

**POST OAK SAVANNA IN TRANSITION: JUNIPER
ENCROACHMENT AND CLIMATE CHANGE ALTER
GRASSLAND SOIL RESPIRATION**

An Honors Fellows Thesis

by

B. CLAY THOMPSON JR.

Submitted to the Honors Programs Office
Texas A&M University
in partial fulfillment of the requirements for the designation as

HONORS UNDERGRADUATE RESEARCH FELLOW

April 2011

Major: Forest Resource Management

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ABSTRACT

Post Oak Savanna In Transition: Juniper Encroachment and Climate Change Alter
Grassland Soil Respiration. (April 2011)

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The amount of carbon flux from soils on a global scale is estimated at over 75×10^{15} g C yr⁻¹. Climate change is projected to affect regional environmental conditions, raising temperatures and altering precipitation patterns. The semi-arid environment of the post oak savannah is an ecotone in transition. As juniper encroachment replaces native grasses, changes in species composition may affect carbon cycling. Given that water is limiting in this warm-temperate climate, changing precipitation patterns coupled with higher temperatures may alter function in addition to the structure of savanna ecosystems. The Texas Warming and Rainfall Manipulation (Texas WaRM) experiment is designed to test global climate change factors and the responses of the dominant tree, eastern red cedar (*Juniperus virginiana*) and grass species, little blue stem (*Schizachyrium scoparium*). We compared respiratory carbon losses of soils between eastern red cedar and little blue stem plots subjected to warming (1.5 °C) and summer drought treatments to determine the effects of climate change on integrated below-ground CO₂ efflux. During the June to August months, soil CO₂ efflux rates were

determined and compared among treatments in relation to soil temperature and moisture. Overall, juniper and grass plots had relatively equal CO₂ respiratory flux, although it generally has more associated roots and microbial biomass. Soil respiration in grass plots appeared more responsive to changes in soil moisture, while juniper maintained more consistent respiration under increasing heat and declining moisture conditions during summer drought. With equivalent soil CO₂ efflux and reduced responsiveness to warming or drought, coupled with increased woody biomass, juniper encroachment might have positive effects on the carbon cycle of this transitional biome through increased carbon sequestration. Determining these transitional characteristics of a changing carbon budget will aid in projecting climate change impacts on carbon cycling and provide management options for native and managed vegetation.

DEDICATION

To my wife Laura who's unending belief in my meager abilities pushes me to achieve great things.

ACKNOWLEDGMENTS

To Laura, my mom Joann, and my daughters for their emotional support throughout this long and arduous process. I thank Dr. Mark Tjoelker for giving me help when I needed it and teaching me how to help myself. I would like to thank Dr. Astrid Volder and her Ph.D. student Andrew Cartmill in the Department of Horticultural Sciences. Dr. Volder gave me direction and help, although she did not have to give me either throughout the length of this project. I extend my thanks to Dr. Tom Boutton and his lab. They were all a great help in providing answers to my questions with the knowledge that only years of experience provide. I would also like to thank the Department of Ecosystem Science and Management for the opportunity to participate in this research project and the resources to complete my work. Finally I would like to thank the Dr. Louis and the Honors office at Texas A&M for the remarkable experience in the Undergraduate Research Fellows program.

NOMENCLATURE

b/d	bulk density
CEC	Cation exchange capacity
C	Carbon

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CHAPTER I

INTRODUCTION

The post oak savannah is a transitional biome between grasslands and deciduous forests in the south central US. The semi-arid environment of the post oak savannah is an ecotone in transition, and as woody trees displace native grasses, this region and its carbon budget will likely be affected. Given that water is a limiting factor in this warm temperate climate, changing precipitation patterns coupled with higher temperatures may alter function in addition to structure of the savannah ecosystem. Thus, this ecosystem is a unique model system in which to test the effects of climate change on an environment at risk. Coupled with changing climate patterns, the species composition of post oak savannah is also in transition. Historically this ecosystem was represented by sparse post oak (*Quercus stellata*) mottes and tall grasses such as little blue stem (*Schizachyrium scoparium*), maintained by fire (Robinson *et al.*, 2001). Over the past century juniper trees, such as eastern red cedar (*Juniperus virginiana*), have been encroaching on grasslands from west to central Texas, including the post oak savannah. The woody encroachment of grasslands and savannas is primarily caused by the restriction of fire in the region, which post oaks are adapted to but juniper trees are not. Post oak and juniper trees have different growth characteristics which cause the decline in grasses under

This thesis follows the style of Ecology.

juniper encroachment. Post oaks thrive in the grass transition zone, creating mottes in the grasslands, while not displacing the grasses. Juniper trees in the grasslands out-compete the regional grasses for water and by casting deep shade that restricts grass growth and survival. Because of the deep rooting profile and taller canopy of both tree species available water, soil carbon, and soil temperature are different from grasslands. Juniper's ability to out-compete the grasses has lead my study to focus on this transitional region of the post oak savannah. Although climate change will potentially lead to an advantage by either grasses or post oak through interspecific competition, the ability of juniper to out-compete them both and change the environment lead to my experimental objective to compare juniper and grass in terms of their below-ground, integrated CO₂ efflux in the context of carbon cycle dynamics.

Woody plant encroachment in grasslands and savannas has been observed as far back as the 19th century (Archer *et al.*, 2000). Encroachment of trees and shrubs in grasslands increases soil carbon because soil nutrients are drawn to the trees through large root system stemflow (Archer *et al.*, 2000). In many semi-arid environments, soil carbon is also increased when wind eroded soil is trapped by the canopy of the tree and deposited on the ground through stemflow (Archer *et al.*, 2000). Carbon gathered by trees is in high concentrations and more easily bound into chemically strong structures or incorporated in microbes in strong organic bonds (Archer *et al.*, 2000). With the increase of nutrients in the area nitrogen accumulation is enhanced because of the shaded environment and brush for animal browsing (Archer *et al.*, 2000). The shade provided by

the canopy encourages macro and micro fauna to seek the lower temperatures; this increases the frequency of defecation under the canopy, increasing nitrogen deposition. The combination of increased nutrients and nitrogen increases net primary production allowing more carbon to be deposited and aggregated into the soil (McCulley *et al.*, 2004). The presence of honey mesquite (*Prosopis glandulosa*), a nitrogen-fixing tree, was shown to increase soil respiration during the rainy season (McCulley *et al.*, 2004). Honey mesquite requires large amounts of water to fix nitrogen, which in a moisture-limited environment indicates that other potential processes are at work in the aggregation of nutrients. In many savanna and woodland systems, root density and biomass are typically greater with woody shrubs and trees over grasses at equal depths (Jackson *et al.*, 1996), while the relative turnover of grass roots is generally higher than trees and shrubs (Gill and Jackson, 2000). Greater amounts of woody root biomass that are slower to turnover would suggest that greater carbon could be sequestered in woody encroached lands. Woody species such as eastern red cedar (*Juniperus virginiana*) also have higher amounts of tannin in their detritus in comparison to grasses, promoting greater amounts of soil carbon storage at higher soil temperatures (Davidson and Janssens, 2006). Carbon compounds, such as tannin, require higher activation energies and Q_{10} values (temperature sensitivity coefficient) for decomposition, (Davidson and Janssens, 2006) suggesting that higher temperatures could volatilize carbon more rapidly than predicted. An alternate hypothesis has been presented that as temperatures increase, soil carbon might become more stable through physiochemical processes (Thornely and Cannell, 2001) leading to reduced soil CO₂ efflux. This theory seems to be in agreement

with observations of increased long-term soil organic carbon in McCulley *et al.* (2004). As soil temperatures rise, if water is not limited, respiration could increase; however, with an increase in temperature, soil carbon could be bound at a quicker rate, allowing for the increase in respiration to be balanced by the decrease in carbon volatilization (Thornley and Cannell, 2001). In the water limited environment of the post oak savannah, I hypothesized that soil respiration be limited by soil water content, but that the little bluestem grass might still have the ability to respire at lower moisture levels due to its C₄ photosynthetic pathway, characteristic of warm-season grasses in the region. However, if juniper roots and associated microbial communities are able to respire at lower moisture levels, the soil CO₂ efflux rates and carbon budgets between grass-dominated and juniper-dominated ecosystems may be closer than expected.

Water is a limited resource in semi-arid and savanna environments. Woody shrubs movement into grassland potentially increases evapotranspiration, especially when soil water tables are deep (Huxman *et al.*, 2005). With less water being available during the summer time coupled with higher temperatures, greater evaporation from leaf area could have a potentially limiting factor on NPP (Huxman *et al.*, 2005). In a study on the Chinese steppe region comprised of a water-limited (300mm/yr) grassland, soil respiration pulsed when rainfall events occurred (Chen *et al.*, 2009). The pulsed respiration in that study primarily came from a heterotrophic response with an autotrophic response coming 2 to 3 days later; presumably after soil moisture spread deeper (Chen *et al.*, 2009). If water was not able to make it to deeper soils, owing to

canopy interception, then as temperature increases, grasses might not receive the soil water pulse in the root profile to continue summertime growth as is typical of little blue stem. When grasslands and woodlands are compared in upland savannas, grasses are typically more responsive to pulses than woodlands (Jenerette *et al.*, 2008), suggesting that grasses are more sensitive to rain events than trees. The activation energy for soil respiration declines in woodlands after precipitation events, suggesting grasslands have greater loss of soil carbon directly after rainfall pulse events (Jenerette *et al.*, 2008). In a separate study, grasses were also confirmed to have higher NPP during summer conditions over woody species in a riparian environment (Jenerette *et al.*, 2009), suggesting that when water was not limiting grasses, autotrophic respiration of grasses is higher. In contrast to some studies in semi-arid environments, where water was limited, the respiration of velvet mesquite (*Prosopis velutina*) declined so that the ecosystem became a source of carbon to the atmosphere (Scott *et al.*, 2009). Little bluestem grass grows during the drier summer months; however, if water is not a limiting factor, encroachment of a woody C₃ species like eastern red cedar would allow for more carbon sequestration. If NPP is lower in juniper compared to grasses during summer, more carbon could be sequestered on an annual basis when considering the winter months, as autotrophic respiration would potentially be greater in the evergreen juniper than in the dormant grasses.

As encroachment by woody species has continued, net gains on a global scale have been observed totaling 0.05 Pg/C/yr from 1700-1990, due to fire suppression (Houghton *et*

al., 1999). Because of higher carbon stores in trees than grasses, a potential net gain of 0.122 Pg/C/yr is sequestered in woody encroached sites (Houghton *et al.*, 1999). Before European settlement, the carbon balance of grasslands was estimated to be 0 Pg/C/yr because of the frequent fires in North American grasslands (Houghton *et al.*, 1999)).

When temperate forests and temperate grasslands are compared, grasslands have higher net primary production (NPP) (Raiche and Schlesinger, 1992). However, in a semi-arid environment where water is limited, the physiological effects of resistance strategy of trees over the resilience strategy of grass may change those relationships. Because mean annual temperatures are expected to rise anywhere from 1.1 – 6.4 °C over the next century (Bates *et al.*, 2008), a resilience strategy may allow grass species to adapt to the overall changing climate, but if conditions are not as harsh, the resistance to drought of woody species may allow them to slowly overtake the NPP of the grass species. It has been shown that temperature has the greatest effect on respiration, followed by precipitation (Raiche and Potter, 1995; Almagro *et al.*, 2009). The effects of increased moisture lowering soil temperature and low soil moisture increasing temperatures result in the release of soil air and associated CO₂ to the atmosphere. At the same time heating up soils volatilizes carbon held in heterotrophs (Almagro *et al.*, 2009). With the given trends of increased temperature and potentially reduced soil water content, fire frequency could possibly increase. The carbon pools that had traditionally been lost in low intensity frequent fires could be lost in high intensity fires (in fire-suppressed systems common throughout savanna regions) scorch the earth and prevent further sequestration. However, woody encroachment also creates deeper soil profiles of rooting

depth and carbon. Thus, while fire would volatilize the carbon on the surface, deep roots and the associated microbes at lower depths would still contribute to soil carbon pools. This study focuses on quantifying soil respiration under drought and warming in contrasting grass and juniper ecosystems, as an integrated measure of belowground soil CO₂ efflux. As such, the study does not directly resolve all soil carbon pools and fluxes, but focuses on identifying the potential effects of climate change and species change on soil CO₂ efflux, a major component of net ecosystem exchange of carbon to the atmosphere. If the soil respiration of grasses responds more positively to climate change scenarios and is associated with increased grass productivity, then management techniques to control juniper could aid the region in terms of maintaining grass dominance, productivity, and carbon sequestration. However, if juniper is better adapted to future warming and drought scenarios than grass, then mixed management of rangelands and juniper-dominated woodlands could promote carbon sequestration and benefit for carbon credit allowances for land managers along with traditional economic benefits. Soil respiration integrates the amount of below ground activity and represents a robust measure of the amount of total carbon flux from soils. Increased sequestration of carbon could be encouraged through management of either species, in part, depending on the effects of respiration and growth of the dominant species and associated microbial communities. If the grassland soils respire more and exhibit decreased NPP in response to drought and warming, a decrease in sequestration could result. Alternatively, if the juniper encroachment increases belowground productivity, roots and associated microbial communities may exhibit higher rates of soil CO₂ efflux than grasslands. My

hypothesis is that changing the tree-grass composition of vegetation to juniper-dominated vegetation, will increase integrated soil respiration, decrease soil pH (owing to their acidic litter inputs), increase soil CEC (through increased fine root inputs), and decrease soil bulk density (through root proliferation) compared to grass-dominated systems.

CHAPTER II

METHODS

The study was conducted at the Texas Warming and Rainfall Manipulation experiment (Texas WaRM Experiment) site located on a remnant post oak savanna site (30°34'N 96°21'W) in College Station, TX. The site contains eight permanent rainout shelters (18m x 9m x 4.5m) covered with clear polypropylene plastic. The walls are open up to 1.5m to maintain microclimate conditions. The 4.5 m high ends of each shelter are protected with a fine mesh to prevent wind blown precipitation from entering the sites. Five species combinations were planted in ten 2x2m plots under each shelter and two control plots that lack shelters. For this study I used the monoculture plots of eastern red cedar (*Juniperus virginiana*) and little blue stem. Two precipitation treatments are applied. The long-term mean treatment emulates the mean precipitation regime of the previous 50 years. The altered precipitation treatment, representing climate change, lowers total rainfall for the summer period (May-September) by 40%, and redistributes that rainfall amount into the preceding spring (March-April) and following fall (October-November). The altered precipitation treatment amplifies summer drought. One half of experimental plots are warmed 24 hours a day with overhead infrared heaters (model MRM-1208L, Kalgo Electronics, Bethlehem, PA, USA) outputting 100W m⁻² of radiant heat at 1.5m in height and raising canopy temperatures by ca. 1.5 °C.

Respiration study

For my experiment, the eastern red cedar and little blue stem plot monocultures were used to provide an experimental contrast of two vegetation types in the oak savannah biome. The plots tested were four different combinations of heated and unheated plots with future precipitation and current precipitation patterns for each of the two species plots. Thus for each species, there were four replicate plots of each of four treatment combinations. In total, from all treatments and replicates, 32 individual plots were tested. In order to quantify integrated soil respiration and its relationship to environmental parameters and related soil characteristics, I measured soil CO₂ efflux, along with soil moisture, and soil surface temperature. Soil respiration was measured during the most active time of the day, as determined by initial sampling, from 10:00-16:00. Soil respiration was measured with an automated portable soil CO₂ flux device (LI-8100, LI-COR, Lincoln, NE, USA) at prepared PVC pipe inserts (20 cm diameter), which circumscribe the soil surface area over which the CO₂ released is measured. Respiration measurements were taken in three cycles with each cycle having three measurements, all over a 10-min period, totaling 9 measures per plot to calculate a mean flux rate. While soil respiration was measured, soil temperature was taken using a stainless steel 30.48 cm x 1.59 mm thermocouple (KQSS-116U-12, Omega, Stamford, CT, USA) connected to a thermometer (HH309A, Omega, Stamford, CT, USA). Soil moisture was taken twice a week during two weeks of the study with time domain reflectometry (TDR) probes (Soil Moisture Corp., Santa Barbara, CA, USA) located in each plot (0 to 20 cm depth). The first week of testing was conducted from July 6 through July 9, 2010 with

each treatment of 8 plots being selected at random from one of the eight covered shelters daily with all the experimental plots being sampled throughout the course four-day period. During week 2 of sampling (July 19, 2010 – July 22, 2010) all plots were tested each daily on each of four successive days ($n = 32$). Soil respiration measurements were not taken the two days following a rain event in order to avoid any pulse effect.

Bulk density and independent soil water content study

In order to determine the effects of species on soil bulk density and potential effects on CO₂ flux and to confirm soil water content, a separate set of measures were conducted. The TDR that was used has a margin of error $\pm 2\%$ with most soils, having an average of less than 10% volumetric water content. Thus, separate soil moisture content was taken to confirm the data collected. On July 27 and August 6, soil moisture was determined with bulk density determined on the August 6 sample. A soil sample with a volume of ca. 334 cm³ was collected with a slide hammer corer from each plot ($n = 32$) to a depth of 10 cm. The samples were collected and immediately placed into Ziploc bags and put into a cooler. After collecting all the soil samples, the total sample was weighed and recorded. Following that soils were broken up in the bag to homogenize the soil structure then a subsample (10 g) was weighed out, organic matter was picked out of the sample, and extra soil was added from the sample to bring the sample to roughly 10.0 ± 0.2 g. The subsample was then dried in an oven for 48 hr. at 102 °C. After drying, the weight of the subsample minus the tin weight was calculated to determine the percent water (Pw) of the sample. After determining the Pw, it was multiplied by the weight of the

total sample to estimate the amount of water in the total sample, assuming that the subsample was representative of the full sample. After the amount of water weight was subtracted from the sample the dry weight of the soil was divided by the size of the cylinder to determine the bulk density in g/cm^3 .

Effects of shading on soil respiration

During the initial measures and checks of the respiration study, cloud cover seemed to be creating potential changes to soil respiration readings. Consequently, I designed a one-week study on the effect of solar irradiance on soil respiration. To determine the effects of solar irradiance on the two species, one plot of the control treatments for both a grass and juniper were selected for repeated measures under sunlit and shaded conditions. A 2x2x2m cage was constructed and shade cloth with 75% shade factor was zip-tied to a pole frame. The study was conducted from August 2 – August 8, 2010. On day one of the study, the selected juniper plot had the cage placed over it and soil respiration and soil temperature were measured. Light levels (photosynthetically active radiation) were measured with a quantum sensor (see below) inside and outside the shelter throughout the course of the four-day study periods for each species. On day 1 for each species, respiration was measured without the shade cloth on it for 24 hrs. On days 2 to 4, respiration was measured under continuous 75% shade. Soil respiration was measured in the way described above, the soil temperature probe (LI-1400-101, LI-COR, Lincoln, NE, USA) was inserted 5 cm into the soil, light level was taken inside the shelter next to the LI-8100 with a quantum light sensor (Apogee QSO2849, Apogee, Logan, UT, USA)

and outside the shelter with a quantum light sensor (LI-191, LI-COR, Lincoln, NE, USA) to compare the different light levels. For each plot, respiration measurements were recorded as mean values (of 3) every 15 min for 72 hr. Soil moisture was taken twice during the study on each plot.

Soil nutrient and CEC estimates

The soils that had been collected for bulk density measurements were stored in refrigeration and then taken to the Texas A&M Soil and Crop Science Lab for nutrient analysis. Soil nutrients P, K, Ca, Mg, Na and S were extracted using the Mehlich III process (Mehlich, 1978). Soil pH was determined with a hydrogen selective rod. To estimate cation exchange capacity (CEC), the pH of each sample was used to determine the base saturation as recorded in Milford (2007). The base nutrients, as recorded in ppm, were then divided by their individual atomic weights and summed. This total was multiplied by the base saturation to estimate CEC.

Data analysis

The nine daily measures of soil respiration and temperature were averaged by day per sample plot. LI-8100 chamber temperature averages were included into data analysis to ensure the accuracy of independent measurements. Spot measures of soil moisture and bulk density were compiled with the other daily averages. Soil moisture measurements from the TDR and independent volumetric measures were not differentiated between days. While the measures were not consistent from a single plot between days when

TDR and volumetric measures were taken, the relationships among all plots on a daily basis were consistent between the two methods. The shade study was analyzed separately as an independent study. Soil respiration and temperature were taken as an average over the month along with soil moisture. Bulk density, CEC, and soil nutrients do not fluctuate greatly over such a short time, so they were assumed to stay constant over the length of the month-long study. After all data was compiled, JMP 8 (JMP 8.02, SAS Institute Inc., Cary, NC, USA) was used to determine statistical correlations between variables. Separately light data was compared to respiration, temperature, and moisture measures collected from the two plots measured in the shade study.

CHAPTER III

RESULTS

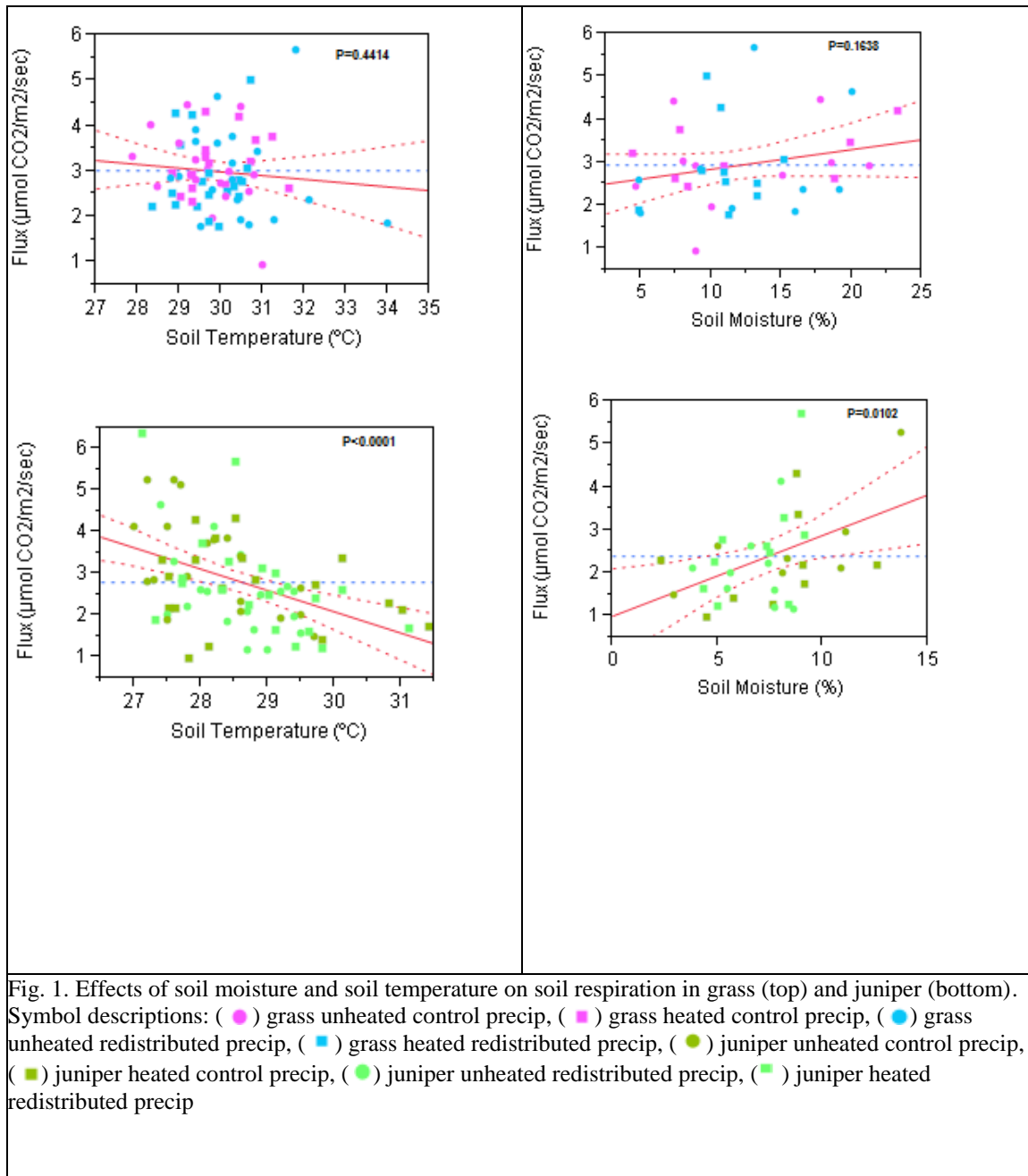
Respiration study

The results of the respiration study showed that overall soil CO₂ efflux rates did not decline in the grasses but did decline in the juniper under increased temperature (Fig. 1). Bulk density was lower in juniper species when compared to grasses (Table 1), but was unrelated to soil respiration rates (data not shown). Moisture had a limiting overall effect on soil respiration in the juniper ($r = 0.19$, $P = 0.0091$), but seemed to have a limited effect on soil respiration in the grass ($r = 0.05$, $P = 0.1638$) (Fig. 1). Increasing soil temperature resulting in declining rates of soil respiration in juniper plots ($r = 0.20$, $P < 0.0001$), while not greatly effecting a change in soil respiration in grass plots ($r = 0.01$, $P = 0.4414$) (Fig. 1).

Table 1: Average soil respiration (Col. 1), average soil moisture (Col. 2), average soil temperature (Col. 3), and average soil bulk density (Col. 4) on whole species and under the individual treatments of grass (G) and juniper (J) and as a whole. Individual symbols include (●) (G1) grass unheated control precip, (■) (G2) grass heated control precip, (●) (G3) grass unheated redistributed precip, (■) (G4) grass heated redistributed precip, (●) (J1) juniper unheated control precip, (■) (J2) juniper heated control precip, (●) (J3) juniper unheated redistributed precip, (■) (J4) juniper heated redistributed precip.

Week	Treatment	Avg_Flux ($\mu\text{mol CO}_2/\text{m}^2/\text{sec}$)	Avg_Moisture (%)	Avg_Temp ($^{\circ}\text{C}$)	Avg_b/d (g/cm^3)
1/2	G	2.98	12.02	29.94	1.53
1	● G1	2.99	8.45	29.45	1.54
	■ G2	2.57	9.50	29.20	1.51
	● G3	2.53	16.30	30.93	1.55
	■ G4	2.51	11.25	29.65	1.55
2	● G1	2.93	12.96	29.76	1.53
	■ G2	3.39	13.49	30.12	1.50
	● G3	3.08	11.84	30.31	1.54
	■ G4	2.97	10.76	29.70	1.54
1/2	J	2.78	7.36	28.58	1.47
1	● J1	2.93	8.05	28.30	1.42
	■ J2	2.25	8.30	28.55	1.40
	● J3	2.18	6.05	28.43	1.53
	■ J4	2.58	7.75	28.25	1.53
2	● J1	3.29	8.78	28.13	1.42
	■ J2	2.82	7.36	28.85	1.40
	● J3	2.50	6.98	28.59	1.54
	■ J4	2.83	6.60	28.97	1.54

Although grass did not respond to the climate warming treatment juniper responded with declining respiration, and the control precipitation treatment of both grass and juniper decreased respiration in response to warming treatments (grass, $r = 0.19$, $P = 0.063$; juniper, $r = 0.36$, $P = 0.006$) (data not shown). The juniper control precipitation and temperature treatment did respond with higher overall flux rates when compared to grass (Fig. 2), but juniper also decreased respiration more steeply in response to increased soil temperature. Respiration rates were generally lower in the juniper plots, with average flux rates at least $1 \mu\text{mol CO}_2/\text{m}^2/\text{sec}$ lower compared to grass plots of similar treatments (Fig. 2).



Although the control precipitation, unheated grass plots, responded negatively to soil surface temperature with a positive correlation, all other grass plots had no correlation between increased temperature and flux rates to any significance which lead to the

overall lack of a statistically significant relationship between soil respiration and temperature in grass (Fig. 1). Increased soil temperature had a significant effect on eastern red cedar with average respiration rates reaching nearly $1.5 \mu\text{mol CO}_2/\text{m}^2/\text{sec}$ at 31°C ($r = 0.20$, $P < 0.0001$) (Fig. 1). Increased soil water content was correlated with increased respiration in both species, with grass respiration only increasing slightly in the grass ($r = 0.05$, $P = 0.1638$) and juniper responding with a more positive slope ($r = 0.19$, $P = 0.0091$) (Fig. 1). The effects of declining soil moisture during summer drought did not appear to limit the grass respiration rates, which averaged $3.0 \mu\text{mol CO}_2/\text{m}^2/\text{sec}$ at 12% soil moisture, while juniper reached an average flux of $2.8 \mu\text{mol CO}_2/\text{m}^2/\text{sec}$ at roughly 7% soil moisture (Table 1).

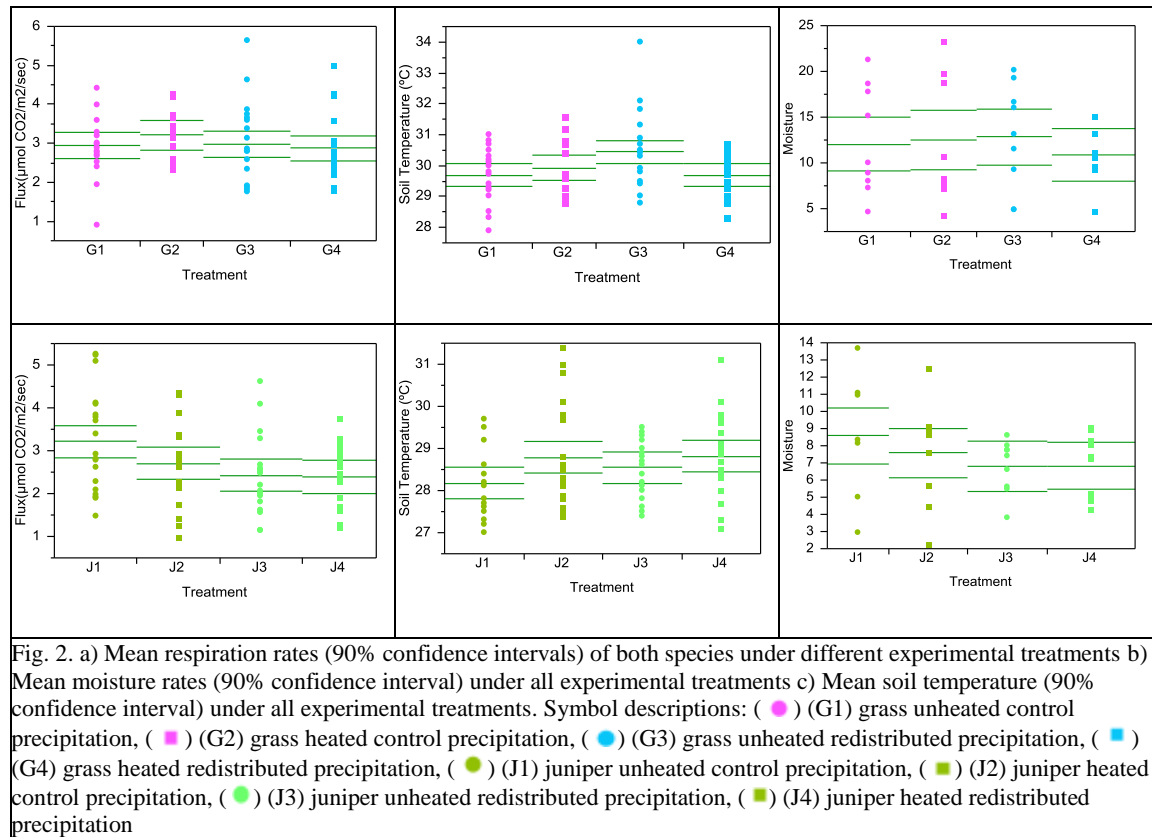


Fig. 2. a) Mean respiration rates (90% confidence intervals) of both species under different experimental treatments b) Mean moisture rates (90% confidence interval) under all experimental treatments c) Mean soil temperature (90% confidence interval) under all experimental treatments. Symbol descriptions: (●) (G1) grass unheated control precipitation, (■) (G2) grass heated control precipitation, (●) (G3) grass unheated redistributed precipitation, (■) (G4) grass heated redistributed precipitation, (●) (J1) juniper unheated control precipitation, (■) (J2) juniper heated control precipitation, (●) (J3) juniper unheated redistributed precipitation, (■) (J4) juniper heated redistributed precipitation

The effects of the different treatments did not produce large differences between the grass and juniper treatments (Fig. 2a). When comparing the average flux across all treatment combinations juniper has slightly lower respiration rates than similar grass treatments but it was not significant at the 90% confidence level (Fig. 2a). Soil temperature rates are lower overall in juniper plots versus the corresponding grass plots and heated plots are typically warmer than unheated plots in both species, with the exception of heated and unheated under the redistributed precipitation treatment in grass (G3/G4) (Fig. 2b). Average moisture was generally lower in juniper plots than in the

comparable grass treatments, but moisture rates were not significantly different between the G1/J1 and G4/J4 treatments (Fig. 2c).

Bulk density of soils was lower in juniper than grass plots, but was unaffected by warming and precipitation treatments (Fig. 3c). CEC and pH might be altered by changing species composition, but did not differ between species or among treatments, juniper soil pH averaged 5.86 compared to 5.79 for grass plots (Fig. 3a).

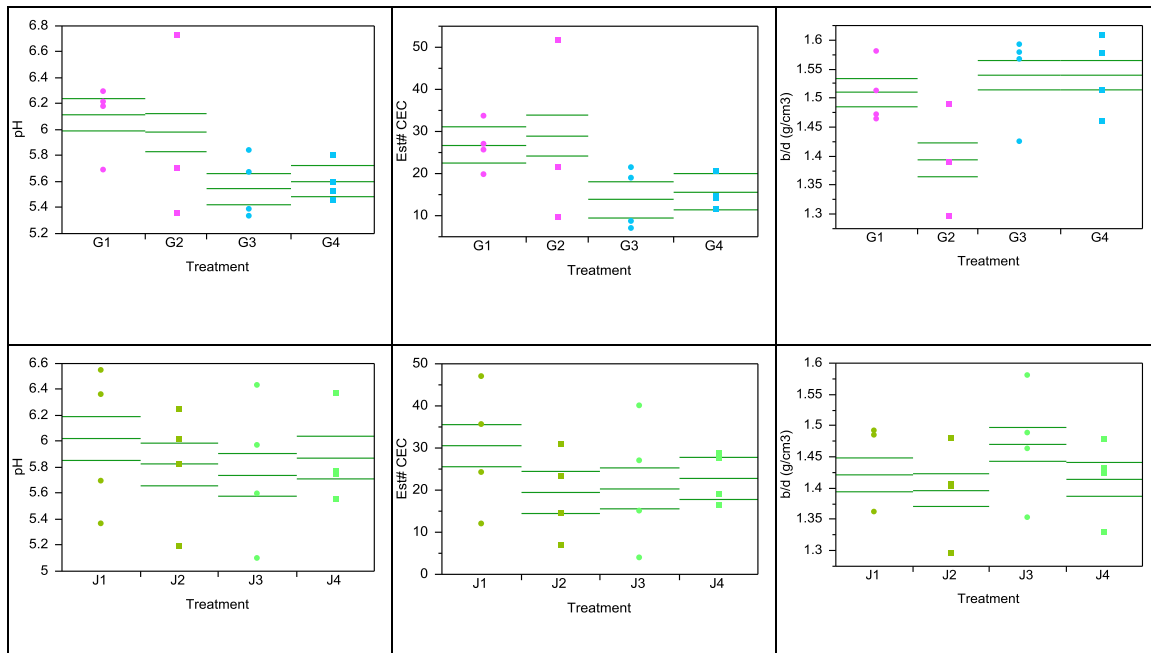
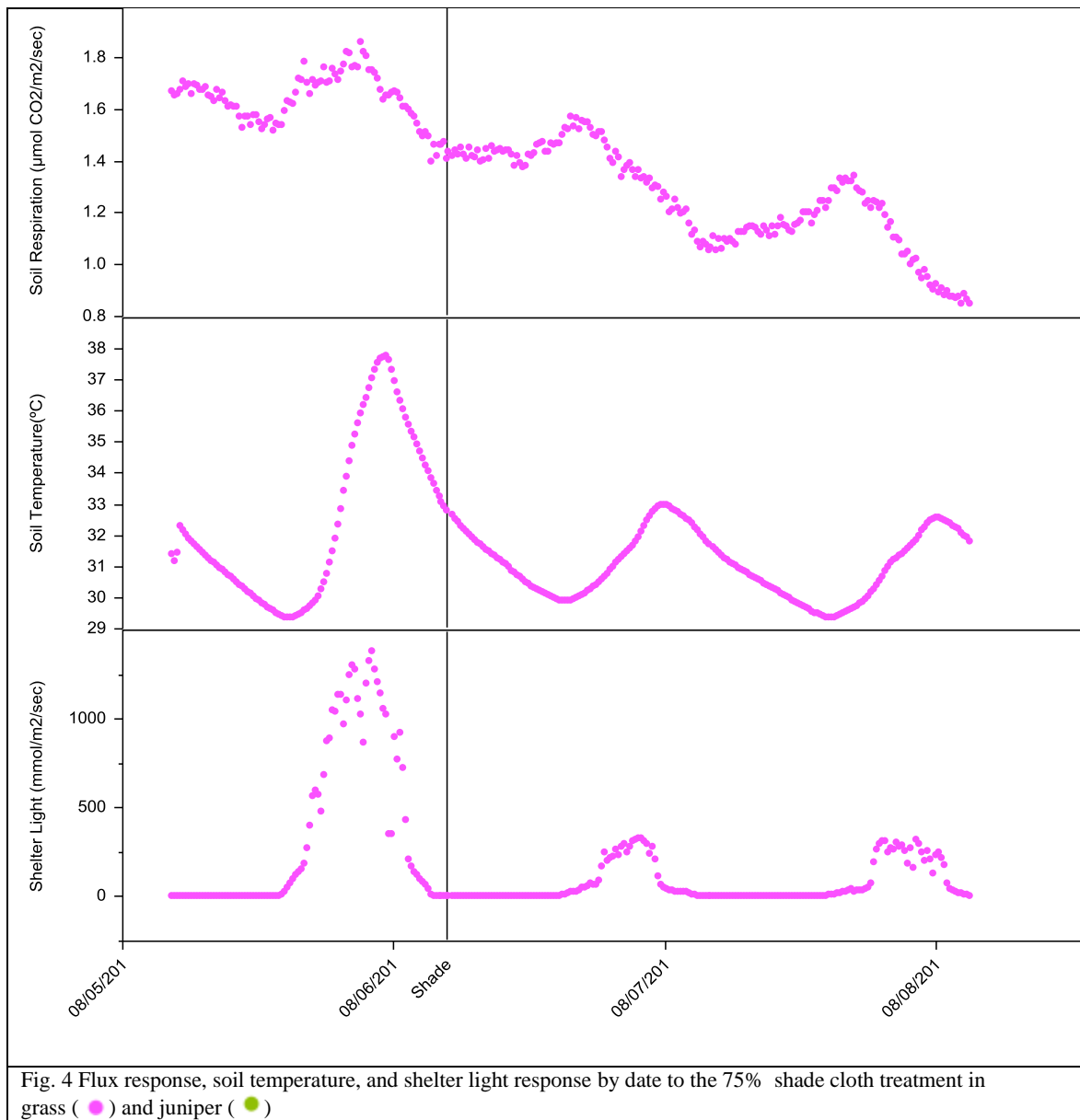
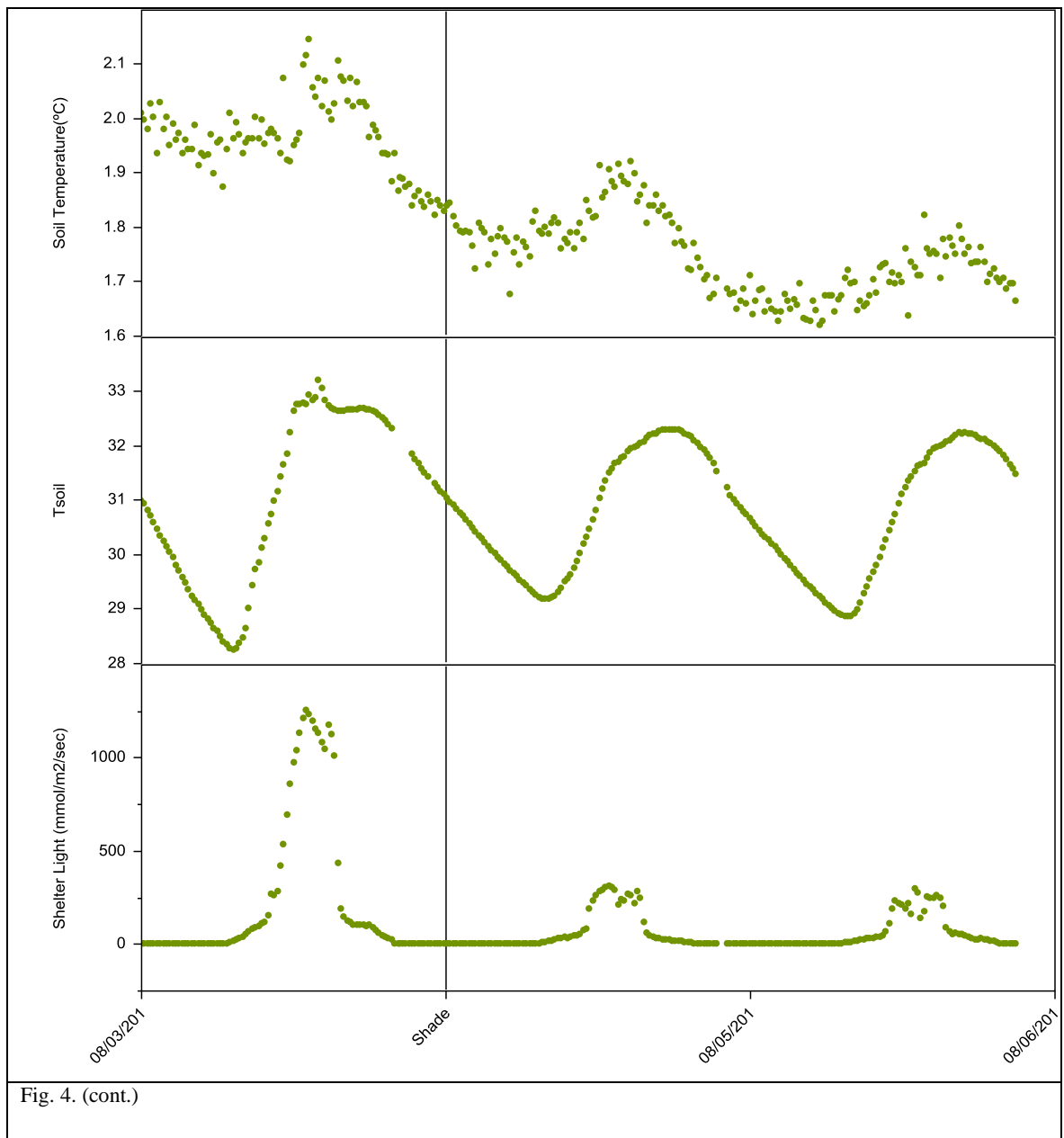


Fig. 3. a) Mean pH (90% confidence intervals) of both species under different experimental treatments b) Mean estimated CEC rates (90% confidence interval) under all experimental treatments c) Mean bulk density (90% confidence interval) under all experimental treatments. Symbol descriptions: (●) (G1) grass unheated control precipitation, (■) (G2) grass heated control precipitation, (●) (G3) grass unheated redistributed precipitation, (■) (G4) grass heated redistributed precipitation, (●) (J1) juniper unheated control precipitation, (■) (J2) juniper heated control precipitation, (●) (J3) juniper unheated redistributed precipitation, (■) (J4) juniper heated redistributed precipitation

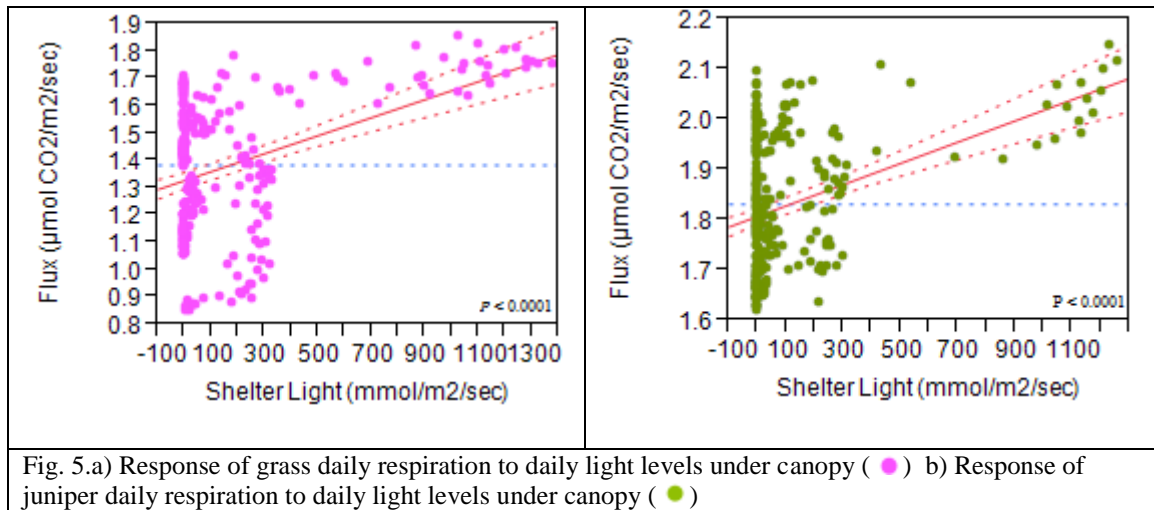
Light study

The effect of shade on soil respiration was manifested in progressive declines in rates over the course of the 2-day period of 75% shade compared to initial rates measured in full sunlight. Each day exhibited a diurnal pattern (Fig. 4). Juniper had higher soil CO₂ efflux rates than the grass plot over the full length of the study, while the grass respiration declined below 1 $\mu\text{mol CO}_2/\text{m}^2/\text{sec}$ by the fourth day of shade compared to 2 $\mu\text{mol CO}_2/\text{m}^2/\text{sec}$ under unshaded conditions at the beginning of the study (Fig. 4).





Temperature did not change greatly across treatments by date, but respiration still declined (Fig. 5), suggesting a strong correlation of soil respiration to light levels.



Each species showed a significant correlation of soil respiration (Fig. 5) to solar irradiance on a daily basis with marked declines in rates with each successive day of shading (grass, $r = 0.18$, $P < 0.0001$; juniper, $r = 0.17$, $P < 0.0001$)(Fig. 5).

CHAPTER IV

DISCUSSION AND CONCLUSION

The effects of the different treatments did not elevate the soil respiration under juniper plots when compared to grass plots, contrary to my initial, hypothesized prediction. Although woody plants typically have more roots and more microbial life forms associated with them (Archer *et al.*, 2000), surprisingly, summertime soil CO₂ efflux rates did not differ between grass and juniper. Species differences in soil respiration may, in part, be influenced by soil water content. The grasses had generally higher soil moisture (>10%) compared to the lower soil moisture (<10%) of juniper, which exhibited large declines in rates at low soil water contents. Without separate soil microbial respiration measures, the actual effects of soil temperature and moisture cannot be directly associated to plant respiration. However, in separate studies at this site, microbial biomass was observed to be greater in juniper plots (unpublished data). With cooler soil temperatures and potentially more soil carbon available under juniper, the comparable respiration rates could result from a limited autotrophic respiration component under juniper compared to the grass. In a study of above ground photosynthesis at the same site, photosynthesis rates were also found to be higher under grass treatments than juniper treatments, particularly following intermittent rainfall pulses during summer drought, which was linked to greater water use efficiency (WUE) in C₄ grasses (Volder *et al.*, 2010). The lower level of soil moisture associated with juniper is caused by a number of possibilities including increased canopy interception and evaporation or increased water use by the larger juniper plants. In either case, the

lowered soil moisture during summer conditions would limit the amount of available water in potential understory plants and soil microbes. On the other hand, lower soil moisture could also create more carbon loss through volatilization of soil carbon (Scott *et al.*, 2009) with lower activation energies.

The lower soil temperature and associated declining CO₂ flux rates as soil temperature rise under juniper is difficult to attribute to direct effects of temperature alone. Soil temperature would be expected to be lower under canopy of a 5-year-old juniper when compared to a bunchgrass. Nonetheless, the observed declines of respiration as soil temperature increased only 2-3 °C can perhaps best be explained by concurrent reductions in soil moisture, because respiration was likely already limited by moisture such that increases in soil temperature only heightened the effects. Although the opposite effect of increasing temperatures in limiting soil moisture is also possible, the effects of comparably high temperatures did not produce a limiting effect on soil moisture in grass. Bulk density did decline under the juniper treatment, but the greater pore space associated with reduced bulk density appeared unrelated to overall flux as predicted. With increased bulk density, grass roots would have less area for soil air and water and perhaps a net limiting effect on respiration of both heterotrophic and autotrophic respiration. Likewise, with the increased surface area of low bulk density soil, soil air and water should have had more binding sites. The cation exchange capacity (CEC) of the different treatments did not show any statistical significance with an average juniper plots CEC of 23.3 and grass plot average of 20.5. Because both CECs are so similar they

have little effect on available nutrients, which could be associated with the activity and soil respiration.

The effects of shading on the two species were the opposite of my hypothesis. By reducing light, respiration declined through time in both species, but soil CO₂ efflux rates in grass declined more steeply than juniper. This finding suggests a closer coupling of soil CO₂ efflux from roots and associated microbial communities to recently fixed photosynthate in grass than juniper. Despite the shade treatment, soil temperature was similar between the two plots suggesting that species differences in soil respiration were linked to light availability and strongly related to photosynthesis. The low rates of soil CO₂ efflux after 4 days of shading, may be approaching flux values dominated by autotrophic respiration, which for the grasses fell below 1 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$, and was lower than that of juniper 1.75 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$, although differences in carbon pools and lag times remain to be ruled out. Because grass responds so with such low rates of respiration under shaded conditions, the effects of juniper could have a two-part effect on reduction of grasses. It has already been suggested that juniper alters the soil environment so that grasses are unable to survive the biophysical alterations (Boutton, 2011), but also by blocking out sunlight from the light-dependent little blue stem, juniper reducing productivity. Unlike West Texas, the post oak savannah has other understory species which were not tested in this study, which have the capability to replace outcompeted bunchgrasses. However, in more arid portions of Texas the effects of

juniper encroachment could potentially alter the abundance and distribution of light-demanding grasses and forbs.

Woody encroached lands often exhibit increased soil nutrients and decreased soil bulk density than many grassland environments, but have also turned traditional rangelands into ungrazable properties. If an intercropping strategy would be favored for juniper management, more research would be needed to determine the drought tolerant and shade tolerant species that may exist under juniper encroached lands to rehabilitate former rangelands.

The comparable respiration rates of the juniper treatment when compared to grass suggest that summertime soil CO₂ efflux (and net loss to the atmosphere) may be more comparable in juniper-dominated and grass-dominated ecosystems than predicted based on their observed differences in biomass and carbon sequestration. Because grass is most active in the summer months, the long term integrated effects of annual soil respiration in evergreen juniper might exceed that of the grass, although this would need to be balance against an extended growing season that might increase productivity and create greater carbon sequestration over multiple years. Separation of autotrophic and heterotrophic respiration below ground activity could provide needed insight into the mechanisms underlying the observed patterns of respiration, especially those of the shade study.

Current practices of mechanical and herbicide treatments to slow woody encroachment have limited but not stopped woody encroachment. With the absence of large scale fire in the populated regions of Central and West Texas, juniper encroachment will continue and more research is needed to determine the effects of encroachment on this very heterogeneous landscape and its carbon cycling and linkages to land management choices and the livelihood of its residents.

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APPENDIX

Table 2: Soil Data Report including b/d

Species	Precip	Heat	Shelter	Label	pH	E.C. Cond (umhos/cm)	NO3-N (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	S (ppm)	Na (ppm)	BaseSat	Est.CEC	B/D (g/cm ³)
G	C	N		1 g10	6.29	44	3.06	5.3	29.73	638.25	69.95	11.02	134.1	0.76	33.6796	1.5128
G	C	N		1 g35	6.18	54	10.14	7.91	55.36	407.28	72.55	10.82	151.01	0.74	25.4258	1.472
G	C	N		3 g55	6.21	38	3.22	17.01	80.99	455.51	72.4	11.74	127.56	0.74	26.9205	1.5795
G	C	N		8 g88	5.69	45	8.57	7.24	28.22	407.33	69.18	15.53	187.37	0.56	19.5907	1.4639
G	C	Y		9 g4	6.74	41	3.46	7.74	95.54	939.16	81.63	8.95	130.56	0.84	51.933	1.2974
G	C	Y		2 g52	5.71	60	4.22	6.99	49.78	466.72	97.1	11.38	132.64	0.56	21.526	1.49
G	C	Y		7 g87	5.36	32	3.95	7.47	49.98	345.38	66.83	14.56	143.85	0.32	9.7093	1.3915
G	R	N		4 g15	5.67	53	5.98	34.57	77.25	518.97	64.76	11.79	116.47	0.56	21.4705	1.5779
G	R	N		4 g30	5.33	56	8.45	6.9	36.24	303.04	45.39	11.39	117.81	0.28	6.9895	1.4256
G	R	N		8 g68	5.39	26	3.74	5.62	56.01	309.29	51.44	8.78	136.03	0.32	8.661	1.5928
G	R	N		3 g79	5.84	33	5.15	8.44	40.65	428.36	71.12	10.75	127.45	0.61	20.6801	1.5663
G	R	Y		6 g20	5.47	83	8.48	15.48	58.9	452.29	63.41	8.74	119.72	0.42	14.522	1.514
G	R	Y		9 g23	5.53	68	7.21	8.04	59.57	421.1	83.48	9.66	128.95	0.42	14.7449	1.6096
G	R	Y		7 g66	5.81	29	4.1	7.71	31.17	414.44	59.33	15.49	176.4	0.61	20.81	1.462
G	R	Y		2 g72	5.6	39	4.75	8.74	36.83	266.96	45.97	9.83	123.92	0.5	11.7437	1.5784
J	C	N		4 j3	6.36	44	3.06	7.01	59.06	641.64	66.24	11.28	150.94	0.78	35.6001	1.3613
J	C	N		6 j36	6.55	118	2.87	10.87	116.98	676.82	136.73	13.83	206.8	0.82	46.864	1.3617
J	C	N		2 j57	5.69	42	2.61	33.02	46.94	577.71	84.62	11.63	135.06	0.56	24.0704	1.4911
J	C	N		8 j84	5.36	49	2.54	7.7	36.57	403.01	95.79	15.77	186.71	0.32	11.8928	1.4846
J	C	Y		1 j33	6.02	64	1.77	9.64	52.8	374.28	74.66	9.48	184.82	0.69	23.6611	1.2968
J	C	Y		9 j5	6.25	42	2.32	11.35	69.03	547.84	63.95	9.32	150.08	0.76	31.1391	1.4801
J	C	Y		3 j58	5.2	57	2.08	11.14	56.28	291.29	62.02	12.8	175.81	0.25	7.1959	1.406
J	C	Y		7 j81	5.83	26	2.55	7.64	28.27	294.79	54.73	10.57	148.67	0.56	14.8237	1.4043
J	R	N		4 j17	5.97	35	2.45	31.62	64.2	512.65	63.85	11.16	147.87	0.69	26.901	1.4632
J	R	N		6 j21	5.6	40	2.12	6.91	30.6	352.56	51.7	12.96	162.79	0.5	14.8894	1.5806
J	R	N		7 j61	5.1	31	2.69	7.86	29.08	123.31	46.33	9.48	141.61	0.23	3.8047	1.3518
J	R	N		2 j77	6.43	40	2.45	9.16	47.05	741.41	72.05	9.83	160.8	0.78	39.9688	1.4879
J	R	Y		1 j14	5.56	50	2.73	16.73	66.57	421.92	64.47	11.05	113.54	0.5	16.5345	1.4339
J	R	Y		9 j28	5.76	49	2.31	8.78	39.75	337.44	60.18	11.9	198.69	0.61	19.2268	1.3318
J	R	Y		8 j70	6.38	44	2.79	12.92	64.02	464.06	72.77	11.64	143.78	0.78	28.9527	1.4245
J	R	Y		3 j80	5.77	60	2.41	8.63	43.28	586.23	129.02	15.76	195.21	0.56	27.7942	1.4796
J Avg.					5.86	49	2.48	12.56	53.15	459.18	74.94	11.78	162.7	0.59	23.3324	1.4275
G Avg.					5.79	47	5.63	10.34	52.41	451.6	67.64	11.36	136.92	0.55	20.5604	1.5022

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