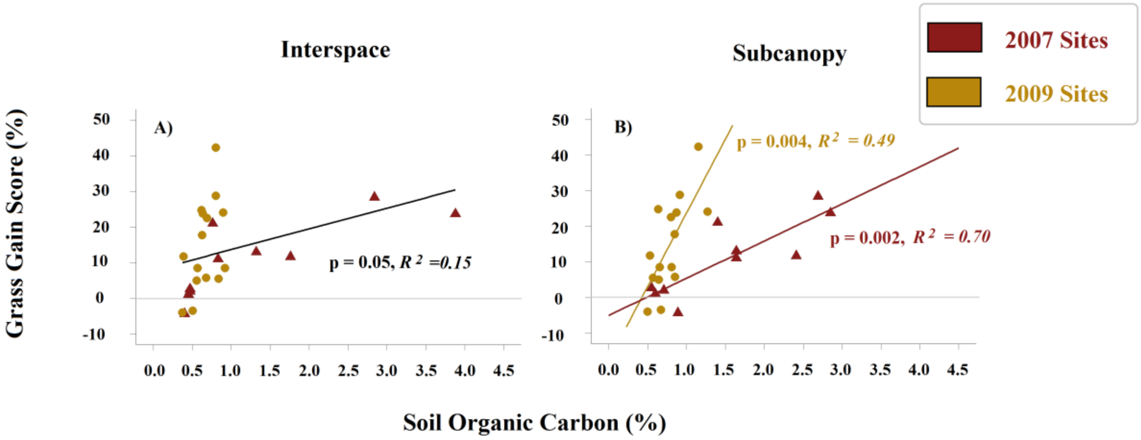

Figure 2.1: Relationship between Grass Gain Score ((*Δ Final and Initial %Grass cover at shrub removal plots)* - *(Δ Final and Initial %Grass cover at no shrub removal plots*)) and soil organic carbon in control plot soils from Interspace (a) and beneath Subcanopy (b) microsite types in a ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Ten of the study sites received shrub removal treatments in 2007 ("2007 sites"), and fifteen of the study sites received shrub removal treatments in 2009 ("2009 sites"). Statistical significance of relationships is denoted by bold font (p=<0.05). If relationships did not differ significantly between site groups (2007 vs. 2009), both site groups were pooled together for analyses (a). If the relationships differed significantly between site groups, the analyses were separated by site group (b).

There was a significant difference in average annual rainfall between the 2007 and 2009 RNM site groups **(**$F_{1,24} = 4.38, p = 0.05$) – the 2007 sites overall had higher average annual rainfall. Average annual rainfall at the 2007 sites ranged from 264.39 – 285.16 mm and the average across these sites was 277.30 mm. Average annual rainfall at the 2009 sites ranged from 230.38 – 297.04 mm and the average across these sites was 263.35 mm. There was no significant relationship between GGS and rainfall across all RNM sites ($R^2 = 0.11, p = 0.11$).

There was a significant difference in site-level elevation between the 2007 and 2009 RNM site groups ($F_{1,24} = 19.7, p = <0.001$) – the 2007 sites were overall higher in elevation. Elevation at the 2007 sites ranged from 1446 – 1733 m and on average was 1614 m. Elevation at the 2009 sites ranged from 1340 – 1580 m and on average was 1438 m. GGS was positively correlated with elevation across all RNM sites (Figure 2.2).

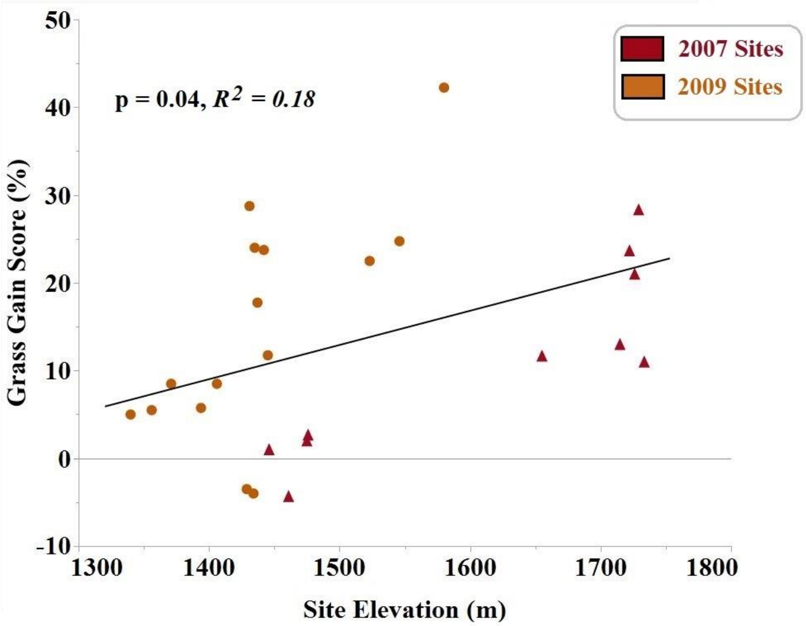

Figure 2.2 Relationship between Grass Gain Score ((*Δ Final and Initial %Grass cover at shrub removal plots*) - (*Δ Final and Initial %Grass cover at no shrub removal plots*)) and site-level elevation in meters across 25 study sites that were part of ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Ten of the study sites received shrub removal treatments in 2007 ("2007 sites"), and fifteen of the study sites received shrub removal treatments in 2009 ("2009 sites"). Statistical significance of relationships is denoted by bold font (p=<0.05).

There was a significant difference in the slope of the regression between site groups for the relationships between elevation and soil texture, organic carbon, and bulk density so these analyses were separated. Elevation at the 2007 sites had significant relationships with % sand, % silt, and soil organic carbon; but not with % clay (Table 2.1a). Elevation at the 2009 sites showed no significant relationships with any of the soil texture variables or soil organic carbon (Table 2.1b). Elevation was not related to plot-level bulk density at either of the site groups (Table 2.1a, b). Across all RNM sites, elevation was positively related to soil pH (Table 2.1C) and average annual rainfall (Figure 2.3).

Table 2.1: The relationships between site-level elevation and pre-treatment site and soil characteristics in a ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Ten of the study sites received shrub removal treatments in 2007 (“2007 RNM sites”) (a), and fifteen of the study sites received shrub removal treatments in 2009 (“2009 RNM sites”) (b). If the relationships differed significantly between site groups, the analyses were separated out by site group (a, b); if not, then site groups were pooled together for analyses (c). Statistical significance of relationships is denoted by bold font (p=<0.05).

	A) 2007 RNM Sites			**B) 2009 RNM Sites**		
	P-value	R^2	*Equation*	*P-value*	R^2	*Equation*
Sand~Elevation	**<0.001**	**0.78**	**Y= -0.08x + 191.97**	0.93	0.00	Y= 0.003x + 63.87
Silt~Elevation	**<0.001**	**0.79**	**Y= 0.08x - 89.38**	0.57	0.01	Y= 0.013x + 7.53
Clay~Elevation	0.37	0.04	Y= 0.01x – 2.59	0.08	0.11	Y= -0.016x + 28.60
Soil Organic Carbon~Elevation	**<0.001**	**0.48**	**Y = 0.01x – 7.48**	0.38	0.03	Y = 0.001x - 0.001
Plot Bulk Density~Elevation	0.43	0.08	Y = -0.0001x + 1.59	0.24	0.10	Y = 0.001x -1.22
C) All RNM Sites						
Average Annual Rainfall~Elevation	**0.009**	**0.26**	**Y = 0.07x + 165.23**			
Soil pH~Elevation	**0.002**	**0.18**	**Y = 0.001x + 6.51**			

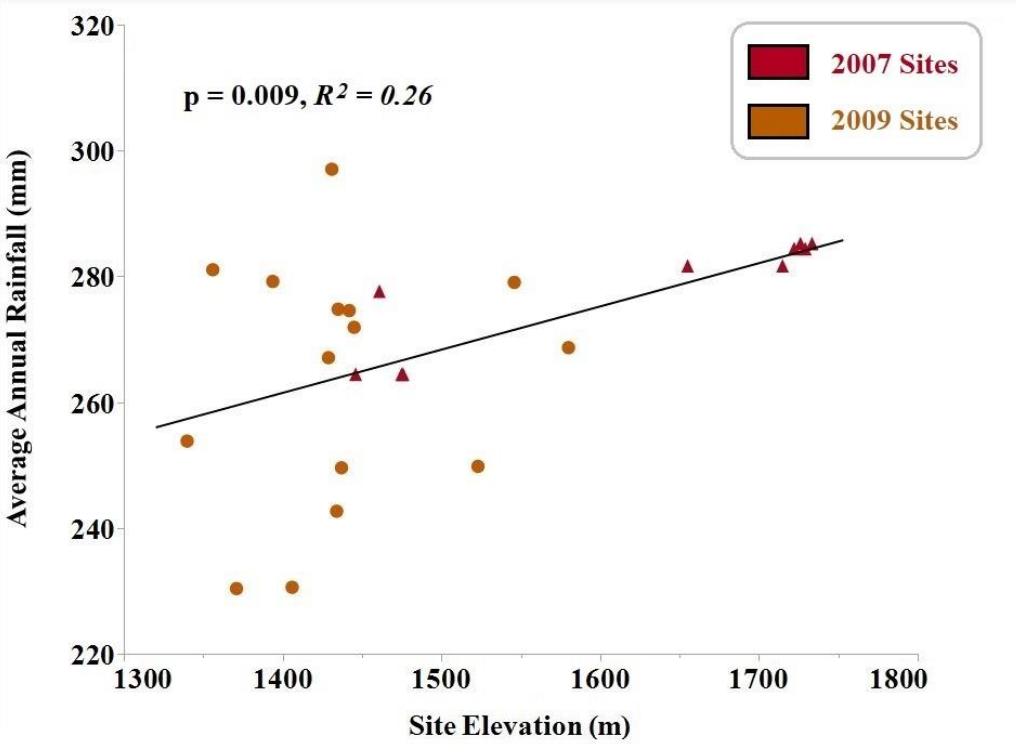

Figure 2.3: Relationship between Average Annual Rainfall (mm) and site-level elevation in meters across 25 study sites that were part of a ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Ten of the study sites received shrub removal treatments in 2007 ("2007 sites"), and fifteen of the study sites received shrub removal treatments in 2009 ("2009 sites"). Statistical significance of relationships is denoted by bold font (p=<0.05).

When we used multiple regression analyses to test multiple indicators simultaneously for relationships with GGS, we found that at both the 2007 and 2009 sites, elevation and soil organic carbon were related to GGS, and at the 2009 sites only, rainfall was also related to GGS (Table 2.2; Supplemental Tables 2.2 and 2.3). In this 2009 Sites model, it should be noted that the model adjusted R^2 significantly decreased when we attempted to remove the last non-significant variable (Average Annual Rainfall, *p = 0.09*). Since this *p-value* was marginal, and the VIF for that variable remained below 2, we opted to include the variable to present the model of best fit (Supplemental Table 2.3).

Table 2.2: Summary of multiple linear regression (MLR) models showing the relationship between Grass Gain Score and two or more indicator variables, at two groups of study sites that were part of ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Ten of the study sites received shrub removal treatments in 2007 (“2007 RNM sites”), and fifteen of the study sites received shrub removal treatments in 2009 (“2009 RNM sites”). Analyses note: In the 2009 Sites model, the adjusted R^2 decreased significantly when we removed the last non-significant relationship (Average Annual Rainfall, coefficient $p = 0.09$). Since this *p-value* was marginal, and the VIF for that variable remained below 2, we determined to keep it in the model to present the model of best fit.

MLR Model	Adjusted R^2	Formula	Overall Significance (ANOVA)
2007 RNM Sites			
Grass Gain Score ~ Elevation + Soil Organic Carbon (SOC)	**0.82**	Grass Gain Score = 0.05 (Elevation) + 3.77 (SOC) -77.85	$(F_{2,19} = 44.23, p = <0.0001)$
2009 RNM Sites			
Grass Gain Score ~ Rainfall + Elevation + Soil Organic Carbon (SOC)	**0.71**	Grass Gain Score = 0.12 (Avg Annual Rainfall) + 0.11 (Elevation) +27.17 (SOC) – 200.84	$(F_{3,29} = 24.15, p = <0.0001)$

There was also a significant difference in the slope of the regression between site groups for the relationship between GGS and %sand (Interspace) therefore those relationships were analyzed separately by site group. GGS was negatively related to % sand in interspace but only at the 2007 sites ($R^2 = 0.61, p = 0.01$) (Supplemental Figure 2.3a), and there was no relationship at the 2009 sites ($R^2 = 0.03, p = 0.51$). Across all RNM sites, GGS was not related to % sand subcanopy ($R^2 = 0.08, p = 0.18$), % silt under either subcanopy ($R^2 = 0.10, p = 0.13$) or interspace ($R^2 = 0.05, p = 0.29$), or with % clay under either subcanopy ($R^2 = 0.00, p = 0.93$) or interspace ($R^2 = 0.09, p = 0.14$) (Supplemental Figure 2.3, b-f). GGS also did not have significant relationships with plot-level bulk density ($R^2 = 0.03$, $p = 0.40$), nor with soil pH subcanopy ($R^2 = 0.05$, $p = 0.30$), or soil pH in interspace ($R^2 = 0.05$, $p = 0.26$).

DISCUSSION

We sought to determine if soil and site characteristics were correlated with the response of grass cover to shrub removal - with an overarching goal of identifying indicator variables for desert grassland restoration potential. The strongest relationship we found was a positive relationship between Grass Gain Score (GGS) and soil organic carbon for soils from both subcanopy and interspace microsites (i.e., higher soil organic carbon correlated with higher grass gain). Relationships between GGS and soil texture were only found at one set of sites (2007 Sites), where less % sand correlated to higher GGS. We also found that across all study sites, GGS was positively related to elevation but not to average annual rainfall. Additionally, elevation was related to several of our other site and soil indicators. At the 2007 sites only, elevation was positively related to soil organic carbon and % silt; and negatively related to % sand. Elevation was also positively correlated to soil pH and average annual rainfall across all RNM sites. Below we discuss why soil organic carbon (SOC), and site elevation could be valuable indicator variables in future restoration studies.

Significant indicators of grassland restoration potential

We predicted that site and soil properties that are known to affect soil moisture and nutrient content in semi-desert soils (e.g., SOC and soil texture) may control grass establishment and growth (Smith & Waring, 2019) after shrub removal. Chihuahuan Desert grass establishment is constrained by a lack of soil moisture and water retention, which is largely due to high evaporation rates via wind and rising temperatures that push soil moisture below levels needed for grass establishment and growth (Chappell et al., 2019; Kidron & Gutschick, 2017). We suggest that the positive relationship we found between SOC and grass response to shrub removal is likely related to soil water retention - as SOC increases soil moisture, infiltration, and nutrient storage (Costantini et al., 2016; Wiesmeier et al., 2019). Higher SOC is indicative of better nutrient retention (Gavrilescu, 2014), and greater resource availability for microbial communities - which could in turn positively influence nutrient cycling for re-establishing grass species (Bell et al., 2008; Kästner & Miltner, 2018).

Site level elevation was also a strong indicator for GGS, which complements previous studies that emphasize how closely elevation is tied to plant community structure in this region; Chihuahuan Desert perennial grasses have historically colonized at middle to higher elevations (Campbell et al., 2013; Desmond & Montoya, 2006), and less so at lower elevations where encroaching shrub species have had a competitive advantage. Additionally, we saw that elevation correlated positively with SOC, % silt, and soil pH; and negatively with % sand. This is consistent with findings from other desert systems that show soil properties like soil organic matter (i.e., soil carbon) are closely linked to elevation (Campbell et al., 2013; Collins & Cavigelli, 2003). Although we found no direct relationship between average annual rainfall and GGS the importance of elevation for GGS, and the positive correlation between elevation and rainfall suggests that long-term variation in microclimate associated with elevation exerts an important control on grass recovery. Higher elevations in this region have generally been associated with wetter-cooler microclimates (Litvak, 2015). Overall, subtle differences in local altitude and related soil conditions could foster the growth of perennial grasses such as black grama (*Bouteloua eriopoda*), which are said to have originally established under much wetter and cooler conditions than today (e.g., during the “Little Ice Age”) (Neilson, 1986). Except for soil pH, the relationship between elevation and soil variables was only found in the 2007 sites where the elevational gradient was generally bimodal. Consequently, using elevation as an indicator for grass response and soil properties may be suited to restoration sites with pronounced differences in elevation (i.e., steeper gradient) - a trend that has already been seen in other biome types (Zhang et al., 2021).

Our multiple linear regression analyses showed that combinations of site and soil indicators were related to grass responses following shrub removal. At the 2007 sites, soil organic carbon and elevation were related to GGS. At the 2009 sites, soil organic carbon, elevation, and rainfall were related to GGS. Soil organic carbon and elevation remained predictive of GGS in both models and were the strongest indicators of grass response of the variables we examined. In the 2009 sites model, rainfall was only marginally significant; however, we note that there were more data points overall in this model compared to the 2007 sites model (i.e., there are five more sites in the 2009 site group). As sample size greatly affects the overall model of multiple linear regression analyses (Duan et al., 2022), we suspect that rainfall might have been a significant variable if the sample size was higher; however, further sampling would be needed to test this prediction.

Soil physical variables were less correlated with grass gain

Soil texture across all RNM sites was not a strong indicator of GGS, but some significant relationships were found at the 2007 sites only – where GGS was negatively related to % sand. These results support previous studies which show that soils made up of less sand and more silt or clay (i.e., loams) may support grass seed establishment by providing optimal infiltration and retention - especially for perennial grass species (Peters & Gibbens, 2006). Although the relationships between soil texture and GGS were not as strong as we initially expected, it still provides valuable information on soil porosity and infiltration (Brady & Weil, 2008).

Neither soil pH nor bulk density were strong indicators for GGS. This lack of relationship for pH is likely due to the relatively limited range of soil pH across all the RNM sites. All soils were consistently alkaline, within a range that perennial desert grasses typically grow (Zhou et al., 2012). We also anticipated that soil bulk density would be related to GGS, as it is often related to soil texture and indicative of compaction (Martín et al., 2017); however, we did not find that it was related to grass response at either of the site groups in our study (2007 vs. 2009). Although our results did not support using soil pH or bulk density as indicators for GGS, they are still widely used soil measurements in restoration studies and have value as monitoring variables (Costantini et al., 2016).

Microsite Sampling Scheme

In our study, we stratified sampling by microsite type (subcanopy and interspace) in anticipation that we would measure contrasting soil characteristics. This prediction derives from the well documented "Island of Fertility" effect wherein soils under shrub canopies stabilize and accumulate soil nutrients as they are lost from eroding interspaces (Walker et al., 2001). However, we found no significant differences in SOC between subcanopy and interspace patches, although there were differences in soil organic carbon relationships with GGS between the two patch types. The similarity in SOC between the two patch types could be explained as a "balancing out" of soil resources through the transfer of shrub and other vegetation inputs. Some studies have shown that the amount of soil carbon in interspace patches is directly connected to the shrub individuals that exist between them (i.e., carbon % under shrubs correlate to carbon % in their interspace – relative to species of shrub and their unique carbon inputs) (Norton et al., 2008). Additionally, interspace patches may also be subject to their own organic carbon inputs as interspaces in shrubland areas can be temporarily occupied by short-lived perennial or annual plant species (e.g., forbs or weeds)

(Demarco et al., 2016). Collectively, these findings indicate that the most effective way to evaluate our proposed soil indicator variables is to account for any microsite type (patch-scale) variability at a potential restoration site. This sampling method would reduce sampling bias and account for the heterogeneity in soils between microsite types.

Value and limitations of suggested indicator variables

Variables such as SOC are ideal indicators for long-term restoration studies, as it is a reasonably slow changing variable, due to water limitation in these semi-desert regions, with turnover rates ranging from decades to centuries (Brazier et al., 2014; Frank et al., 2012). SOC is an accessible and relatively inexpensive measure of soil properties, increasing the value of its use in restoration efforts; SOC is easily measured in a lab using a muffle furnace (Loss of Ignition method) or combustion analyzer (e.g., LECO SC632) and commercial options are also available (Bianchi et al., 2008). Additionally, SOC has long been considered an indicator of soil health and quality (Jenny, 1941; Wiesmeier et al., 2019), as well as an indicator of grassland productivity (Tessema et al., 2020). Soil organic matter (i.e., SOC) is already being considered as an indicator variable to estimate soil loss from erosional processes in Drylands undergoing degradation (Billings et al., 2021; Lorenz et al., 2019).

Lastly, we recommend using site elevation as an indicator for grass response because it may be indicative of soil variables (% sand, % silt, soil organic carbon, soil pH) and environmental characteristics (microclimate) - with the caveat that the study or restoration region exists along a reasonably variable elevational gradient. Site level elevation can be easily measured (using most GPS devices) and is often already included as a descriptive site variable in many restoration studies.

While we do recommend that these indicator variables are useful for restoration planning, there are still significant caveats that restoration planners should be aware of. For instance, soil properties in the Chihuahuan Desert are subject to patch scale variation (subcanopy vs. interspace) and regional variability (e.g., soil carbon in one region may be significantly lower than others) (Havstad et al., 2006). This indicates that correlations between soils and response variables may be more apparent in larger-scale management projects, where sites capture heterogeneity within the landscape. To minimize these limitations, we recommend that restoration planners continue to select sites that are comparable within their study region (e.g., Restore New Mexico selected sites based on similar soils, landform, ecological state, and plant community) and consider using our proposed indicator variables as qualitative reference points for identifying potential restoration sites.

In conclusion, soil and site-level properties remain widely underused as indicator variables for restoration potential, yet there is a consistent call from the science community to include them in the planning process (Gornish & Shaw, 2017; Mendes et al., 2019; Stanturf et al., 2021). Based on our study's findings, we recommend that land managers and stakeholders consider soil organic carbon and site elevation when identifying sites that are potential candidates for desert perennial grass restoration.

MANAGEMENT IMPLICATIONS

It is imperative that land managers of dryland systems continue to build upon their toolbox for estimating restoration success, especially at a time when Drylands are faced with increased climate and anthropogenic pressures. In restoration practices, site indicators are frequently used to measure or predict outcomes, such as vegetation structure, diversity, and abundance, as well as ecological processes (Wortley et al., 2013). However, there is a growing emphasis in the literature that stresses that site and soil characteristics (e.g., soil carbon) should have more consideration in the planning for restoration success, particularly in pre-restoration assessments (Brudvig et al., 2017; Ruiz-Jaen & Mitchell Aide, 2005; Rydgren et al., 2020; Wortley et al., 2013).

Our study found that soil organic carbon and elevation were positively correlated to grass gain following large-scale shrub removal in Drylands. These results highlight that site and soil conditions are worth exploring prior to implementing restoration practices. We suggest that these indicators are important for establishing baseline site conditions, and including these variables in pre-restoration assessments may help in identifying or prioritizing potential desert grassland restoration sites. We chose these variables for their general accessibility of analyses as well as their well-known relationships with properties that affect grass seed establishment and growth (Smith & Waring, 2019), making them ideal measurements for large-scale land management programs. However, there may be several additional important site and soil properties that could be tested in future studies to identify other strong indicators of grass response following shrub removal (Costantini et al., 2016; Smith & Waring, 2019).

AUTHOR CONTRIBUTIONS

This Chapter has been submitted for review in a peer-reviewed journal and is co-authored by Kathleen Schaeffer (KS), Brandon Bestelmeyer (BB), Laura Burkett (LB), and Jennie McLaren (JM). The methodology for this specific study was designed by JM and KS, with significant inputs from BB and LB. KS collected and analyzed data; JM and KS interpreted results with additional input from BB and LB; KS led the writing of the manuscript. All authors contributed significantly and gave final approval for publication.

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DATA ACCESSIBILITY

Data from this project will be made available when publication for this chapter is finalized. Potential data centers include National Resources Conservation Service (NRCS) or BLM/USDA affiliated data centers.

Chapter 3: Large-scale shrub removal had no effect on soil organic carbon but could lead to burial of soil inorganic carbon in the Chihuahuan Desert

ABSTRACT

Prior to the 1800s, much of the Chihuahuan Desert of southern New Mexico was perennial desert grasslands, which have since been greatly reduced and displaced by encroaching shrub communities. Recent restoration efforts aim to recover grass and herbaceous species by removing shrubs via herbicide, which often leads to the emergence of novel plant communities. However, there is still much unknown on how this transition will affect valuable ecosystem resources like soil carbon. The aim of our study was to determine how large-scale shrub removal practices are affecting soil organic and inorganic carbon ca. 8 years after shrubs are removed. The study took place at 15 experimental shrub removal sites across the southwest of New Mexico, established by "Restore New Mexico". We sampled surface soils and measured vegetation/ground percent cover at paired no-removal control and shrub removal treated areas and analyzed soils for carbon (organic and inorganic), pH, bulk density, and texture (% sand, silt, and clay). We found that grass and herbaceous cover was higher in shrub removal areas. We found that plot-level soil organic carbon (SOC) did not change; however, soil inorganic carbon (SIC) was lower in shrub removal areas. We suggest here that the SOC inputs following shrub removal came from returning grasses and decomposing shrub skeletons. We also suggest these SOC inputs are comparable to those from preceding shrubland communities; thus, no change was detected. We propose that SIC is likely being buried by an influx of dust and sand that is being captured by recovering grasses in treated areas, which was partially supported by soil texture results. These findings emphasize that large-scale shrub removal practices, at this timescale, may not lead to increases in soil carbon but may protect sequestered inorganic carbon sources from loss due to erosion.

INTRODUCTION

Prior to the 19th century, the Chihuahuan Desert of southwestern New Mexico was primarily perennial desert grasslands (Buffington & Herbel, 1965; Wooton, 1908). These grasslands were greatly reduced over the last few centuries due to cattle grazing, homesteading, and ongoing global climate change (D'Odorico et al., 2012; García Criado et al., 2020). These factors helped create conditions that enabled shrub species such as creosote bush (*Larrea tridentata)* and honey mesquite (*Prosopis glandulosa)* to encroach upon and displace grassland habitats – which has resulted in the shrub-dominated landscapes presently found in the Chihuahuan Desert (Barger et al., 2011). This transition to a shrub-dominant state has largely been viewed as harmful to these desert ecosystems, given that a loss of grass habitat means less forage for cattle, reduced habitat for grass-specific wildlife, and a loss of soil and water storage potential (Rango et al., 2005).

Preserving the remaining grassland is of prime concern for local land managers, who have been actively attempting to reduce shrubs and increase grass cover since the early 1900s (Buffington & Herbel, 1965; Lister et al., 2012; Wooton, 1908). Since the 1980s, shrub removal through the aerial application of herbicide has been a common practice of the New Mexico Bureau of Land Management (BLM) (Bestelmeyer et al., 2019). In 2005, the BLM joined forces with the USDA and several local stakeholders to establish intensive monitoring of these ongoing shrub removal practices in a program called "Restore New Mexico".

These large-scale shrub removal practices create novel plant communities – which include living (surviving) shrubs, dead shrub skeletons, re-establishing forbs, grasses, and the unvegetated interspace between them. These unique emerging landscapes are distinctive from both the shrub-dominated areas they were preceded by as well as the perennial desert grasslands of the past

(Bestelmeyer, 2015; Hobbs et al., 2014). Recent studies have shown that this transition to novel plant communities affects many aspects of the aboveground habitat structure, especially if grass or herbaceous species increase after shrubs are removed. For instance, grass recovery can have positive effects on grass-specific species of birds and lizards but negative effects on shrub-specific species, which can ultimately alter the community structure of the local wildlife (Coffman et al., 2014; Cosentino et al., 2013). While it is apparent that this change in plant community identity can, in turn, modify the identity of the aboveground fauna, it is unclear how it will affect the belowground properties of these desert ecosystems.

When this region shifted from grassland to shrubland, it affected belowground processes and properties in several ways. The dominant shrubs (creosote bush and honey mesquite) have physical and biochemical characteristics that significantly influence soil resources. For example, the understory of the honey mesquite shrub efficiently captures eroded sand, which over time can lead to the burial of grass species and the formation of coppice sand dunes (stands of mesquite in large areas of sand deposits) (Gibbens et al., 2007; Okin & Gillette, 2001). Creosote bush similarly collects traveling soil and plant debris under its canopy, which concentrates organic matter under shrubs (i.e., the island of fertility effect) (Walker et al., 2001). Additionally, creosote bush may also interfere with the seed germination of other plants through the release of toxins into the soil around its understory (i.e., allelopathy) (Hyder et al., 2002). Shrub encroachment may have shifted not only the physical properties of the soils around them but also the distribution of soil resources such as soil carbon.

Although on an individual basis, Drylands hold relatively low levels of soil organic carbon (less than 0.5 % SOC content), combined Drylands contribute greatly to the inter-annual variability of the terrestrial global carbon cycle (Lal, 2019; Poulter et al., 2014). Recent estimates show that despite their low SOC content, collectively, Drylands make up ~27-33% of the global organic carbon stocks because of their great extent (Plaza et al., 2018; Safriel, 2005). Dryland soil organic carbon plays a significant role in regulating soil structure and temperature, as well as retaining water and nutrients for plants and soil organisms (Lal, 2019).

In addition to contributions to global SOC stocks, Drylands additionally account for ~97% of the world's terrestrial soil inorganic carbon (i.e., calcium carbonates) – which is a much less studied form of soil carbon (Plaza et al., 2018). In the Chihuahuan Desert, inorganic soil carbonates can form from parent rock material like limestone; however, they can also form through chemical reactions sequestering atmospheric carbon (i.e., pedogenic carbonates) (Monger & Martinez-Rios, 2000). The alkalinity of desert soils allows calcium-rich dust (namely from silicates) to deposit on soils without significant disturbance (i.e., relative to forest soils where leaf litter-derived acids quickly leach carbonates through the soil profile) (Schlesinger & Bernhardt, 2013). When water and carbon dioxide mix in desert soils (i.e., form carbonic acid – H_2CO_3), they can dissolve these calcium-rich deposits, along with bicarbonates - in a process that can eventually precipitate different forms of soil inorganic carbonates (e.g., filaments, caliche layers). This process can sequester CO_2; however, the length of the process varies from weeks to thousands of years depending on the type of inorganic carbonate (Kraimer et al., 2005). Soil inorganic carbon has historically been understudied because of this vast timescale and has generally been thought to be an inactive pool of carbon (i.e., high mean residence times make carbonates inaccessible to microbes) (Zamanian et al., 2021). Regardless of these perspectives, soil inorganic carbon is increasingly gaining notice as an underappreciated soil resource that should be more widely considered in global soil carbon estimates and conservation efforts (Gao et al., 2017; Pilli et al., 2023; Zamanian et al., 2021), namely because losses of these carbonate pools may negatively affect global CO_2 sequestration or regional carbon stocks in Drylands (Liu et al., 2020; Wu et al., 2009).

Shrub encroachment can have variable effects on soil carbon, and the direction of the effect (i.e., positive vs. negative) often depends on regional differences in soil properties (e.g., soil depth, texture, pH), history of land use, and the biophysical properties of the encroaching shrubs themselves (Eldridge et al., 2011; Hu et al., 2021; Li et al., 2016). In shrub-dominated areas, there exist large patches of unvegetated interspace between shrubs, which leaves both organic and inorganic soil carbon vulnerable to loss by wind and water erosion (Havstad et al., 2006; Okin et al., 2001). Shrubs do, however, capture a portion of eroded soils and nutrients (Wallace et al., 1980), which indicates their removal could impact the rate of erosion in these regions if grass and herbaceous regrowth does not occur following treatment.

The effects of shrub removal on dryland ecosystems can vary and may not always result in grass recovery (e.g., shrub removal may lead to a landscape of dead shrub skeletons and interspace patches (*see* Supplemental Figure 3.1)) (Bestelmeyer et al., 2019). The unpredictable nature of restoration practices makes it difficult to estimate how shrub removal practices could influence resources like soil carbon. Studies from other deserts with similar shrub-dominated states, like the Sonoran Desert, have found that shrub removal can decrease soil organic carbon by disturbing the potential inputs and storage capacity of shrub-derived soil carbon (Demarco et al., 2016). There is also evidence that shrubs may be more effective at sequestering inorganic soil carbon under their canopies for longer periods than historical grassland systems (Throop et al., 2013), meaning shrub removal may reduce inorganic soil carbon sequestration. These uncertainties underline a need for regionally based comparisons in soil carbon between shrublands and areas where shrubs have been removed (i.e., novel plant communities).

The goal of our study was to determine if large-scale shrub removal practices in the Chihuahuan Desert of New Mexico result in vegetation and ground cover changes and also changes in soil organic and inorganic carbon. We tested the following hypotheses and predictions below:

Hypothesis 1 (H1) Soil organic carbon (SOC) will increase with shrub removal due to:

1. Changes within a ground or vegetation type (i.e., local level) [***H1a***]. For example, if interspace soils in treated plots have higher SOC than interspace soils in control plots.
2. Changes in proportional ground and vegetation cover following shrub removal (e.g., increase in grasses) will, in turn, increase soil organic carbon at the plot-level due to differences between ground cover types in SOC [***H1b***].

Hypothesis 2 (H2) Soil inorganic carbon (SIC) will not differ between treatment plots, as the precipitation rate of inorganic carbon occurs at relatively long timescales.

We tested both these hypotheses using a shrub removal experiment ~8 years after shrubs were removed. From control and treated plots, we collected and analyzed soils for soil carbon (organic and inorganic), as well as soil pH, bulk density, and texture, as those properties are related to soil carbon retention (Lorenz & Lal, 2022). Finally, we estimated entire plot-level soil carbon values, after adjusting for ground cover type specific soil carbon values along with the proportional cover of each ground cover type.

STUDY AREA AND RNM EXPERIMENTAL DESIGN

We conducted this study in the Chihuahuan Desert of southwestern New Mexico, at 15 experimental shrub removal sites established by the Restore New Mexico Initiative (RNM). The elevations of our study sites range from 1340 to 1580 m, and the average annual rainfall ranges from 200-350 mm. The dominant vegetation varies across the study sites, but the most prevalent shrub species are creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), and tarbush (*Flourensia cernua*). The dominant grass species present are short-lived perennials, including fluff-grass (*Dasyochloa pulchella*) and perennial grasses like bush muhly (*Muhlenbergia porteri*). The soils within this region are classified as gravelly to loamy. Each of the 15 RNM sites consists of two paired 9 ha (300 x 300 m) plots. One plot underwent shrub removal treatment (treated plots), and the other served as the control (no shrub removal). Herbicide (tebuthiuron (N(tebuthiuron (N-[5-(1-1-dimethylethyl)-1,3,4 thiadiazol-2-yl]-N,N'-dimethylurea) (0.56 -0.84 kg - ha)) application occurred at the treatment plots only in the winter or fall of 2009 and 2010. Removing livestock from the plots after herbicide application was also common practice after the initial setup.

METHODS

At each of the 15 paired shrub removal and control plots, we established two 50-m transects (avoiding any inconsistent landforms such as sharp gullies or high hillslopes) that ran parallel but were a minimum of 15 m away from previously established permanent RNM transects. We collected vegetation cover using the line transect method between June and November of 2017, where we recorded the ground cover category (living shrub, dead shrub, forbs/grasses, and unvegetated interspace) along the entire length of the transect, with the constraint that ground cover category needed to cover at least a contiguous meter to be included. We then used this vegetation and ground cover data to calculate the proportional cover of different ground cover types and their representative soil carbon content - to estimate plot-level soil carbon values (g C/m^2) for each control and shrub removal area (*see* details below).

On the same day as vegetation sampling, soils were collected to 5 cm depth from 9 haphazardly selected patches of each vegetation and ground cover type along our transects, ensuring that samples were relatively evenly distributed across both transects. Shrubs were sampled at dripline, and other cover types were sampled in the center of the cover patch. These 9 individual samples were randomly pooled into 3 composite samples that were used for soil carbon and texture analyses. In addition, we sampled soil at 3 locations per ground cover type for bulk density.

Soil Analyses

Soil pH and Bulk Density: We measured soil pH on 15 grams of soil in a 1:2 slurry of soil to DI water, which was left to stand for 30 minutes after stirring to equilibrate to the ambient atmospheric CO2. We calculated soil bulk density as the dry weight of the soil samples (dried at 60 °C for 72 hours) divided by its measured field volume. In the field, we used trowels and rulers to measure and excavate soil as an approximately 5x5x5cm cube - two times, yielding an approximate volume of 250cm^3 and actual excavated volume was recorded.

Soil Carbon*:* We sieved soils at 2mm, dried at 60 °C for 72 hours, and then ground into a fine powder (less than 150 um grain size). We analyzed soils for total soil carbon (TC) and soil organic carbon (SOC). TC was measured using a LECO SC632 carbon and sulfur determinator (LECO CO., St. Joseph, MI), and SOC was measured following the same procedure after leaching soil inorganic carbon (SIC, primarily inorganic carbonates) from the soil with 10 ml of 10% HCL. For both TC and SOC analysis, pure calcium carbonate (12% Carbon), synthetic carbon (5% carbon, ore tailings (0.50% Carbon), and LECO Soil (0.926 % Carbon) were used as calibration standards, and synthetic carbon (5% Carbon) and pure calcium carbonate (12% Carbon) used as check and drift standards. An additional check standard of pure calcium carbonate leached with 10 ml of 10% HCL was used in the SOC analysis to ensure that the leaching process removed all inorganic carbon. SIC was calculated as the difference between TC and SOC.

Soil Texture (Particle Size): We mixed a known weight (30-50 grams) of soil with 100 mL of DI water, breaking up larger soil aggregates manually. Soil was placed in an ultrasonic bath for 10 minutes to further break up larger aggregates and then stirred to break up residual aggregates. We then passed the solution through a 63µm mesh sieve, collecting the sand on the sieve, and the clay/silt suspension that passed through was centrifuged at 750 rpm for 7 minutes, resulting in a silt pellet with the clay suspended in liquid. Sand and silt components were dried (60°C for at least 72hrs) and weighed, and the clay portion was determined by subtracting the sum of silt and sand weights from the initial weight.

Estimating Plot Level Surface Soil Carbon:

For each site, we calculated the surface soil carbon (top 5 cm) per m^2 for each ground cover type using the ground cover specific average measured soil carbon (organic and inorganic) and average bulk density (g/cm^3), independently for control and treated plots within each site. We then calculated the proportion of land area covered by each ground cover type at both the control and treated plots using transect ground cover data, resulting in a calculated g C/m^2 per ground cover type. Plot level soil carbon was then calculated by summing across all cover types, the soil carbon contained in the top 5 cm of each cover type. Example of calculating plot-level soil carbon:

Step 1: Calculate ground cover specific carbon values

$$\text{Shrub } (g\ C/m^2) = \frac{Avg.\%Carbon\ under\ Live\ Shrub}{100} * \text{Avg. bulk density of live shrub } (g/cm^3) * 50{,}000\ (cm^3) \quad \textbf{[1]}$$

Step 2: Account for proportional land cover and sum across cover types

$$\text{Plot level soil carbon } (g\ C/m^2) = \sum [(\%\text{area covered by shrubs} * \text{Shrub } (g\ C/m^2)), (\%\text{area covered by grasses} * \text{Grass } (g\ C/m^2)), \text{etc.}\ldots] \quad \textbf{[2]}$$

Note: 50,000 cm^3 is the calculated soil in 1m^2 at a 5cm depth

Statistical Analyses

For all analyses, we averaged soil variables by ground cover type, by treatment type (control or treated), and by site - with each site acting as a single replicate within each cover type – treatment combination. We used paired t-tests to compare the average percent cover of vegetation and ground cover types (e.g., forbs/grass, shrubs, interspace) between control and treated plots. To analyze for differences in soil carbon between ground cover types within a single treatment type, we used full factorial ANOVAs with the main effects of ground cover type and site on soil carbon (both organic and inorganic) (e.g., soil carbon compared between interspace and live shrubs at the control plot only). Effects of ground cover type and site on soil carbon were analyzed separately for the treated and control sites because most control sites were missing multiple ground cover types (i.e., dead shrubs, forbs/grass). Similarly, sites that were missing ground cover types (e.g., shrub removal plots with no forbs/grass present) were omitted from these analyses to maintain equal sample sizes (Gotelli and Ellison, 2012). To examine the effects of shrub removal on soil carbon within a ground cover type, we used paired t-tests to directly compare average soil carbon within a ground cover type, between control and treated areas, using only subcanopy (live shrub) and interspace soils, as these were the common ground cover types found at both control and treated plots. (e.g., we compared interspace % carbon at the control to interspace % carbon at the treatment). Finally, we used paired t-tests to test for the effects of shrub removal on estimated plot-level soil organic and inorganic carbon. A two-sided p-value was reported for all analyses. All analyses were conducted using JMP®, Version <*16.2.0*>. SAS Institute Inc., Cary, NC, 2020–2021.

RESULTS

Vegetation and Ground Cover

Cover differed between control and treated plots for some, but not all, ground cover types. There was no significant difference in % interspace between control and treated plots (Figure 3.1a), but average % live shrub cover was lower, and % dead shrub and forbs/grass cover was higher in treated plots than the controls (Figure 3.1b -d). When shrub types are combined (live and dead), the total % shrub cover did not differ between control and treated plots (Figure 3.2).

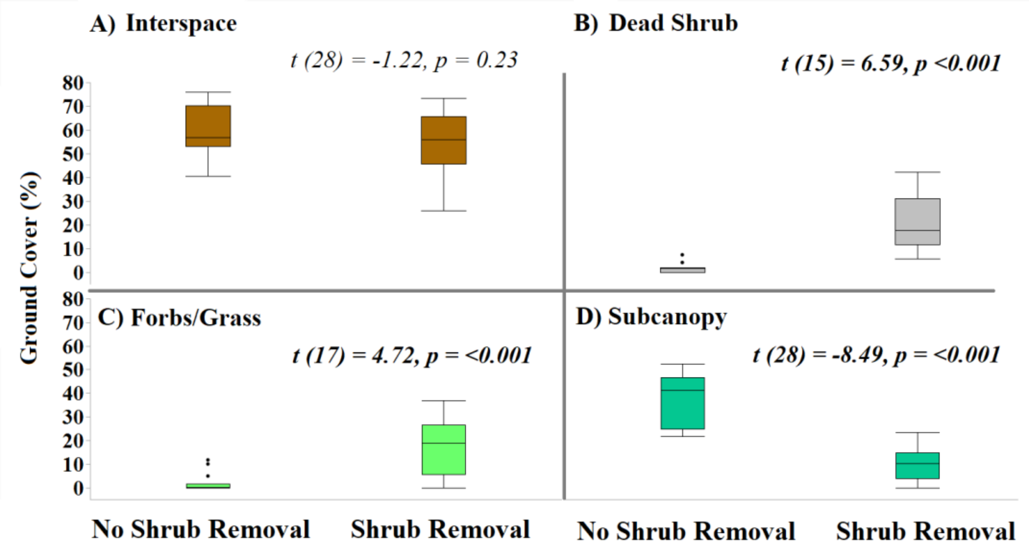

Figure 3.1: Boxplots comparing individual percent cover of dominant vegetation and ground types between no shrub removal (*control*) and shrub removal (*treated*) plots that were part of an ~8 year old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. The most dominant vegetation and ground cover types included unvegetated interspace (**a**), dead shrub skeletons (**b**), forbs/grass (**c**), and live shrub subcanopy (**d**). *Note:* Some shrub removal sites did not have all types present. Significant differences are denoted in bold font (p-value <0.05).

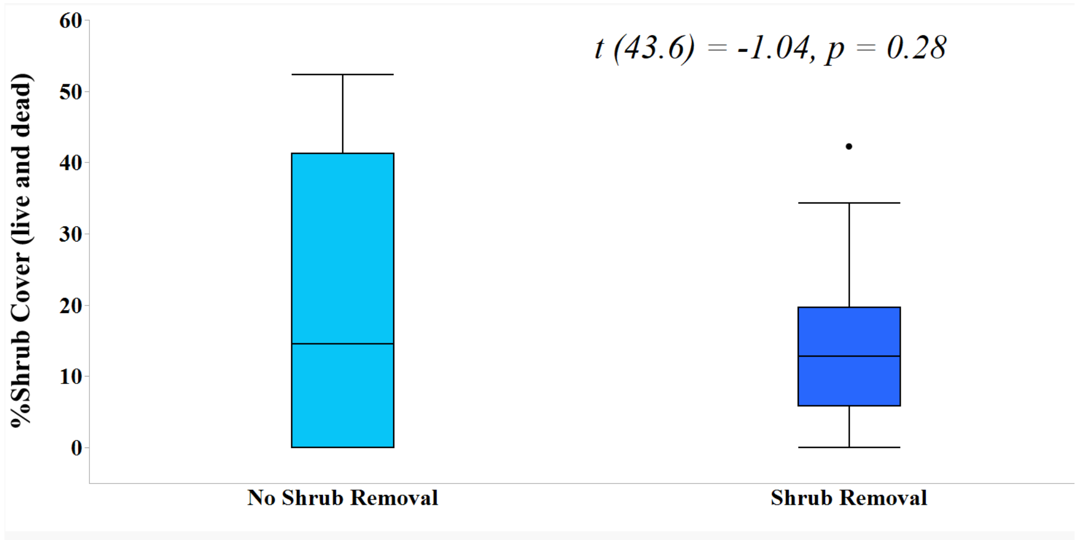

Figure 3.2: Boxplots comparing total percent shrub cover (live and dead shrub skeletons) between no shrub removal (*control*) and shrub removal (*treated*) plots that were part of an ~8 year old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico.

Soils were consistently alkaline (average 8.2, range 7.6 – 9.2) across sites, and soil pH did not differ between control and treated plots ($t_{(262)} = 1.62, p = 0.11$). Soil bulk density (average 0.87 g/cm^3, range 0.34 – 1.81) also did not differ between control and treated plots ($t_{(162.2)} = -0.05, p = 0.96$).

Differences in soil carbon between ground cover types within a treatment type

At the control plots, soil organic carbon (SOC) ranged from 0.35 – 1.5% and on average was 0.72%. We found that subcanopy soils had higher SOC than interspace soils ($F_{1,14} = 11.75, p = 0.001$), and that there was an effect of site ($F_{1,14} = 6.42, p = <0.001$) on SOC, but there was no interaction between site and ground cover type ($F_{1,14} = 1.32, p = 0.22$) (Figure 3.3a). At the treated plots, SOC ranged from 0.36 – 5.35% and on average was 0.88%. There was an effect of ground cover type ($F_{1,3} = 2.87, p = 0.04$), and site ($F_{1,9} = 4.11, p =<0.001$) on SOC, and no significant interaction between the main effects was found ($F_{1,27} = 1.11, p = 0.36$) (Figure 3.3b).

Soil inorganic carbon (SIC) at the control plots ranged from 0 – 3.26% and on average was 1.06%. Interspace soils had higher SIC ($F_{1,14} = 61.67, p = <0.001$), and there was an effect of site ($F_{1,14} = 21.15, p = <0.001$) on SIC, but no interaction between the main effects was found ($F_{1,14} = 1.11, p = 0.37$) (Figure 3.3c). SIC at the treated plots ranged from 0 – 1.81% and on average was 0.34%. There was an interaction found between the two main effects, ground cover type and site ($F_{1,27} = 1.93, p = 0.01$) indicating that the effect of ground cover on SIC differed across sites (Figure 3.3d, Supplemental Table 3.1).

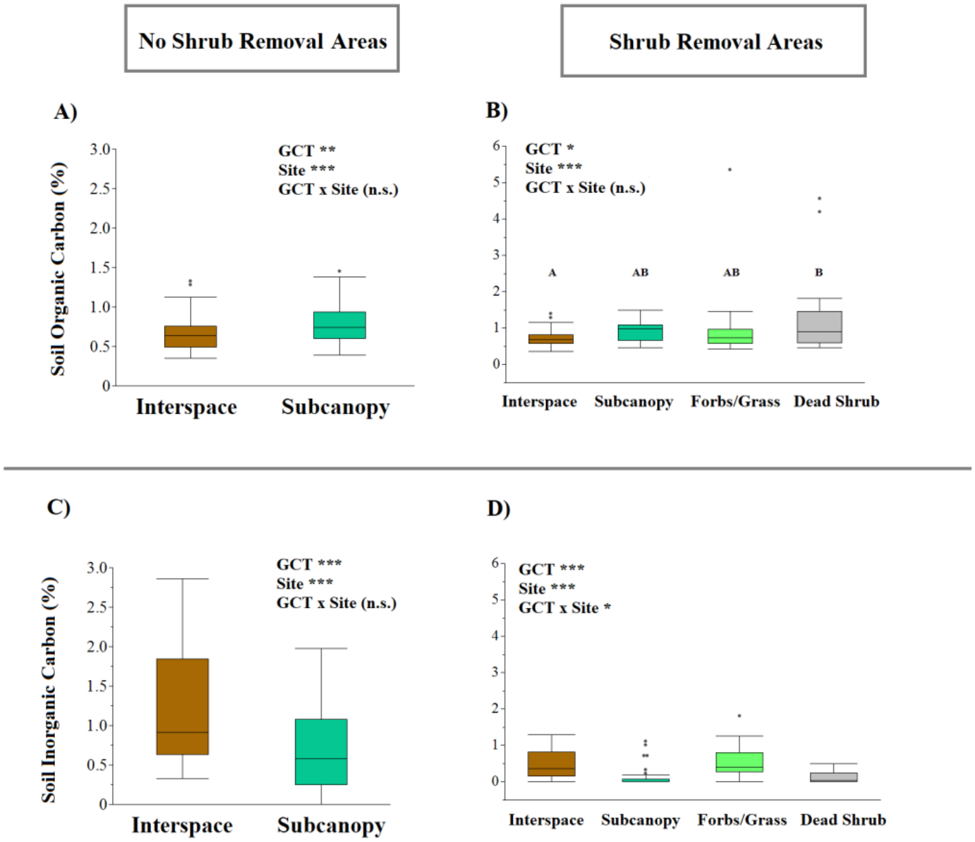

Figure 3.3: Boxplots showing soil organic (**a, b**) and inorganic carbon (**c, d**) between ground and vegetation cover patches within no shrub removal control plots (**a, c**); and shrub removal treatment plots (**b, d**) that were part of an ~8 year old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Significant differences in soil carbon between ground and vegetation types (GCT) and/or site are denoted by asterisks (p-value < 0.05 denoted as *, <0.01 as **, and <0.001 as ***). No statistical significance is denoted as "n.s.". Note: Only 10 out of 15 study sites were included in the shrub removal analyses, because not all ground cover types were present at some sites.

Differences in soil carbon at the local level

For interspace or subcanopy (live shrub) soils, there was no significant difference in SOC between control and treated plots (Figure 3.4a), but SIC was higher in control plots for both (Figure 3.4b).

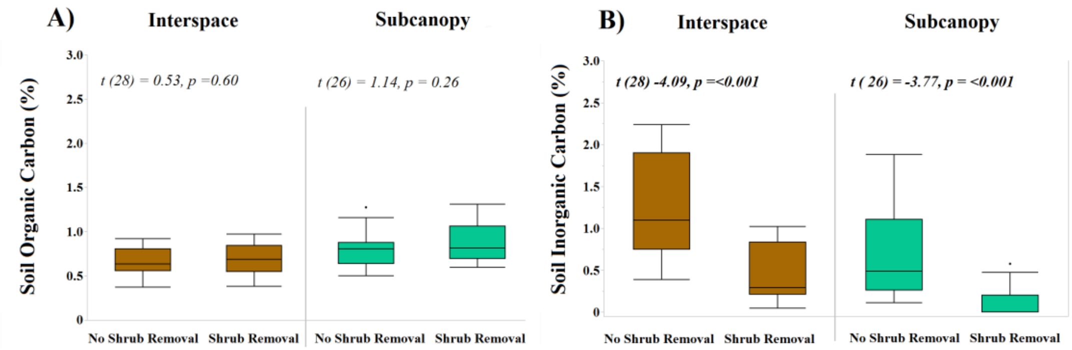

Figure 3.4: Boxplots showing local level soil organic (**a**) and inorganic carbon (**b**) within interspace and live shrub (subcanopy) patches between no shrub removal control and shrub removal treatment plots that were part of an ~8 year old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Significant differences within a ground or vegetation type are denoted in bold (p-value < 0.05).

Differences in soil carbon at the plot-level

Plot level SOC at the control plots ranged from 203 – 768 g C/m^2 and on average was 305 g C/m^2. Plot level SOC at the treated plots ranged from 226 – 763 g C/m^2 and on average was 361 g C/m^2. There was no significant difference in plot-level SOC between the control and treated plots (Figure 3.5a). Plot level SIC at the control plots ranged from 103 – 909 g C/m^2 and on average was 431 g C/m^2. Plot level SIC at the treated plots ranged from 13 – 364 g C/m^2 and on average was 159 g C/m^2. Plot level SIC was higher in the control plots than the treated plots (Figure 3.5b).

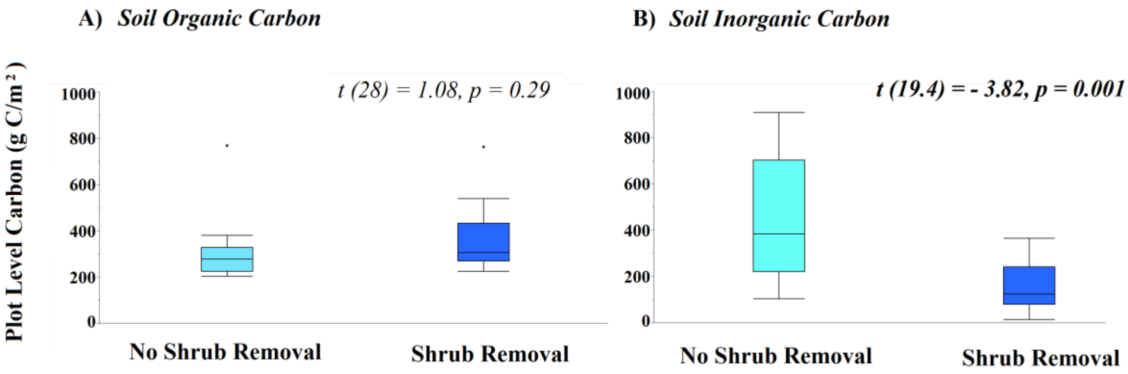

Figure 3.5: Boxplots showing plot-level soil organic carbon (**a**) and soil inorganic carbon (**b**), between 15 paired no shrub removal (control) and shrub removal (herbicide treated) plots in an ~8 year old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Significant differences (paired t-tests) are denoted by bold font ($p = <0.05$).

Differences in soil texture between control and treated areas

Treated and control plots differed in ground cover type specific particle size, where treated plots had higher average % sand than control plots – for both interspace (Figure 3.6a) and subcanopy soils (Figure 3.6b). Treated plots also had marginally higher average % silt than control plots, however, this was only found in interspace soils (Figure 3.6c) There was no significant difference in % silt subcanopy (Figure 3.6d), or average % clay (interspace or subcanopy), between the control and treated plots (Figures 3.6e, f).

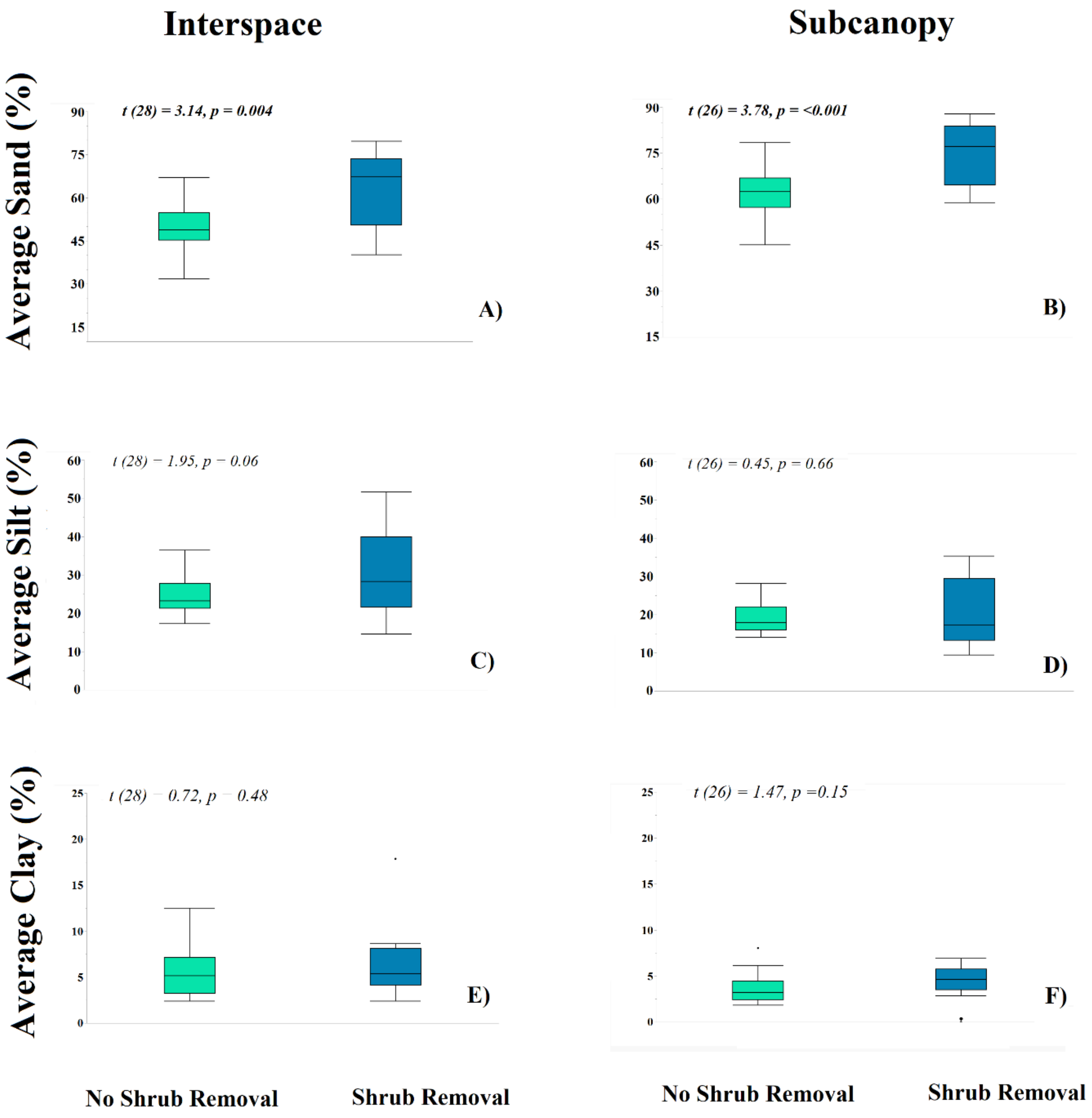

Figure 3.6: Boxplots that show the difference in interspace (**a, c, e**) and living shrub (subcanopy) (**b, d, e**) soil texture portions of average % sand (**a, b**), % silt **(c, d)** and % clay (**e, f**) between 15 paired no shrub removal (*control*) and shrub removal (*treated*) plots, that were part of a ca.8 year old restoration experiment in the Chihuahuan Desert of southwestern New Mexico.

DISCUSSION

The aim of our study was to determine if large-scale shrub removal practices in the Chihuahuan Desert of New Mexico result in vegetation and ground cover changes and changes in soil organic and inorganic carbon over the short term (8 years after removal). Contrary to our first hypothesis, we found that shrub removal had no effect on soil organic carbon at either the local or the plot-level. Also, contrary to our second hypothesis, soil inorganic carbon was lower at shrub removal areas. Below we discuss why soil organic carbon (SOC) appears to be unaffected by these large-scale shrub removal practices, as well as how vegetation cover differences and soil textural changes caused by these restoration practices could have resulted in lower observed levels of soil inorganic carbon (SIC).

Shrub removal did not affect SOC at local or plot-level (*Hypothesis 1*)

Our data did not support our first hypothesis that SOC would be higher at the local level within individual ground cover types, between control and treated plots (e.g., interspace soils in treated plots would have higher SOC than interspace soils in control plots). Instead, we found no difference in SOC within a cover type between treated and control plots. We also found no effect of shrub removal treatment on either of the physical properties we measured (soil pH and bulk density), both of which can affect the rate at which plant material is converted to SOC (Berg & McCLaugherty, 2003).

The second part of our first hypothesis was that SOC might increase with shrub removal treatment if the proportion of these cover types changed with shrub removal treatment (e.g., grass to shrub cover proportionally increases with treatment) and there are differences in SOC between vegetation cover types (i.e., grass cover has higher SOC than shrub cover). For example, we expected that there would be increases in the cover of grasses and forbs with shrub removal, which due to their typically higher SOC compared with shrublands (Liang et al., 2021; Sainepo et al., 2018), would lead to proportionally more SOC in plots where shrubs had been removed. In support of the first part of this mechanism, we found increases in grass cover and decreases in living shrub cover with shrub removal treatments.

In support of the second part of this mechanism, we also found differences in SOC between vegetation types in both treated and control plots. In the control plots, we found that surface soils under living shrubs had higher SOC than unvegetated interspace soils. The higher SOC under living shrubs than interspace soils complement previous studies that have shown organic matter accumulates under shrub canopies (i.e., island of fertility effect) (Field et al., 2012; Throop et al., 2013; Walker et al., 2001). However, the effect of grass on SOC was not as predicted, where soil under grasses would have the highest SOC. In the treated plots where there was measurable grass cover, we found no difference in SOC in surface soils underneath grasses relative to under shrubs (live or dead), and only soil under dead shrubs had significantly higher SOC than the unvegetated interspace soils. The higher SOC under dead shrubs than in the unvegetated interspace we found in the treated plots may partially result from ephemeral grasses and weeds, which can occupy the space beneath dead shrubs, temporarily increasing plant matter inputs (e.g., nurse plant effect) (Badano et al., 2016). Further, despite no longer contributing senesced leaves to the litter pool, dead shrubs can still have high inputs of plant litter from decaying branches or roots. In support of this, we found that there was no difference in SOC in surface soils under living vs. dead shrubs, suggesting that even after death, the physical structures of shrubs persist and continue to contribute to SOC inputs in treated plots.

We suspect that with the relatively recent (ca. 8 years) shrub removal, that living and dead shrubs may still have comparable litter inputs, leading to the similar SOC beneath their canopies. In shrublands, senesced leaves, flowers, and branches that fall below the shrub canopy make up the concentrated litter of fertility islands. While in other biomes, decomposition is often positively related to rainfall, it has been found that dryland rates of plant litter decomposition greatly depend on a combination of environmental conditions (i.e., UV radiation, rainfall), location of the litterfall (e.g., litter covered by soil) (Whitford & Steinberger, 2021), as well as the seasonal presence of prominent decomposers (i.e., subterranean termites) (Hewins et al., 2013; Moorhead & Reynolds, 1991). Estimates do concur that leaf litter decomposition from shrubs occurs rapidly in the Chihuahuan Desert. For example, in a long-term decomposition study, it was found that honey mesquite and creosote bush lost 40% and 22% of their leaf litter, respectively, over a 5-month period (Kemp et al., 2003). Leaf decomposition rates markedly outpace those of woody material decomposition (Hall et al., 2020; Vanderbilt et al., 2008). For example, over a six-month period, honey mesquite and creosote bush branch litter can lose ~10.55 – 12.75 percent mass to decomposition, respectively (Schaefer et al., 1985). However, despite the slow decomposition of woody tissue, we suggest here that because the annual leaf litter inputs from shrubs are markedly smaller than branch litter inputs (Havstad et al., 2006), the absence of leaf inputs from dead shrubs may have no negative effect on SOC. If inputs of plant litter are dominated by woody material, then soils in novel plant communities would retain some of these carbon inputs from surviving shrubs and would also receive inputs from dead shrubs.

In sum, although we did find higher grass cover in treated plots compared with control plots, this did not translate to higher SOC when we estimated surface soil carbon at the plot-level (accounting for proportional differences in ground and vegetation cover). This may partly be due to our finding that SOC was higher under grasses than shrubs (as we initially expected), so the transition from shrub cover to grass cover would not affect SOC. Further, we found that dead shrubs and living shrubs have similar effects on SOC, likely because the leaf litter inputs from living shrubs are small compared with woody inputs, which may be comparable between living and dead shrubs. Because shrub cover, living or dead, is similar between the two treatment types, and because living and dead shrubs have similar effects on SOC, shrub removal may not affect SOC, at least in the short term. However, dead shrubs are no longer producing new woody tissue and we expect that after decades, when most of the woody material has decomposed in the treated plots, we may then find a difference in SOC.

SIC was lower in shrub removal areas at both the local and plot-level (*Hypothesis 2*)

Our second hypothesis was that SIC was unlikely to change with shrub removal treatments, given the long periods of time required for SIC to accumulate in the soil (Durand et al., 2018; Kraimer et al., 2005). However, in contrast with this hypothesis, we found that surface level SIC was significantly lower in shrub removal areas at the local and plot-level. Similar to SOC, vegetation cover affected SIC, where SIC was higher in the unvegetated interspace between shrubs. This could be due to the lack of vegetation structure in interspace soils, which fails to protect upper layers of soil from eroding away (e.g., clays and light material are lost to runoff or wind) – leading to the gradual exposure of inorganic carbonates in lower soil depths (Hussain et al., 2019). SIC under shrubs could also be buried (i.e., protected) by organic matter inputs and other non-carbonate rich sources of dust (e.g., sandy silicates collected by shrub understory) (Gillette, 2004). However, there was an interaction between the effects of site and ground cover type on SIC, where some sites showed strong effects of ground cover type and other sites did not

- indicating that other inherent site-level properties may also be influencing SIC (Okin & Gillette, 2001).

Both within vegetation types (local level) and at the plot-level, SIC was significantly higher in the control plots. We suggest that the lower SIC found in the treated plots may be due to recovered grasses capturing more loose sediment from wind and rain, burying SIC deeper in the soil profile (as suggested above for soils under shrubs). Throughout the Chihuahuan Desert soil profile, soil inorganic carbonate content generally increases with depth but may also be laterally heterogeneous (e.g., some topsoil layers may be calcium carbonate-rich) (Monger, 2006). In the uppermost soil layers (0-10 cm depth), SIC can exist as fine powder, filaments, or nodules – that can be sourced from parent materials or relatively young atmospherically-derived carbonates (e.g., micro precipitates from calcium and bicarbonate dissolution). Specific estimates of SIC differ by soil unit type (e.g., Regosol, Vertisol), but on average, SIC can make up ~50 – 60% of total carbon in a dryland soil across a 30 cm or 100 cm depth range, respectively (Nieder & Benbi, 2008). From this, we suggest that the lower SIC in treated plots is likely due to a change in soil layer height caused by increased soil capture (i.e., grasses capture sediments that, in turn, bury SIC). Although there was no significant difference in % interspace cover between control and treated plots, we note that interspaces in control often existed as large stretches of interspace, whereas treated plots had smaller patches (i.e., interspace connectivity is lower in treated plots due to patches of grasses). The difference in this connectivity is in line with previous studies and suggests that smaller patches of interspace equate to less overall soil loss from erosion (Ludwig et al., 2005). This supports our reasoning that the unvegetated interspace we found in the control plots has likely been subjected to significant erosion from wind and runoff, resulting in the exposure of lower soil horizons that are richer in inorganic carbonates.

We found further support for soil transport as a mechanism for changes in SIC with comparisons of soil texture between control and treated plots. Treated plots had higher % sand and marginally higher % silt (at interspace patches) than the control plots. This suggests the change in vegetation following treatments (e.g., increase in grasses) may have led to more soil capture from sand saltation (i.e., sand particles jumping with the wind) (Gillette, 2004) and loose dust (e.g., light particles such as silt are captured by re-establishing grasses and surviving shrubs) (Field et al., 2012). We do not suspect that the SIC has disappeared from the ecosystem entirely - typical processes of SIC dissolution (at this magnitude) would require either significant sources of acidification (i.e., acid rain) or would occur at timescales much larger than the duration of this experiment (Kraimer et al., 2005) - making burial (i.e., protection) by sand and dust deposition the most likely mechanism for the observed lower SIC in treated plots.

In conclusion, our results emphasize that the changes in vegetation communities that follow large-scale treated practices have variable effects on soil carbon (organic and inorganic), and these effects may not directly correlate to re-establishing plant species (i.e., recovery of grasses may not always equate to more SOC). The null effect we found of shrub removal on SOC implies that soil carbon storage may not be increased by these restoration practices; however, these results may have been temporally constrained and 8 years following shrub removal may not be enough time to successfully observe changes in SOC. We also found that these developing novel plant communities (grasses, live and dead shrubs) could be capturing more sand and dust than shrublands – meaning they effectively bury and protect SIC from erosional loss (e.g., dissolution of carbonates releases CO_2). This has positive implications for management goals that aim to conserve already sequestered soil stocks in these regions. We recommend that, when possible, dryland management should regularly incorporate soil carbon assessments during shrub removal practices to account for the variable effects of restoration on these vulnerable yet significant soil resources.

AUTHOR CONTRIBUTIONS

A version of this Chapter will be submitted for review in a peer-reviewed journal and is co-authored by Kathleen Schaeffer (KS) and Jennie McLaren (JM). The methodology for this specific study was designed by JM and KS. KS collected and analyzed data; JM and KS interpreted results; KS led the writing of the manuscript.

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DATA ACCESSIBILITY

Data from this project will be made available when publication for this chapter is finalized. Potential data centers include National Resources Conservation Service (NRCS) or BLM/USDA affiliated data centers.

Chapter 4: Soil organic carbon is positively related to time since shrub removal in the Chihuahuan Desert

ABSTRACT

Since the 1980s, land managers in the New Mexican Chihuahuan Desert have applied large-scale herbicide treatments to remove shrub species that have displaced native perennial grasslands over the last century. If successful, these treatments would not only increase grass and herbaceous species but could positively affect vulnerable resources such as soil carbon. However, the timescale for this recovery is uncertain. We set out to determine if the effects that large-scale shrub removal practices have on vegetation cover and soil carbon vary at different time points (ages) of restoration. Our study took place at 14 shrub removal study sites that made up a chronosequence of treatment ages (16-32 years old) and one reference grassland site in the southwest of New Mexico. We sampled soils from each site and analyzed them for soil organic (SOC), inorganic carbon (SIC), and bulk density. We also collected vegetation and ground percent cover at both shrub removal and control areas, which we used to calculate relative live vegetation cover and soil carbon at the plot-level. There was no relationship between relative vegetation cover and time since shrub removal treatment (TST). Relative SOC was positively related to TST; however, there was no relationship between relative SIC and TST. Our results show that relative vegetation cover did not vary at different time points of restoration, which suggests that early vegetation responses to shrub removal may be maintained over time. The positive relationship we found between TST and relative SOC (which was not found with relative SIC) suggests that the response of SOC to shrub removal could gradually increase over time. These findings could help strategize desert grassland restoration planning, particularly in estimating the time to recovery for individual response variables (like soil carbon).

INTRODUCTION

Large-scale shrub encroachment has affected many dryland systems across the globe (Eldridge et al., 2011). These landscape level changes are often attributed to drivers such as excessive cattle grazing and climate change (Van Auken, 2009). In the Chihuahuan Desert of New Mexico, the encroachment of shrubs on perennial desert grasslands has been occurring since the late 1800s (Bestelmeyer et al., 2018; Branscomb, 1956; Fisher, 1950). This displacement of grasses by shrubs has been a longstanding concern for land managers, as it can alter soil resources and biodiversity in these habitats (Peters et al., 2013), as well as limit the availability of palatable forage for livestock (McIntosh et al., 2019). To mitigate the negative effects of shrub encroachment, local land managers have focused efforts on large-scale shrub removal practices. Historically, these shrub removal treatments have led to the establishment of novel plant communities, often composed of any surviving shrubs, dead shrub skeletons, re-established grasses, or forbs, and the unvegetated interspace between them. From a land management perspective, a novel plant community that is dominated by grass and herbaceous cover could be an indication of restoration success (i.e., more herbaceous cover benefits livestock) (Bestelmeyer et al., 2019; Gann et al., 2019). However, the degree of grass return may vary at each treated site and perhaps even vary by time since shrub removal treatment (i.e., areas that were treated more recently may still show the signs of early succession with mainly weedy or ephemeral plants) (Luken, 1990). In many plant restoration projects, it can take several decades to observe any significant re-establishment of target plant species (Tilley et al., 2022; Verdoodt et al., 2009).

Accounting for the temporal dynamics in site response to dryland restoration practices is challenging due to the temporal variation of ecosystem factors (internal and environmental) that co-occur along with the effects of restoration treatments (Suding, 2011). For example, the variability in soil legacy (soil properties linked to past plant communities that remain after those communities are removed) between restoration sites may affect the extent of grass recovery seen following shrub removal (in ‘t Zandt et al., 2020). Additionally, in a previous study, we found that the gain in grass and forbs cover following shrub removal treatments was positively related to average site-level precipitation (Chapter 1). Emphasizing that factors like spatial and temporal variability in climate (temperature and precipitation) likely also affect grass species re-establishment following shrub removal. To characterize temporal trends in restoration treatment effects, chronosequences (i.e., gradients of treatment ages) can be a valuable tool.

Chronosequences can be used to estimate the trajectory of ecosystem and plant community succession. Under ideal study conditions, each site within a chronosequence would be similar in landform and ecological state and only differ by the “time since disturbance” or “time since restoration treatment” (Walker et al., 2010). Chronosequences present a space for time substitution that can help land managers estimate temporal patterns of effects that come from restoration treatments (Walker et al., 2010). When evaluating these temporal patterns in restoration ecology, it is also recommended that a site that represents the target ecosystem condition should be included in analyses (e.g., a reference desert grassland used in a grass restoration study) (Lal, 2016). It is pertinent that this baseline or reference site represent the condition that managers believe their disturbed areas would be in, had the disturbance never occurred, rather than selecting it based on ideal past conditions (Gann et al., 2019; Lal, 2016,).

Within a chronosequence, the age of treatment (or time since treatment was applied) is a valuable metric for gauging recovery, or relapse, of response variables. For example, a study that used a chronosequence of shrub removals in the Jornada Basin of the Chihuahuan Desert found that creosote bush (*Larrea tridentata)* had re-encroached ~65 years after an aggressive mechanical shrub removal treatment was applied in the 1930s (Rango et al., 2005). These findings emphasize that time to recovery is not necessarily a linear process and, therefore, should be considered when assessing how different ecosystem properties, such as vegetation and soils, may respond to shrub removal treatment. It is well known that shrub encroachment has affected the distribution of soil resources (Li et al., 2016; Sankey et al., 2012); however, there is still a need to understand whether large-scale shrub removal practices restore affected soil properties and the timeline of this recovery.

The overarching goal of our study was to determine whether large-scale shrub removal practices affect soil carbon differently at different time points (ages) of restoration. We tested the following three hypotheses:

(1) Shrub removal treatments will lead to increases in the grass and herbaceous cover and decreases in shrub cover, and the difference between control and shrub removed plots would increase over time [**H1a**]. Previous grass restoration studies have found that full grass recovery was gradual, sometimes taking decades or more (Valone et al., 2002), and that shrub cover continues to decline over time (Perkins et al. 2006). An alternative hypothesis was that we would find a positive relationship between relative shrub cover and time since removal, if shrubs were not effectively killed or shrubs recovered/re-encroached at later time points, which has been observed in previous shrub removal studies [**H1b**] (Rango et al., 2005).

(2) Our second hypothesis was that the relative increase in soil organic carbon with shrub removals would increase with time since removal [**H2**] due to our hypothesized increase in recovered grasses, which are typically associated with higher SOC (Yang et al., 2019).

(3) Lastly, we predicted that the relative soil inorganic carbon would be negatively related with time since removal [**H3**] because in a previous study (Chapter 3) we suggested that soil inorganic carbon had been buried with sediment trapped by recovering vegetation ~8 years after shrub removal occurs.

To test these predictions, we calculated a relative difference in vegetation cover between no shrub removal and removal areas and examined whether these relative differences varied by time since shrub removal treatment. We also tested for relative differences in plot-level surface soil carbon between ground and vegetation types at shrub removal and non-removal areas. We also explored relationships between relative plot-level surface soil carbon (both organic and inorganic) and time since shrub removal treatment.

STUDY AREA

We conducted this study in the Chihuahuan Desert of southwestern New Mexico, at 14 historical Restore New Mexico (RNM) sites that make up a chronosequence of shrub removal herbicide treatments which were implemented from 1982 to 2002 (see details on treatments below). We also sampled one grassland site, as a reference point for pre-shrub encroachment conditions, at the Bosque Del Apache Wildlife Refuge in San Antonio, New Mexico. The elevations of our study sites range from 1260 to 1756 m, and the average annual rainfalls range from 200-350 mm. The dominant vegetation varies across the study sites and the most prevalent shrub species present across these sites are creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), and tarbush (*Flourensia cernua*). The dominant grass species present are short-lived perennials, fluffgrass (*Dasyochloa pulchella*), and perennial grasses like bush muhly (*Muhlenbergia porteri*). The soils within this region are classified as gravelly to loamy. Historically, these areas have been used primarily for livestock and recreation (Unnasch, 2017)

RNM Shrub Removal Treatments

From the 1980s to the early 2000s, the BLM broadly applied tebuthiuron herbicide (N-[5-(1,1-dimethylethyl)-1,3,4thiadiazol-2-yl]-N,N′-dimethy-lurea) at an application rate of 0.56 kg/ha, to large shrub encroached areas. Although non-treated controls were not designated at the same time as herbicide application, in an earlier study Coffman et al. (2014) paired shrub removal locations to nearby untreated shrub-dominated areas that had similar soil and ecological baseline features. We used these shrub-dominated areas as the paired controls for each shrub removal plot in our study. These 14 sites make up a chronosequence of shrub removal treatments, with the ages of treatments ranging from 16 – 36 years old. We will refer to these 14 sites collectively as the “RNM chronosequence”.

METHODS

Vegetation Sampling

We used pre-existing RNM transect coordinates (subset of Coffman et al., 2014) to navigate to the approximate center of each no shrub removal (control) and shrub removal area (treated). We established two parallel 50 m transects that were approximately 25 m apart, avoiding any inconsistent landforms such as sharp gullies or high hillslopes. We used the line transect method to record the length of vegetation and ground cover covering the transect, limiting cover recorded to those that made up at least 1 meter in sum along the transect. The major ground and vegetation cover types present were: live shrub, dead shrub, forbs/grass, and unvegetated interspace. Live shrub and interspace were found at both control and treated areas, but dead shrub and forbs/grass cover was mainly present at treated areas, and only occasionally present at control areas. Combined, these transects equated to 100 m from which we estimated proportion cover (e.g., 100 m = 100% total cover at treatment area).

From these values, we calculated a Relative Vegetation Cover Difference between no shrub removal and shrub removal areas for each category of live vegetation (forbs/grass and live shrub) independently.

$$\textit{Relative Vegetation Cover Difference} = \frac{\%\text{ Cover at treated area} - \%\text{ Cover at control area}}{\%\text{ Cover at control area}} \quad \textbf{[1]}$$

Soil Sampling

Between June and October 2018, we sampled soils across the RNM chronosequence and the reference grassland site. We haphazardly selected 15 patches of each ground and vegetation cover type from the vegetation sampling transects, ensuring the patches were evenly distributed across both 50 m transects. At each location, we collected a single soil core (2.54 cm diameter) to 5 cm depth from each patch. From these 15 samples, we randomly composited samples together in sets of 3 while in the field, yielding 5 samples per ground and vegetation cover type. We also collected 3 separate samples per cover type for soil bulk density. Sampling under shrubs was consistently done at the dripline (canopy edge).

Soil Analyses

Soil Carbon: Prior to soil carbon (C) analysis, soils were sieved at 2 mm, dried at 60 ℃ for a minimum of 72 hours, and then ground into a fine powder (less than 150 µm grain size). We analyzed samples for both total soil carbon (TC) and soil organic carbon (SOC). TC was measured using a LECO SC632 carbon and sulfur determinator (LECO CO., St. Joseph, MI), and SOC measured following the same procedure after leaching inorganic carbon (inorganic carbonates) from the soil with 10 ml of 10% HCL. For both TC and SOC analysis, pure calcium carbonate (12% Carbon), ore tailings (0.50% Carbon), and LECO Soil (0.926 % Carbon) were used as calibration standards, and synthetic carbon (5.03% Carbon) used as a check standard. An additional check standard of pure calcium carbonate (12% Carbon) leached with 10 ml of 10%

HCL was used in the SOC analysis to ensure that the leaching process removed all inorganic carbon. Soil inorganic carbon (SIC) was calculated as the difference between total and organic carbon (TC – SOC = SIC).

Soil Bulk Density: We calculated soil bulk density as the dry weight of the soil samples (dried at 60 °C for 72 hours) divided by its measured field volume. Soil volume was determined using a soil corer method (the soil ring yielded an approximate volume of 25.34cm^3).

Statistical Analysis

To test for the overall effects of shrub removal on vegetation cover, we compared each ground and vegetation type between the no shrub removal and shrub removal areas using a t-test, without reference to time since removal (see Supplemental Figures 4.1 & 4.2). We then used linear regressions to explore relationships between time since shrub removal treatment (in years) and relative vegetation cover difference (described above) for each group of living plants (live shrub and forbs/grass). When we measured vegetation cover in 2018, some control areas had no forbs/grass cover – in those cases, we used a standard % forbs/grass cover based on the minimum value we found across all other control areas (~0.5 % forbs/grass) to avoid indefinite numbers.

For all soil analyses, we first averaged soil variables by ground cover type within the control and treated areas at each site, with each site-treatment combination acting as a single replicate. To estimate plot-level surface (top 5 cm) soil carbon, we calculated the surface soil carbon per m^2 for each ground cover type using the ground cover specific average measured soil carbon (organic and inorganic) and average bulk density (g/cm^3), independently for control and treated areas within each site. We then calculated the proportion of land area covered by each ground cover type at the control and treated areas using line transect ground cover data. Plot level carbon (g C/m^2) was then calculated by summing across all cover types, the soil carbon contained in the top 5 cm of each cover type (*described above in Chapter 3)*.

From these plot-level carbon values we calculated Relative Soil Carbon values for each site, that we tested for relationships against time since shrub removal treatment using linear regressions.

$$(Relative\ Soil\ Carbon = \frac{Soil\ Carbon\ in\ treated\ area - Soil\ Carbon\ in\ control\ area}{Soil\ Carbon\ in\ control\ area}) \quad \textbf{[2]}$$

A positive value for relative soil carbon means that there was an increase in soil carbon following shrub removal, whereas a negative value means there was a decrease in soil carbon. Relative soil carbon of zero indicates that there is no difference in soil carbon between shrub removed and non-removed areas.

RESULTS

Hypothesis 1: In treated areas, grass percent cover was higher and shrub percent cover lower, regardless of the time since treatment occurred (Supplemental Figure 4.1). Total shrub cover (live and dead shrub combined) was also lower in treated areas (Supplemental Figure 4.2). Dead shrub cover in treated areas marginally decreased with time since treatment (Supplementary Figure 4.3). There were no significant relationships between relative live vegetation cover and time since shrub removal treatment for either forbs/grass or live shrub ground cover types (Figure 4.1a, b).

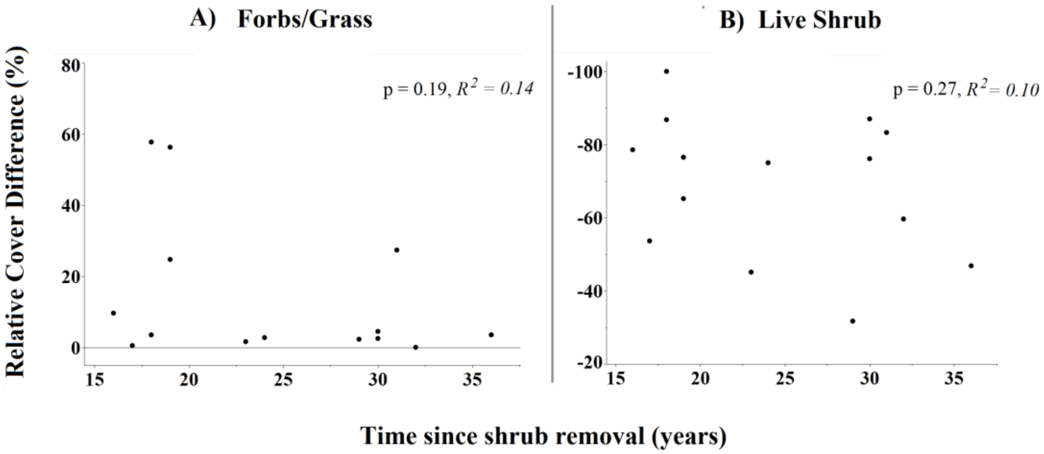

Figure 4.1. Relationships between time since shrub removal treatment (in years) and relative cover difference $(\frac{\%\ cover\ at\ treated\ area - \%\ cover\ at\ control\ area}{\%\ cover\ at\ control\ area})$ for forbs/grass (**a**) and live shrub (**b**), across 14 shrub removal sites established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico. Shrub removal treatments were applied once at each site at establishment, making a chronosequence of treatment ages.

Hypothesis 2: Plot level soil organic carbon (SOC) at the control areas ranged from 295 – 797 g C/m^2 and averaged 527 g C/m^2. Plot level SOC at treated areas ranged from 264 – 870 g C/m^2 and averaged 588 g C/m^2. Plot level SOC at the remnant grassland site was 984 g C/m^2 (Figure 4.2a). Relative plot-level SOC was positively related to time since shrub removal treatment (Figure 4.2b). Vegetation cover specific SOC used in plot-level calculations can be found in Supplemental Figure 4.4.

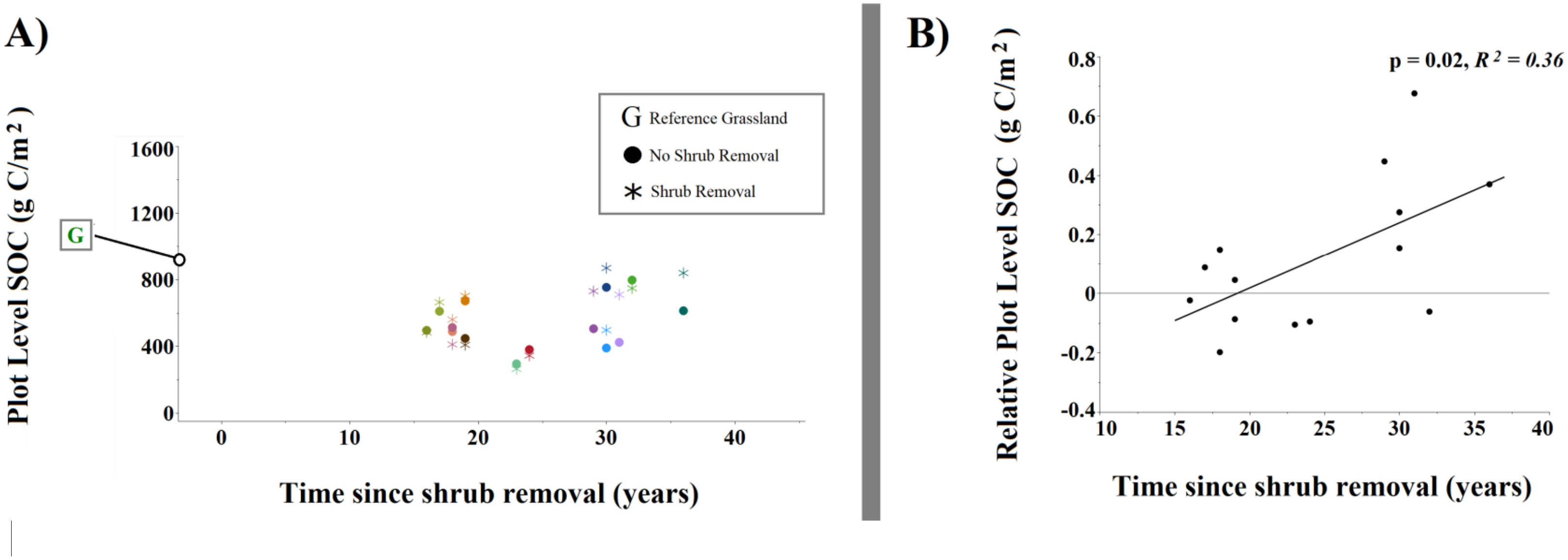

Figure 4.2: Scatterplots showing plot-level soil organic carbon (SOC) at a reference grassland, in comparison with 14 restoration sites established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico (**a**); and the relationship between time since shrub removal treatment in years, and relative plot-level SOC ($\frac{\text{Soil Carbon in treated area} - \text{Soil Carbon in control area}}{\text{Soil Carbon in control area}}$) across these 14 restoration sites (**b**). In panel A, no shrub removal and shrub removal areas that are within the same site have the same color, and the plot-level SOC value for the reference grassland is indicated on the Y axis by a black line and dot outside the graph. In panel B, statistical significance is denoted by bold font ($p \leq 0.05$). Relative soil carbon is positive with an increase in soil carbon following shrub removal, whereas a negative value means there was a decrease in soil carbon following shrub removal.

Hypothesis 3: Plot level soil inorganic carbon (SIC) at the control areas ranged from 34 –1170 g C/m^2 and averaged 361 g C/m^2. Plot level SIC at the treated areas ranged from 1.64 – 1405 g C/m^2 and averaged 429 g C/m^2. Plot level SIC at the remnant grassland site was 21 g C/m^2 (Figure 4.3a). There was no significant relationship between time since shrub removal and relative plot-level SIC (Figure 4.3b). Vegetation cover specific SIC used in plot-level calculations can be found in Supplemental Figure 4.4.

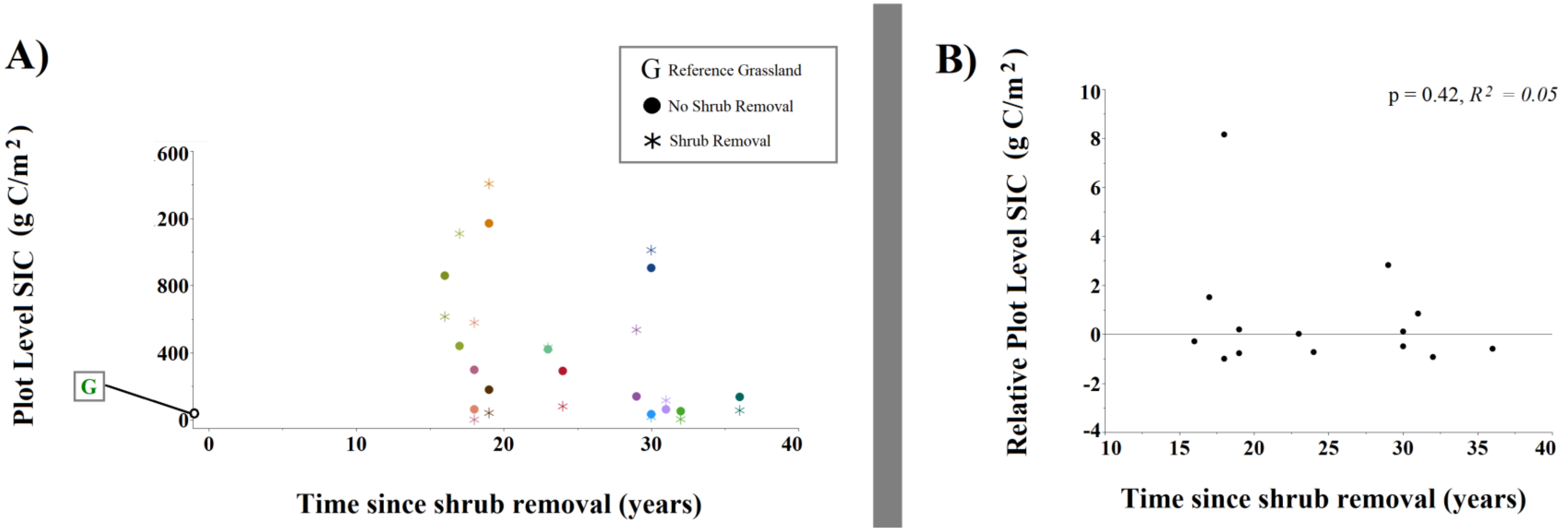

Figure 4.3: Scatterplots showing plot-level soil inorganic carbon (SIC) at a reference grassland, in comparison with 14 restoration sites established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico (**a**); and the relationship between time since shrub removal treatment in years, and relative plot-level SIC ($\frac{Soil\ Carbon\ in\ treated\ area\ - Soil\ Carbon\ in\ control\ area}{Soil\ Carbon\ in\ control\ area}$) across these 14 restoration sites (**b**). In panel A, no shrub removal and shrub removal areas that are within the same site have the same color, and the plot-level SIC value for the reference grassland is indicated on the Y axis by a black line and dot outside the graph. In panel B, soil carbon is positive with an increase in soil carbon following shrub removal, where a negative value means there was a decrease in soil carbon following shrub removal.

DISCUSSION

The aim of our study was to determine whether the effect of large-scale shrub removal practices in the Chihuahuan Desert varies at different time points (ages) of restoration. Although we found that grass cover was higher and shrub cover was lower in treated areas, neither our first hypothesis nor the alternative hypothesis was supported as the relative changes in live vegetation cover (forbs/grass and live shrub) were not related to time since treatment. We found support for our second hypothesis in that relative soil organic carbon (SOC) was higher in older restoration sites. However, our third hypothesis that soil inorganic carbon (SIC) would be lower in more recently treated areas (i.e., younger treatments) was not supported. Below we discuss 1) why relative vegetation cover does not vary with time since treatment, 2) how differences in vegetation and ground cover following shrub removal could be affecting soil carbon (SOC and SIC), and 3) what these findings mean for future desert grassland restoration.

H1: Relative vegetation cover did not correlate with age of restoration treatment

We expected to see relationships between relative vegetation cover and time since treatment, as previous studies have shown that desert grasslands can take decades to re-establish or recover (Guo, 2004; Ott et al., 2019). Our study did not find support for this relationship; however, we did find higher forbs/grass cover in treated areas relative to no-removal controls, although most shrub removal plots only had ca. 10% more grass than found in the paired shrub desert. This finding implies that shrub removal treatments had limited success in increasing grass and forbs cover, but there may not be additional gains in herbaceous cover following initial increases right after removal, even after decades have passed (i.e., after 36 years).

It is important to note that the relative increase in grass % cover we observed with shrub removal may have been constrained by environmental and climate factors. For instance, legacy effects from soil conditions formed under shrublands could affect grass recovery. In prior studies, it has been found that invasive shrubs can alter the microbial communities in soil through changes in litter quality and abundance (Xiang et al., 2018). Once shrubs are removed, their associated microbial communities may not immediately be replaced by microbe assemblages that benefit native or recovering species (Bashan & de-Bashan, 2010). The legacy of soil physical properties like soil texture and structure that shrublands leave behind are also likely to affect the pace of grass recovery following treatment (Baer et al., 2010). Additionally, grasses and forbs are more palatable species than shrubs, and the grazing that many of these plots are subjected to, may have limited their recovery (Abercrombie et al., 2019). On a broader scale, climate factors could have also contributed to grass cover constraints, as there has been a megadrought occurring over the last few decades (e.g., 2000 – 2022) in the southwest of North America (Gremer et al., 2015; Williams et al., 2022) which is likely to restrict herbaceous growth.

We found support for our prediction that shrub removal would lead to decreases in live shrub cover, and again there was no relationship between time since treatment and relative shrub cover. This indicates that shrubs were effectively reduced, and re-encroachment (or recovery) of shrubs may not be occurring at these time points (e.g., up to 36 years). Living shrubs were not entirely eliminated from shrub removal plots, however. Individual differences in live shrub cover between the treated areas is likely related to site-specific differences in shrub recovery (re-encroachment) (Perkins et al., 2006). Some of the living shrubs may also be those that were not killed by the herbicide treatments; shrubs like creosote bush are typically resilient and long-lived (i.e., can live from decades to centuries years old) (DeLisle, 2015). Mortality rates of creosote shrubs via Tebuthiuron herbicide can vary between individuals (Gibbens et al., 1987). This variability was also reflected in our estimates of relative shrub cover, where differences in shrub cover between treated and untreated plots ranged from 31 -100% across sites.

H2: Older restoration treatments correlated with higher relative soil organic carbon

Our prediction that older restoration areas would hold more SOC was supported, which we attribute here to shifts in vegetation cover, including general increases in forbs and grass cover and increases in dead shrub skeletons following shrub removal. In undisturbed or established grasslands (e.g., prairies), soil organic matter inputs mainly come from the turnover of belowground plant materials (i.e., roots and their exudates) (Qi et al., 2019). This is due to the belowground biomass of grasses being markedly higher than their aboveground structures, which can easily be lost to herbivory or other external factors (e.g., desiccation from extreme heat) (Mason & Zanner, 2005.). This high root-to-shoot ratio is also found in desert perennial species, where root systems can significantly outweigh aboveground grass biomass (Gibbens & Lenz, 2001). In both Chihuahuan Desert shrublands and grasslands, it is estimated that belowground turnover from roots is equal to or higher than turnover from aboveground inputs (Havstad et al., 2006). However, the belowground turnover from grasslands is likely considerably higher than that from shrublands; Rough estimates show that the roots of grasses like bush muhly turnover at a rate of 30 kg N/ha/yr, relative to creosote bush and honey mesquite that have root turnover rates of 15.5 and 27 kg N/ha/yr respectively (Havstad et al., 2006). More recent studies have also found that soil litter mixing (mixing of soil and litter via erosional deposition) can often accelerate the rate of decomposition, particularly in shrublands where erosion is greater due to the high percentage of unvegetated interspace (Hewins et al., 2013). Increases in grass and herbaceous cover following shrub removal would presumably lead to less erosion and higher belowground turnover rates, which could correlate to increases in soil organic matter (i.e., soil carbon). Our findings are also in line with previous studies that show soil organic matter (i.e., carbon) recovery can take decades or more, particularly in cases where ecosystems have undergone significant disturbances or changes (i.e., shrub encroachment, shrub removal) (Lorenz & Lal, 2022).

We also suggest that the gradual increase in relative SOC with time may be related to the shift in soil carbon inputs following shrub removal – namely via the decomposition of dead shrub skeletons. In support of this, we found that shrub cover was overall lower in treated areas – regardless of type (living or dead shrubs) and that dead shrubs had a marginal negative relationship with time since treatment. In the field, we observed that dead shrub skeletons varied in structure- i.e., some were reduced to stumps while others still retained their branch structure. This variance in dead shrub structure is likely due to the slow decomposition rates of woody tissue over time (Hall et al., 2020), which suggests dead shrubs could also provide inputs of SOC for many years as they decompose. In shrub removal areas, soil under dead shrubs held the most SOC relative to the other ground cover types (Supplemental Figure 4.4). We propose here that SOC overall will continue to increase with time since shrub removal treatment due to the slow recovery of SOC facilitated by recovering grasses, forbs, and the coinciding decay of dead shrubs.

H3: Restoration treatment age did not correlate to relative soil inorganic carbon

In a previous study, we found that soil inorganic carbon (SIC) in surface soils was lower in treated areas ~8 years after shrub removal treatments occurred (Chapter 3). We suggested that carbonates in the uppermost soil layers (e.g., top 5cm) were likely buried by an increase of dust and sand capture that was facilitated by recovered grasses and forbs (Chapter 3). From this, we predicted that SIC may negatively correlate with time since treatment, assuming regular increases in grass following shrub removal would equate to higher burial rates of SIC. This was not supported by our results, however, as no relationship was found with time since treatment for either relative grass cover or SIC. It may be that soils that continue to be captured by recovered grasses/forbs may not be carbonate-rich (i.e., silicates) or that additional soils were not captured on the longer term (> 8 years after shrub removal). It is also unlikely that carbonates would form chemically (e.g., pedogenic carbonate precipitation), as these processes occur at very large timescales (Kraimer et al., 2005). Overall, we suggest that lower SIC in surface soils deriving from shrub removal may only be observable at relatively short time points – perhaps only in the few years directly following shrub removal events.

Implications for desert grassland restoration

Our study highlights that even though grass cover may not continue to change with time since shrub removal, you may still see changes through time in relative SOC. This is significant as grassland restoration goals may not only include increasing herbaceous cover but also often aim to establish regular gains in herbaceous cover to support specific services (i.e., consistent gains in grass each year can continue to support both wildlife and livestock) (Copeland et al., 2021; Resch et al., 2021). Our results suggest that significant regular gains in herbaceous cover may not be the only indication of restoration success, and soil properties may also offer insights on site responses to shrub removal treatments. There are a few caveats we would note when considering these findings. While we suggest that dead shrub decomposition may be contributing to this positive relationship, eventually, they will decay completely, making them a temporary contributor to soil organic matter stocks following shrub removal. Lastly, it is important to recognize that although shrub removal sites correlated with higher relative plot-level soil carbon, some sites had negative relative carbon values regardless of treatment age (i.e., SOC was lower with shrub removal at some sites). This implies that within site differences of SOC may be dependent on other underlying factors (e.g., micro-climate or site soil characteristics) apart from the time since treatment was applied.

In conclusion, desert grassland restoration practices could be aided by a better understanding of how the time since restoration treatment influences our assessment of restoration success. Although grass cover may not continue to change (i.e., increase) with time since shrub removal, changes through time in relative SOC – are likely suggesting that the time point at which system recovery is assessed is critical. Overall, these findings could help strategize desert grassland restoration planning, particularly in cases where the management goal includes monitoring vulnerable soil resources such as soil carbon. Lastly, we recommend that assessments on restoration success for specific response variables (i.e., vegetation cover, soil carbon) be consistently framed within a time dependent context, as short-term effects of restoration may not be indicative of long-term effects.

AUTHOR CONTRIBUTIONS

A version of this Chapter will be submitted for review in a peer-reviewed journal and is co-authored by Kathleen Schaeffer (KS) and Jennie McLaren (JM). The methodology for this specific study was designed by JM and KS. KS collected and analyzed data; JM and KS interpreted results; KS led the writing of the manuscript.

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DATA ACCESSIBILITY

Data from this project will be made available when this chapter is submitted for publication. Potential data centers include National Resources Conservation Service (NRCS) or BLM/USDA affiliated data centers.

Chapter 5: Conclusions

SUMMARY OF DISSERTATION FINDINGS

Soil carbon and other soil properties are affected by large-scale shrub removal practices in the Chihuahuan Desert – and these soil properties can also provide support for desert grassland restoration planning. Predicting restoration success in desert regions is challenging, particularly when successes or failures may be attributed to differences in inherent restoration site properties (i.e., soil carbon, elevation). Soil properties like carbon (both organic and inorganic) are understudied properties in dryland regions, yet they are essential resources that provide services such as soil water and nutrient retention, structure, and energy for the decomposers (i.e., microbes) that drive primary productivity. To address these restoration challenges and gaps in research, we used three main objectives to determine if 1) inherent soil and site-level properties could act as indicators for desert grassland restoration outcomes; 2) if the vegetation shifts that follow large-scale shrub removal treatments affect soil carbon (organic and inorganic) ~8 years after treatments; and 3) if relative soil carbon (i.e., treatment effects on carbon) vary with treatment age. Below I will summarize how my dissertation projects (i.e., chapters) addressed each of the above objectives along with their findings– as well as discuss what broad implications our results have for dryland restoration research.

In Chapter 2, we explored the first objective by testing inherent site and soil properties for relationships with our calculated grass response score (i.e., Grass Gain), a measure of restoration success found in shrub removal areas. We selected a suite of site and soil variables based on their known relation to factors that could optimize grass seed establishment (i.e., soil moisture and structure, microclimate). We found that soil organic carbon and site-level elevation were significant indicators of grassland restoration potential. Higher soil organic carbon and elevation correlated to higher grass responses. We also found that site elevation was predictive of several soil properties in general (soil carbon included), which we predict could affect restoration success. Additionally, we found that the presence or strength of relationships between grass response and soil/site indicators varied by ground cover type (i.e., microsite), indicating that sampling scheme may affect observations in dryland restoration studies. These findings underline that these soil and site-level properties can be used as qualitative reference points for identifying potential restoration sites (prior to shrub removal treatments).

In Chapter 3, we explored the second objective by determining whether soil carbon (organic and inorganic) differed between no shrub removal and shrub removal areas ca. 8 years after shrub removal treatments occurred. We hypothesized that treatment-initiated changes in vegetation composition would lead to increases in soil organic carbon but no change in soil inorganic carbon. We compared both local (within ground cover type) and plot scale differences in soil carbon between these treated and untreated areas. Contrary to our predictions, we found that shrub removal treatment did not affect soil organic carbon at the local or plot scale; however, soil inorganic carbon was lower in shrub removal areas – at both the local and plot scales. We attributed the null effect on soil organic carbon to the death and subsequent decay of shrubs following herbicide treatments. We suggest that after 8 years following shrub removal, dead shrubs are likely contributing approximately the same magnitude of soil organic carbon inputs that living shrubs did before treatment. We also suggest that the lower levels of soil inorganic carbon observed in shrub removal areas are not due to a loss through chemical mechanisms (i.e., leaching), but due to an increase in dust and sand capture by recovered grasses – ultimately burying soil inorganic carbonates below our sampling depth (5 cm). These findings are significant, particularly for projects where soil carbon conservation or recovery is included as a land management goal.

In Chapter 4, we set out to answer our third objective by exploring relationships between shrub removal treatment effect on soil carbon (organic and inorganic) and the time since shrub removal treatment was imposed (i.e., treatment age). We calculated treatment effects on soil carbon at different time points using a chronosequence of shrub removal treatments. We found that shrub removal had a positive effect on soil organic carbon over time; however, there was no effect on soil inorganic carbon. We suggest that the gradual increase of soil organic carbon with time since removal is driven by the decomposition of shrub skeletons. Overall, these results show that the short-term effects of shrub removal treatments may not be indicative of long-term effects, highlighting the value of these historically treated areas.

SOIL CARBON MUST BE CONSIDERED IN DESERT GRASSLAND RESTORATION PRACTICES

Restoring desert grasslands is an undertaking that requires significant planning, time, and resource allotment (Resch et al., 2021). It is also important to explicitly recognize that the subsequent changes in vegetation following shrub removal (i.e., creation of novel plant communities) may not lead to the same conditions that the perennial desert grasslands of the past may have had (Petrie et al., 2015). This variation in restoration results requires the expansion of the tools we use to estimate restoration success and effects. This dissertation underlines that there is a need to include properties beyond vegetation composition in both the planning and assessment of desert grassland restoration practices. When selecting ideal grassland restoration sites, inherent site-level properties like soil organic carbon and elevation can provide insight on how effective shrub removal treatment may be.

We also found overall, the observed effects of shrub removal on soil carbon may not be evident until many years after shrub removal occurred. This is likely due to the legacy effects from shrub encroachment as well as from their removal. For instance, dead shrub skeletons likely contribute to soil organic carbon inputs long after they were initially removed via herbicide (e.g., even 32 years after treatment). This indicates that shrub removal via herbicide does not eliminate the presence of soil organic carbon inputs from shrubs and that shrubs may continue to make significant soil carbon contributions even after death. These inputs, however, may only be present for a few decades (or however long it takes herbicide-removed shrubs to decompose). However, more research is needed to determine if soil carbon changes after dead shrubs diminish completely (i.e., more than 32 years after shrubs were removed).

We also found that dryland soil carbon sequestration may also be positively influenced by shrub removal practices. In terms of carbon sequestration and soil resources, soil inorganic carbon in Drylands has been considered to be a static resource pool relative to organic carbon (Várallyay, 2005). This is because soil inorganic carbon is inaccessible to microbes, and sequestration rates are difficult to measure due to massive timescales (e.g., soil carbonates can take thousands of years to accumulate) (Monger, 2014). However, Drylands cumulatively make up ~97% of the global soil inorganic carbon stock (Plaza et al., 2018). Although it may take significant amounts of time for atmospheric CO_2 to be sequestered as inorganic carbonates, it only takes a few years for existing carbonates to be lost back to the atmosphere (e.g., the acidification of carbonates releases CO_2) (Liu et al., 2020). We found that removing shrubs may lead to higher rates of sand and dust capture by novel plant communities (e.g., recovered forbs and grasses). From our results, we also suggest that shrublands are likely to expose more soil carbonates to deterioration (i.e., rain, wind) than novel plant communities. The decrease in unvegetated interspace following shrub removal will likely help conserve this sequestered soil carbon source if novel plant communities persist (i.e., shrubs do not re-encroach).

In conclusion, it is essential that researchers and land managers continue to monitor site-level variables, including soil carbon, to fully capture the observed effects of large-scale shrub removal practices both in the Chihuahuan Desert and other Drylands. This is especially important as Drylands provide several essential services and functions to a wide range of organisms as well as to humans.

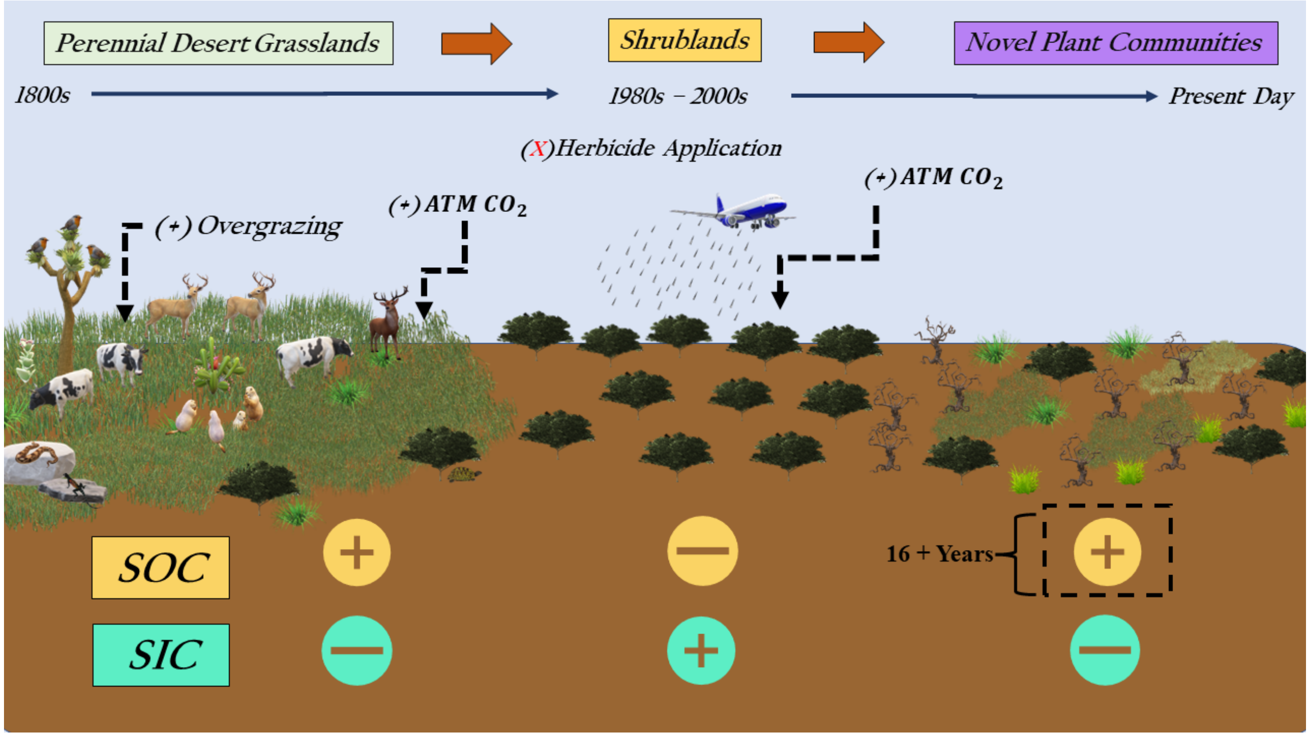

Figure 5.1: Vegetation community regime shifts in the Chihuahuan Desert over ~200-year period, with differences in associated plot-level surface soil carbon (organic and inorganic) inferred from our study. Plot-level soil surface measurements (i.e., sampled at the top 5cm) are shown for both soil organic carbon (SOC) and inorganic carbon (SIC). Plot-level soil surface carbon values are categorized as "more" (denoted by **"+"**) or "less" (denoted by "**-** ") to show respective higher and lower plot values in each soil carbon type, at each regime stage. Soil carbon estimates for perennial grasslands were calculated from a reference grassland we sampled in Fall of 2018, and these values represent pre-shrub encroachment conditions in this region. Shrubland and novel plant community soil carbon estimates are calculated from a group of 15 experimental shrub removal sites established ca.8 years before we sampled them in Fall 2017. Each site had a control (shrubland) area, as well as an herbicide treated area where shrubs were removed – making a "novel" plant community made up of recovering grasses/forbs, dead shrub skeletons, and surviving shrubs. We additionally sampled at a chronosequence of 14 shrub removal treatments that varied in age (ranged from 16 - 32 years since treatment), where we found that novel plant communities had higher SOC but only after 16+ years following shrub removal (this condition of time is denoted by the dashed line box). Lastly, drivers of shrub encroachment are preceded by **"*(+)*"** and include overgrazing by introduced herbivores in perennial grasslands, increases in atmospheric (ATM) CO_2 (both factors were beneficial for encroaching shrubs).

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Supplemental Tables

Supplemental Table 2.1. Summary of how Grass Gain Score (GGS) was calculated using pre-treatment (baseline) and post treatment perennial grass cover (%) data at no shrub removal (CTL) and shrub removal (TRT) areas, that were part of a ca.8-year shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Ten of the study sites received shrub removal treatments in 2007 ("2007 Sites"), and fifteen of the study sites received shrub removal treatments in 2009 ("2009 Sites").

	Perennial Grass Cover (%)						
Site Group	**Pre-Treatment CTL**	**Post Treatment CTL**	**Grass (%) Δ CTL** *(post – pre)*	**Pre-Treatment TRT**	**Post-treatment TRT**	**Grass (%) Δ TRT** *(post – pre)*	**Grass Gain Score** ***(Grass (%) Δ TRT - Grass (%) Δ CTL)***
2007 Sites	**22.7**	**30.3**	**7.7**	**20.0**	**38.7**	**18.7**	**11.0**
	13.0	**4.7**	**-8.3**	**14.0**	**18.7**	**4.7**	**13.0**
	30.7	**30.0**	**-0.7**	**31.0**	**51.3**	**20.3**	**21.0**
	46.7	**19.7**	**-27.0**	**63.0**	**64.3**	**1.3**	**28.3**
	39.0	**18.0**	**-21.0**	**43.3**	**46.0**	**2.7**	**23.7**
	35.3	**12.3**	**-23.0**	**47.3**	**36.0**	**-11.3**	**11.7**
	31.7	**18.7**	**-13.0**	**25.0**	**14.0**	**-11.0**	**2.0**
	13.3	**2.7**	**-10.7**	**27.0**	**12.0**	**-15.0**	**-4.3**
	22.3	**5.0**	**-17.3**	**21.0**	**6.3**	**-14.7**	**2.7**
	18.3	**7.7**	**-10.7**	**24.7**	**15.0**	**-9.7**	**1.0**
2009 Sites	**3.3**	**5.3**	**2.0**	**8.8**	**6.8**	**-2.0**	**-4.0**
	14.3	**9.5**	**-4.8**	**10.5**	**17.5**	**7.0**	**11.8**
	3.5	**4.5**	**1.0**	**8.3**	**27.0**	**18.8**	**17.8**
	10.0	**4.0**	**-6.0**	**4.3**	**6.8**	**2.5**	**8.5**
	3.0	**0.0**	**-3.0**	**6.5**	**0.0**	**-6.5**	**-3.5**
	20.5	**14.3**	**-6.3**	**13.8**	**49.8**	**36.0**	**42.3**
	16.8	**6.8**	**-10.0**	**6.0**	**18.5**	**12.5**	**22.5**
	0.0	**4.8**	**4.8**	**0.3**	**10.5**	**10.3**	**5.5**
	12.8	**3.0**	**-9.8**	**5.8**	**4.5**	**-1.3**	**8.5**
	25.3	**15.3**	**-10.0**	**22.0**	**36.8**	**14.8**	**24.8**
	47.5	**18.0**	**-29.5**	**31.5**	**30.8**	**-0.8**	**28.8**
	12.8	**10.0**	**-2.8**	**10.0**	**13.0**	**3.0**	**5.8**
	6.3	**6.0**	**-0.3**	**8.5**	**32.3**	**23.8**	**24.0**
	19.8	**8.0**	**-11.8**	**9.5**	**21.5**	**12.0**	**23.8**
	6.8	**2.0**	**-4.8**	**3.5**	**3.8**	**0.3**	**5.0**

Supplemental Table 2.2: Summary statistics of multiple linear regressions between Grass Gain Score (GGS) and soil and site indicator variables (rainfall, elevation, and soil organic carbon) and their respective coefficients (*Estimate* column) at ten “2007 RNM” study sites that were part of ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Statistical significance of relationships is denoted by an asterisk (Prob>|t| = ≤ 0.05).

2007 RNM Sites					
Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**	**VIF**
Intercept	-77.85151	16.66213	-4.67	0.0002*	.
Site Elevation (m)	0.0517246	0.011114	4.65	0.0002*	1.9056178
Soil Organic Carbon (%)	3.7654128	1.38799	2.71	0.0148*	1.9056178

Supplemental Table 2.3: Summary statistics of multiple linear regressions between Grass Gain Score (GGS) and soil and site indicator variables (rainfall, elevation, and soil organic carbon) and their respective coefficients (*Estimate* column) at fifteen “2009 RNM” study sites that were part of ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. In this 2009 Sites model, it should be noted that the model adjusted R^2 decreased significantly when we attempted to remove the last non-significant relationship (Average Annual Rainfall, $p = 0.09$). Since this *p-value* was marginal, and the VIF for that variable remained below 2, we opted to include the variable to present the model of best fit. Statistical significance of relationships is denoted by an asterisk (Prob>|t| = ≤ 0.05).

2009 RNM Sites					
Term	**Estimate**	**Std Error**	**t Ratio**	**Prob>|t|**	**VIF**
Intercept	-200.844	30.71709	-6.54	<.0001*	.
Avg Annual Rainfall (mm)	0.1170829	0.068537	1.71	0.0995	1.0701472
Site Elevation (m)	0.1148656	0.019817	5.80	<.0001*	1.0508926
Soil Organic Carbon (%)	27.168853	6.515764	4.17	0.0003*	1.0667956

Supplemental Table 3.1: Average percent soil organic carbon (a) and inorganic soil carbon (b) found in each ground cover and vegetation type between no shrub removal (control) and shrub removal (treatment) areas that were part of a ca.8 year old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Note: not all ground cover types were found in control and treatment areas, and this absence is denoted by "~".

	A) Average Organic Soil Carbon (%)		**B)** Average Inorganic Soil Carbon (%)	
	No Shrub Removal	Shrub Removal	No Shrub Removal	Shrub Removal
Interspace	0.66	0.69	1.20	0.46
Subcanopy (live shrub)	0.78	0.89	0.70	0.12
Forbs/Grass	~	0.92	2.19	0.62
Dead Shrub	~	1.03	~	0.17

List of Supplemental Figures

Supplemental Figure 2.1: Perennial grass cover difference (%) over an 8-year period at ten experimental shrub removal sites established in 2007 (“2007 RNM Sites”), in the Chihuahuan Desert of southwestern New Mexico. “Year 0” shows baseline grass cover (pre-treatment), and “Year 8” shows grass cover ca.8 years after shrubs were removed via herbicide. For each site, Control (no shrub removal) areas are denoted in blue and Treated (shrub removal) areas are denoted in orange. The darker/thicker lines and markers show the overall site-level averages for control and treated perennial grass cover (%) at both time points.

Supplemental Figure 2.2: Perennial grass cover difference (%) over an 8-year period at fifteen experimental shrub removal sites established in 2009 (“2009 RNM Sites”), in the Chihuahuan Desert of southwestern New Mexico. “Year 0” shows baseline grass cover (pre-treatment), and “Year 8” shows grass cover ca.8 years after shrubs were removed via herbicide. For each site, Control (no shrub removal) areas are denoted in blue and Treated (shrub removal) areas are denoted in orange. The darker/thicker lines and markers show the overall site-level averages for control and treated perennial grass cover (%) at both time points.

Supplemental Figure 2.3: Relationships between Grass Gain Score (*(Δ Final and Initial %Grass cover at shrub removal plots) - (Δ Final and Initial %Grass cover at no shrub removal plots))* and soil texture components of % sand (**a, b**), % silt (**c, d**) and % clay (**e, f**) in control plots from soil sampled from interspace (**a, c, e**) and under subcanopy (**b, d, f**) microsites; in a ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. Ten of the study sites received shrub removal treatments in 2007 (“2007 RNM sites”), and fifteen of the study sites received shrub removal treatments in 2009 (“2009 RNM sites”). Statistical significance of relationships is denoted by bold font (p=<0.05). If relationships did not differ significantly between site group (2007 vs 2009), both site groups were pooled together or analyses (**b-f**). If the relationships differed significantly between site group, the analyses were separated out by site group (**a**).

Supplemental Figure 2.4: Comparison photos of no shrub removal (*left)* and shrub removal (*right*) areas that were part of a ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. No shrub removal areas often consist of living shrub vegetation with large patches of unvegetated interspace between shrubs. Shrub removal areas consist of "novel plant communities" made up of varying proportions of surviving shrubs, dead shrub skeletons, forbs, grasses, and the unvegetated interspace between them. (Photo credit: K. Schaeffer, Oct. 2017)

Supplemental Figure 3.1: Comparison photos of no shrub removal (*left)* and shrub removal (*right*) areas that were part of a ca. 8-year-old shrub removal experiment in the Chihuahuan Desert of southwestern New Mexico. No shrub removal areas often consist of living shrub vegetation with large patches of unvegetated interspace between shrubs. Shrub removal areas consist of "novel plant communities" made up of varying proportions of surviving shrubs, dead shrub skeletons, forbs, grasses, and the unvegetated interspace between them. This shrub removal area however was mainly composed of dead shrubs (Photo credit: K. Schaeffer, Nov. 2017)

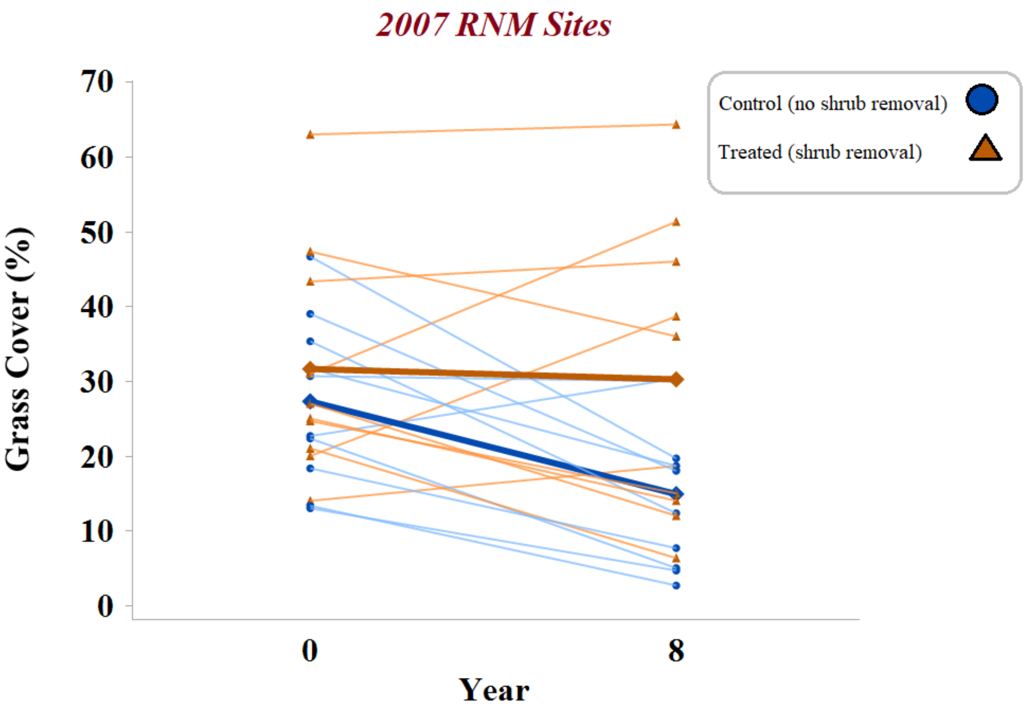
Supplemental Figure 4.1: Boxplots comparing individual percent cover of dominant vegetation and ground types between no shrub removal and shrub removal areas across 14 shrub removal sites established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico. Shrub removal treatments were applied once at each site across multiple years, making a chronosequence of treatment ages. The most dominant vegetation and ground cover types included unvegetated interspace (a), dead shrub skeletons (b), forbs/grass (c), and live shrub subcanopy (d). Note: Some shrub removal sites did not have all types present. Significant differences are denoted in bold font (p-value <0.05).

Supplemental Figure 4.2: Boxplots comparing total percent shrub cover (both dead and living) at no shrub removal and shrub removal areas across 14 shrub removal sites established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico. Shrub removal treatments were applied once at each site across multiple years, making a chronosequence of treatment ages.

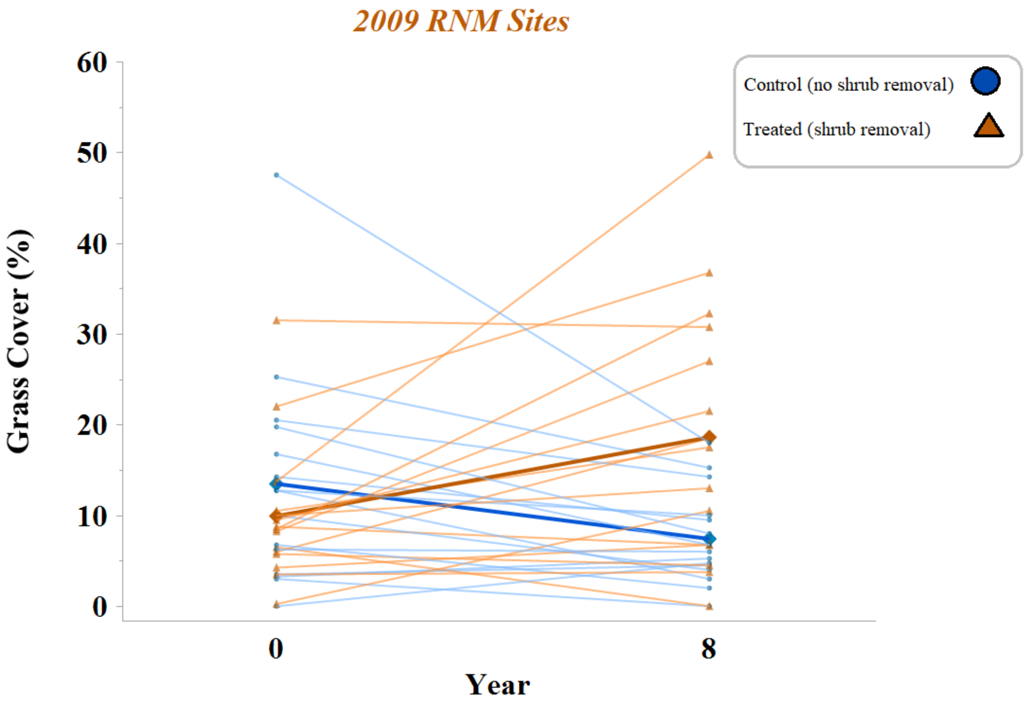
Supplemental Figure 4.3: Relationship between time since shrub removal treatment (in years) and total percent dead shrub cover at 14 shrub removal areas that were established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico. Shrub removal treatments were applied once at each site at establishment, making a chronosequence of treatment ages.

Supplemental Figure 4.4: Boxplots showing soil organic (**a, b**) and inorganic carbon (**c, d**) between ground and vegetation cover patches within no shrub removal control plots (**a, c)**; and shrub removal treatment plots (**b, d**) at 14 shrub removal sites that were established between 1982 – 2002 in the Chihuahuan Desert of southwest New Mexico. Shrub removal treatments were applied once at each site at establishment, making a chronosequence of treatment ages. Significant differences in soil carbon between ground and vegetation types (GCT) and/or site are denoted by asterisks (p-value < 0.05 denoted as *, <0.01 as **, and <0.001 as ***). No statistical significance is denoted as “n.s.”.

Supplemental Figure 2.1



Supplemental Figure 2.2



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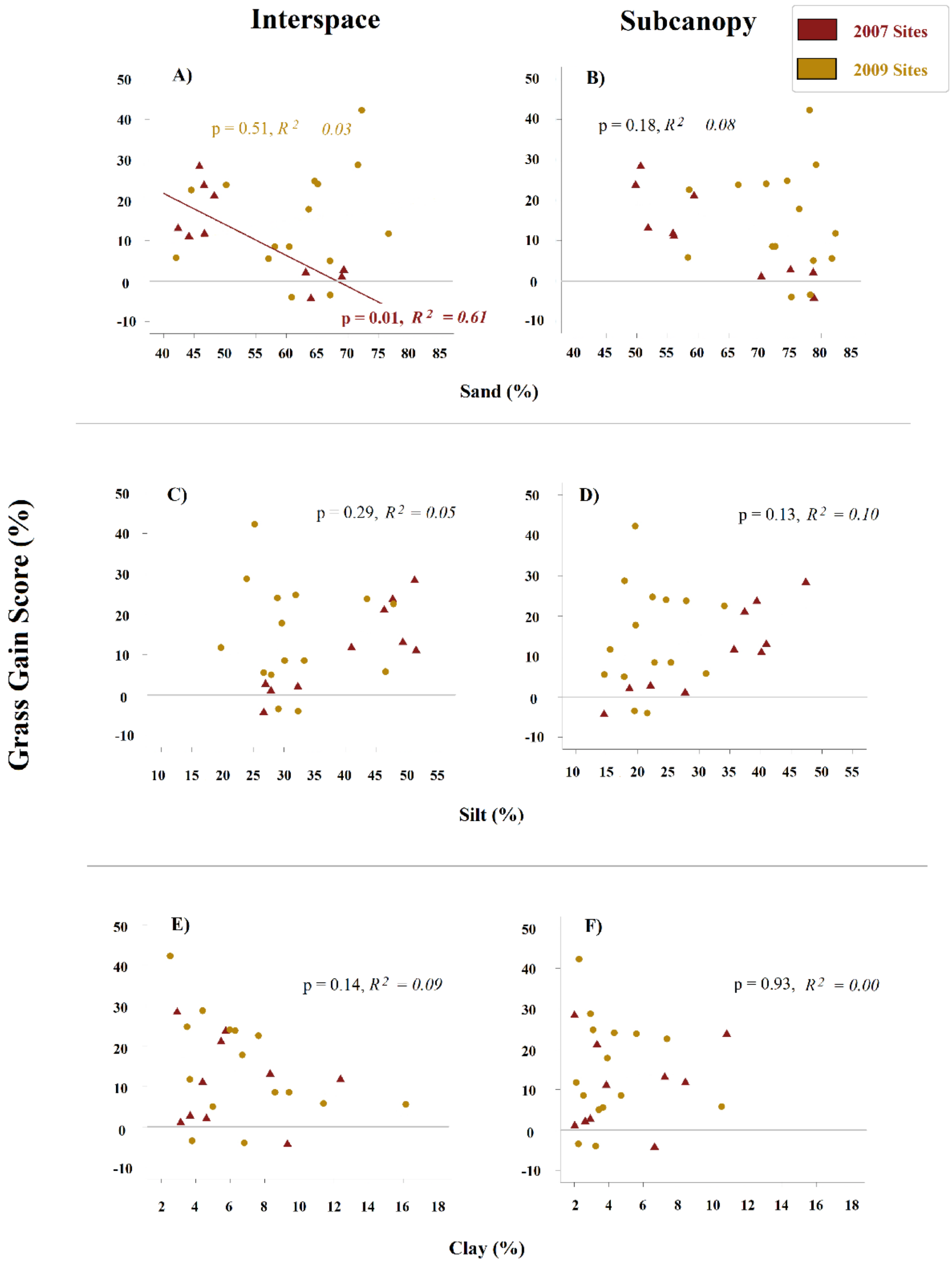

Supplemental Figure 2.4:

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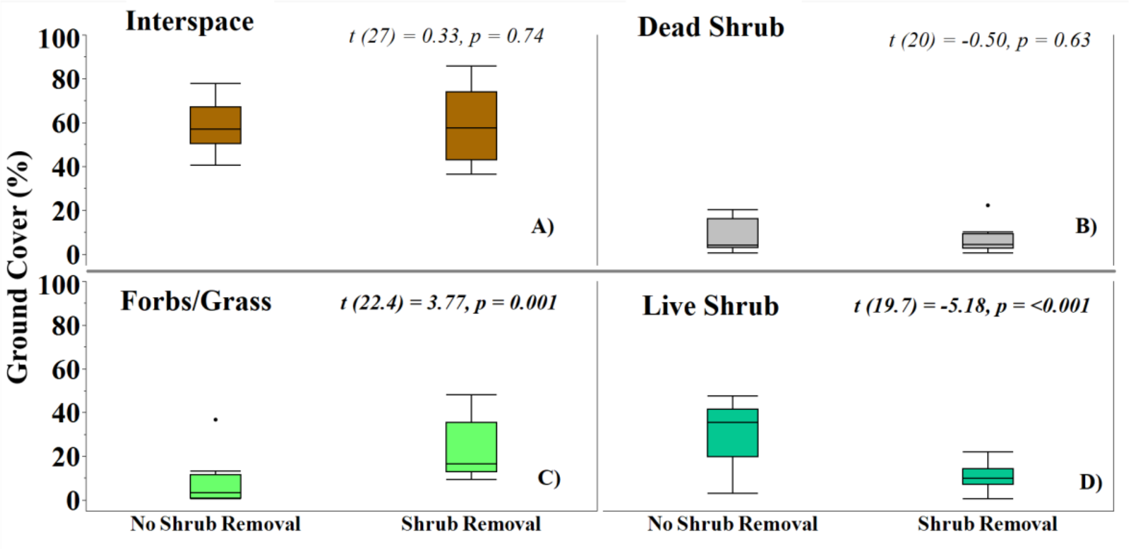

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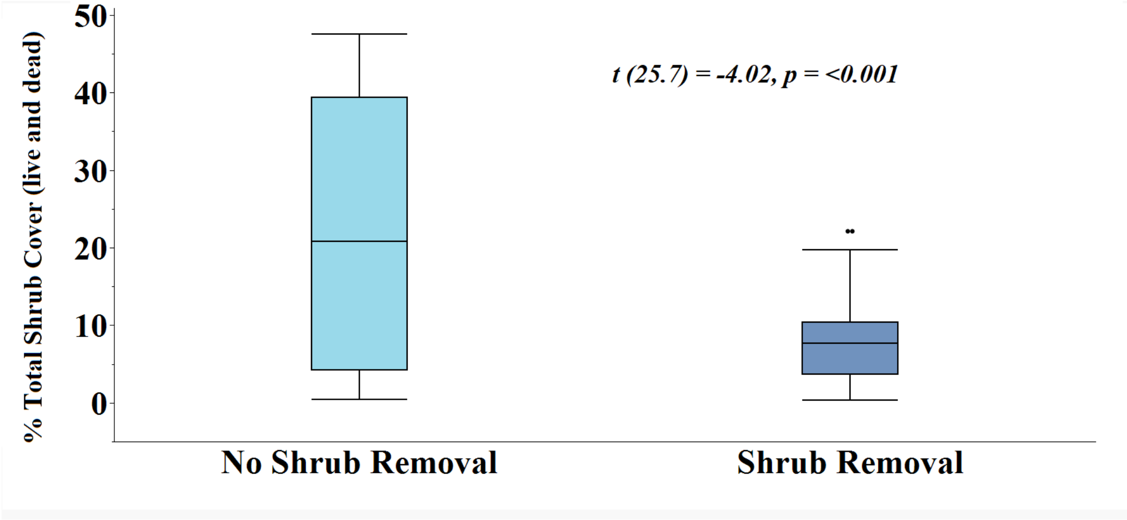

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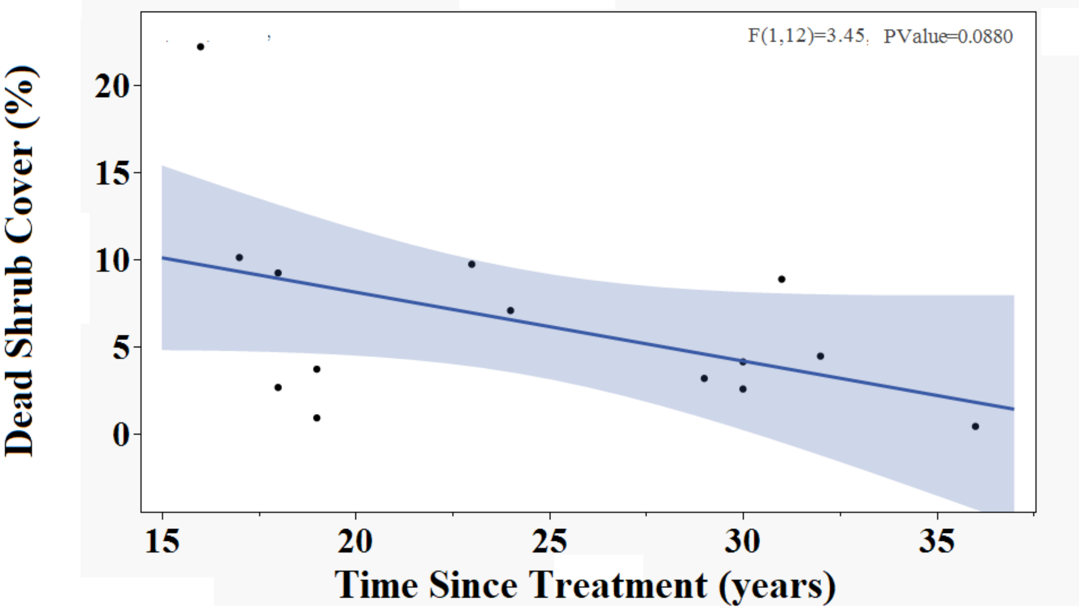

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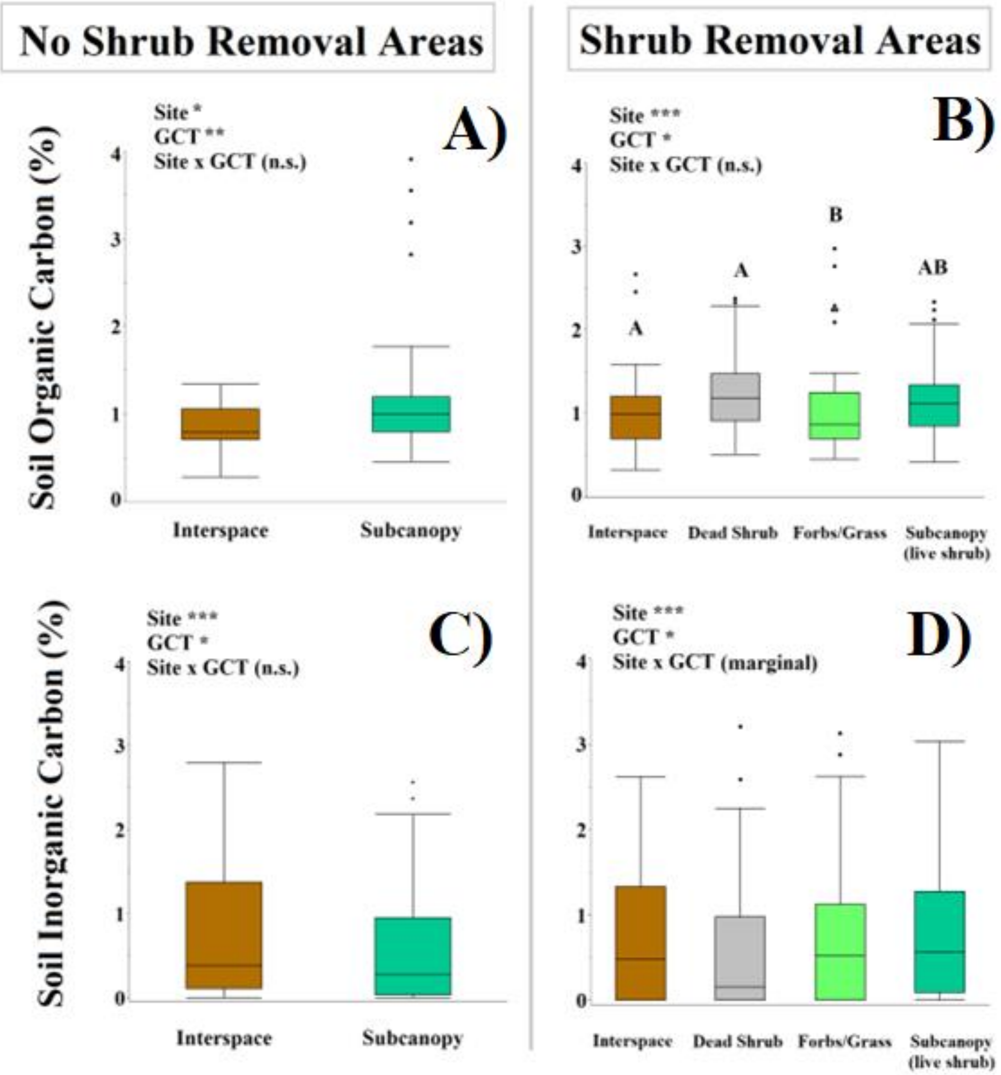

Vita

Kathleen Schaeffer received a Bachelor of Science with a concentration in Ecology and Evolution from the University of Texas at El Paso (UTEP) in 2016. Before coming to UTEP, Kathleen earned an Associate degree in science from El Paso Community College (EPCC) in 2014. While at UTEP, Kathleen worked as a Graduate Teaching Assistant for the courses Topics in Study in Life, Ecology, and Plant Ecology and was a guest lecturer for Ecology. Kathleen was a recipient of the Prairie Biotic Research and Native Plant Society Grant in 2018. In 2020, she was accepted to the Hispanic Alliance for Graduate Education and the Professoriate (H-AGEP) fellowship. During her time in the fellowship, she created ecology-based labs and a workshop for biology students at EPCC. In 2021, Kathleen and her fellow graduate students were awarded the UTEP Graduate School Summer Enhancement Grant, for which they created and facilitated an on-boarding workshop for new graduate teaching assistants. Kathleen has presented her doctoral research at the *Jornada LTER Annual Conference 2018,* the *JER Desert Ecology Short Course 2021*, and the *H-AGEP Annual Conference 2022*. Kathleen also collaborated with her fellow graduate teaching assistants to host a panel discussion on the challenges of transitioning to online teaching during the pandemic, in the *UTEP SOL (Support for Online Learning) Conference 2021.* Kathleen was a co-founder of the Biology, Environmental, and Engineering Graduate Student Group (BEE) at UTEP, whose mission was to both advocate and provide networking opportunities for graduate students. She was also a co-founding member of the 500 Women Scientists El Paso Pod, a community group that advocates for the advancement and success of women in science. From 2019 – 2023, Kathleen volunteered for several science focused University, and community outreach events hosted by the UTEP Biodiversity Collections, El Paso Audubon, and El Paso Insights Museum. Kathleen was also elected by her peers to be the Graduate Student Assembly representative for the Ecology and Evolutionary Doctoral Program in 2019 and 2021.