EFFECT OF WARMING AND PRECIPITATION DISTRIBUTION ON SOIL RESPIRATION AND MYCORRHIZAL ABUNDANCE IN POST OAK SAVANNAH

A Dissertation

by

ANDREW DAVID CARTMILL

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2011

Major Subject: Horticulture

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Approved by:

Chair of Committee,	Astrid Volder
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ABSTRACT

Effect of Warming and Precipitation Distribution on Soil Respiration and Mycorrhizal Abundance in Post Oak Savannah. (May 2011)
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Projected climate change may alter soil carbon dioxide (CO_2) efflux from terrestrial ecosystems; yet disentangling effects of plant species from climate drivers remains a key challenge. We explored the effects of the dominant plant species, warming, and precipitation distribution on soil CO_2 efflux, its underlying components, and mycorrhizal abundance in southern post oak savannah. Post oak savannah in the south-central US are dominated by three contrasting plant functional types: *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) a C_4 grass, *Quercus stellata* Wangenh. (post oak) a C_3 deciduous tree, and *Juniperus virginiana* L. (eastern redcedar) a C_3 evergreen tree. Monocultures and tree-grass plots were warmed using infrared heaters and precipitation events were manipulated to intensify summer drought and augment cool season precipitation. Soil CO_2 efflux, the root, bacterial and hyphal components of CO_2 efflux, and mycorrhizal abundance were measured. Soil CO_2 efflux varied with seasonal changes in soil volumetric water content and temperature, with higher soil CO_2 efflux rates in the spring and lower rates in both the cooler winter season and at the end of the dry summer period. There was no relationship between root length density or root mass density and soil CO_2 efflux during the short term precipitation distribution campaigns. Partitioning of root, fungal, and bacterial component contribution to soil CO_2 efflux indicated a substantial contribution of bacterial respiration to soil CO_2 efflux within this system. There was no relationship between microbial biomass (microbial dissolved organic carbon) and soil CO_2 efflux, or root length (or mass) density and microbial biomass. This suggests that species and climatic effects on root and microbial activity drive soil CO_2 efflux. As plant species within this system differed in their association with mycorrhizal fungi and had a strong effect on the individual components of soil CO_2 efflux, we conclude that shifts in vegetation cover and growth and the response of vegetation to long term warming and potential future extreme precipitation events (e.g., large

preciptation events, prolonged drought) will be major drivers of changes in soil carbon (C) dynamics and associated soil CO_2 efflux.

DEDICATION

This dissertation is dedicated to my parents, family, and friends for their support and encouragement.

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CHAPTER I
INTRODUCTION AND LITERATURE REVIEW

Introduction

Natural and human-induced changes to the global environment are complex, multi-factorial, and of increasing economic, social, and ecological significance. Increasing concentrations of greenhouse gases are projected to elevate global surface temperatures (~1.4 to ~5.8 °C) and potentially increase the intensity and variability of precipitation and drought events (Solomon *et al.*, 2007; Bates *et al.*, 2008). Advanced climate models project that, for the South Western United States, an intensification of summer drought periods coupled with intensification of individual precipitation events in spring and autumn is more probable than a substantial change in mean annual precipitation (Manabe & Wetherald, 1986; Easterling *et al.*, 2000). It remains unclear what the relative effects of climate warming and potential precipitation redistribution, both independently and in combination, will have on ecosystem processes. Furthermore, current research into the response of terrestrial ecosystems to climate change frequently focuses on the response of the aboveground components with little consideration on the response of the belowground component. The belowground component, the soil and related flora and fauna, has numerous functions, and is an integral part of terrestrial ecosystems (Wardle *et al.*, 2004). Thus, there is a need to quantify what the effect of projected climate change will be on terrestrial ecosystems, both above- and belowground.

OAK SAVANNAHS

Savannahs are geographically extensive and socioeconomically important ecosystems and comprise over one eighth of the Earth's surface, occupying some 50 million ha in North America alone (McPherson, 1997; Scholes & Archer, 1997). Savannahs form a tension zone/ecotone between grasslands and forest ecosystems and are among the most striking ecosystems where contrasting plant life forms co-dominate (Scholes & Archer, 1997). The co-occurrence of these contrasting plant life forms creates a complex web of both intra- and inter-specific interactions (Scholes & Archer, 1997), which have been linked to climate (precipitation amount and seasonality), soils (depth and fertility), herbivory (balance between grazing and browsing) and fire (McPherson, 1997; Scholes & Archer, 1997).

This dissertation follows the format and style of *New Phytologist*.

Oak savannahs are one of the most endangered ecosystems of North America, with less than 0.02% of its original area remaining (Nuzzo, 1986; Dickie *et al.*, 2009). Texas post-oak savannahs are dominated by three species, *Schizachyrium scoparium* (Michx.) Nash. (little bluestem, a C_4 grass), *Juniperus virginiana* L. (eastern redcedar, a C_3 evergreen tree), and *Quercus stellata* Wangenh. (post oak, a C_3 deciduous tree). Post oak savannah has seen an increase in the abundance of woody species and an increase in the density of *J. virginiana* in particular (McPherson, 1997; Briggs *et al.*, 2002). Increasing abundance and/or encroachment of woody plants into grasslands and savannahs as a result of urbanization and agronomic practices, coupled with fire suppression has the potential to alter ecosystem structure and function, nutrient cycling and availability, primary productivity, resource competition, and species composition and diversity (Scholes & Archer, 1997; Van Auken, 2000). Through its effects on all these ecosystem processes, woody plant encroachment may potentially alter the spatial distribution and productivity of the herbaceous species.

Woody plant (*J. virginiana*) encroachment into oak savannah may suppress both *Q. stellata* and *S. scoparium* growth and regeneration in several ways, their relatively large trunks (with age), canopy architecture, dense foliage, thick litter layer, and extensive root system, may physically overwhelm and competitively exclude other vegetation by limiting light, water, nutrients, and physical space (Rykiel & Cook, 1986; Belsky, 1994; Scholes & Archer, 1997; Norris *et al.*, 2001b). In addition, woody plants may potentially modify the microclimate beneath their canopies [soil volumetric water content (VWC) and temperature] through shading/reduced soil temperature, canopy interception, stemflow, and evapo-transpiration rates (Vetaas, 1992; Belsky, 1994; Scholes & Archer, 1997; Hibbard *et al.*, 2001). The resulting changes in soil water availability may lead to enhanced drought conditions for the herbaceous vegetation growing below a woody plant canopy, particularly when this canopy is very dense and intercepts large amounts of water. Furthermore, the effect of woody encroachment on herbaceous vegetation may be negative, neutral, and/or even positive, depending on woody plant age, size, density, and time (Scholes & Archer, 1997). For example, when woody plants are small, there may be few changes in microclimate, but if the woody plants are exhibiting hydraulic lift (lifting of water from lower soil layers to upper drier soil layers by roots) more water may become available to the surrounding herbaceous vegetation. As woody plants increase in size, the microclimate will be progressively more altered; increasing shade below the woody plant, increasing competition

for physical space, increasing canopy precipitation interception, and potentially increasing competition for belowground resources.

SOIL CO_2 EFFLUX

Terrestrial ecosystems play a critical role in the global carbon (C) cycle. On a global basis, the pool of soil C is vast [~1500 gigatons of C (GtC) versus ~500 GtC in vegetation] and soil C flux is an order of magnitude greater than anthropogenic C emission (~68 GtC $year^{-1}$ versus 5.4 GtC $year^{-1}$) (Raich & Schlesinger, 1992; Raich & Potter, 1995). Carbon dioxide (CO_2) release from soils (soil respiration) exceeds all other terrestrial to atmospheric C exchanges except for photosynthesis (Raich & Schlesinger, 1992). Due to the extent of this soil-to-atmosphere CO_2 flux, and the large pool of potentially mineralizable C in the soil, any increase in soil CO_2 emissions in response to climate change has the potential to exacerbate increasing atmospheric CO_2 levels and potentially provide a positive feedback to global warming and enhance further release of CO_2 from terrestrial C pools (Raich & Schlesinger, 1992; Rustad *et al.*, 2000; Schlesinger & Andrews, 2000).

Belowground processes strongly affect terrestrial C cycling. Plants send an estimated 35-80% of the C fixed in photosynthesis belowground for root production, associations with mycorrhizae, and root exudation (Raich & Tufekcioglu, 2000). Plants also lose approximately 10% of annually fixed photosynthates as leaf litter (Raich & Tufekcioglu, 2000). The C stored in the litter and the labile and recalcitrant soil C pool is a large fraction of the C stored in forests (30-90%) (Dixon, 1994; Raich & Tufekcioglu, 2000) and an even greater fraction of the C stored in grasslands (>90%) (Raich & Tufekcioglu, 2000), because grasslands do not have the aboveground standing woody C pool that forests have.

Soil CO_2 efflux rates are dependent on soil type, soil temperature and soil VWC (Carlyle & Than, 1988; Raich & Tufekcioglu, 2000). Seasonal changes in climate affect soil CO_2 efflux rates as the fractions of C supply to the roots vary seasonally, as do soil temperature and soil water availability (Raich & Potter, 1995). Other factors that influence soil CO_2 efflux rates include C source availability and/or density of roots, population of soil organisms, soil chemical and biological properties, and soil drainage (Rai & Srivastava, 1981; Boudot *et al.*, 1986; Freeman *et al.*, 1993; Benasher *et al.*, 1994).

Soil CO_2 efflux is determined by two major components, autotrophic (mostly root related) respiration and heterotrophic respiration that is associated with soil microbes. Rates of

soil respiration are associated with the size of both the root and microbial pool and the activity of each pool. Young roots are generally the ones with the highest respiration rates (Volder *et al.*, 2005) and the root component of soil respiration is suggested to be largely in sync with periods of high root production, with generally a peak production rate of roots during early spring (e.g, Eissenstat & Caldwell, 1988; Zogg *et al.*, 1996; Jarvis *et al.*, 1997; Fitter *et al.*, 1999). The size of the microbial pool is largely dependent on the availability of substrates, while activity of both microbes and roots is strongly affected by temperature, provided adequate moisture is available.

Temperature directly affects respiration processes as the respiratory system involves numerous temperature-dependent enzymes that drive processes such as glycolysis, the TCA cycle, and the electron transport chain (Ryan, 1991). Studies have shown that respiration generally increases exponentially with increasing temperatures and reaches a maximum at approximately 45 to 50°C before declining (Nobel & Palta, 1989). Soil temperature may also indirectly affect root respiration due to its effect on root growth, with root growth increasing with increasing temperatures until an optimal temperature is reached, which varies depending on plant species (McMichael & Burke, 1998). Autotrophic and heterotrophic respiration may have a reduced response to higher temperature as a result of acclimation which may result in relatively reduced C loss at sustained higher temperatures (Tjoelker *et al.*, 1999; Atkin & Tjoelker, 2003).

Soil VWC is another factor that influences soil CO_2 efflux rates. Precipitation events and soil water content also affect soil CO_2 efflux directly. Small precipitation events on dry soils may result in relatively sudden increases in soil CO_2 efflux, as the result of displacement of O_2 and CO_2 in soil pore spaces (Liu *et al.*, 2002; Xu *et al.*, 2004). Therefore, under drought conditions, soil CO_2 efflux rates may increase rapidly for a short period after relatively small precipitation events that do not saturate the soil. However, following relatively large soil saturating precipitation events, the resulting water saturated soil may inhibit CO_2 diffusion through the soil and decrease soil CO_2 efflux (Liu *et al.*, 2002; Hirano *et al.*, 2003). In general, rates of soil respiration are low in dry conditions and then reach a maximum rate under intermediate soil VWC levels (near field capacity), and then decrease at high soil VWC due to anaerobic conditions decreasing aerobic microbial activity (Davidson *et al.*, 2000). Anaerobic soil conditions also slow down root growth and root respiration (Drew, 1997). Soil VWC from precipitation can lower diffusion rates and decrease CO_2 efflux (Hirano *et al.*, 2003). Most soil fungi are active at a soil water potential as low as -1.5 MPa, while most bacteria are inactive below -1.0 to -1.5 MPa (Swift *et al.*, 1979).

Soil temperature, moisture, and oxygen content all interact to affect soil CO_2 efflux. In wet soils, an increase in soil temperature may reduce soil VWC content which in turn may increase soil oxygen diffusion which could stimulate soil CO_2 efflux, whereas in dry soils, increasing temperatures and resulting decreases in soil water content, may negatively impact soil respiration rates (Liu *et al.*, 2002; Hirano *et al.*, 2003; Xu *et al.*, 2004).

Temperature and light influence seasonal effects on belowground processes which varies among plant species and developmental stages (Edwards *et al.*, 2004). Increasing spring temperatures and longer days result in increased shoot growth, photosynthetic activity, and also soil CO_2 efflux during the first flush of growth in deciduous trees (Yuste *et al.*, 2004). This seasonal effect is greater on root growth in deciduous trees when compared to coniferous trees (Coleman *et al.*, 2000). It is unclear whether increased spring soil CO_2 efflux rates are a function of higher soil temperatures or increasing light availability since the two are generally confounded. Edwards *et al*. (2004) demonstrated that any positive response to temperature was short-lived and that over a full growing season, soil warming led to a reduction in root number and mass due to increased root death during autumn and winter in temperate grasslands. They also reported that root respiration was insensitive to soil temperature over much of the year.

Soil CO_2 efflux also varies with different biome types (Raich & Tufekcioglu, 2000), mostly along broad patterns of vegetation cover and climatic conditions. Although rates of soil CO_2 efflux have been shown to differ within biomes as species composition and local climatic conditions were different (Hibbard *et al.*, 2005), these differences have not been as large as expected. Raich & Tufekcioglu (2000) compiled results from different studies performed under comparable conditions (site, methodology, topography) and reported that grasslands had 20% greater soil CO_2 efflux rates compared to forests, and that broadleaf forests had 10% greater soil respiration rates than coniferous forests. Given the structural, physiological, and phylogenetic differences between grasses, angiosperms, and gymnosperms, the relatively small differences in CO_2 efflux observed, suggest that soil CO_2 efflux rates are affected more by climatic and inherent soil conditions with plant species causing a secondary effect (Raich & Tufekcioglu, 2000). For example, Smith and Johnson (2004) reported a 38% lower soil CO_2 efflux from *J. virginana*-dominated sites when compared to adjacent grassland sites. They suggested that in this study soil temperatures, rather than soil VWC, explained most of the variability in soil CO_2 efflux, as soil water content tended to be only marginally/slightly higher in the grassland.

Observed differences in soil CO_2 efflux rates between plant communities growing on the same soil type and within the same climatic conditions are likely due to differences in root production, specific root respiration and standing root length, as well as potential species effects on microclimatic changes, and changes in microbial biomass and composition. Some species are known to exude allelopathic compounds which may alter rates of microbial respiration (Kraus *et al.*, 2003). *Juniperus virginiana* (Stripe & Bragg, . 1989) and *Q. stellata* (McPherson & Thompson, 1972), may release alellopathic compounds through leaching and volatilization of compounds from foliage by precipitation, breakdown/decomposition of litter, and/or through exudation from roots, which may suppress the diversity and activity of other species, and/or reduce fungal and microbial diversity and activity (Inderjit & Weiner, 2001), potentially affecting soil CO_2 efflux rates. *Juniperus virginiana* leaves are also high in Ca (Read & Walker, 1950; Millar, . 1974) and litter accumulation beneath *J. virginiana* trees has been reported to raise soil Ca concentration and pH (Coile, 1933; Spurr, 1940; Read & Walker, 1950; Sauer *et al.*, 2007). Increasing soil Ca concentration and associated increase in pH may potentially decrease root growth, and/or decrease the availability and uptake of nutrients to other plants (Marschner, 1995). Furthermore, increasing pH and Ca in the soil profile may potentially increase earthworm activity (Springett & Syers, 1984; Reich *et al.*, 2005), which in turn may potentially decrease surface runoff, and increase infiltration, structural porosity, and storage of water in pores (increase soil VWC), and thus potentially enhance fungal and microbial activity, root growth, incorporation (decomposition and humification) and storage of organic matter in the soil profile (Lavelle *et al.*, 1997; Lavelle *et al.*, 2006), potentially increasing soil CO_2 efflux rates.

AUTOTROPHIC AND HETEROTROPHIC RESPIRATION

Soil CO_2 efflux is the major pathway for C exiting terrestrial ecosystems. Soil CO_2 efflux is the release of C dioxide at the soil surface and is the cumulative result of several belowground processes (Ryan & Law, 2005). The interactions of autotrophic and heterotrophic organisms in soil CO_2 efflux are poorly understood (Pendall *et al.*, 2004) and makes modelling complex. Autotrophic respiration (root and mycorrhizal) is dependent on current photosynthates for substrate supply, but stored carbohydrates can temporarily be used when environmental conditions are unfavourable for photosynthesis (Ryan & Law, 2005). On average across ecosystems, 50% of soil respiration is derived from metabolic activity to support and grow roots

and associated mycorrhizae (Hanson *et al.*, 2000). The majority of the remaining soil respiration is linked with heterotrophic respiration from microbial communities utilizing organic matter as a substrate (Trumbore, 2000) and is dependent on the supply of decomposable labile substrate and its chemical composition. Only a small fraction (~10%) of soil CO_2 efflux is derived from decomposition of older more recalcitrant C compounds (Gaudinski *et al.*, 2000; Trumbore, 2000).

The contribution of the autotrophic and heterotrophic components of soil CO_2 efflux may vary with vegetation type. It is reported that soil CO_2 efflux resulting from live root respiration ranges from 33-50% in broad-leaved forests, 35-62% in pine forests, and 17-40% in grasslands (Buyanovsky *et al.*, 1987; Bowden *et al.*, 1993; Striegl & Wickland, 1998). Across a range of studies, the heterotrophic contribution varies from 10 to 95% and averages 54% annually and 40% during a growing season (Hanson *et al.*, 2000). The variability in the contributions of the autotrophic and heterotrophic components can be partially attributed to the seasonality of the factors controlling them. For example, labile biomass inputs change seasonally, which will have a large effect on heterotrophic respiration (Ryan & Law, 2005). In a study comparing soil respiration rates in oak and pine forest, soil CO_2 efflux was higher in the oak forest in autumn after leaf drop when compared to CO_2 efflux in the spring (Yuste *et al.*, 2005). This was not reported for pine forests as leaf litter was more resistant to decay and was produced continuously.

Microorganisms are divided into three groups based upon their optimum temperature ranges. Cryophiles develop at temperature <20°C, mesophiles grow optimally at 20°C to 40°C, and thermophiles grow optimally at >40°C. Research studies reported a wide range of optimal temperatures for microbial respiration (-10°C to 23°C to 65°C) (Mikan *et al.*, 2002; Flanigan & Veum, 1974).

The effects of water stress vary in regards to microbial growth. In general, soil microorganisms that have the ability to adapt to a wide range of soil VWC levels have a cell-wall membrane complex and are capable of osmotic regulation through constitutive production of compatible solutes (Harris, 1981). Drought may induce spore formation, dormancy, and/or dehydration (Stark & Firestone, 1995; Schjonning *et al.*, 2003), which may result in reduced microbial respiration.

Root respiration is controlled by aboveground processes when environmental conditions are favourable for photosynthesis. Allocation of recently fixed photosynthates stimulates root

growth and respiration (Ryan & Law, 2005). Root respiration is related to temperature and tissue N concentrations due to the dependence on amino acids and proteins for metabolism (Ryan *et al.*, 2004). Nitrogen (N) concentration can alter root and mycorrhizal biomass as a result of reduced C allocation to roots (Ryan *et al.*, 2004). During periods of unfavourable environmental conditions such as drought, there is a decrease in photosynthetic activity resulting in the use of stored carbohydrates to maintain living tissue and a decoupling of root respiration from aboveground photosynthetic activity (Hogberg *et al.*, 2001). Soil VWC affects soil CO_2 efflux both directly in physiological processes of roots and microorganisms, and indirectly in diffusion of substrate and oxygen (Liu *et al.*, 2002; Xu *et al.*, 2004). Root respiration can be affected by drought as a result of reduced photosynthetic activity and resulting reduced root growth and respiration. Soil respiration is reported to increase following precipitation events in dry climates, possibly as a result of rapid microbial responses to water availability, with the recovery of root respiration lagging behind (Kelliher *et al.*, 2004).

Analysis of carbon 14 (^{14}C) content has shown that most extramatrical hyphae of arbuscular mycorrhizal (AM) fungi live approximately 5-6 days (Staddon *et al.*, 2003a), although lifespan may be longer under certain conditions. Turnover estimates of extraradical hyphae of AM appear to be in the order of weeks (Friese & Allen, 1991; Staddon *et al.*, 2003a; Staddon *et al.*, 2003b; Steinberg & Rillig, 2003). So-called runner hyphae, that may function more as framework than actual nutrient uptake, may have longer life spans (Friese & Allen, 1991). Soil desiccation affects hyphae directly by dehydrating them (Juniper & Abbott, 1993) and indirectly by decreasing in-host net primary production and C allocation from host plant to the fungus. Langley and Hungate (2003) suggest that the lifespan of ectomycorrhizal (EM) hyphae may be longer than that of AM hyphae, because EM fungi form comparatively massive structures that envelop fine roots. Roots infected by EM have higher N concentrations than non-mycorrhizal roots, which would be expected to increase decomposition rates, but much of this N is bound in recalcitrant forms, such as chitin, so the net effect on decomposition is difficult to predict. Arbuscular mycorrhizal fungi lack elaborate, macroscopic structures and may not alter root chemistry as profoundly. However, like AM hyphae, EM hyphae are also affected by drought. Hunt and Fogel (1983) reported that the total length of soil hyphae in EM-dominated coniferous forest decreased over threefold within four months during the dry summer period. Baath *et al* (2004) estimated that 60-70% of EM hyphae in the soil of a Swedish mixed forest fully decomposed within 3-6 months after C supply from host plant was interrupted. The

exudation and/or transfer of hydraulically lifted water by plants into the upper dry soil layer may protect fungal hyphae from desiccation (Querejeta *et al.*, 2003; Egerton-Warburton *et al.*, 2007).

On a global scale, woody vegetation dominated by EM fungi CO_2 fluxes is primarily influenced by changes in temperature, while in AM-dominated grasslands and woody vegetation CO_2 fluxes are primarily influenced by changes in precipitation (Vargas *et al.*, 2010). Thus, in savannah areas, where AM and EM vegetation are both present, the effects of climate change on belowground responses may be different depending on the specific host-fungal symbiosis and the change in temperature and water availability. *Quercus* spp. usually form EM associations (Mitchell *et al.*, 1984; Daughtridge *et al.*, 1986; Egerton-Warburton & Allen, 2001), however some *Quercus* spp. are reported to form both EM and AM associations (Grand, 1969; Rothwell *et al.*, 1983; Dickie *et al.*, 2001). *Schizachyrium scoparium* commonly form symbiotic associations with AM fungi and are frequently considered to be obligate mycotrophs (Dhillion *et al.*, 1988; Anderson & Liberta, 1992; Dhillion, 1992; Meredith & Anderson, 1992; Anderson *et al.*, 1994). *Juniperus* spp. have been reported to form associations with EM fungi (Thomas, 1943) and AM fungi (Reinsvold & Reeves, 1986; Pregitzer *et al.*, 2002; Caravaca *et al.*, 2006; Wubet *et al.*, 2006). This suggests that changes in temperature may have stronger impact on the soil CO_2 fluxes in plots with *J. virginiana*, while precipitation changes may have a stronger impact on plots dominated by *S. scoparium* and *Q. stellata*.

ROOT DYNAMICS

Fine roots are a key link for plant water and nutrient uptake, soil C input, and soil microbial activity (Norby, 1994; Eissenstat & Yanai, 1997). Turnover of fine roots (< 2.0 mm in diameter) plays a critical role in regulating ecosystem water and nutrient fluxes, and C balance (Eissenstat & Yanai, 1997; Gill & Jackson, 2000; Pendall *et al.*, 2004) and may influence sequestration of atmospheric CO_2. It is estimated that as much as 33% of global annual net primary production (NPP) is used for the production of fine roots (Jackson *et al.*, 1997). Globally >90 % of all soil profiles have at least 50 % of all roots in the upper 0.3 m and 95 % of all plant roots in the top 2 m (Schenk & Jackson, 2002a; Schenk & Jackson, 2005).

Vegetation types differ in total and fine root biomass, root turnover, vertical root distribution, and maximum rooting depth (Stone & Kalisz, 1991; Canadell *et al.*, 1996), and deeper rooting depths are usually associated with water limited conditions (Schenk & Jackson, 2002a; Schenk & Jackson, 2002b; Schenk & Jackson, 2005). For example, *J. virginiana* roots

are usually shallow, fibrous, and spreading (Fowells, 1965), sometimes developing penetrating and lateral tap roots, depending on soil conditions and age. Roots from mature specimens have been reported to penetrate up to ~7.6 m (Yeager, 1935) and lateral roots may reach ~6 m (Bunger & Thomson, 1938). *Quercus stellata* are reported to be coarse rooted with thick penetrating tap roots (Arnold & Struve, 1993; Pallardy & Rhoads, 1993; Arnold, 2008), but are frequently established on sites with a dense/thick clay pan, which hinders downward growth and forces development of the bulk of the root system at shallower depth above the underlying clay layer (Coile, 1937). *Schizachyrium scoparium* roots are usually fibrous, deeply penetrating, with some lateral extension (Weaver, 1958). Roots from mature specimens have been reported to penetrate up to ~ 2.4 m and lateral roots may reach ~ 0.9 m, depending on soil conditions (Weaver, 1958).

MOISTURE AND ROOT GROWTH

Besides the availability of carbohydrates to support root growth, high mechanical impedance and a low soil water potential are the dominant factors that limit root growth in dry soils. In dry soils, root-to-soil contact decreases either due to shrinking of roots and/or shrinkage of soil and/or growth of root into soil cracks (Faiz & Weatherley, 1982). A lack of direct contact with soil particles and water surrounding the soil particles further exacerbate drought stress and reduce root growth, even if mechanical resistance to root growth is reduced. Root growth is usually less depressed than shoot growth, leading to increased root-to-shoot dry mass ratio in response to drought stress (Marschner, 1995), possibly as a result of a quick osmotic adjustment in roots compared to shoots. However, C allocation to roots is reduced when soil is under drought condition (Kosola & Eissenstat, 1994) and nutrient uptake by the roots is reduced as a result of drought effects on diffusion and transpiration rates (Marschner, 1995).

Drought can also increase root mortality, depending on the species. Drought may have a bigger impact on root mortality in grass roots which lack an exodermis (Hayes & Seastedt, 1987). Plant species which have fine lateral roots of high hydraulic conductivity tend to shed roots in dry soil and re-grow them quickly when soil is rewetted (Nobel *et al.*, 1992). Other species, such as citrus trees, maintain functionality in the fine roots with considerably reduced rates of root maintenance respiration, until more favourable conditions return (Eissenstat *et al.*, 1999). While increasing soil water availability may partially relieve these drought-related factors/stresses, excessive soil water content reduces soil oxygen availability and may impede

root growth (Marschner, 1995; Drew, 1997). Water logging restricts root growth and root branching, and may cause shallow root systems and reduce plant size/growth (Kozlowski, 1999; Kozlowski & Pallardy, 2002).

TEMPERATURE AND ROOT GROWTH

Root growth increases with increasing temperatures until an optimal temperature is reached, which varies depending on plant species (McMichael & Burke, 1998). Optimal temperature for root growth for a given species can be defined on the basis of changes in elongation rates biomass production and branching, as well as water and nutrient uptake characteristics and microbial interactions. Temperature optima tend to be lower for root growth than shoot growth (McMichael & Burke, 1998). At higher than optimum soil temperatures the rate of cell division in the root is reduced, resulting in reduced root elongation (Marschner, 1995; McMichael & Burke, 1998). Higher temperatures are also associated with increased fine-root production and mortality (Gill & Jackson, 2000) and therefore turnover rates (Fitter *et al.*, 1999; Pendall *et al.*, 2004), thus potentially 'returning' more C to the soil.

Effects of temperature are likely to be mediated by other environmental conditions. High light intensity and high supply of N may increase sensitivity of roots to high soil temperature (Marschner, 1995; McMichael & Burke, 1998). Volder *et al.* (2007) found that soil warming increased fine root production of an Australian pasture grass only under elevated CO_2 conditions. Fitter *et al*. (1999) reported that elevated soil temperatures (by 2.8 °C at a 2 cm depth) did not cause a significant change in root lifespan in an upland grass land in the UK and suggested that root production acclimates to warming and is mostly driven by the availability of photosynthates, and that any stimulation of root growth due to soil warming was the result of changes in nutrient availability due to enhanced decomposition. Forbes *et al*. (1997) found that *Lolium perenne* L. (perennial ryegrass) grown in a growth chamber at 15°C had 30% root mortality after 35 days while grasses grown at 27°C had 84 % root mortality. Estimates of fine root life span vary and range from <20 days to 4-8 years (Eissenstat & Yanai, 1997; Gaudinski *et al.*, 2000; Matamala & Schlesinger, 2000), depending on species, environment and root order. A branched (higher order) root lives longer than a non branched root, even within the same diameter class (Eissenstat *et al.*, 2000; Wells & Eissenstat, 2001).

LITTER QUALITY AND DECOMPOSITION

Variation in leaf and fine root traits, such as N concentration, specific leaf area (SLA), specific root length (SRL), and C:N ratio, among others, may have pronounced effects on numerous ecosystem processes (Comas *et al.*, 2002; Comas *et al.*, 2005). Leaf and fine root traits are correlated with specific rates of net CO_2 exchange and resource acquisition and productivity at the ecosystem scale (Craine *et al.*, 2002; Tjoelker *et al.*, 2005). Differences in leaf and fine root tissue chemistry may influence feedbacks to nutrient dynamics through differences in litter decomposition and N availability (Yahdjian *et al.*, 2006). In addition, plant functional types may differ in their spatial and temporal patterns in leaf and fine root production and turnover that, in turn, affect C and water fluxes, such as soil respiratory CO_2 efflux, net ecosystem exchange, and evapotranspiration (Chimner & Welker, 2005; Ryan & Law, 2005). Among tree and grass species, fine root turnover is positively correlated with fine root N concentration and specific respiration rates, but generally unrelated to SRL (Tjoelker *et al.*, 2005).

Lignin content, lignin to N ratios, C:N ratios, and other indices of litter quality have been shown to strongly influence decomposition and the release of N from decomposing litter (Gartner & Cardon, 2004). Tissues with higher lignin:N and C:N ratios have slower decomposition rates and release less N per unit of litter mass (Gartner & Cardon, 2004). Norris *et al.* (2001a) suggested that while the majority of *J. virginana* biomass (trunk) is of low quality (high C:N ratio), greater allocation of biomass N to foliage and roots may result in relatively high quality (low C:N ratio) litter. Litter in *J. virginana* stands averaged about 500 g m^{-2} $year^{-1}$(Norris *et al.*, 2001a). However, while *J. virginana* litter may provide good quality litter (low C:N ratio), the lignin content (3 times greater in foliage and 2 times greater in root when compared to grass species) may slow decomposition and thus N release (Norris *et al.*, 2001b). Thus, despite the potential for large surface litter inputs and accumulation of organic N, surface litter decomposition of *J. virginiana* appears to contribute little to soil inorganic N pools in the short-term, and eventual release of inorganic N from surface litter may require long periods of time due to differences in litter chemistry relative to grassland species (Norris *et al.*, 2001a).

Juniperus virginiana root biomass may also provide significant quantities of organic matter to soil. What remains unclear is the quality, quantity, and time scale/turnover of *J. virginiana* roots, *Q. stellata* roots and *S. scoparium* roots in Texas oak-savannah ecosystems. Without basic information on root litter input, root chemistry and root turnover, and the effects

of climate change on these parameters, it will remain impossible to accurately project how CO_2 fluxes from oak-savannah soils will be affected by projected climate change.

MYCORRHIZAL FUNGI

Mycorrhizal symbioses are ubiquitous in terrestrial ecosystems and are a key component of ecosystem structure and function, potentially mediating plant growth, competition, population and community dynamics (Smith & Read, 2008; van der Heijden *et al.*, 2008). Mycorrhizal fungi exist in symbiotic (mutually beneficial) associations with the fine young roots of most higher plants (Smith & Read, 2008). The plant supplies the fungus with C (from photosynthesis) while the mycorrhiza enhances plant nutrient and water uptake and helps alleviate cultural and environmental stresses (Smith & Read, 2008). A range of forms of mycorrhiza occur and have been grouped/classified by structural characteristics at maturity (and increasingly by molecular/genetic techniques) on the basis of their fungal associates into those involving largely aseptate endophytes (Glomeromycota) and those formed by septate fungi in the (Ascomycetes and Basidiomycetes) (Smith & Read, 2008). The two dominant types of mycorrhizal fungi in temperate ecosystems are arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi (Allen, 1991; Smith & Read, 2008). The AM fungi appear to be obligate symbionts (in the majority of cases), whereas some EM fungi may be able to act as saprotrophs.

Arbuscular mycorrhizal fungi are widespread and form symbiotic associations with ~85% of extant terrestrial plants (Smith & Read, 2008). Ectomycorrhizal fungi are by comparison less common, forming associations with ~5% of extant terrestrial plants (Meyer, . 1973). Ectomycorrhizal fungi are usually associated with woody plants (forest trees and shrubs), and are dominant in coniferous forests in cold boreal or alpine regions, and many broad leaf forests in temperate and Mediterranean regions (Smith & Read, 2008; Meyer, . 1973). Ectomycorrhizal fungi are also common in subtropical and tropical savannah and rainforest regions (Brundrett *et al.*, 1996). Ectomycorrhizal fungi form associations with members of a wide range of economically important plant families, including Betulaceae, Dipterocarpaceae, Ericaceae, Fagaceae, Pinaceae, and Myrtaceae (Brundrett *et al.*, 1996; Smith & Read, 2008). Members of these families are widespread and economically important for forestry (timber) (Meyer, . 1973).

Ectomycorrhizal roots are characterized by the lack of root hairs and presence of a distinctive extraradical mycelium sheath or net-like mantel covering (~20-40 μm thick) around

the frequently pigmented, fine root tips and thick racemose lateral root branches of the host plant (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008). Ectomycorrhizal fungi may also form a distinctive net like structure (Hartig net) between the root cortical cell (hyphae penetrate between epidermal cells in angiosperms or into the cortex in gymnosperms) of the host plant and extraradical mycelium sheath (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008). The invading hyphae of the Hartig net are intercellular, they distort (sometimes radically) but do not penetrate the cortical cell, and colonization does not progress beyond the endodermis into the stele or undifferentiated tissue (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008).

Arbuscular mycorrhizal roots do not 'lose' their root hairs, even when AM fungi (may) form loose hyphal webs over the root surface (not sheath as with EM), but are more commonly characterized by extensive, highly intimate, interior colonization of the root (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008). The fungal hyphae differentiate and form appressoria (swollen hyphal mass) on the root surface and penetrate into the cortical cells of the host plant, between the outer most layer of cells, growing between and within the cells of the root cortex, forming coils of hyphae in the outer to middle cortical layer of the root and are thought to be involved in nutrient transfer (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008). Terminal and intercellular swellings (vesicles and/or spores) either in or between the host cells may also form here. These are lipid-rich and thought to be important for storage and reproduction within cells of the inner cortical layer (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008). Near the central stele, hyphae branch dichotomously and form finely divided relatively thin walled projections which penetrate and invaginate the host cells membrane. These structures are called arbuscules and provide a large surface area of contact between the fungus and the plant, and are thought to be the location of the majority of nutrient and mineral exchange (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008). Meristematic tissue and the stele are not colonized/invaded by AM hyphae (Brundrett *et al.*, 1996; Isaac, 1996; Smith & Read, 2008).

CARBON BALANCE AND MYCORRHIZA

Mycorrhizal fungi are an important part of the belowground response of terrestrial systems to environmental change with the potential to affect numerous belowground processes/cycles, including C balance (Fitter *et al.*, 2004). Mycorrhizal fungi are estimated to act as sinks for 3-20% of host plant photosynthates (Jakobsen & Rosendahl, 1990; Johnson *et al.*, 2002a; Johnson *et al.*, 2002b) and are globally abundant in soils (Treseder & Cross, 2006).

Arbuscular mycorrhizal fungi form a large network of hyphae outside of roots (extraradical hyphae) which is responsible for 20-30% of the soil microbial biomass and as much as 15% of the soil organic C pool (Leake *et al.*, 2004). Staddon *et al.* (2003a) demonstrated that some C may move rapidly through fine hyphae with very short life-spans. In contrast, Olsson & Johnson (2005) suggested that AM fungi may be capable of retaining recently assimilated photosynthetic C in lipids for at least 32 days.

Fungal C may remain in the soil for a longer time period, even after the hyphae are not connected to the host plant anymore, given that mycorrhizal fungal tissue contains recalcitrant compounds such as chitin and glomalin (Steinberg & Rillig, 2003), which may slow microbial degradation. Vesicles and hyphae may contain up to 20% neutral lipids, which are suggested to be more persistent than phospholipids in soil (Olsson & Johansen, 2000; Olsson & Johnson, 2005), suggesting that the proportion, number, and type of mycorrhiza structures in an ecosystem may affect both slow and fast turnover pools of soil organic matter and soil C balance. However, while this mutualistic symbiosis between plant and fungi is widespread, it is also one of the least understood biological associations in terrestrial ecosystems. Thus, how mycorrhizal fungi will respond to climate change is critical to our understanding of how soil C pools and fluxes will respond to climate change.

MOISTURE AND MYCORRHIZA

Effects of moisture on mycorrhizal populations are not straightforward. Allen *et al*. (1987) observed that mycorrhizal populations shifted radically between years of differing precipitation in several successional areas of the Beartooth Mountains, Montana. Most studies suggest that increasing soil water availability enhances mycorrhizal growth, either through direct effects on the fungi themselves, or indirectly via an improved plant C balance. Increased soil VWC increased total root length and mycorrhizal root length in two semi-arid tussock grasses (Allen *et al.*, 1989b). Apple *et al*. (2005) reported that mycorrhizal colonization of Mojave desert shrubs increased after precipitation events during the dry fall and summer season. Reduced mycorrhizal colonization with peak precipitation in spring was suggested to be as a result of increased C allocation to fine root and shoot growth and flowering (Apple *et al*., 2005). Sieverding (1981) reported an increased frequency of mycorrhizal infection on *Sorghum bicolor* (L.) Moench (sorghum) with drier soil, but Allen and Boosalis (1983) reported no difference in the frequency of mycorrhizal infection for greenhouse-grown *Agropyron desertorum* (Fisch.) Schult. (crested

wheatgrass) between wet and dry treatments. Shi *et al*. (2002) reported that drought did influence the composition of mycorrhizae in *Fagus sylvatica* L. (beech) forest, and observed that different mycorrhizal types respond to drought differently in terms of their patterns of occurrence and abundance.

Total length of fungal hyphae /fungal mycelium in the soil has been found to fluctuate seasonally in a wide range of natural ecosystems (Hunt & Fogel, 1983; Staddon *et al.*, 2003b; Li *et al.*, 2005). Much of this variation can be attributed to the influence of abiotic factors, including soil VWC and temperature. Both soil hyphal length and plant biomass co-vary with soil VWC (Berg *et al.*, 1998; Morris & Boerner, 1999) and a decline in mycelia abundance during drought periods may be linked to both soil and plant factors as plants reduce rates of photosynthesis in response to drought (Hunt & Fogel, 1983; Staddon *et al.*, 2003b).

In drought-prone regions (semi-desert shrub land in south western Wyoming), high soil VWC was reported to reduce mycorrhizal spore counts (Allen *et al.*, 1987), although this was suggested to be potentially the result of nematode or parasitic activity at the study site rather than a direct effect of high soil water content. Allen and Allen (1986) observed that higher moisture inhibited mycorrhizal formation in plants from semi arid areas, growing in high nutrient soils. Miller and Bever (1999) observed that water depth is an important factor determining the distribution of mycorrhizal spores along a dry to wet gradient in wetlands dominated by the semi aquatic grass. The presence of flooding was suggested to restrict some mycorrhizal species to drier regions due to differences in the extent to which mycorrhizal species can tolerate flooded conditions.

Robertson *et al.* (2006) demonstrated that the EM community of *Picea mariana* (Mill.) (black spruce) composition and richness varied across the moisture gradient in central British Columbia in response to soil heterogeneity and alternate hosts [*Larix laricina* (Du Roi) C. Koch (tamarack) and *Pinus contorta* Douglas ex Loudon (lodgepole pine)]. Both morphological and molecular analyses showed that EM diversity was greater in upland than in wetland habitats and greater in *P. mariana – L. laricina* wetlands than in *P. mariana*-dominated wetlands. Escudero and Mendoza, (2005) reported similar results (but with a seasonal influence) in that spore density and colonization of *Lotus glaber* L. (bird's foot trefoil), a perennial herbaceous legume naturalized in the Argentinean flooding Pampas, was highest in summer (dry season) and lowest in winter (wet season) with intermediate values in autumn and spring. *Pinus sylvestris* L. (Scots pine) seedlings, grown in a vertical petri dish system, inoculated with different mycorrhizal

fungi [*Thelephora terrestris* Ehrh, *Laccaria laccata* (Scop.) Cooke, and *Hebeloma crustuliniforme* (Bull. ex St Amans.) Quél.] were not sensitive to flooding (2 min./day four times a week), whereas those inoculated with *Suillus flavidus* (Fr.) J. Presl and *S. bovinus* (Pers.) Roussel were highly sensitive to flooding (Stenstrom, 1991). Suggesting that some species of mycorrhizal fungi are more tolerant than others to flooding conditions. Thus, saturating soil conditions may reduce the presence of some species more than other species, and could lead to changes in mycorrhizal abundance and species diversity.

TEMPERATURE AND MYCORRHIZA

Effects of temperature on mycorrhizal populations are not straightforward. Bentivenga and Hetrick (1992) demonstrated that mycorrhizal activity was greatest in cool season grasses during the growing season when temperatures were relatively low. Rillig *et al.* (2002) demonstrated that warming (1.5-2.0 °C at the canopy and 1°C at the soil surface) of an annual grassland with infrared heaters (250 W heater, for a power input of about 80 W m^{-2}) increased AM hyphal length by 40% and root colonization, independently from effect on root mass, length, and average diameter. This was suggested to be the result of a combination of factors including, a change in C resource allocation to the AM hyphae by the plant, changes in AM hyphal growth physiology and/or shift in AM mycorrhiza species composition (more prolific under growth conditions).

Increased hyphal growth may also lead to a higher C input to the soil as AM hyphae have high concentrations of chitin and excrete large amounts of glomalin (Wright & Upadhyaya, 1996; Rillig *et al.*, 2001; Steinberg & Rillig, 2003). Increased soil hyphal growth may therefore lead to accumulation of these compounds, possibly increasing C sequestration. However, Rillig *et al.* (2002) also reported that concentration of the soil protein glomalin (glycoprotein produced by AM hyphae) was decreased in warmed plots. Soil aggregate stability was also significantly decreased in warmed plots, suggesting that glomalin, as with other portions of soil organic matter, may be subject to more rapid decomposition at higher temperatures. Alternatively, hyphal production of glomalin may be reduced as a result of changes in AM hyphae growth physiology and/or shift in AM species composition. Glomalin may act as a C source for soil microbes and thus reduced glomalin production by fungi may reduce the microbial component of heterotrophic soil respiration.

Heinemeyer and Fitter (2004) demonstrated that when *Plantago lanceolata* L. (English plantain) and *Holcus lanatus* L. (velvet grass) and an AM fungus [*Glomus mosseae* (Nicol. & Gerd.) Gerd. & Trappe] were subjected to an 8°C decrease in day and night temperature (from 20/18 °C (day/night to 12/10 °C (day/night) that the impact on the internal and external parts of the AM fungus was related to different plant biomass and root growth dynamics, respectively. When only the extra-radical mycelium was subjected to warming (+8°C), increased extra-radical mycelium growth was reported, percent root colonized did not increase, but specific root length did increase. Gavito *et al.* (2005) also demonstrated that the growth of AM is directly affected by temperature independent of the plant host. They found greater root colonization, more extensive extradical mycelium, and more glucose uptake at higher temperatures (24-30 °C). Hawkes *et al.* (2008) demonstrated that temperature significantly altered the structure and allocation of the AM hyphal network. They observed that as soil temperature increased, an increase in the speed at which plant photosynthates were transferred to and respired by roots and AM, coupled with an increase in the amount of C respired per unit hyphal length was observed. These differences were reported to be largely independent of plant size and rates of photosynthesis, thus suggesting that, under warmed conditions, C loss to the atmosphere from mycorrhizal respiration would increase, both because warming increases rates of hyphal specific respiration and because it increases total hyphal length in the soil.

An increase in long term pools of fungal C may also be likely given that that mycorrhizal fungal tissue contains recalcitrant compounds such as chitin and glomalin (Steinberg & Rillig, 2003)and lipids (Olsson & Johansen, 2000; Olsson & Johnson, 2005). Olsson & Johnson (2005) however, suggest that AM fungi may be able of retaining recently assimilated photosynthates C in lipids for at least 32 days. Hawkes *et al.* (2008) reported a switch from more vesicles (storage) in cooled soils (14-15°C) to more extensive extraradical hyphal networks (growth) in warmed soils (26-27°C). Similar shifts in mycorrhizal structures have been reported in response to drought stress (Staddon *et al.*, 2003a) and water-logging/flooding (Mendoza *et al.*, 2005) and are suggested to allow the fungus to survive in adverse conditions. Thus, a change in the density of lipid-filled vesicles and hyphae may well affect both slow and fast turnover pools of soil organic matter. Heinemeyer *et al.* (2006) tested the direct effect of temperature on extraradical mycelium by allowing hyphae from *P. lanceolata* to grow into a separate root-free compartment/microcosm where a pulse label of the stable isotope ^{13}C was applied, and total C and the ^{13}C:^{12}C ratio of respired CO_2 was measured.

Mycorrhizal colonization remained unchanged in response to warming (+ 6 °C above ambient), while hyphal respiration rate (from root-free compartments) increased initially, but rapidly (within 2 weeks) acclimated to the temperature increase. Moreover, CO_2 concentrations fluctuated diurnally and tended to be higher in the mycorrhizal treatments, but over the period of the experiment were unaffected by temperature, thus suggesting that extraradical mycelium exhibited acclimation to temperature increase, and that light was the key factor controlling C allocation to the fungus.

Indirect effects of temperature shifts may also cause changes in mineralization and nitrification activity that may alter both composition and type of mycorrhiza. The ratio of carbohydrates to N is suggested to affect EM fruiting bodies, external hyphae and root tips (Wallander, 1995; Wallenda & Kottke, 1998). If this ratio declines, EM biomass decreases. Yet, the effect of soil N availability is variable. For both AM and EM, greater N availability may increase, decrease, or have no response on mycorrhizal root infection and production of external hyphae (Wallenda & Kottke, 1998; Treseder & Allen, 2000). Greenhouse studies have demonstrated that EM decrease as N availability increases from deficient to optimal, and then decline at higher N levels (Wallenda & Kottke, 1998). Increased N may also cause a shift in mycorrhizal community composition (Treseder & Allen, 2000). The limited available data on mycorrhizal responses to warming suggest that the effects of temperature are more likely to be indirect, through changes in organic matter decomposition and mineralization, than direct.

ROOT TURNOVER AND MYCORRHIZA

Changes in root turnover rates may have a profound effect upon mycorrhizae. Increased rates of root turnover may increase the rate at which mycorrhizae establish new contacts with a root system, which in turn may lead to loss of less active species. Bruns (1995) suggested that during flushes of root growth (spring and autumn and/or after wetting of dry soil) large numbers of noncolonized root tips may be produced and this in turn may increase mycorrhizal diversity and/or competition/selection for ‘fast’/vigorous mycorrhizal colonizers. Sohn (1981) suggested that a threshold growth limit exists for the extension rate of roots above which mycorrhizal formation maybe progressively restricted as roots may move faster than colonization can take place. This would suggest that host species with very fast growing roots may have reduced colonization rates, or a greater ‘lag’ time between root birth and colonization.

HOST PLANT COMPETITION AND MYCORRHIZA

Little is known about the interactive effects of host-plant competition and mycorrhizal competition. McHugh and Gehring (2006) reported that belowground interactions between an EM *Pinus edulis* Engelm. (Piñon pine) and co-occurring AM colonized shrubs during drought were significant. Field performance and root biomass of pine was lower when in presence of shrubs, suggesting a potential below ground competitive interaction for resources. When shrubs were removed, both above- and belowground *P. edulis* growth increased and EM colonization doubled, although diversity of fungal community was unaffected.

Bergelson & Crawley (1988) suggested that the effects of mycorrhizal colonization on plant diversity are not absolute and are strongly influenced by the responsiveness of the plant species in the community. Bever (2002; 2003) examined community dynamics of co-occurring plants and mycorrhizal species at a grassland site and reported the existence of asymmetric relationships and negative feedback between plant and mycorrhizae. He showed, in general, that mycorrhizae may deliver the greatest benefit to one plant species, but grow better on another. Interestingly, he did not find evidence of positive feedback in which the mycorrhizae that delivered the greatest growth benefits to the plant also received the greatest benefits from the plant. This would seem to be very significant and may explain the specificity, occurrence, and function of mycorrhizae in plant interactions. Under negative feedback, specific advantages would not happen for a given plant species and fluctuation in plant/fungal success may occur in the short term, however co-occurrence of competing/interacting species would be potentially maintained, resulting in species richness of plant and fungal communities. Climate change and the introduction of non-native species may add another variable and potentially disrupt this pattern.

The large diversity of function between different plant fungus combinations as well as selectivity in choice of partners means that changes in fungal community with respect to both number and identity of species as a result of warming and/or moisture could change plant interactions. It is likely that mycorrhizae may be host-specific, efficiencies among mycorrhizal species may vary (colonization strategies, carbohydrate requirements, tolerance of environmental extremes, enzymatic capabilities, and ability to transport water and nutrients), and that each mycorrhizal isolate originating from a specific environment may represent an ecotype adapted to that particular environment.

MYCORRHIZAL STATUS OF THE PLANTS USED IN THIS STUDY

The three dominant plant species of post oak savannah not only have very different growth strategies, but also have very different mycorrhizal relationships. There is limited information on the competitive ability/role of mycorrhizal associations for *Quercus stellata*. Most *Quercus* L. spp. are considered to form associations with EM mycorrhizae (Mitchell *et al.*, 1984; Daughtridge *et al.*, 1986; Bakker *et al.*, 2000; Dickie *et al.*, 2001; Egerton-Warburton & Allen, 2001; Pregitzer *et al.*, 2002). However, while *Q. virginiana* Mill. (live oak) forms EM associations, these were reported to be not beneficial for growth (Gilman, 2001). Furthermore, some *Quercus* spp. will form associations with both EM and AM fungi. For example, *Quercus rubra* L. (red oak) (Dickie *et al.*, 2001), *Q. falcata* Michx. (Spanish red oak) (Grand, 1969), and *Q. imbricaria* Michx. (shingle oak) (Rothwell *et al.*, 1983) are reported to form associations with both EM and AM. In these situations, the fungi occur within the plant root systems as co-dominants and/or successional mycorrhizal associations (Allen *et al.*, 2003). Lapeyrie & Chilvers (1985) suggested that AM colonization of what is typically considered an EM plant may be an important adaptation mechanism to nutrient poor sites. However, dual colonization and the presence of both mycorrhizal types were reported to reduce young *Q. agrifolia* Née (California live oak) survival, possibly as a result of the C cost necessary to maintain the 'dual' association, and it was therefore suggested to be less beneficial to have both mycorrhizal types (Egerton-Warburton & Allen, 2001). As *Q. agrifolia* seedlings benefited most when either AM or EM were present, and were negatively affected when inoculated with both AM and EM (Egerton-Warburton & Allen, 2001). However, it has been demonstrated that AM do not increase nutrient uptake or growth of *Q. rubra* seedlings early in development (Dickie *et al.*, 2001), suggesting that for some *Quercus* spp. there may be a shift in mycorrhizal association depending on maturity of plant material and environmental conditions.

There is limited information on the competitive ability/role of mycorrhizal associations for *J. virginiana*. *Juniperus* L. Spp. have been reported to form associations with both EM and AM, which may enhance plant nutrient uptake, water relations, and help alleviate plant stress. Joint or co-dominants and/or successional mycorrhizal associations may give the host species a competitive advantage, if the C cost is not too high. Lapeyrie & Chilvers (1985) suggested that AM colonization of what is typically considered an ectomycorrhizal plant may be an important adaption/survival mechanism in nutrient-poor sites. We suggest that this may also be a response to other environmental stressors, for example drought.

Ectomycorrhizal associations have occasionally been reported for other *Juniperus* species, such as *J. osteosperma* (Torr.) Little (Utah juniper) (Reinsvold & Reeves, 1986), *J. communis* L. (common juniper), *J. macrocapa* Sibth. & Sm. (prickly juniper), *J. scopulorum* Sarg. (Colorado red cedar), and *J. virginiana* (Thomas, 1943). However, the formations of EM associations with *Juniperus* spp. may be facultative rather than symbiotic (Meyer, . 1973), which may account for the infrequency and low colonization rates observed. Arbuscular mycorrhizal fungi associations with *Juniperus* spp. appear to be more common. Arbuscular mycorrhizal associations have been reported for *J. monosperma* (Engelm) Sarg. (Cherrystone juniper) (Pregitzer *et al.*, 2002; Haskins & Gehring, 2005), *J. procera* Hochst. Ex Endl. (African juniper) (Wubet *et al.*, 2003; Wubet *et al.*, 2006), *J. oxycedrus* L. (prickly juniper) (Caravaca *et al.*, 2006), *J. osteosperma* (Reinsvold & Reeves, 1986), and *J. chinensis* L. (Chinese juniper) (Roncadori & Pokorny, 1982). Thus, the response of other *Juniperus* spp. to mycorrhizal associations is less certain and remains unclear.

Schizachyrium scoparium commonly form symbiotic associations with AM and are frequently consider to be obligate mycotrophs (Dhillion *et al.*, 1988; Anderson & Liberta, 1992; Dhillion, 1992; Meredith & Anderson, 1992; Anderson *et al.*, 1994). However, the degree of AM dependency remains unclear. For example *S. scoparium* grown in steam-treated soil without AM inoculum had enhanced growth when compared to plants inoculated with AM (Anderson & Liberta, 1992; Meredith & Anderson, 1992; Anderson *et al.*, 1994). This was suggested to be the result of a potentially, yet undisclosed antagonistic relationship between the plant or the fungus, and soil microbes (Meredith & Anderson, 1992; Anderson *et al.*, 1994). We suggest that the findings may better be explained as an artefact of the steaming process on soil nutrient content, or competition for inorganic nutrients between plant and microbes, or growth of plants under 'ideal' conditions (i.e., no environmental stress, as would be expected in a field setting and are thus seeing the fungal C cost of the symbiosis).

SUMMARY OF FOLLOWING CHAPTERS

Although annual precipitation totals are expected to remain stable in Texas, advanced climate models project an increase in global surface temperatures and an intensification of summer drought periods and individual precipitation events. Climate warming and changes in precipitation patterns will have a strong impact on the relationship of plants with their environment, and only those species that can effectively cope with intensified summer drought,

coupled with an increased frequency of short-term flooding will be able to persist under the projected new climatic conditions. Many of the responses to projected climatic change will be determined at the soil-water interface. Therefore, this dissertation explores the interactive effects of climate warming and precipitation distribution on some rhizosphere processes in southern oak savannah.

In the last sixty years, the Texas post oak savannah has seen an increase in the abundance of woody species, and in particular an increase in the density of *J. virginiana*. The three dominant species not only have very different growth strategies, but also have very different mycorrhizal relationships. *Schizachyrium scoparium* is exclusively colonized by AM, while both *J. virginiana* and *Q. stellata* are colonized by EM and can possibly also associate with AM.

The following chapters focus on four main questions 1) what are the short term effects of changes in plant species and species mixture on CO_2 efflux from the soil, 2) how are these processes affected by climate change drivers, 3) how are the three components of soil CO_2 efflux (root, fungal, bacterial) affected by plant species and climate change drivers and 4) how are mycorrhizal type and presence altered by plant species and the climate change drivers (Figure 1.1).

In Chapter II we will address the effect of plant-species combination, seasonal variation, and warming and precipitation distribution, both independently and in combination, on soil CO_2 efflux in post oak savannah. In Chapter III we will focus on the effect of short term increased soil VWC as affected by precipitation distribution, plant-species combination, and warming on soil CO_2 efflux in post oak savannah. In Chapter IV we will explore the relative contribution of root, fungal, and microbial respiration to soil CO_2 efflux, and study the effect of plant species combinations, seasonal variations, and precipitation distribution on root, fungal, and bacterial respiration in juniper-grass savannah. In Chapter V we will examine the effect of warming and precipitation distribution, both independently and in combination, on mycorrhizal abundance in post-oak savannah. Ultimately, this dissertation will explore the idea that climate change drivers, specifically altered precipitation patterns and warming, mediate plant species interactions through soil water availability, and thus will be key to understanding the effects of global climate change on terrestrial ecosystems.

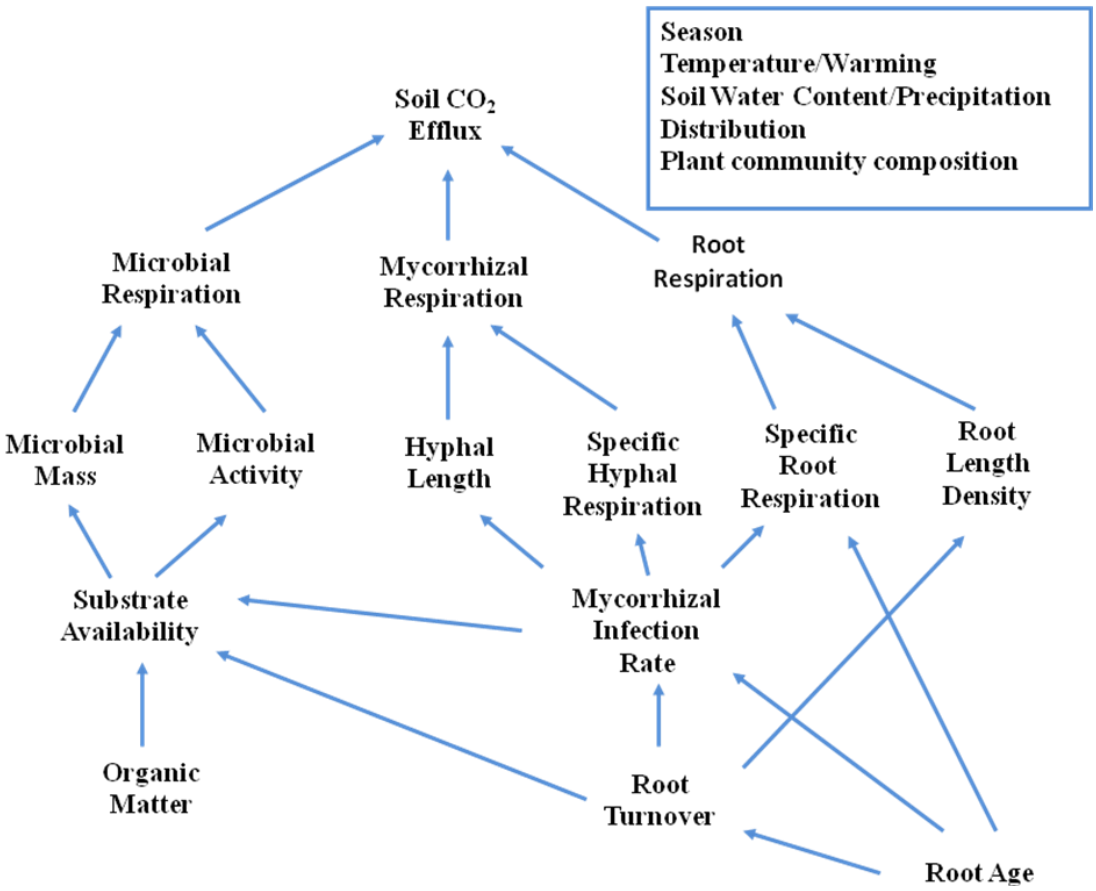

Figure 1.1. Conceptual diagram linking the processes discussed in this dissertation. Overarching treatments include manipulations of leaf and soil temperature, soil water content, and plant species and mixture on top of natural seasonal changes in environmental variables.

CHAPTER II

SOIL CO_2 EFFLUX IN OAK-SAVANNAH RESPONDS MORE STRONGLY TO SPECIES COMPOSITION THAN PRECIPITATION DISTRIBUTION AND WARMING

Introduction

Terrestrial ecosystems play a critical role in the global carbon (C) cycle (Schimel, 1995). Within the next century increasing concentrations of greenhouse gases are projected to elevate global surface temperatures (~1.1 to 6.4 °C) and potentially increase the variability of precipitation and drought events (Bates *et al.*, 2008). In the southern United States, intensification of summer drought coupled with increased variability in size and intensity of precipitation events in spring and autumn is projected to be more probable than substantial changes in the mean annual precipitation (Groisman *et al.*, 2005; Groisman & Knight, 2008). This anticipated climate change may potentially increase soil carbon dioxide (CO_2) efflux, the major pathway for C exiting terrestrial ecosystems, thus increasing atmospheric CO_2 levels and providing a positive feedback to global warming (Cox *et al.*, 2000; Friedlingstein *et al.*, 2006). Soil CO_2 efflux differs within biomes as species and climatic conditions vary (Raich & Schlesinger, 1992; Hibbard *et al.*, 2005). However, given the structural, physiological, and phylogenetic differences between grasses, angiosperms, and gymnosperms, and the relatively small differences in soil CO_2 efflux observed, it is likely that soil CO_2 efflux is affected more by climatic and inherent soil conditions while plant species composition causes a secondary effect (Raich & Tufekcioglu, 2000). In summary, disentangling species effects from effects by altered climatic conditions remains a key challenge.

Soil CO_2 efflux rates are dependent on vegetation type, soil temperature and volumetric water content (VWC) (Raich & Tufekcioglu, 2000; Ryan & Law, 2005). Soil CO_2 efflux in the short term generally increases exponentially with increasing temperatures and reaches a maximum at approximately 45 to 50°C before declining (Nobel & Palta, 1989). Warming has been reported to increase, decrease and have little or no effect on soil CO_2 efflux depending on vegetation and climatic conditions (as reviewed by Rustad *et al.*, 2001). Warming treatments may extend/lengthen the growing season (Norby *et al.*, 2003), increase N availability (Shaw & Harte, 2001; Melillo *et al.*, 2002), and stimulate plant growth (Wan *et al.*, 2005). Soil temperature may also indirectly affect root respiration due to its effect on root growth and root

metabolism, with root growth and rates of respiration increasing with increasing temperatures until an optimal temperature is reached, which varies depending on plant species (McMichael & Burke, 1998) and environmental conditions such as soil water and light availability (Edwards *et al.*, 2004). However, soil CO_2 efflux overall may have a reduced response to higher temperature as a result of acclimation of roots and/or microbes which may result in relatively reduced C loss at sustained higher temperatures (Tjoelker *et al.*, 1999; Luo *et al.*, 2001; Atkin & Tjoelker, 2003).

Soil CO_2 efflux tends to increase with increasing soil volumetric water content (VWC); however, soil temperature and seasonal microbial activity and root growth may confound observed results. In general, small precipitation events on dry soils may result in relatively sudden increases in soil CO_2 efflux, as the result of displacement of CO_2 out of the soil pore spaces (Liu *et al.*, 2002; Xu *et al.*, 2004). Conversely, following relatively large precipitation events, the resulting water saturated soil may increase CO_2 concentration within the soil pores, yet inhibit CO_2 diffusion to the surface, thus decreasing soil CO_2 efflux (Liu *et al.*, 2002; Hirano *et al.*, 2003).

Seasonal changes in climate affect soil CO_2 efflux, as C supply to roots and root exudates varies seasonally, as do soil temperature and water availability (Raich & Potter, 1995). Increasing spring temperatures and longer days result in increased shoot growth, photosynthetic activity, and root activity during the first flush of growth in deciduous trees (Yuste *et al.*, 2004). Thus, soil CO_2 efflux is generally higher in the spring when conditions are closer to optimal for both root and microbial growth and activity (Ryan & Law, 2005). It is unclear whether increased soil CO_2 efflux during spring and summer is a function of higher soil temperatures or increasing light availability since the two are generally confounded (Edwards *et al.*, 2004). This seasonal effect is stronger in deciduous trees when compared to evergreen trees (Coleman *et al.*, 2000) as evergreen trees tend to be moderately active throughout the whole year while deciduous trees have a seasonal pattern of photosynthetic activity (Kiniry, 1998). Seasonal variations in component contribution to CO_2 efflux in our study may also reflect the distinct seasonal differences in *Juniperus virginiana* L. (eastern redcedar) (a C_3 evergreen tree) and *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) (a C_4 grass) leaf structure and longevity, quality of litter inputs, and root growth and turnover (Yuste *et al.*, 2004). In general, grasses allocate a larger portion of their photosynthate below ground (Raich & Tufekcioglu, 2000) and have higher root turnover rates, resulting in greater root litter inputs into the soil,

greater root length density and lower average root age. Higher litter inputs stimulate microbial respiration, while lower average root age increases specific root respiration (Hanson *et al.*, 2000; Volder *et al.*, 2005). Thus, soil CO_2 efflux from grass dominated areas is likely higher than that of tree dominated areas.

Rates of soil CO_2 efflux are associated with the size and activity of both the root and microbial pool. Young roots are generally the ones with the highest respiration rates (Volder *et al.*, 2005; Volder *et al.*, 2009) and the root component of soil respiration is suggested to be largely in sync with periods of high root production, with generally a peak production rate of roots during early spring (e.g, Eissenstat & Caldwell, 1988; Zogg *et al.*, 1996; Jarvis *et al.*, 1997; Fitter *et al.*, 1999). The size of the microbial pool is largely dependent on the availability of substrates, while activity of both microbes and roots is strongly affected by temperature, provided adequate moisture is available.

Climate change, fragmentation of the landscape, and altered land management practices, coupled with fire suppression have resulted in invasion and expansion of woody plant material into grassland and savannah systems of North America (Van Auken, 2000; Heisler *et al.*, 2003). Post oak savannah in the south-central United States are dominated by three contrasting plant functional types: *S. scoparium* a C_4 grass, *Quercus stellata* Wangenh. (post oak) a C_3 deciduous tree, and *J. virginiana* a C_3 evergreen tree. Due to its position as a transition zone between the western grasslands and the eastern deciduous forests, oak savannah may be especially sensitive to climate change. In the past 50 years, *J. virginiana* has strongly increased its presence, often at the expense of *S. scoparium* and, to a lesser extent, *Q. stellata* (Briggs *et al.*, 2002; Briggs *et al.*, 2005).

Oak savannahs are geographically extensive and potentially represent a significant carbon sink. The dominant plant species of this system may be especially sensitive to climate change due to different functional traits, both in growth form and photosynthetic pathways. The broad objective of this study was to determine the effect of warming and precipitation redistribution on CO_2 efflux in southern oak savannah. We collected soil CO_2 efflux data, soil volumetric water content (VWC), and soil temperature, approximately every month from March 2005 – September 2009. The goal was to quantify the effects of plant species interaction, warming, increased intensity of summer drought, and the amount of cool season precipitation on soil CO_2 efflux rates in southern oak savannah. We hypothesised that: (i) soil efflux rates will vary seasonally and will be higher in the spring when conditions will be closer to optimal for

both root and microbial growth and activity, (ii) warming will increase soil CO_2 efflux rates, (iii) while soil CO_2 efflux will generally increase with increasing soil VWC but will be reduced under extreme low and high VWC conditions, and (iv) soil CO_2 efflux will vary with plant species composition.

Materials and Methods

EXPERIMENTAL SITE AND INFRASTRUCTURE

The Texas warming and rainfall manipulation experiment (Texas WaRM Experiment) is located on a remnant post oak savannah site (30°34 N 96°21 W) near the Texas A&M University campus, College Station, Texas. This facility was constructed in 2003 to investigate the combined effects of altered precipitation distribution and warming on tree grass dominants of southern oak savannah. The research infrastructure included eight permanent 18 × 9 × 4.5 m (L × W × H) rainout shelters covered with clear polypropylene film. The side walls below 1.5 m were open to maintain microclimate conditions as near ambient as possible, but effectively exclude precipitation (Fay *et al.*, 2000; Weltzin & McPherson, 2003). A fine-mesh shade cloth, matching the radiation attenuation of the film (70% transmittance), excludes windblown precipitation from entering two 4.5 m high open ends of each shelter. Sheet metal flashing 40 cm in height, was inserted 30 cm into the soil penetrating the clay hardpan, to isolate each shelter from surface and subsurface water flow.

Ten 2 × 2 m plots with five species combinations were located beneath each shelter in the native soil (Volder *et al.*, 2010). Soil consisted of a shallow layer (< 20 cm) of Boonville fine sandy loam, with a thick clay pan below (Chervenka, 2003). An overhead irrigation system (17 pressure regulated spray nozzles per shelter) simulated precipitation regimes by supplying reverse osmosis (RO) treated ground water, from four 11,500 L holding tanks, to each shelter. A weather station (EZ Mount GroWeather, Davies Instruments, Hayward, CA) on site recorded precipitation, air temperature, and humidity. Solar radiation (total PPFD), air temperature, and relative humidity were continuously monitored in each shelter and control plots using data logger (Hobo U12, Onset Company Corp., Bourne, MA). Soil water content was measured twice weekly for each plot using permanently installed time domain reflectometry (TDR) probes (Soil Moisture Corp., Santa Barbara, CA) which were inserted vertically to give an integrated measure of soil VWC in the top 20 cm of the soil profile. The rainout shelter design preserves natural

variation in the microenvironment that is for the most part similar to ambient conditions (Fay *et al.*, 2000). Mean daily temperature in the shelters was on average 0.3 °C higher, RH values were 2% lower, and PPFD levels were 30% lower than ambient.

PRECIPITATION AND WARMING TREATMENT

Simulated precipitation regimes included two patterns that varied in season distribution and event size, but not in total annual precipitation (1018 mm) or total number of events. The long-term (50 yr) precipitation events were also simulated from the regional long-term precipitation record. The frequency and intensity (amount) of precipitation events were also simulated from the regional long-term precipitation record (Figure 2.1a). Precipitation redistribution treatment imposed beneath the other four shelters had 40% of the summer (May – September) precipitation withheld from each event and evenly redistributed to the preceding spring (March and April) and autumn (October and November) (Figure 2.1a). The redistribution treatment effectively increased the intensity of the summer drought (redistribution dry phase) and the amount of precipitation that occurred during the cooler season of the year (redistributed wet phase). Each precipitation regime was replicated within four rainout shelters. Precipitation regimes were initiated in March 2004.

One half of the experimental plots beneath each shelter were continuously warmed (24 h per day) with overhead infrared lamps (models MRM 1208L, Kalglo Electronic, Bethlehem, PA) that output 400 W (100 W m^{-2}) of radiant energy from a height of 1.5 m above the soil surface (Figure 2.1b) (Harte *et al.*, 1995; Shaw & Harte, 2001; Wan *et al.*, 2002). Due to increasing height of both *J. virginiana* and *Q. stellata*, all heaters were raised to 2 m (from 1.5 m) in February 2008, while output of heaters was doubled from 400 W to 800 W.

PLANT SPECIES COMBINATIONS

Two sets of five species combinations were grown in 2 × 2 m plots beneath each of the rainout shelters and two unsheltered controls. One set of plots was warmed with overhead infrared lamps while the other set was fitted with dummy lamps. *Schizachyrium scoparium*, *Q. stellata*, and *J.virginiana* were each grown in monoculture (25 plants per plot). In addition, each of the tree species was grown with the grass in separate mixed species plots (13 trees and 12 grasses) to investigate tree grass interactions.

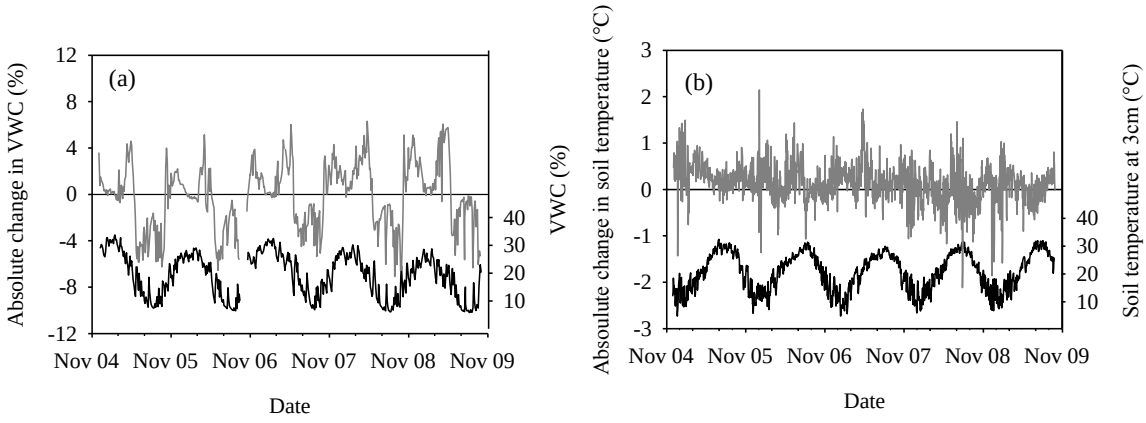

Figure 2.1. Effect of (a) precipitation on soil volumetric water content (VWC) over time averaged across plant species mixture and warming. The grey line depicts absolute change in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal soil VWC pattern. Effect of (b) warming treatment on soil temperature at 3 cm depth averaged across plant species mixture and precipitation distribution. The grey line depicts absolute change in soil temperature due to the warming treatment and the black line depicts the seasonal soil temperature pattern.

The plots were established in 2003 one year prior to the start of experiment treatments March 2004) from local transplants of *S. scoparium*, 1-yr-old bare root containerized *Q. stellat* and *J. virginiana* grown from native, regional seed sources. Monocultures of *J. virginiana* were thinned in December 2007. Twelve trees were removed from each monoculture plot. The remaining trees had the same spacing as the trees in the mixture plots (stem/trunk of each tree that were left were now 0.8 m apart, instead of 0.4 m). One year old transplant/replacement bare root *Q. stellata* seedlings were replanted as necessary in February 2008.

SOIL CO_2 EFFLUX

Collars (20 cm in diameter, 8 cm high, PVC pipe, with one drain hole at soil surface) were inserted 4 cm into the soil, in the central portion of each plot in May 2005. Collars were weeded 48 h prior to measurement being taken and drain holes were plugged during measurements. Soil CO_2 efflux was measured monthly from May 2005 to September 2009 using a soil chamber [Survey Chamber 8100-103 (20 cm diameter); LI-COR Inc., Lincoln, NE] connected to a CO_2 unit [LI-8100 Analyzer Control Unit; LI-COR Inc., Lincoln, NE] for data collection and storage. Soil temperature at 5 cm depth was measured using the attached soil temperature probe. Data collection problems occurred between March 2007 and July 2008 where unreliable temperature data were recorded. For all soil temperature analyses, these data were omitted from the dataset. Soil temperature after July 2008 was recorded at 5 cm depth with a hand held temperature probe (model no. SC-GG-K-30-36-PP Thermocouple and model no. HH309 Data Logger OMEGA Engineering, Inc., Stamford, CT). Annual soil CO_2 efflux was calculated from March to March, and seasonal averages were calculated and weighted according to length of season (2× spring, 5× summer, 2× autumn, 3× winter and divided by 12). Soil CO_2 effluxes were not directly averaged across year due to uneven measurement number across seasons and between years.

STATISTICAL DESIGN

Effect of precipitation redistribution, warming, and species mixtures on soil CO_2 efflux were analyzed using a mixed model with precipitation treatment, warming, and species mixtures as fixed effects and between shelter variations as a random effect. The precipitation, warming, and species treatment were arranged as a split-plot factorial, with a completely randomized design. The precipitation regimes constitute the whole plot factors (with four replications), while warming and species combination were assigned within-plot factors. Soil temperature and VWC

were used as covariates. All analysis were conducted with statistical analysis software (JMP 7.02 SAS Institute, Cary, NC).

Results

SOIL CO_2 EFFLUX AS AFFECTED BY THE TREATMENTS

Soil CO_2 efflux followed a general trend of lows in winter and highs in spring/summer regardless of warming and precipitation treatments (Tables 2.1 – 2.5; Figure 2.2 and Figure 2.3). Across the whole experiment, soil CO_2 flux rates were higher in *Q. stellata* mixture and lowest in the *Q. stellata* monoculture. There was no difference between *J. virginiana* monoculture and mixture and *S. scoparium* monoculture. Surprisingly, as the vegetation increased in size and cover, soil CO_2 efflux rates did not show a large increase over time. Soil CO_2 efflux was highest in year 1 and lowest in year 2 for *S. scoparium* monoculture and mixtures (Table 2.6; Figure 2.4a, c, and e). Soil CO_2 efflux was highest in years 1, 3, and 4 and lowest in year 2 for *J. virginiana* monoculture (Table 2.6; Figure 2.4b). Soil CO_2 efflux was highest in year 3 and lowest in year 1 and 2 for *Q. stellata* monoculture (Table 2.6, Figure 2.4d). Soil CO_2 efflux was inconsistently affected by precipitation and warming treatment across species (Table 2.6; Figure 2.5).

EFFECT OF SOIL VOLUMETRIC WATER CONTENT AND TEMPERATURE ON SOIL CO_2 EFFLUX

Soil CO_2 efflux showed a curvilinear relationship with VWC for all species and treatments (Table 2.7; Figures 2.6 and 2.7). Optimal soil CO_2 efflux rates were generally reached at a VWC of 15% after which soil CO_2 efflux rates started to decline. Soil CO_2 efflux was slightly higher with increasing soil VWC in the control precipitation treatment for *S. scoparium* monocultures(Table 2.7; Figure 2.6a). Soil CO_2 efflux was higher in the redistributed precipitation treatment when compared to the control precipitation treatment with increasing soil VWC for *J. virginiana* mixture (Table 2.7; Figure 2.6c), while precipitation distribution did not affect the relationship between soil VWC and soil CO_2 efflux in both tree monocultures and the *Q. stellata* mixture (Figure 2.6).

The relationship between soil VWC and soil CO_2 efflux was unaffected by the warming treatment in S. scoparium and J. virginiana monoculture and the J. virginiana-S. scoparium

Table 2.1. Probability values (*P*-values) and F-ratios determined using ANCOVA for annual soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) in 2005.

	CO_2 efflux					
	Spring 2005[z]		Summer 2005		Autumn 2005[z]	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.26	0.619	1.95	0.191	0.03	0.858
Warming (W)	0.11	0.742	0.16	0.691	0.14	0.712
P × W	1.91	0.997	1.99	0.159	0.03	0.871
Mixture (M)	1.63	0.211	5.48	**<0.001**	0.80	0.545
P × M	0.53	0.718	1.41	0.231	0.11	0.977
W × M	0.24	0.913	1.08	0.364	0.15	0.959
P × W × M	0.43	0.787	0.17	0.953	0.53	0.718
Soil VWC[y]	0.44	0.515	17.7	**<0.001**	0.00	0.972
P × VWC	1.98	0.176	11.2	**<0.001**	0.84	0.372
W × VWC	0.06	0.806	1.32	0.251	0.22	0.647
P × W × VWC	0.12	0.734	0.71	0.402	0.06	0.808
M × VWC	0.16	0.958	0.80	0.524	0.09	0.985
P × M × VWC	0.17	0.952	1.25	0.289	0.24	0.911
W × M × VWC	0.10	0.980	0.45	0.771	0.18	0.944
P × W × M × VWC	0.82	0.528	0.23	0.919	0.03	0.998
Soil temperature (T)	0.02	0.896	0.42	0.519	0.12	0.729
P × T	0.00	0.994	0.82	0.365	0.10	0.756
W × T	0.01	0.909	0.73	0.393	0.01	0.914
P × W × T	0.95	0.342	0.64	0.425	0.54	0.470
M × T	0.40	0.808	0.72	0.578	0.44	0.779
P × M × T	0.56	0.693	0.17	0.955	1.55	0.236
W × M × T	0.12	0.973	0.37	0.831	0.16	0.958
P × W × M × T	0.10	0.981	1.39	0.236	0.59	0.677
T × VWC	-	-	0.16	0.686	-	-
P × T × VWC	-	-	2.84	0.093	-	-
W × T × VWC	-	-	0.19	0.662	-	-
P × W × T × VWC	-	-	2.14	0.145	-	-
M × T × VWC	-	-	1.33	0.258	-	-
P × M × T × VWC	-	-	1.00	0.410	-	-
W × M × T × VWC	-	-	0.24	0.914	-	-
P × W × M × T × VWC	-	-	1.08	0.369	-	-

P-values ≤ 0.05 are printed in bold.

[z] Insufficient data collect in Spring and Autumn 2005 (only 1 survey) to allow running of volumetric water content (VWC) × soil temperature interaction.

[y] Soil volumetric water content (VWC).

Table 2.2. Probability values (*P*-values) and F-ratios determined using ANCOVA for annual soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) in 2006.

	CO_2 efflux							
	Winter 2006		Spring 2006		Summer 2006		Autumn 2006	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	3.08	0.107	0.01	0.913	0.47	0.505	0.29	0.602
Warming (W)	0.29	0.588	0.11	0.737	0.41	0.524	0.62	0.434
P × W	5.55	**0.020**	0.05	0.829	0.06	0.803	0.01	0.970
Mixture (M)	3.94	**0.005**	0.60	0.665	1.96	0.101	5.65	**<0.001**
P × M	4.01	**0.004**	1.06	0.385	1.37	0.244	0.68	0.610
W × M	0.40	0.809	1.20	0.319	1.48	0.208	0.89	0.475
P × W × M	1.58	0.183	0.42	0.796	2.61	**0.036**	0.23	0.921
Soil VWC[z]	2.49	0.120	0.54	0.465	1.38	0.240	0.08	0.777
P × VWC	0.59	0.445	3.19	0.079	2.28	0.132	1.18	0.281
W × VWC	1.95	0.165	0.57	0.452	0.04	0.841	0.06	0.804
P × W × VWC	0.59	0.444	0.82	0.368	1.51	0.219	1.38	0.244
M × VWC	0.33	0.860	1.38	0.252	0.38	0.824	0.82	0.518
P × M × VWC	0.32	0.863	0.20	0.938	0.54	0.709	0.91	0.465
W × M × VWC	0.64	0.637	1.18	0.328	0.75	0.558	0.12	0.976
P × W × M × VWC	0.69	0.599	0.87	0.487	1.33	0.260	0.32	0.863
Soil temperature (T)	2.66	0.105	0.17	0.683	7.48	**0.007**	2.69	0.105
P × T	0.08	0.783	0.23	0.632	1.17	0.280	0.99	0.324
W × T	0.32	0.570	0.22	0.641	1.70	0.193	0.60	0.441
P × W × T	1.74	0.189	0.50	0.481	1.06	0.303	4.92	**0.029**
M × T	1.78	0.136	0.19	0.944	1.71	0.147	1.80	0.137
P × M × T	1.07	0.372	1.80	0.140	1.15	0.335	0.28	0.893
W × M × T	1.42	0.229	0.29	0.884	0.96	0.429	1.20	0.319
P × W × M × T	0.72	0.580	0.44	0.776	0.89	0.472	0.60	0.662
T × VWC	1.31	0.255	0.16	0.689	7.97	**0.005**	0.04	0.836
P × T × VWC	2.26	0.135	0.56	0.458	6.84	**0.009**	0.29	0.592
W × T × VWC	6.54	**0.011**	0.46	0.501	2.67	0.104	1.67	0.201
P × W × T × VWC	0.39	0.535	0.17	0.678	1.22	0.269	7.25	**0.009**
M × T × VWC	0.64	0.635	0.63	0.641	1.26	0.285	0.97	0.431
P × M × T × VWC	0.67	0.615	0.72	0.584	0.86	0.488	1.06	0.380
W × M × T × VWC	4.65	**0.001**	0.23	0.922	1.22	0.302	1.34	0.263
P × W × M × T × VWC	3.79	**0.006**	0.23	0.920	0.69	0.596	1.87	0.123

P-values ≤ 0.05 are printed in bold.

[z] Soil volumetric water content (VWC).

Table 2.3. Probability values (*P*-values) and F-ratios determined using ANCOVA for annual soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) in 2007.

	CO_2 efflux							
	Winter 2007		Spring 2007[z]		Summer 2007[z]		Autumn 2007[z]	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.49	0.503	9.69	0.016	1.91	0.213	0.32	0.573
Warming (W)	0.00	0.978	0.08	0.777	0.29	0.593	0.29	0.594
P × W	0.13	0.719	0.02	0.888	0.37	0.544	2.70	0.103
Mixture (M)	1.17	0.332	14.1	**<0.001**	8.89	**<0.001**	1.00	0.410
P × M	1.33	0.267	1.57	0.183	1.16	0.328	1.43	0.229
W × M	0.58	0.676	2.27	0.062	2.53	**0.041**	2.32	0.061
P × W × M	1.35	0.259	2.77	**0.028**	3.28	**0.012**	1.23	0.304
Soil VWC[y]	21.6	**<0.001**	10.26	**0.002**	30.2	**<0.001**	0.61	0.435
P × VWC	0.36	0.550	2.36	0.126	9.14	**0.003**	0.64	0.425
W × VWC	0.43	0.514	1.21	0.272	0.03	0.865	0.27	0.602
P × W × VWC	0.13	0.723	0.23	0.629	0.52	0.470	0.05	0.830
M × VWC	0.27	0.899	7.78	**<0.001**	2.31	0.058	0.49	0.740
P × M × VWC	0.25	0.908	1.23	0.300	0.76	0.551	1.71	0.152
W × M × VWC	1.60	0.185	0.73	0.573	0.42	0.795	0.08	0.987
P × W × M × VWC	0.41	0.800	0.16	0.958	1.77	0.136	2.18	0.075
Soil temperature (T)	4.31	**0.041**	-	-	-	-	-	-
P × T	0.77	0.382	-	-	-	-	-	-
W × T	0.04	0.840	-	-	-	-	-	-
P × W × T	0.53	0.470	-	-	-	-	-	-
M × T	1.07	0.376	-	-	-	-	-	-
P × M × T	0.29	0.883	-	-	-	-	-	-
W × M × T	0.37	0.830	-	-	-	-	-	-
P × W × M × T	1.67	0.167	-	-	-	-	-	-
T × VWC	5.91	**0.018**	-	-	-	-	-	-
P × T × VWC	5.25	**0.025**	-	-	-	-	-	-
W × T × VWC	0.23	0.634	-	-	-	-	-	-
P × W × T × VWC	0.01	0.927	-	-	-	-	-	-
M × T × VWC	1.00	0.415	-	-	-	-	-	-
P × M × T × VWC	1.85	0.128	-	-	-	-	-	-
W × M × T × VWC	0.65	0.625	-	-	-	-	-	-
P × W × M × T × VWC	1.96	0.110	-	-	-	-	-	-

P-values ≤ 0.05 are printed in bold.

[z] Soil temperature not collected due to probe malfunction in Spring, Summer, and Autumn 2007.

[y] Soil volumetric water content (VWC).

Table 2.4. Probability values (*P*-values) and F-ratios determined using ANCOVA for annual soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) in 2008.

	CO_2 efflux							
	Winter 2008[z]		Spring 2008[z]		Summer 2008		Autumn 2008	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	2.44	0.138	0.18	0.679	0.14	0.712	0.46	0.500
Warming (W)	0.06	0.802	5.06	**0.026**	0.06	0.804	0.02	0.892
P × W	0.71	0.401	0.24	0.625	0.08	0.777	0.07	0.795
Mixture (M)	1.35	0.256	3.35	**0.012**	0.42	0.796	1.12	0.352
P × M	1.82	0.129	1.53	0.198	0.94	0.445	0.33	0.854
W × M	0.67	0.614	2.23	0.070	0.81	0.524	0.25	0.907
P × W × M	0.52	0.720	1.61	0.178	0.75	0.561	0.48	0.752
Soil VWC[y]	20.4	**<0.001**	0.01	0.913	0.12	0.727	0.02	0.902
P × VWC	4.58	0.035	2.37	0.126	4.80	**0.032**	0.24	0.624
W × VWC	0.56	0.457	2.89	0.092	0.28	0.597	0.12	0.735
P × W × VWC	3.73	0.056	0.01	0.924	0.56	0.457	0.10	0.758
M × VWC	0.85	0.498	0.97	0.425	0.59	0.671	0.04	0.996
P × M × VWC	0.94	0.444	0.79	0.531	0.68	0.611	0.10	0.983
W × M × VWC	1.79	0.135	1.04	0.387	0.37	0.832	0.07	0.991
P × W × M × VWC	0.99	0.418	0.62	0.648	0.25	0.912	0.04	0.997
Soil temperature (T)	-	-	-	-	0.80	0.375	0.00	0.982
P × T	-	-	-	-	0.09	0.767	0.18	0.672
W × T	-	-	-	-	0.18	0.675	0.08	0.784
P × W × T	-	-	-	-	0.37	0.543	0.59	0.446
M × T	-	-	-	-	0.27	0.895	0.09	0.984
P × M × T	-	-	-	-	0.32	0.866	0.88	0.483
W × M × T	-	-	-	-	0.14	0.966	0.13	0.972
P × W × M × T	-	-	-	-	0.42	0.792	0.71	0.590
T × VWC	-	-	-	-	0.20	0.660	5.44	0.999
P × T × VWC	-	-	-	-	0.38	0.541	1.16	0.286
W × T × VWC	-	-	-	-	0.01	0.912	0.01	0.937
P × W × T × VWC	-	-	-	-	0.11	0.737	0.50	0.482
M × T × VWC	-	-	-	-	0.13	0.971	0.11	0.977
P × M × T × VWC	-	-	-	-	0.33	0.856	1.00	0.412
W × M × T × VWC	-	-	-	-	0.54	0.710	0.06	0.994
P × W × M × T × VWC	-	-	-	-	0.32	0.862	0.48	0.748

P-values ≤ 0.05 are printed in bold.

[z] Soil temperature not collected due to probe malfunction in Winter and Spring 2008.

[y] Soil volumetric water content (VWC).

Table 2.5. Probability values (*P*-values) and F-ratios determined using ANCOVA for annual soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) in 2009.

	CO_2 efflux					
	Winter 2009		Spring 2009		Summer 2009	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.01	0.920	0.35	0.560	0.06	0.812
Warming (W)	0.05	0.829	1.05	0.309	0.07	0.790
P × W	0.11	0.746	2.22	0.141	0.00	0.968
Mixture (M)	6.13	**<0.001**	1.96	0.112	0.91	0.457
P × M	0.80	0.526	0.41	0.801	0.62	0.645
W × M	1.49	0.209	0.21	0.932	3.03	**0.018**
P × W × M	0.42	0.797	0.35	0.843	2.02	0.092
Soil VWC[z]	13.16	**<0.001**	0.00	0.969	5.08	**0.025**
P × VWC	1.66	0.200	0.80	0.375	0.30	0.586
W × VWC	0.05	0.826	0.01	0.931	3.75	0.054
P × W × VWC	0.01	0.926	0.25	0.616	0.33	0.564
M × VWC	0.99	0.416	0.28	0.889	3.41	**0.009**
P × M × VWC	0.26	0.905	0.66	0.621	1.19	0.316
W × M × VWC	0.43	0.786	0.11	0.978	0.60	0.666
P × W × M × VWC	0.62	0.651	0.32	0.865	0.32	0.865
Soil temperature (T)	40.9	**<0.001**	13.0	**<0.001**	7.90	**0.005**
P × T	1.57	0.212	0.95	0.334	0.10	0.749
W × T	0.27	0.603	1.48	0.228	3.55	0.061
P × W × T	0.20	0.654	1.93	0.169	0.05	0.818
M × T	1.04	0.389	1.22	0.310	3.04	**0.018**
P × M × T	0.69	0.598	0.84	0.505	1.03	0.390
W × M × T	0.57	0.688	0.92	0.456	1.34	0.254
P × W × M × T	1.26	0.289	0.91	0.463	0.38	0.820
T × VWC	0.30	0.584	1.01	0.318	48.3	**<0.001**
P × T × VWC	0.42	0.519	0.00	0.981	0.77	0.381
W × T × VWC	0.62	0.432	1.30	0.258	1.57	0.211
P × W × T × VWC	0.46	0.498	2.22	0.141	0.09	0.766
M × T × VWC	0.29	0.884	1.14	0.347	0.24	0.917
P × M × T × VWC	0.51	0.726	0.35	0.626	0.06	0.881
W × M × T × VWC	0.58	0.678	1.05	0.546	0.07	0.663
P × W × M × T × VWC	0.76	0.553	2.22	0.600	0.00	0.781

P-values ≤ 0.05 are printed in bold.

[z] Soil volumetric water content (VWC).

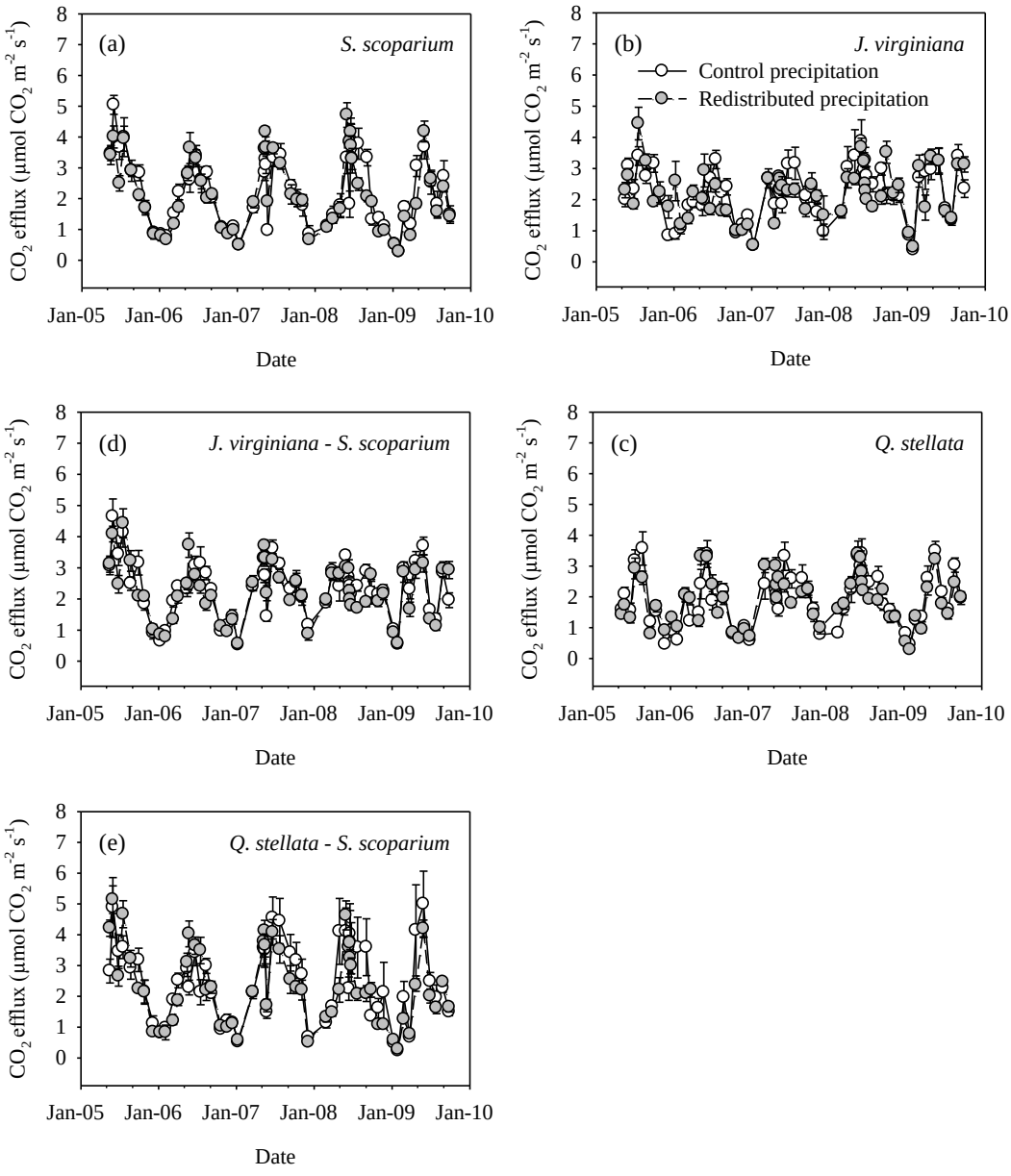

Figure 2.2. Soil CO_2 efflux ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$) through time for control precipitation (unfilled circle) and redistributed precipitation (filled circle) treatments averaged across warming treatments in (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium* (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* (means ± SE).

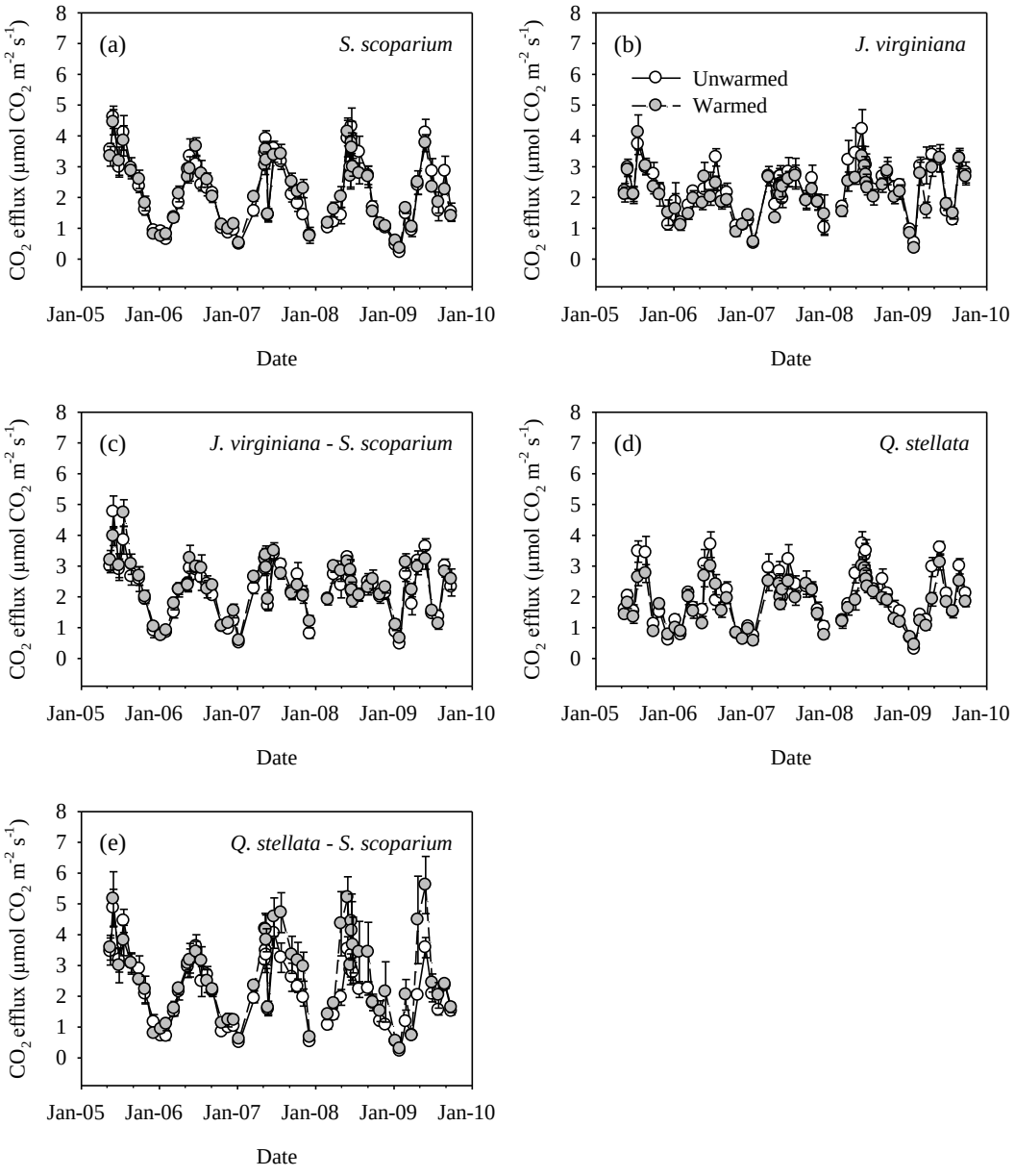

Figure 2.3. Soil CO_2 efflux ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$) through time for unwarmed (unfilled circle) and warmed (filled circle) treatments averaged across precipitation treatments in (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium* (d) *Quercus stellata* in a monoculture, and (e) *Q. stellata* grown with *S. scoparium* (means ± SE).

Table 2.6. Probability values (*P*-values) and F-ratios determined using ANOVA for annual soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}).

	Soil CO_2 efflux	
Treatment	F-ratio	*P*-value
Precipitation (P)	0.02	0.885
Warming (W)	0.30	0.583
P × W	4.23	**0.041**
Mixture (M)	17.5	**<0.001**
P × M	0.14	0.969
W × M	4.96	**<0.001**
P × W × M	10.2	**<0.001**
Year (Y)	22.8	**<0.001**
Y × P	0.39	0.760
Y × W	0.35	0.787
Y × P × W	0.86	0.462
Y × M	3.18	**<0.001**
Y × P × M	0.79	0.658
Y × W × M	0.73	0.724
Y × P × W × M	0.70	0.753

P-values ≤ 0.05 are printed in bold.
Data was log transformed.
Data was analyzed with soil volumetric water content as a covariate and was not significant (data not shown).

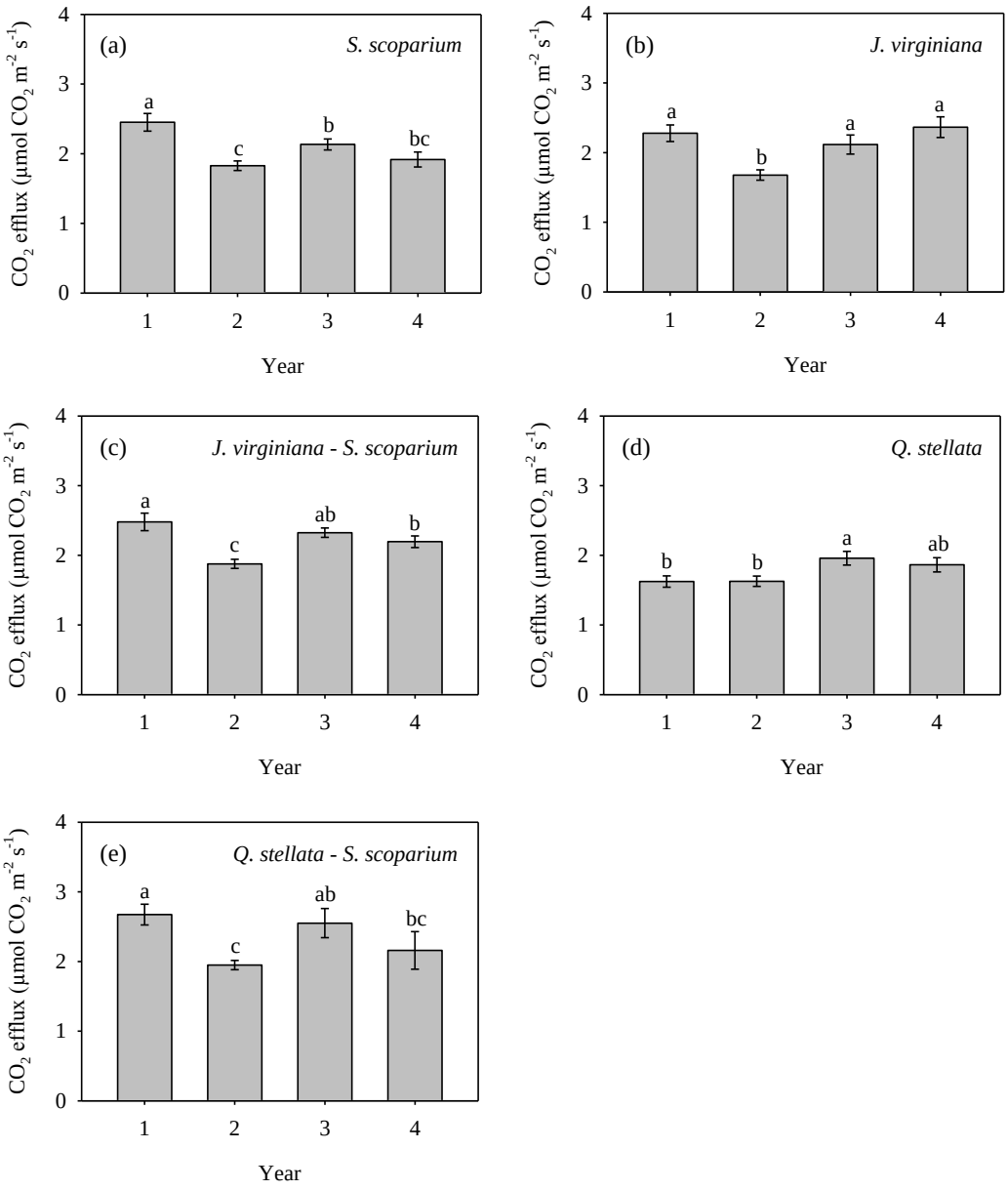

Figure 2.4. Effect of year on annual soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across warming and precipitation treatments in (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium* (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* from May 2005 to February 2009 (means ± SE). Years with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

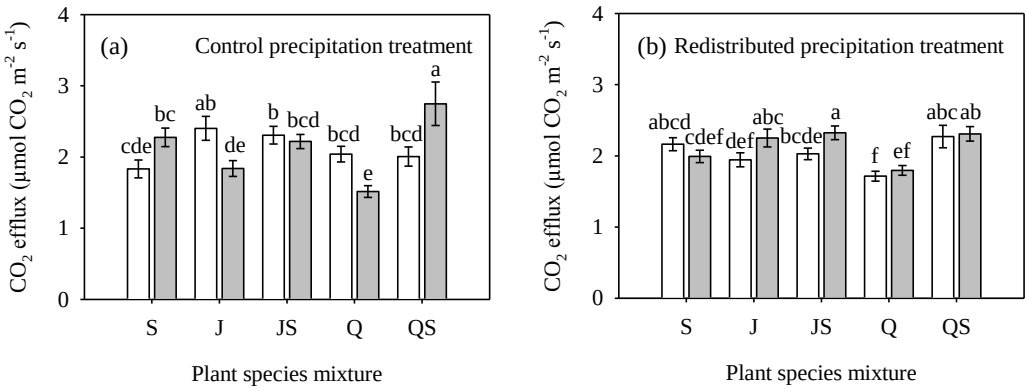

Figure 2.5. Effect of plant species mixture, warming, and (a) control precipitation treatment and (b) redistributed precipitation treatment on annual soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) from May 2005 to February 2009 (means ± SE). *Schizachyrium scoparium* monoculture (S), *Juniperus virginiana* monoculture (J), *J. virginiana* grown with *S. scoparium* (JS), *Quercus stellata* monoculture (Q), and *Q. stellata* grown with *S. scoparium* (QS). Filled bars depict warmed treatment (IR lamp 100 W m^{-2}) and unfilled bars depict unwarmed treatment. Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

Table 2.7. Probability values (*P*-values) and F-ratios determined using ANCOVA for survey soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) for May 2005 to September 2009.

	CO_2 efflux									
	S. scoparium		*J. virginiana*		*J. virginiana – S. scoparium*		*Q. stellata*		*Q. stellata – S. scoparium*	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	7.01	**0.038**	0.05	0.832	6.06	**0.050**	3.50	0.111	1.07	0.340
Soil VWC[z]	85.9	**<0.001**	30.3	**<0.001**	66.8	**<0.001**	18.2	**<0.001**	58.8	**<0.001**
P × VWC	0.03	0.868	0.83	0.364	0.13	0.714	3.27	0.071	0.16	0.6882
Warming (W)	0.93	0.337	2.50	0.115	0.06	0.813	17.9	**<0.001**	6.37	**0.012**
W × P	17.9	**<0.001**	16.6	**<0.001**	4.88	**0.028**	13.0	**<0.001**	8.24	**0.004**
W × VWC	0.93	0.336	0.20	0.657	0.31	0.582	0.59	0.444	0.01	0.910
Soil temperature (T)	32.8	**<0.001**	23.8	**<0.001**	37.6	**<0.001**	133.1	**<0.001**	17.7	**<0.001**
P × T	1.85	0.175	4.89	**0.028**	8.27	**0.004**	0.37	0.544	0.18	0.671
W × T	1.57	0.211	0.74	0.390	0.10	0.748	0.23	0.631	0.38	0.540

P-values ≤ 0.05 are printed in bold.

[z] Soil volumetric water content (VWC).

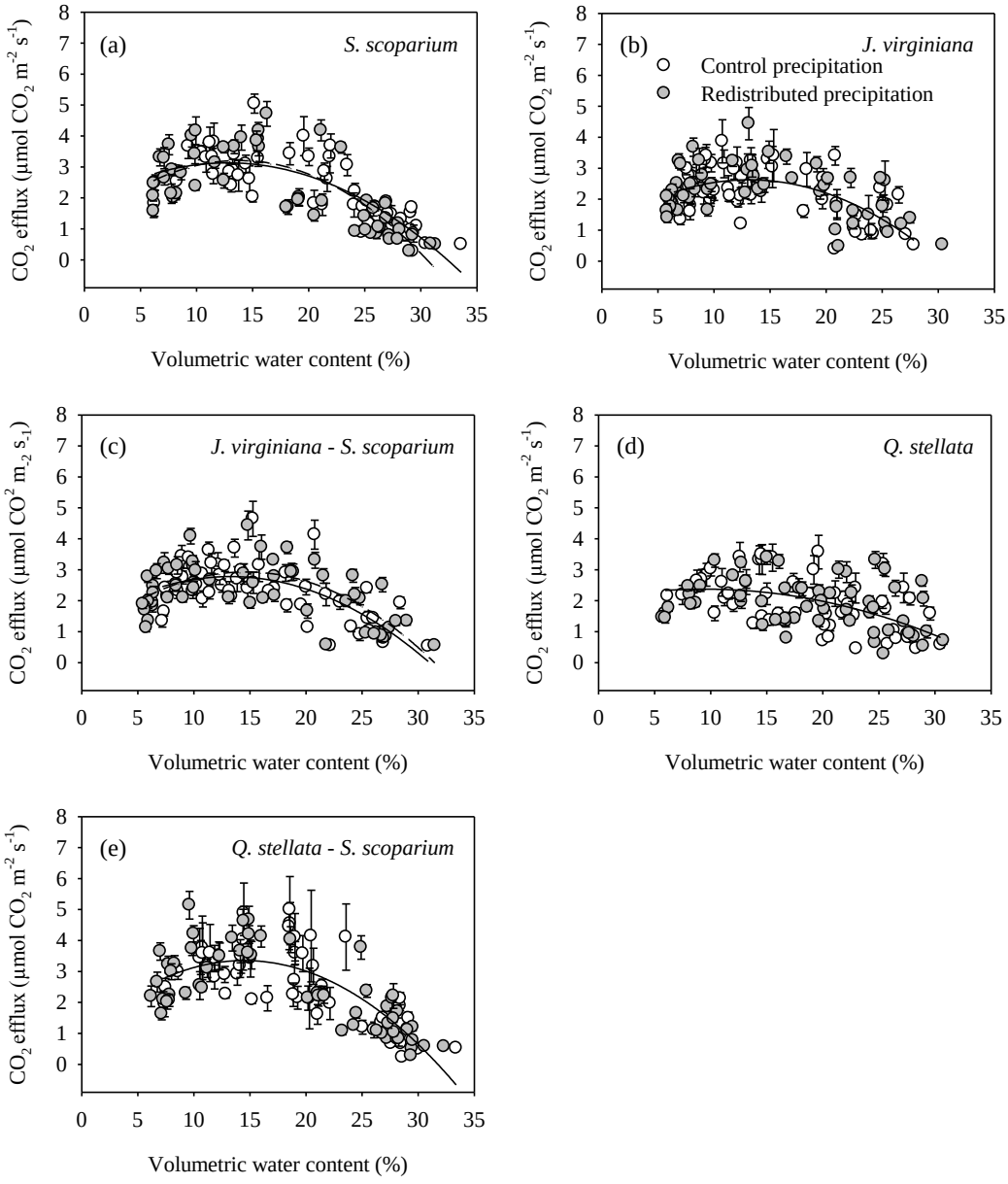

Figure 2.6. Effect of volumetric water content (%) on CO_2 efflux ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$) for control precipitation (unfilled circle) and redistributed precipitation (filled circle) treatments averaged across warming treatments in (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium* (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* (means ± SE). Statistically significant ($P < 0.05$) regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (a) *S. scoparium* control precipitation, $r^2 = 0.653$; redistributed precipitation, $r^2 = 0.626$ and (c) *J. virginiana – S. scoparium* control precipitation, $r^2 = 0.465$; redistributed precipitation $r^2 = 0.476$. Single line depicts significant trend for (b), *J. virginiana*, $r^2 = 0.357$, (d) *Q. stellata*; control precipitation, $r^2 = 0.268$, and (e) *Q. stellata – S. scoparium* control precipitation $r^2 = 0.603$.

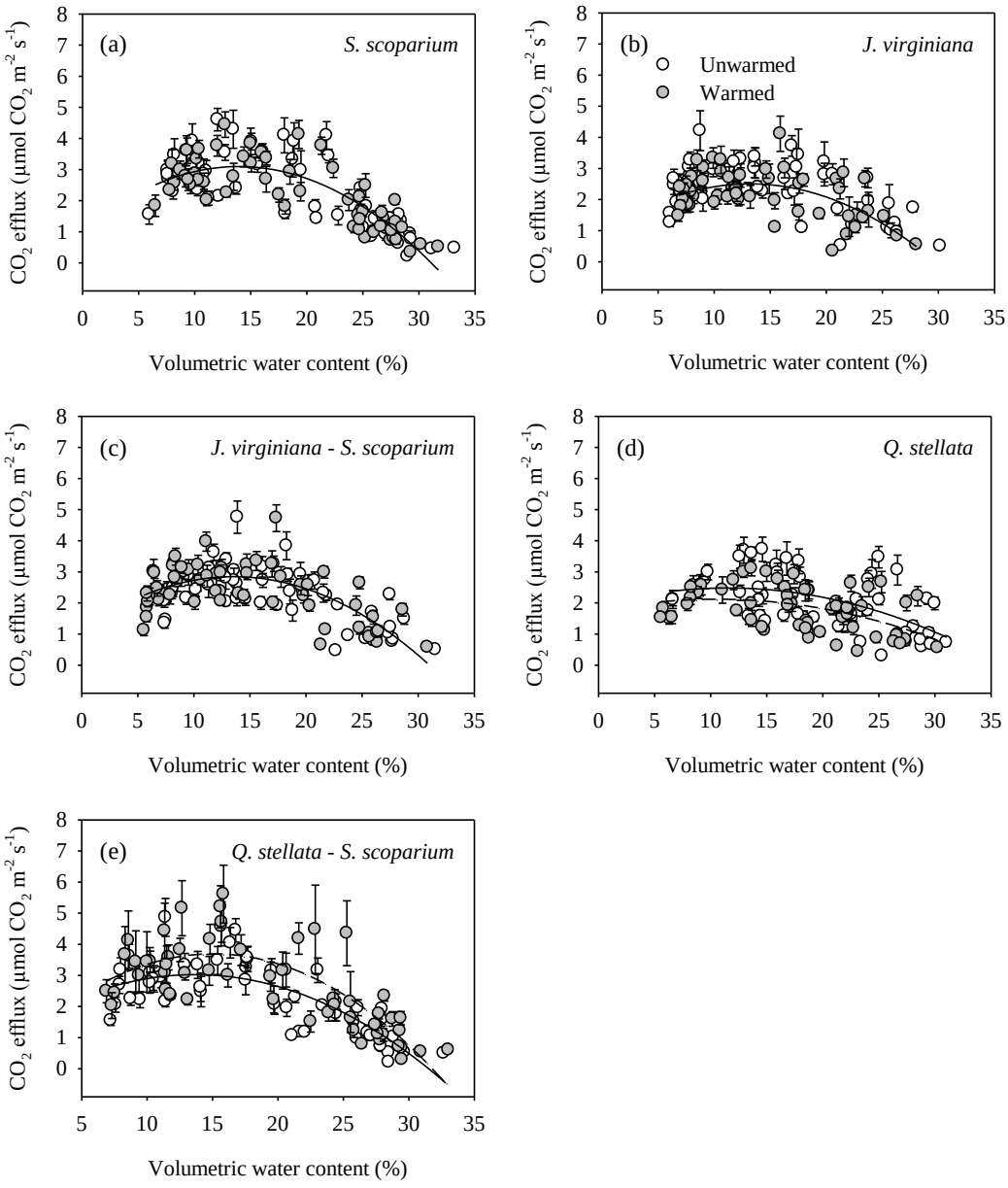

Figure 2.7. Effect of volumetric water content (%) on CO_2 efflux ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$) for unwarmed (unfilled circle) and warmed (filled circle) treatments averaged across precipitation treatments in (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium* (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* (means ± SE). Statistically significant ($P < 0.05$) regression relationships are depicted for unwarmed (solid line) and warmed (dashed line) treatments; (d) *Q. stellata*; unwarmed $r^2 = 0.269$; warmed $r^2 = 0.232$ and (e) *Q. stellata – S. scoparium* unwarmed, $r^2 = 0.630$; warmed, $r^2 = 0.610$. Single line depicts significant trend for (a) *S. scoparium*, $r^2 = 0.683$, (b) *J. virginiana* $r^2 = 0.324$ and (c) *J. virginiana – S. scoparium*, $r^2 = 0.465$.

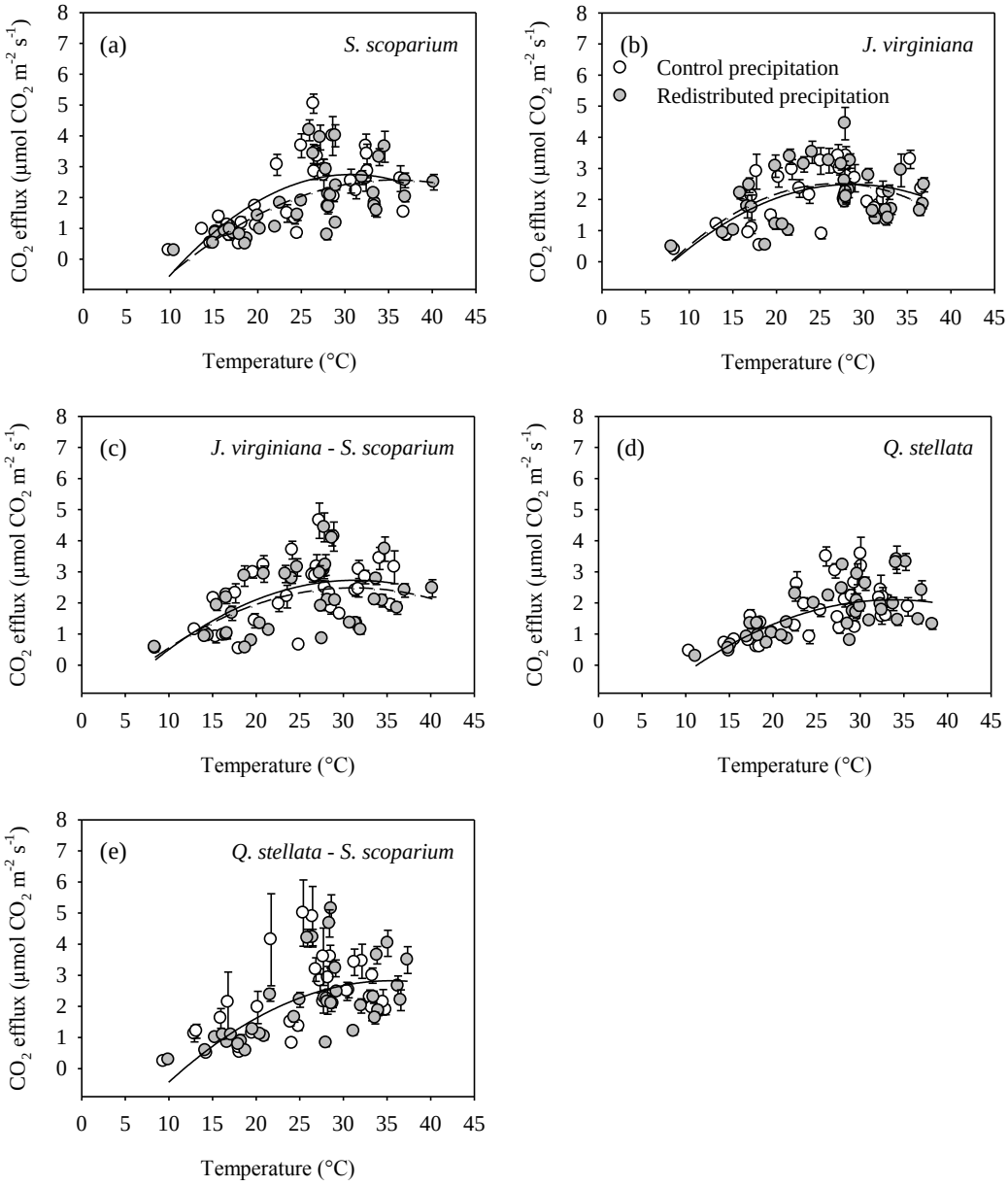

Figure 2.8. Effect of soil temperature (°C) on CO_2 efflux ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$) for control (unfilled circle) and redistributed precipitation (filled circle) treatments averaged across warming treatments in (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium* (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* (means ± SE). Statistically significant ($P < 0.05$) regression relationships are depicted for control (solid line) and redistributed precipitation (dashed line); (a) *S. scoparium* control, $r^2 = 0.4996$; redistributed precipitation, $r^2 = 0.457$, (b) *J. virginiana* control, $r^2 = 0.385$; redistributed precipitation, $r^2 = 0.276$, and (c) *J. virginiana – S. scoparium* control, $r^2 = 0.348$; redistributed precipitation, $r^2 = 0.239$. Single line depicts significant trend for (d) *Q. stellata*, $r^2 = 0.456$ and (e) *Q. stellata – S. scoparium*, $r^2 = 0.411$.

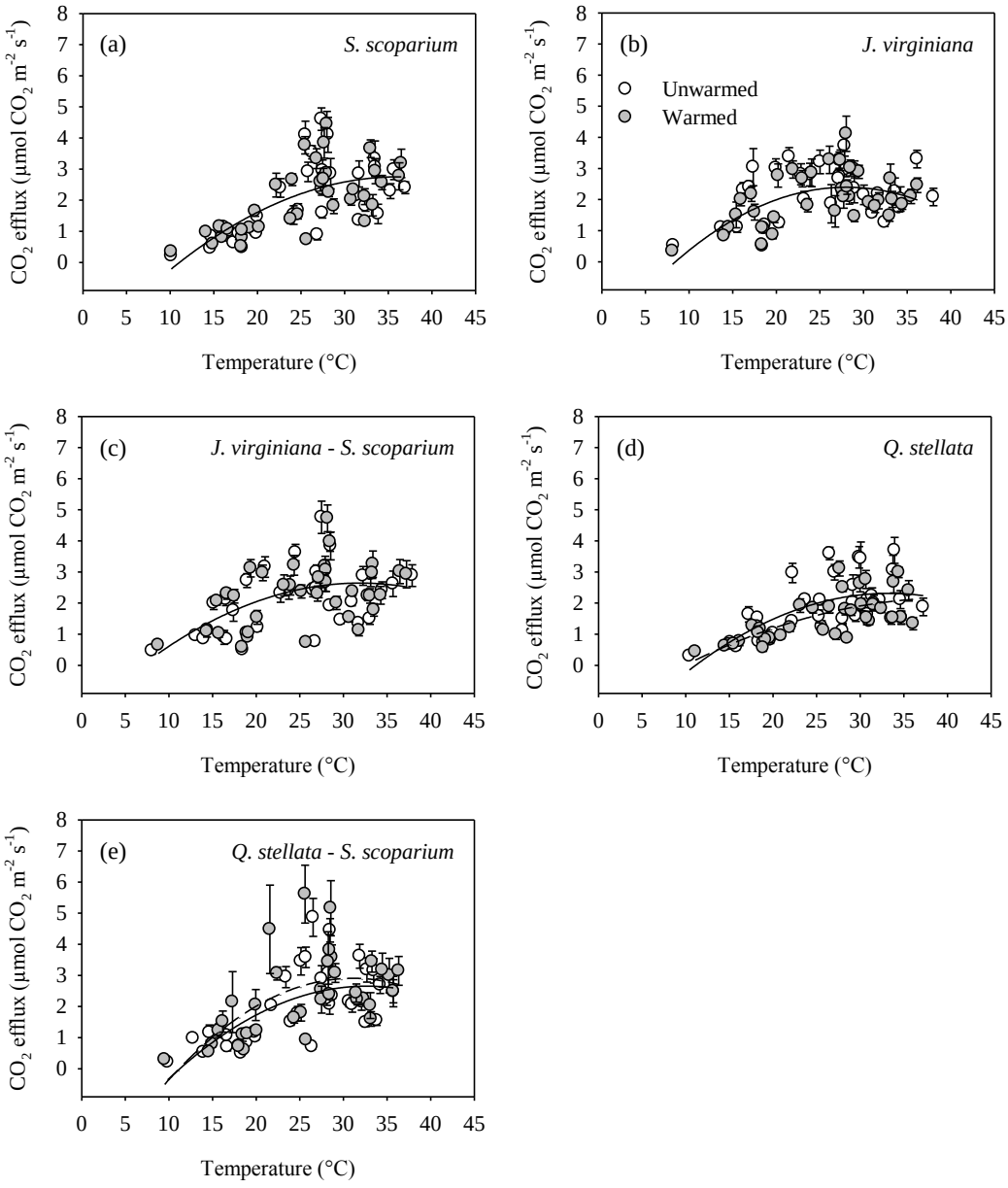

Figure 2.9. Effect of soil temperature (°C) on CO_2 efflux ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$) for unwarmed treatment (unfilled circle) and warmed treatments (filled circle) averaged across precipitation treatments in (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium* (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* (means ± SE). Statistically significant ($P < 0.05$) regression relationships are depicted for unwarmed (solid line) and warmed (dashed line) treatments; (d) *Q. stellata* unwarmed, $r^2 = 0.435$; warmed, $r^2 = 0.495$ and (e) *Q. stellata* – *S. scoparium* unwarmed, $r^2 = 0.453$; warmed, $r^2 = 0.377$. Single line depicts significant trend for (a) *S. scoparium*, $r^2 = 0.493$, (b) *J. virginiana*, $r^2 = 0.372$, and (c) *J. virginiana* – *S. scoparium*, $r^2 = 0.284$.

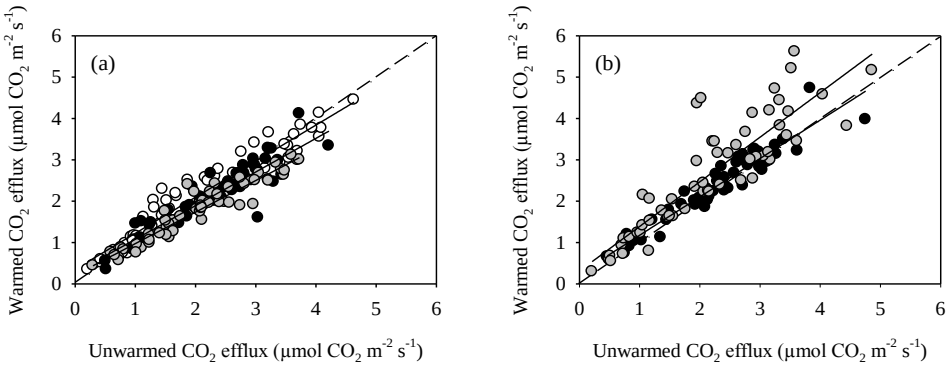

Figure 2.10. Relationship between unwarmed soil CO_2 efflux (µmol·CO_2·m^{-2}·s^{-1}) and warmed soil CO_2 efflux (µmol·CO_2·m^{-2}·s^{-1}) averaged across precipitation treatments for (a) *Schizachyrium scoparium* monoculture (white circles), *Juniperus virginiana* monoculture (black circles), *Quercus stellata* monoculture (grey circles) and (b) *J. virginiana* grown with *S. scoparium* (black circles), *Q. stellata* grown with *S. scoparium* (grey circles) (means). Statistically significant ($P < 0.05$) regression relationships are depicted for (a) *S. scoparium* monoculture, $r^2 = 0.932$; *J. virginiana* monoculture CO_2, $r^2 = 0.835$; *Q. stellata* monoculture, $r^2 = 0.906$ and (b) *J. virginiana – S. scoparium* mixture, $r^2 = 0.912$; *Q. stellata – S. scoparium* mixture, $r^2 = 0.774$. Dashed line is 1:1 line. The mean slope was 0.89 ± 0.024, intercept 0.027 ± 0.057. The slope for the *Q. stellata* monoculture was less than the mean slope ($P = 0.012$) and the slope for the *Q.* stellata mixture was greater than the mean slope ($P < 0.001$).

mixture. However, soil CO_2 efflux at the same VWC was lower in the warmed treatment when compared to the unwarmed treatment for *Q. stellata* monoculture (Table 2.7; Figure 2.7d), while soil CO_2 efflux at the same VWC was higher in the warmed treatment when compared to the unwarmed treatment in the *Q. stellata – S. scoparium* mixture (Table 2.7; Figure 2.7e). Soil CO_2efflux showed a curvilinear relationship with soil temperature for all species and treatments (Table 2.7; Figures 2.8 and 2.9). Optimum temperature for soil CO_2 efflux ranged from 35 to 40°C (Figures 2.8 and 2.9). The redistributed precipitation pattern reduced soil CO_2 efflux for *S. scoparium* monoculture and *J. virginiana* mixture at the same soil temperature (Table2.7; Figure 2.8a and c). Soil CO_2 efflux was inconsistently affected by precipitation treatment as soil temperature increased for *J. virginiana* monoculture (Table 2.7; Figure 2.8b). Soil CO_2 efflux was lower in the warmed treatment when compared to the unwarmed treatment at the same soil temperature for *Q. stellata* monoculture (Table 2.7; Figure 2.9d). Soil CO_2 efflux was higher in the warmed treatment when compared to the unwarmed treatment at the same soil temperature for *Q. stellata* mixture (Table 2.7; Figure 2.9e). Soil CO_2 efflux was inconsistently affected by precipitation and warming treatments for all species (Table 2.7). Warming reduced soil CO_2 efflux in *J. virginiana* and *Q. stellata* monoculture and enhanced soil CO_2 efflux in *Q. stellata* mixture (Figure 2.10). *Schizachyrium scoparium* monoculture and mixture and *J. virginiana* monoculture slope were not different from the mean slope (mean slope 0.89 ± 0.024; intercept 0.27±0.057). *Quercus stellata* monoculture slope was less than the mean slope ($P = 0.012$) and the *Q.* stellata mixtureslope was greater than the mean slope ($P < 0.001$).

Discussion

Soil CO_2 efflux in this study followed a general seasonal trend of lows in winter and highs in spring/summer regardless of additional warming and precipitation. On a seasonal basis the effects of temperature on soil CO_2 efflux rates may be confounded by the effects of shoot and root growth and changes in root biomass (Epron *et al.*, 2001). Soil temperature and moisture alone frequently do not explain the difference in soil CO_2 efflux between sites (Raich & Schlesinger, 1992; Davidson *et al.*, 1998; Janssens *et al.*, 2001) as resource pulses from the dominant vegetation also exert temporal effects on belowground organisms and processes and may be the main driver of soil CO_2 efflux while environmental conditions modulate the response to these pulses (Yang *et al.*, 2008). For example, increasing spring temperatures and longer days

result in increased shoot growth, photosynthetic activity, and also soil respiration during the first flush in deciduous trees (Yuste *et al.*, 2004). C supply to the roots varies seasonally, as do soil temperature and soil water availability, thus making it difficult to separate direct effects of soil parameters during overlapping periods of optimal plant growth conditions (Raich & Potter, 1995; Ryan & Law, 2005). Edwards *et al*. (2004) suggested that increased soil CO_2 efflux during spring and summer is a function of increasing light availability and greater photosynthetic activity and C allocation, rather than a soil warming effect Changes in plant productivity would not only affect soil CO_2 efflux related to root activity, but also alter the supply of C to the soil through root exudates and thus the structure and activity of microbial communities and associated CO_2 release (Bardgett *et al.*, 2008).

In our study the initially high soil CO_2 efflux in year 1 followed by low soil CO_2 efflux in year 2 may reflect an artefact of the experimental system with collar installation disturbance (Guo & Gifford, 2002). Inter-annual variability in soil CO_2 efflux has been observed in various mature ecosystems, including; grasslands (Flanagan *et al.*, 2002), mixed temperate forest (Savage & Davidson, 2001), and pine forest (Irvine & Law, 2002), and in most cases has been attributed to climatic variation, changes in soil temperature and soil VWC, and/or duration of growing season, and subsequent changes in leaf emergence, and/or stand structure (Raich & Schlesinger, 1992; Raich & Potter, 1995; Raich & Tufekcioglu, 2000). In our study, soil CO_2 efflux was initially highest in plots with *S. scoparium,* however as the plants matured soil CO_2 efflux was highest in plots with *J. virginiana*. Surprisingly, over time soil CO_2 efflux remained at a steady state in the tree monocultures, even though standing aboveground biomass increased more than 9-fold for *J. virginiana* and 115-fold for *Q. stellata* over the same time period (Volder *et al.*, unpublished data).

In our study rates of soil respiration were low in dry conditions and then reached a maximum rate under intermediate soil VWC levels, and then decreased at high soil VWC levels, likely due to anaerobic conditions which reduce microbial and root activity (Davidson *et al.*, 2000). Soil water content directly influences soil CO_2 efflux through drought water limitation stress on plant roots and microbes and indirectly through plant productivity and C allocation (Liu *et al.*, 2002; Xu *et al.*, 2004). Anaerobic soil conditions slow down root growth and root respiration (Drew, 1997) and may cause shallow root systems and reduce plant size/growth (Kozlowski, 1999; Kozlowski & Pallardy, 2002). High soil VWC can lower gas diffusion rates (Hirano *et al.*, 2003) and decrease soil CO_2 efflux (Liu *et al.*, 2002; Hirano *et al.*, 2003).

Soil CO_2 efflux was inconsistently affected by precipitation treatment with increasing soil VWC for *S. scoparium*, while soil CO_2 efflux was higher in redistributed precipitation treatment when compared to the control precipitation treatment with increasing soil VWC for *J. virginiana* mixture. Reflecting that plant species in our study differ in their response to the long term effects of the precipitation distribution, i.e., receiving more precipitation in the spring and fall and less in the summer. Furthermore, low VWC does not have a strong negative effect on soil CO_2 efflux when compared to high soil VWC. Suggesting that in our system, with drought adapted plants, soil CO_2 efflux will respond more negatively to soil saturated conditions than drought conditions.

Soil CO_2 efflux increased with increasing soil temperature for all species and treatments, probably reflecting increased root and microbial activity at higher soil temperatures (Boone *et al.*, 1998), or availability of photosynthates as daylight hours also increase as soil temperature increases (Fitter *et al.*, 1999; Edwards *et al.*, 2004). Soil CO_2 efflux declined or reached a steady state across all species at higher temperatures (>35°C), suggesting generally suboptimal temperatures for root growth and microbial activity in our system. Thus, we expected soil warming to generally increase soil CO_2 efflux.

Although our warming treatment did not strongly heat the soil, particularly as the plants grew larger in canopy, adding experimental warming did increase soil CO_2 efflux in the *Q. stellata* mixture. Conversely, soil CO_2 efflux was lower in the warmed *Q. stellata* monoculture when compared to the unwarmed treatment. This may have been related to aboveground responses to warming where trees in the *Q. stellata* monoculture exhibited reduced growth when exposed to warming (unpublished data), while grass growth in the mixed plots may have been stimulated by warming. Soil CO_2 efflux was higher in the control precipitation when compared to the redistributed precipitation treatment at the same soil temperature for *S. scoparium* monoculture and *J. virginiana* mixtures. As the redistributed precipitation treatment was exposed to more extreme flooding and drought conditions it may be less capable of rewetting (Goebel *et al.*, 2011). Soils dry faster as they increase in temperature, causing a decrease in the rate of diffusion of soluble substrates as the soil water films thin, thus reducing soil CO_2 efflux. Warming may have mitigated the effects of precipitation redistribution during the wet spring months, and exacerbated the effects of rainfall redistribution during the dry summer months. In that, soil CO_2 efflux is less sensitive to temperature at low soil VWC and is more responsive to

temperature at high soil moisture (Carlyle & Than, 1988; Harper *et al.*, 2005) (see also Figure 2.7e).

Alternatively, this study reflects the problems and inconsistent results reported in the literature, in that a variety of experimental warming treatments have been reported to increase, or have inconsistent to no effect on soil CO_2 efflux depending on plant cover and climatic conditions (Rustad *et al.*, 2001). The lack of a consistent relationship between soil temperature and soil CO_2 efflux in this study may reflect the lack of an effective warming treatment in a already 'warm' environment (i.e. ambient temperature at study site was already relatively high and the infrared heater failed to consistently raise soil temperatures, but it did increase canopy temperatures). In addition, it remains unclear whether higher soil CO_2 efflux in dry soil represent CO_2 from deeper soil layers and root systems even when upper soil layer roots and microbes are under significant drought stress. Soil temperature may also indirectly affect root respiration due to its effect on root growth, with root growth increasing with increasing temperatures until an optimal temperature is reached, which varies depending on plant species (McMichael & Burke, 1998). Furthermore, the lack of response to the warming treatment may reflect reduced response to higher temperature as a result of acclimation (Tjoelker *et al.*, 1999; Atkin & Tjoelker, 2003), and/or depletion of soil organic matter and C substrates (Kirschbaum, 2004; Eliasson *et al.*, 2005) which may result in relatively reduced CO_2 efflux at sustained higher temperatures.

Conclusion

In our study we observed inter-annual variability in soil CO_2 efflux, probably as a result of climatic variation, changes in soil temperature and soil VWC content, and/or duration of growing season, and subsequent changes in plant growth. Surprisingly, over time annual soil CO_2 decreased in the *S. scoparium* monoculture and mixtures and remained at a steady state in the tree monocultures, probably reflecting the plant establishment period and potentially stabilization of the belowground system irrespective of above ground activity. Soil CO_2 efflux in this study varied with seasonal changes in soil VWC and temperature, with higher respiration rates in the spring and lower rates in both the cooler winter season and at the end of the dry summer period. We suggest that observed differences in soil respiration rates between plant communities growing on the same soil type and within the same climatic conditions were likely due to differences in root production, specific root respiration and standing root length, as well

as potential species effects on microclimatic conditions and changes in microbial biomass and composition. Overall, the effect of species combination was greater than that of either treatment. These findings suggest that soil CO_2 efflux in oak savannah will likely respond more to changes in species composition than to direct effects of climate drivers. Further progress in understanding the spatial and temporal patterns of soil CO_2 efflux respiration in post oak savannah will require separating out the effect of climate drivers on the autotrophic and heterotrophic components of soil CO_2 efflux.

CHAPTER III
SHORT-TERM CHANGES IN SOIL CO_2 EFFLUX IN RESPONSE TO INCREASED SOIL VOLUMETRIC WATER CONTENT AS AFFECTED BY PRECIPITATION DISTRIBUTION, PLANT SPECIES, AND WARMING

Introduction

Oak savannah in the south-central United States is dominated by three contrasting plant functional types: *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) a C_4 grass, *Quercus stellata* Wangenh. (post oak) a C_3 deciduous tree, and *Juniperus virginiana* L. (eastern redcedar) a C_3 evergreen tree. Increasing woody plant encroachment has been observed in these ecosystems in the last decades (McPherson, 1997; Scholes & Archer, 1997). The oak-savannah ecosystem is an ecotone where the grasslands of the west meet the deciduous forests of the east, and thus represents a unique ecosystem where species composition may be especially sensitive to changes in temperature and soil water availability. Climate change models project an increase in the intensity and variability of summer drought and precipitation events in the United States (Groisman *et al.*, 2005; Groisman & Knight, 2008).

A major concern is whether changes in species composition may lead to enhanced release of carbon dioxide (CO_2) from the soil. In general, soil CO_2 efflux rates are dependent on soil conditions such as temperature, moisture, and chemical and biological properties, as well as species composition, and seasonal changes in climate (Raich & Schlesinger, 1992; Raich & Tufekcioglu, 2000; Ryan & Law, 2005). Seasonal changes in climate affect soil CO_2 efflux directly through soil water availability and temperature effects on both microbial and root respiration and indirectly as new root production and carbon (C) supply to the roots vary seasonally (Raich & Potter, 1995). Rates of soil CO_2 efflux are associated with the size of both the root and microbial pool and the activity of each pool (Hanson *et al.*, 2000). Thus, soil water availability may inconsistently affect soil CO_2 efflux depending on the seasonal timing of the rainfall or drought event.

Precipitation events and soil water content (VWC) also affect soil CO_2 flux directly. Small precipitation events on dry soils may result in relatively sudden increases in soil CO_2 efflux, as the result of displacement of oxygen (O_2) and CO_2 in soil pore spaces (Liu *et al.*, 2002; Xu *et al.*, 2004). Therefore, under drought conditions, soil CO_2 efflux rates may increase rapidly

for a short period after relatively small precipitation events that do not saturate the soil. However, following relatively large soil saturating precipitation events, the resulting water saturated soil may inhibit CO_2 diffusion through the soil and decrease soil CO_2 efflux (Liu *et al.*, 2002; Hirano *et al.*, 2003).

Carbon flux to both the roots and microbes may also be affected by soil water conditions. Drought events may lead to a decoupling of root growth and respiration from aboveground photosynthetic activity and root growth and respiration may become more dependent on stored carbohydrate reserves (Hogberg *et al.*, 2001). Reduced photosynthetic activity can reduce the flow of C into the roots and rhizosphere, and thus induce soil microbe dormancy or mortality, resulting in reduced microbial growth and activity. Thus, following a precipitation event, reported increases in soil CO_2 efflux may, in part, primarily be due to rapid a microbial response to increased substrate availability due to resumption of plant photosynthesis and C flow into the rhizosphere (Kelliher *et al.*, 2004). Relatively more C would temporarily become available to the microbes since root growth and respiration resume more slowly than photosynthetic activity (Ryan & Law, 2005).

Soil VWC is also likely to affect temperature sensitivity of soil CO_2 efflux. Under conditions of low VWC, drought restrictions on photosynthetic activity, which provides substrates to a portion of microbes in the rhizosphere, and microbial activity may lead to a reduced response to increasing soil temperatures. Similarly, under saturated soil conditions limitations, on CO_2 diffusion may limit responsiveness to increased soil temperature conditions. Thus, we expect that CO_2 efflux is most sensitive to soil temperature in soils of medium soil water content.

The size and frequency of precipitation and drought events may induce considerable variability in soil CO_2 efflux, which may be attributed to a variety of interactive responses, including duration and intensity of precipitation and drought events and dominant plant species interactions. The broad objective of this study was to explore the effects of plant species and soil VWC on soil CO_2 efflux rates in southern oak savannah. We collected soil CO_2 efflux data and soil VWC, before and after precipitation events in May 2006, May 2007, and June 2008. The goal was to quantify the effects of plant species composition and summer precipitation distribution on soil CO_2 efflux rates in southern oak savannah. We hypothesized that: (i) soil CO_2 efflux will generally increase with increasing soil VWC but will be reduced under extreme low and high VWC conditions, (ii) warming will generally increase soil CO_2 efflux, but the

magnitude of this response will be dependent on VWC conditions, and (iii) soil CO_2 efflux will vary with plant species mixture according to rooting density.

Materials and Methods

EXPERIMENTAL SITE AND INFRASTRUCTURE

The Texas warming and rainfall manipulation experiment (Texas WaRM Experiment) is located on a remnant post oak savannah site (30°34 N 96°21 W) near Texas A&M University, College Station, Texas. This facility was constructed in 2003 to investigate the combined effects of altered precipitation distribution and warming on tree grass dominants of southern oak savannah. The research infrastructure included eight permanent 18 × 9 × 4.5 (L × W × H) rainout shelters covered with clear polypropylene film. The side walls below 1.5 m were open to maintain microclimate conditions as near ambient as possible, but effectively exclude precipitation (Fay *et al.*, 2000; Weltzin & McPherson, 2003). A fine mesh shade cloth matching the radiation attenuation of the film (70% transmittance), excludes windblown precipitation from entering two 4.5 m high open ends of each shelter. Sheet metal flashing 40 cm in height, was inserted 30 cm into the soil penetrating the clay hardpan, to isolate each shelter from surface and subsurface water flow.

Ten 2 × 2 m plots with five species combinations were located beneath each shelter in the native soil (Volder *et al.*, 2010). Soil consisted of a shallow layer (< 20 cm) of Boonville fine sandy loam, with a thick clay pan below (Chervenka, 2003). An overhead irrigation system (17 pressure regulated spray nozzles per shelter) simulated precipitation regimes by supplying reverse osmosis (RO) treated ground water, from four 11,500 L holding tanks, to each shelter. A weather station (EZ Mount GroWeather, Davies Instruments, Hayward, CA) on site recorded precipitation, air temperature, and humidity. Solar radiation (total PPFD), air temperature, and relative humidity were continuously monitored in each shelter and control plots using data logger (Hobo U12, Onset Company Corp., Bourne, MA). Soil water content was measured for each plot using permanently installed time domain reflectometry (TDR) probes (Soil Moisture Corp., Santa Barbara, CA,) which were inserted vertically to give an integrated measure of soil VWC in the top 20 cm of the soil profile. Soil VWC was measured on the15 and 24 of May during the 2006 campaign, 10, 14, 16 and 24 of May during the 2007 campaign and 12, 16, 18, and 24 June during the 2008 campaign. The rainout shelter design preserves natural variation in

the microenvironment that is for the most part similar to ambient conditions (Fay *et al.*, 2000). Mean daily temperature in the shelters was on average 0.3 °C higher, RH values were 2% lower, and PPFD levels were 30% lower than ambient.

PRECIPITATION AND WARMING TREATMENT

Simulated precipitation regimes included two patterns that varied in season distribution and event size, but not in total annual precipitation (1018 mm) or total number of events. The long-term (50 yr) precipitation events were also simulated from the regional long-term precipitation record. The frequency and intensity (amount) of precipitation events were also simulated from the regional long-term precipitation record. Precipitation redistribution treatment imposed beneath the other four shelters had 40% of the summer (May – September) precipitation withheld from each event and evenly redistributed to the preceding spring (March and April) and autumn (October and November). The redistribution treatment effectively increased the intensity of the summer drought (redistribution dry phase) and the amount of precipitation that occurs during the cooler season of the year (redistributed wet phase) (Figure 3.1). Each precipitation regime was replicated within four rainout shelters. Precipitation regimes were initiated in March 2004. Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on the 19, 20, 22, and 23 of May, respectively, for the 2006 and 2007 campaigns. Precipitation event size for the control treatment were 9.7 and 29.7, and redistributed treatment were 5.8 and 17.8, on the 10 and 11 of June, respectively, for the 2008 campaign.

One half of the experimental plots beneath each shelter were continuously warmed (24 h per day) with overhead infrared lamps (models MRM 1208L, Kalglo Electronic, Bethlehem, PA) that output 400 W (100 W m^{-2}) of radiant energy from a height of 1.5 m above the soil surface (Harte *et al.*, 1995; Shaw & Harte, 2001; Wan *et al.*, 2002) (Figure 3.2). Due to increasing height of both *J. virginiana* and *Q. stellata*, all heaters were raised to 2 m (from 1.5 m) in February 2008, while output of heaters was doubled from 400 W to 800 W.

PLANT SPECIES COMBINATIONS

Two sets of five species combinations were grown in 2 × 2 m plots beneath each of the rainout shelters and two unsheltered controls. *Schizachyrium scoparium*, *Q. stellata*, and *J. virginiana*

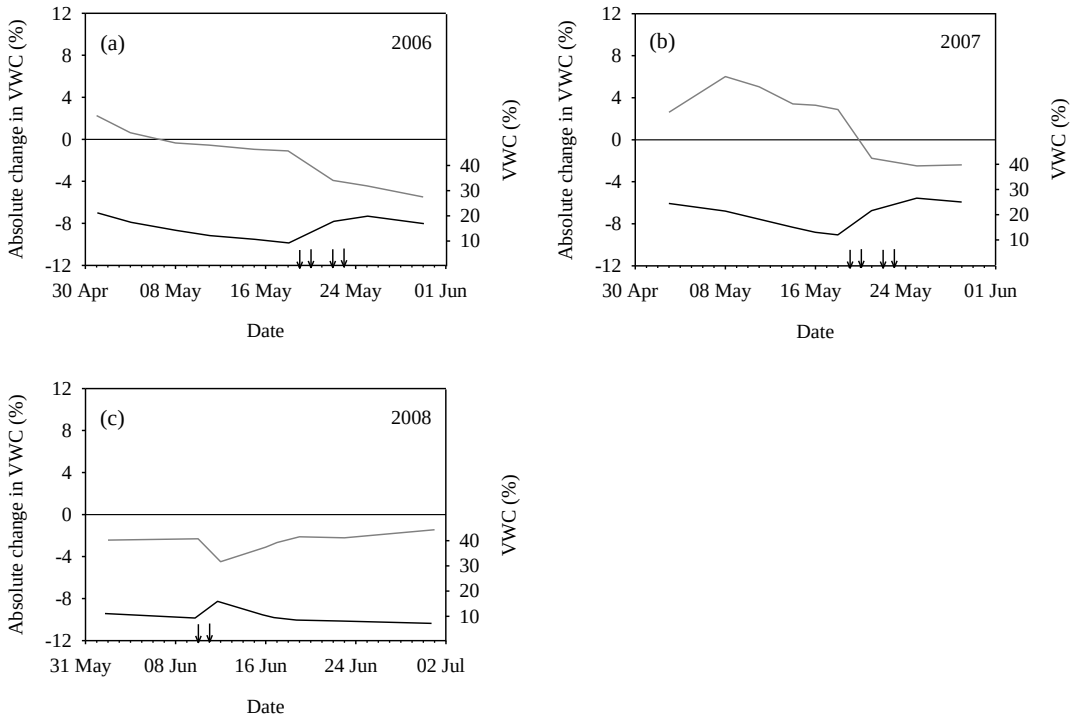

Figure 3.1. Effect of precipitation on soil volumetric water content (VWC) over time averaged across plant species mixture and warming treatment during (a) 2006, (b) 2007, and (c) 2008 campaigns. The grey line depicts absolute change in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal soil VWC pattern. Arrows denote precipitation events. Precipitation event sizes for the control precipitation treatment were 34.1, 30.9, 29.8, and 20.5 mm, and for the redistributed precipitation treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2006 and 2007 campaigns. Precipitation event size for the control precipitation treatment were 9.7 and 29.7 mm, and redistributed precipitation treatment were 5.8 and 17.8 mm, on 10 and 11 June, respectively, for the 2008 campaign.

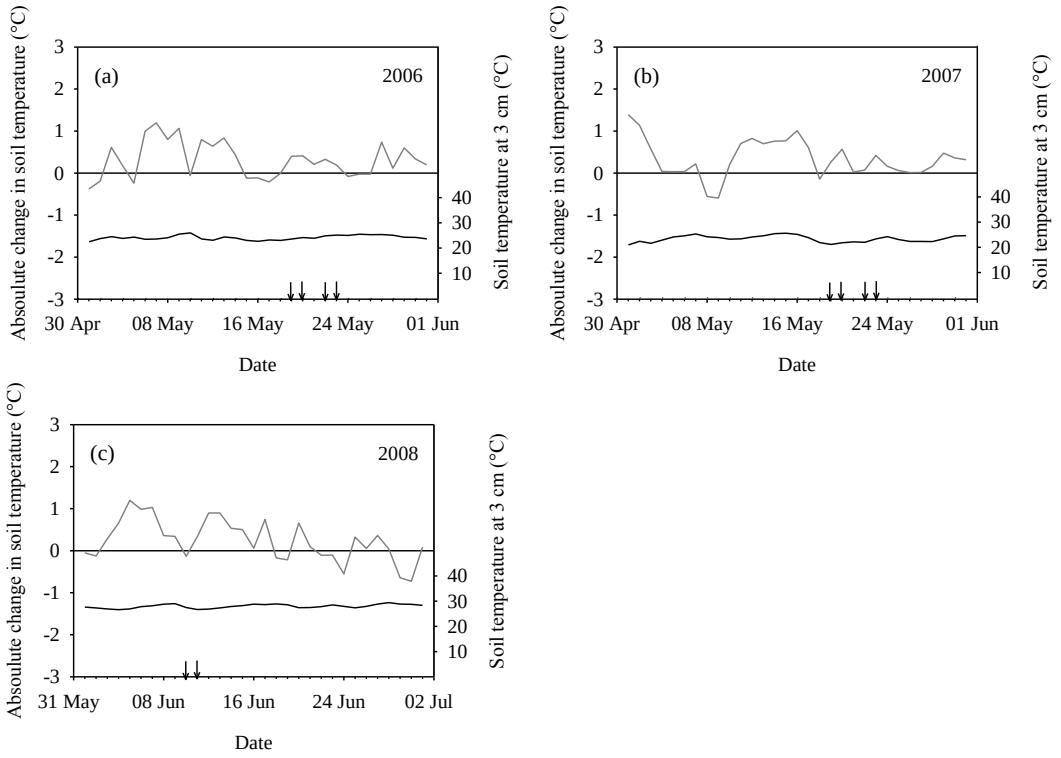

Figure 3.2. Effect of warming on soil temperature (°C) over time averaged across plant species mixture and precipitation treatment during (a) 2006, (b) 2007, and (c) 2008 campaigns. The grey line depicts absolute change in soil temperature due to warming treatment and the black line depicts the seasonal soil temperature pattern. Arrows denote precipitation events. Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and for the redistributed precipitation treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2006 and 2007 campaigns. Precipitation event size for the control precipitation treatment were 9.7 and 29.7 mm, and redistributed precipitation treatment were 5.8 and 17.8 mm, on 10 and 11 June, respectively, for the 2008 campaign.

were each grown in monoculture (25 plants per plot). In addition, each of the tree species was grown with the grass in separate mixed species plots (13 trees and 12 grasses) to investigate tree grass interactions. One set of plots was warmed with overhead infrared lamps while the other set was fitted with dummy lamps.

The plots were established in 2003 one year prior to the start of experiment treatments (in March 2004) from local transplants of *S. scoparium*, 1-yr-old containerized *Q. stellata*, and *J. virginiana* grown from native, regional seed sources. Monocultures of *J. virginiana* were thinned to 13 trees in December 2007. The remaining trees had the same spacing as the trees in the mixture plots (stems of each tree were left 0.8 m apart). One year old transplant/replacement bare root *Q. stellata* seedlings were replanted as necessary in February 2008.

SOIL CO_2 EFFLUX

Collars (20 cm in diameter, 8 cm high, with one drain hole at soil surface) were inserted 4 cm into the soil, in the central portion of each plot in May 2005. Collars were weeded if required 48 h prior to measurement and drain holes were plugged during measurements. Soil CO_2 efflux and soil temperature at 5 cm depth were measured during three intensive campaigns, on 15 and 24 May during the 2006 campaign, 10, 14, 16 and 24 May during the 2007 campaign, and 12, 16, 18, and 24 June during the 2008 campaign, using a soil chamber [Survey Chamber 8100-103 (20 cm diameter); LI-COR Inc., Lincoln, Nebraska] connected to a CO_2 unit [LI-8100 Analyzer Control Unit ; LI-COR Inc., Lincoln, Nebraska].

ROOT COLLECTION

Three soil cores (5 cm diameter × 20 cm length; AMS soil core sampler kit, AMS Inc., American Falls, ID) were collected from each plot during the May 2006, May 2007, and June 2008 campaigns. Cores were sealed in plastic bags and refrigerated at ~5 °C until processed (within 2 weeks). Soil cores were checked for roots and carefully separated from the bulk soil. Roots were carefully separated from the bulk soil, rinsed in nanopure water, and sorted where applicable by species, into fine (< 2 mm) and coarse (> 2 mm) and root fresh mass (Model CX 301, Laboratory Balance, Citizen Scale Inc., Edison, NJ) and length (WinRHIZO, Régent Instruments Inc., Québec City, Québec, Canada) were determined.

STATISTICAL DESIGN

Effect of precipitation redistribution, warming, and species mixture on soil CO_2 efflux were analyzed using a mixed model with precipitation treatment, warming, and species mixtures as fixed effects and between shelter variations as a random effect. The precipitation, warming, and species treatment were arranged as a split-plot factorial, with a completely randomized design. The precipitation regimes constitute the whole plot factors (with four replications), while warming and species combination were assigned within-plot factors. Soil temperature and soil VWC were used as covariants. All analysis were conducted with statistical analysis software (JMP 7.02 SAS Institute, Cary, NC).

Results

EFFECT OF PRECIPITATION TREATMENT, SPECIES MIXTURE AND WARMING ON SOIL VOLUMETRIC WATER CONTENT

Soil VWC was greater following precipitation events in May 2006 and June 2008 (precipitation effect, $P = 0.030$, $P = 0.006$, respectively; Figure 3.3a and e). For the June 2008 campaign, soil VWC was allowed to decrease over time following the precipitation event (Figure 3.3e), while in the 2006 and 2007 campaigns the effect of precipitations was measured after a period of drought (Figure 3.3a and c). Soil VWC was lower in the precipitation redistribution treatment after the precipitation event during the May 2006 and May 2007 campaigns, and consistently lower in the redistributed treatment in the June 2008 campaign (Figure 3.3). Soil VWC was 6.9% lower in the warmed treatment when compared to the unwarmed treatment during the June 2008 campaign.

Soil VWC was greater in *Q. stellata* monoculture and mixture when compared to *J. virginiana* monoculture and mixture during the May 2006 campaign (species mixture effect, $P < 0.001$; Figure 3.3a and b). Soil VWC was greater in *Q. stellata* mixture and *S. scoparium* monoculture when compared to *J. virginiana* monoculture and mixture, during the May 2007 campaign (species mixture effect, $P < 0.001$; Figure 3.3c and d). Soil VWC was greater in *S. scoparium* monoculture and *Q. stellata* monoculture and mixture when compared to *J. virginiana* monoculture and mixture, during the June 2008 campaign (species mixture effect, $P < 0.001$; Figure 3.3e and f).

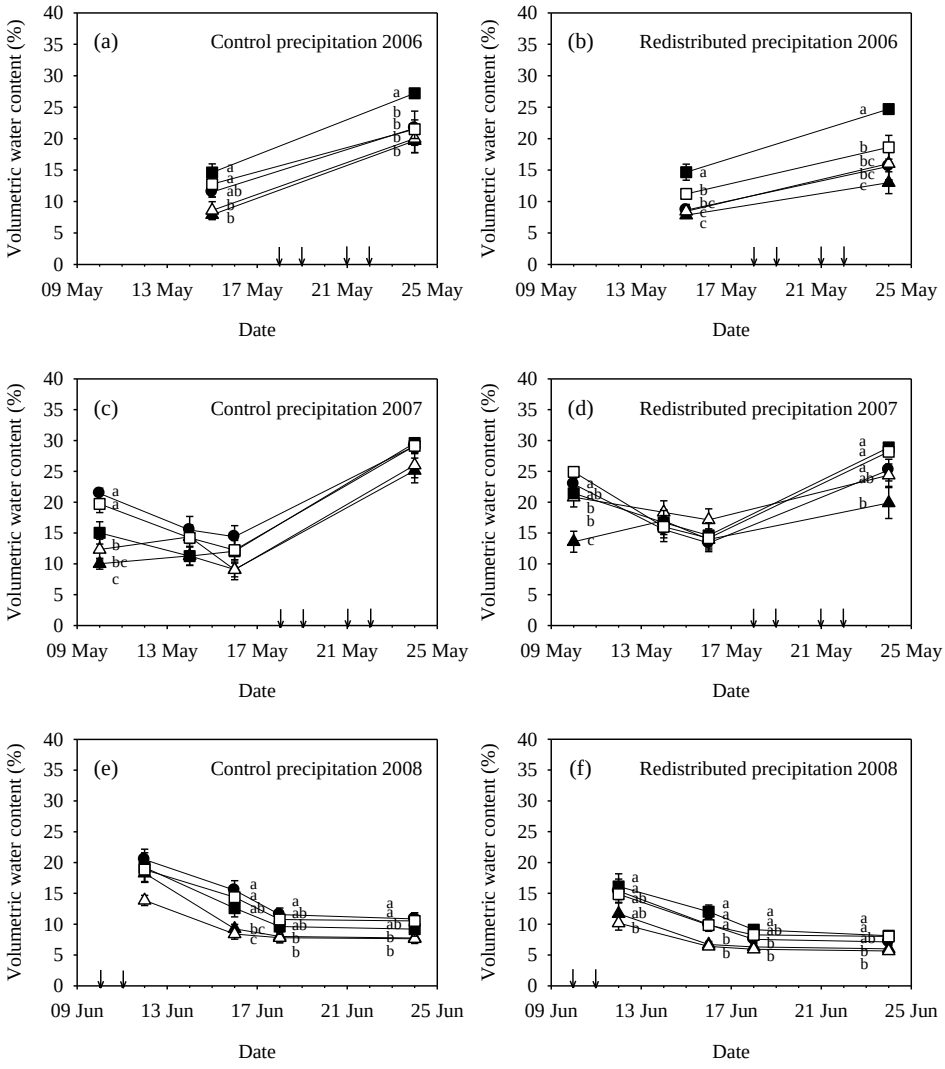

Figure 3.3. Effect of species mixture on soil volumetric water content (%) averaged across warming treatments for (a) control precipitation and (b) redistributed precipitation during the May 2006 campaign, (c) control precipitation and (d) redistributed precipitation during the May 2007 campaign, and (e) control precipitation and (f) redistributed precipitation during the June 2008 campaign (means ± SE). Arrows denote precipitation events. The symbols depict the species as follows: filled circles *Schizachyrium scoparium* monoculture, filled triangles *Juniperus virginiana* monoculture, unfilled triangles *J. virginiana* grown with *S. scoparium*, filled squares *Quercus stellata* monoculture, unfilled squares *Q. stellata* grown with *S. scoparium*. Letters indicate significant ($P \leq 0.05$) differences in response for a species within date measured according to student's t-test.

EFFECT OF SPECIES MIXTURE, PRECIPITATION DISTRIBUTION, WARMING AND SOIL VOLUMETRIC WATER CONTENT ON SOIL CO_2 EFFLUX

Overall soil CO_2 efflux was greater in *S. scoparium* monoculture and mixtures and *J. virginiana* monoculture when compared to *Q. stellata* monoculture during the May 2006 campaign (Table 3.1, Figure 3.4). Soil CO_2 efflux was greater in *S. scoparium* monoculture and mixtures when compared to the trees in monoculture during the May 2007 campaign (Table 3.1, Figure 3.5). Soil CO_2 efflux was greater in *S. scoparium* monoculture when compared to *J. virginiana* monoculture and mixture and *Q. stellata* in monoculture during the June 2008 campaign (Table 3.1, Figure 3.6). Overall, soil CO_2 efflux was greater in the redistributed precipitation treatment and lower in the control precipitation treatment during the May 2007 campaign (Table 3.1, Figure 3.5).

Soil CO_2 efflux increased with increasing soil VWC in the tree monocultures regardless of precipitation treatment during the May 2006 campaign (VWC effect, $P = 0.029$, $P \leq 0.001$; Figure 3.4b and d, respectively). Soil CO_2 efflux increased with increasing soil VWC in *J. virginiana* grown with *S. scoparium* and was greater in the redistributed precipitation treatment when compared to the control precipitation treatment during the May 2006 campaign (precipitation effect, $P = 0.042$; Figure 3.4c). Soil CO_2 efflux increased with increasing VWC in *Q. stellata* grown with *S. scoparium* in the redistributed precipitation treatment and decreased with increasing VWC in the control precipitation treatment, and was greater in the redistributed precipitation treatment when compared to the control precipitation treatment during the May 2006 campaign (precipitation effect, $P = 0.028$; Figure 3.4e).

Soil CO_2 efflux decreased with increasing soil VWC in *S. scoparium* monoculture and *Q. stellata* grown with *S. scoparium* regardless of precipitation treatment during the May 2007 campaign (VWC effect, $P \leq 0.001$, $P \leq 0.001$; Figure 3.5a and e, respectively). Soil CO_2 efflux decreased with increasing soil VWC in *J. virginiana* grown with *S. scoparium* and was greater in the redistributed precipitation treatment when compared to the control precipitation treatment during the May 2007 campaign (precipitation effect $P = 0.008$, VWC effect $P = 0.003$; Figure 3.5c).

Soil CO_2 efflux increased with increasing soil VWC in the *J. virginiana* grown with *S. scoparium* and *Q. stellata* in monoculture regardless of precipitation treatment during the June 2008 campaign (VWC effect, $P = 0.004$, $P = 0.008$; Figure 3.6c and d, respectively). Soil CO_2

Table 3.1. Probability values (*P*-values) and F-ratios determined using ANCOVA for soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) during the May 2006, May 2007, and June 2008 campaigns.

	Soil CO_2 efflux					
	May 2006		May 2007[z]		June 2008[z]	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	5.54	0.051	13.1	**0.010**	0.73	0.420
Warming (W)	0.05	0.832	0.55	0.457	0.02	0.892
W × P	0.00	0.995	1.13	0.289	0.02	0.879
Mixture (M)	9.40	**<0.001**	13.3	**<0.001**	5.09	**0.001**
P × M	0.95	0.440	0.71	0.586	1.10	0.357
W × M	1.39	0.244	1.31	0.267	3.30	**0.012**
P × W × M	0.31	0.869	2.63	0.035	7.73	**<0.001**
VWC[y]	12.9	**<0.001**	67.5	**<0.001**	5.34	**0.022**
P × VWC	3.03	0.084	1.89	0.171	10.8	**0.001**
W × VWC	2.22	0.139	0.35	0.554	0.18	0.672
M × VWC	2.51	**0.046**	6.38	**<0.001**	3.14	**0.015**
P × W ×VWC	0.09	0.767	0.86	0.354	0.15	0.701
M × P × VWC	0.64	0.633	1.92	0.109	1.15	0.332
M × W ×VWC	0.86	0.488	0.26	0.904	0.17	0.952
M × P × W × VWC	0.93	0.450	0.54	0.703	0.74	0.566

P-values ≤0.05 are printed in bold.

[z] Data was log transformed.

[y] Soil volumetric water content.

Data was analyzed with root length density (RLD; km m^{-3}) as a covariate and RLD was not significant (data not shown).

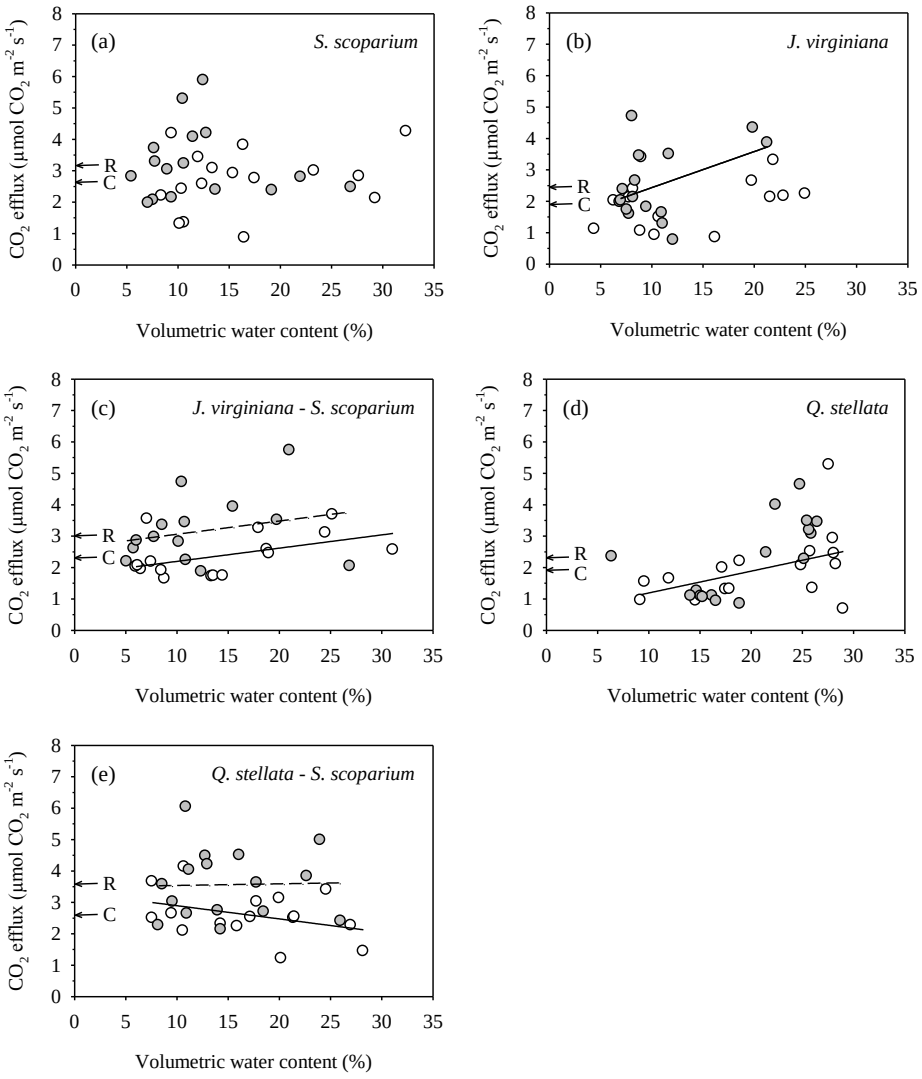

Figure 3.4. Effect of volumetric water content (%) on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2006 campaign. Unfilled symbols are the plants in control precipitation and filled symbols are plants in redistributed precipitation treatments. Arrows indicate mean soil CO_2 efflux for control (C) and redistributed (R) precipitation treatments. Significant regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (c) *J. virginiana – S. scoparium* control precipitation, r^2 = 0.236; redistributed precipitation, r^2 = 0063 and (e) *Q. stellata – S. scoparium* control precipitation, r^2 = 0.140; redistributed precipitation, r^2 = 0.001. Significant regression relationships are depicted across precipitation treatments; (b) *J. virginiana* monoculture, r^2 = 0.187, and (d) *Q. stellata* monoculture, r^2 = 0.206.

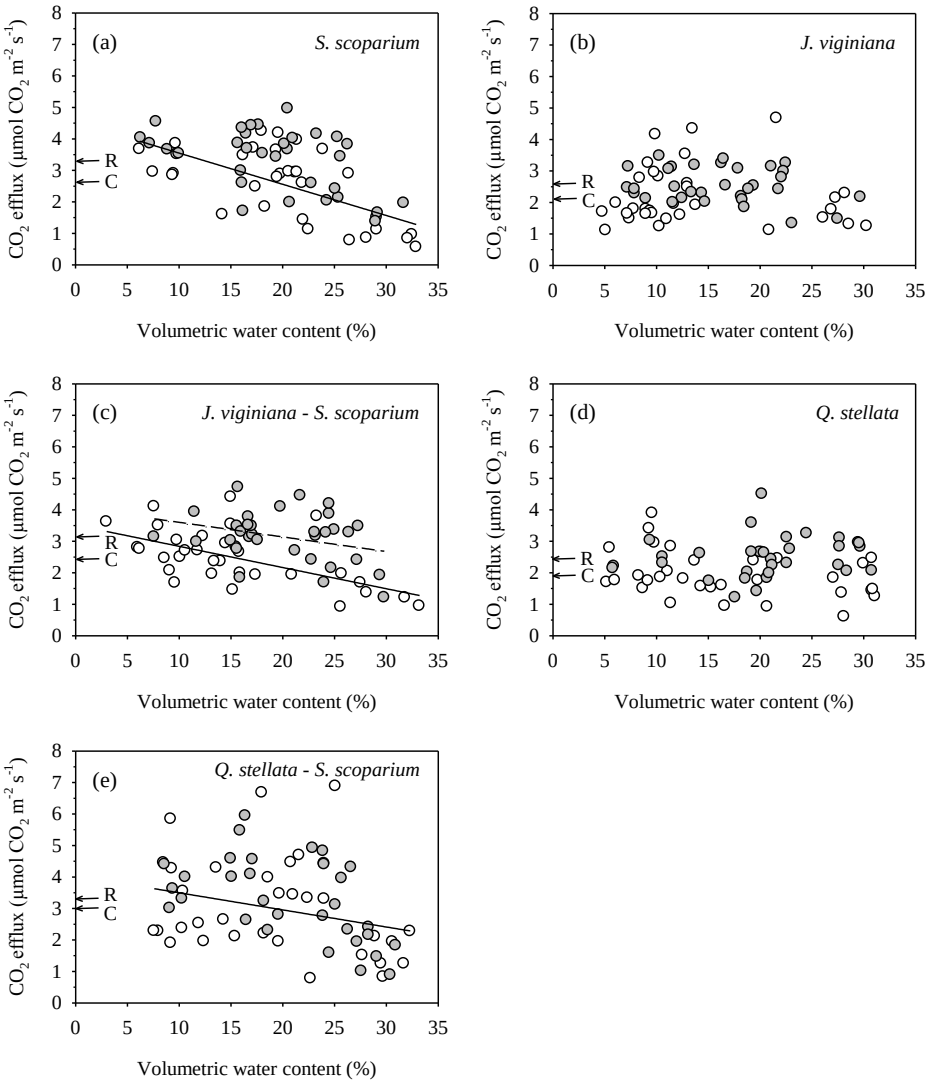

Figure 3.5. Effect of volumetric water content (%) and soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2007 campaign. Unfilled symbols are the plants in control precipitation and filled symbols are plants in redistributed precipitation. Arrows indicate mean soil CO_2 efflux for control (C) and redistributed (R) precipitation treatments. Significant regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (c) *J. virginiana* – *S. scoparium* control precipitation, $r^2 = 0.348$; redistributed precipitation, $r^2 = 0.103$. Significant regression relationships are depicted across precipitation treatments; (a) *S. scoparium*, $r^2 = 0.404$ and (e) *Q. stellata* – *S. scoparium*, $r^2 = 0.075$.

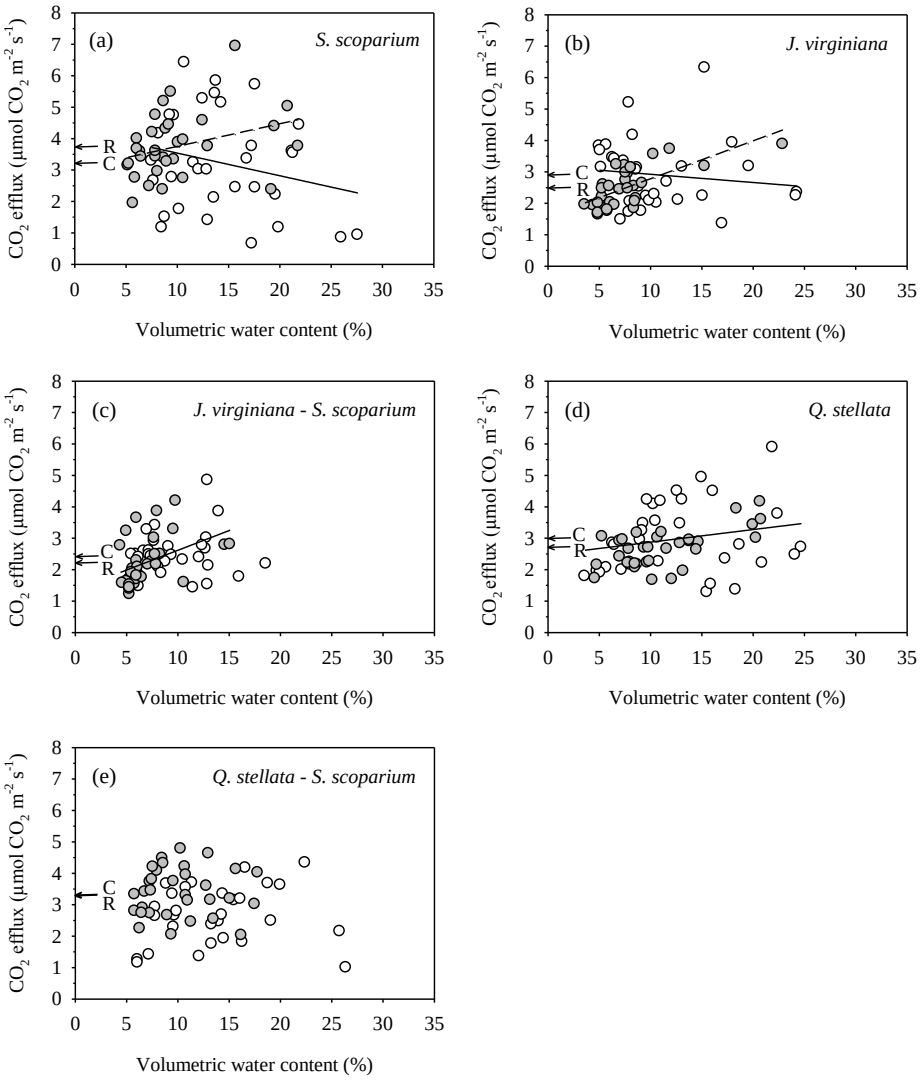

Figure 3.6. Effect of volumetric water content (%) and soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the June 2008 campaign. Unfilled symbols are the plants in control precipitation and filled symbols are plants in redistributed precipitation. Arrows indicate mean soil CO_2 efflux for control (C) and redistributed (R) precipitation treatments. Significant regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (a) *S. scoparium*; control precipitation, $r^2 = 0.056$; redistributed precipitation, $r^2 = 0.104$ and (b) *J. virginiana* control precipitation, $r^2 = 0.014$; redistributed precipitation, $r^2 = 0.479$. Statistically significant regression relationships are depicted across precipitation treatments; (c) *J. virginiana – S. scoparium*, $r^2 = 0.176$ and (d) *Q. stellata*, $r^2 = 0.044$.

efflux increased with increasing soil VWC in *S. scoparium* and *J. virginiana* monoculture in redistributed precipitation treatment and decreased in control precipitation treatment during the June 2008 campaign (precipitation × VWC effect, $P = 0.009$, $P = 0.001$; Figure 3.6a and b, respectively).

Soil CO_2 efflux increased with increasing soil VWC in the *J. virginiana* and *Q. stellata* monocultures regardless of warming treatment during the May 2006 campaign (VWC effect, $P = 0.029$, $P \leq 0.001$, respectively). Soil CO_2 efflux decreased with increasing soil VWC in the *S. scoparium* monoculture, *J. virginiana* mixture and *Q. stellata* mixtures regardless of warming treatment during the May 2007 campaign (VWC effect, $P \leq 0.001$, $P = 0.003$, $P \leq 0.001$, respectively). Soil CO_2 efflux increased with increasing soil VWC in *J. virginiana* monoculture and mixture and *Q. stellata* monoculture regardless of warming treatment during the June 2008 campaign (VWC effect, $P \leq 0.001$, $P = 0.004$, $P = 0.008$, respectively). Soil CO_2 efflux increased with increasing soil VWC in *Q. stellata* grown with *S. scoparium* and was greater in the warmed treatment when compared to the unwarmed treatment (warming effect, $P = 0.042$).

Root length density (RLD) (Figure 3.7) and root mass density (RMD) (data not shown) were not related to soil CO_2 efflux in any of the years, neither before nor after a precipitation event. Within species there was no relationship between species soil CO_2 efflux and RLD and RMD, except for CO_2 efflux and RLD in the *J. virginiana* mixture in the May 2007 campaign before precipitation event and in the June 2008 campaign after the precipitation event.

Discussion

The size and frequency of precipitation events and plant species mixture had a distinct effect on soil VWC and CO_2 efflux during the May 2006, May 2007, and June 2008 campaigns. Soil VWC varied with plant species mixture. In general, soil VWC was higher in *Q. stellata* monocultures and mixtures and lower in the *J. virginiana* monoculture and mixtures, potentially reflecting a greater canopy and litter layer precipitation interception rate and higher evapotranspiration rates in *J. virginiana* dominated plots (Owens *et al.*, 2006).

In general, soil CO_2 efflux increased with increasing soil VWC during the May 2006 and June 2008 campaigns, while soil CO_2 efflux decreased with increasing soil VWC during the May 2007 campaign. Soil CO_2 efflux usually increases with increasing soil VWC but can be reduced

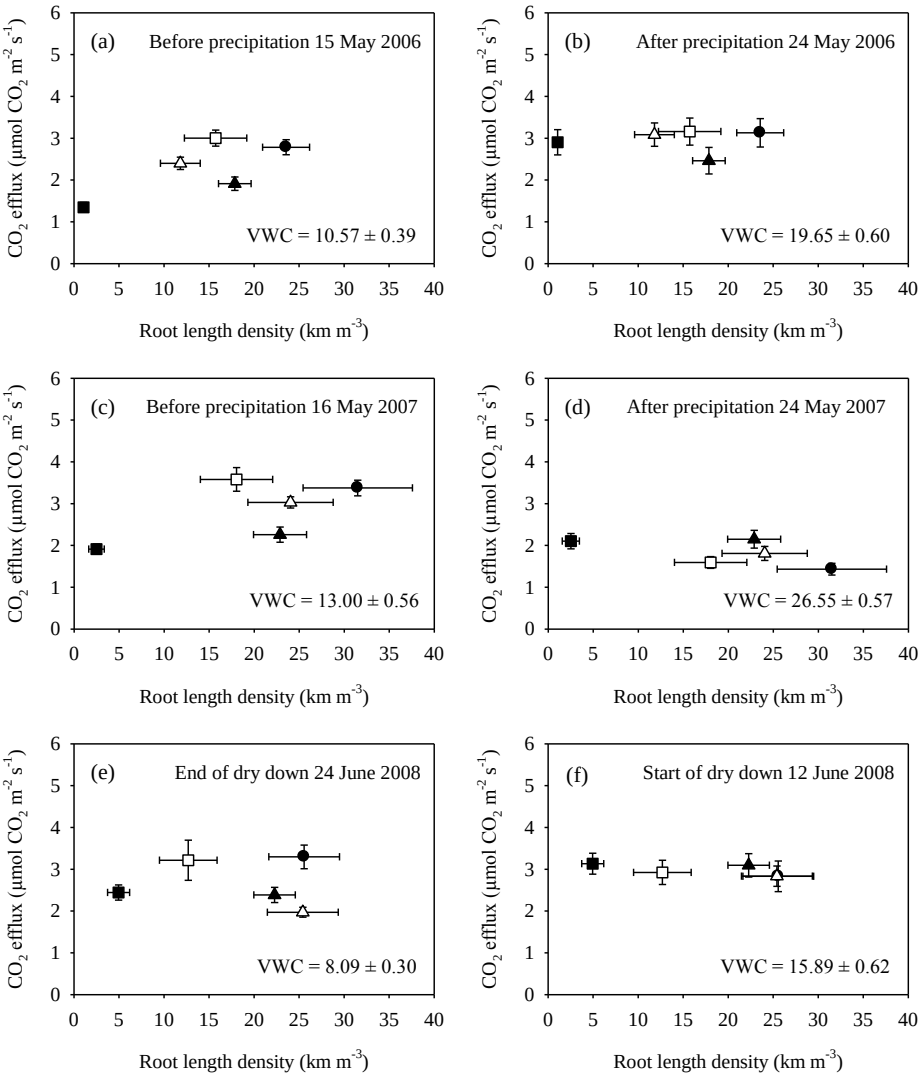

Figure 3.7 Effect of root length density (km m^{-3}) on soil CO_2 efflux (μmol CO_2 $m^{-2}s^{-1}$) averaged across species mixture, precipitation, and warming treatments. (a) before precipitation events 15 May 2006, (b) after precipitation events 24 May 2006, (c) before precipitation events 16 May 2007, (d) after precipitation events 24 May 2007, (e) end of dry down 24 June 2008, and (f) start of dry down 12 June 2008 (means ± bi-directional SE). The symbols depict the species as follows: filled circles *Schizachyrium scoparium* monoculture, filled triangle *Juniperus virginiana* monoculture, unfilled triangles *J. virginiana* grown with *S. scoparium*, filled square *Quercus stellata* monoculture, unfilled squares *Q. stellata* grown with *S. scoparium*.

under extreme low and high VWC conditions (Davidson *et al.*, 2000; Liu *et al.*, 2002; Xu *et al.*, 2004). Soil water content directly influences soil CO_2 efflux through drought water limitation stress on plant roots and microbes and indirectly through plant productivity and C allocation. However, we did not find any relationship between root length density or root mass density and soil CO_2 flux, before or after precipitation events, suggesting that in our system soil CO_2 efflux is not strongly linked to standing root length and that the root component of soil CO_2 efflux is unresponsive to soil water content unless root and microbial responses to the precipitation event were cancelling each other out.

Rewetting a relatively dry soil in the May 2007 campaign resulted in a general decrease in soil CO_2 efflux several days after the precipitation event in the grass monocultures and mixtures, while soil CO_2 efflux remained at a steady state for tree monocultures. Thus, there may be a plant species and microbial specific response to drying and rewetting within the oak savannah system. In wet soils, above field capacity, oxygen deficiencies inhibit root (Drew, 1997) and microbial aerobic respiration (Skopp *et al.*, 1990). In our experiment, *S. scoparium* roots and associated microbes may have been more susceptible to oxygen deficiency than roots and associated microbes of either tree species.

Soil CO_2 efflux was inconsistently affected by precipitation treatment. There was a general trend of higher soil CO_2 efflux in the redistributed precipitation treatments and lower soil CO_2 efflux in the control precipitation treatments during the May 2006 and May 2007 campaigns. Greater soil CO_2 efflux in the redistributed precipitation treatments at the same VWC content as control precipitation treatment in the *S. scoparium* mixtures and *J. virginiana* mixture during the May 2006 and May 2007 campaigns, respectively, may reflect that higher soil CO_2 efflux is not due to any physical effects of water content that affects soil CO_2 diffusion, but rather a carry-over effect of the redistributed precipitation treatment enhancing microbial activity, resulting in greater respiration rates. Potentially reflecting a recovery and renewal of microbial activity with increased water availability (Fierer & Schimel, 2002; Fierer & Schimel, 2003) in the May 2006 and May 2007 campaign. In general, soil microbes have the ability to adapt to a wide range of soil VWC (as reviewed by Harris, . 1981). Soil CO_2 efflux is reported to increase following precipitation events in dry climates, possibly as a result of rapid microbial responses to water availability, with the recovery of root respiration lagging behind (Kelliher *et al.*, 2004).

This potentially reflects a broad range of 'near' optimum soil VWC where changes in soil VWC have limited effect, if any, on soil CO_2 efflux, suggesting that soil VWC is only important when it is at an extreme high or low. Similarly, Davidson *et al.* (2000) also showed that optimum soil VWC for soil respiration is normally found at intermediate values for water content . What remains unclear is whether soil CO_2 efflux correlates with photosynthetic rates and soil VWC. Of particular interest is whether there is delay and if any, the duration of the delay and recovery between the onset of drought conditions, photosynthetic activity, and allocation of C to the roots/rhizosphere. The species in this study are drought tolerant and have been reported to maintain leaf gas exchange at low VWC during early summer (Volder *et al.*, 2010). However, prolonged summer drought reduced leaf gas exchange for *S. scoparium* and *Q. stellata*, while *J. virginiana* was largely unaffected (Volder *et al.*, 2010). Light-saturated rates of leaf level net photosynthesis were closely coupled to water stress in *S. scoparium* when compared to the tree species (Volder *et al.*, 2010). Thus, since substrate availability is often closely linked to recent assimilation of photosynthates (Hogberg *et al.*, 2001), soil CO_2 efflux may be strongly affected by VWC as drought progresses.

Soil VWC content may affect the rate of soil CO_2 efflux as well as its response to temperature due to interaction between moisture and temperature. Soil warming treatments inconsistently affected soil VWC. Soil VWC was higher in the unwarmed plots and lower in the warmed plots during the June 2008 campaign. During the May 2006 and May 2007 campaigns there was a similar (non-significant) trend of higher soil VWC in the unwarmed plots when compared to the warmed plots. Warming did not strongly affect soil CO_2 efflux, as the study site was already relatively warm and campaigns were conducted when air temperatures were already relatively high (air temperature 24.85±0.50 °C, 24.13±0.33 °C, and 29.69±0.13 °C during May 2006, May 2007, and June 2008, respectively). Numerous studies have shown a transient response of soil CO_2 efflux to warming (McHale *et al.*, 1998; Luo *et al.*, 2001; Melillo *et al.*, 2002; Eliasson *et al.*, 2005).

Soil CO_2 efflux has been reported to vary with different biome types (Raich & Tufekcioglu, 2000), mostly along broad patterns of vegetation cover and climatic conditions, although these differences have not been as large as expected (Hibbard *et al.*, 2005). Observed differences in soil CO_2 efflux between plant species in this study, may have been due to differences in root production, root density, as well as potential species effects on microclimatic conditions, and changes in microbial biomass and composition. However, while difference in

species composition did influence root density, soil CO_2 efflux was more responsive to the precipitation events and subsequent changes in soil VWC and not related to root length or root mass density either before or after a rainfall event.

Soil CO_2 efflux was greater in the warmed treatment when compared to the unwarmed treatment for *Q. stellata* mixture during the June 2008 campaign, potentially reflecting a positive relationship between warming, fine root turnover, and root respiration (Gill & Jackson, 2000). The warming treatments may have indirectly increased soil CO_2 efflux through enhanced photosynthetic activity, and allocation of C to the roots and soil microbes. Thus, even though we did not find a significant increase in soil temperature as a result of our warming treatment (Figure 3.2; see also Chapter II) there may still have been a contributory effect of the warming treatment.

Conclusion

Observed differences in soil CO_2 efflux rates between savannah species during intensified summer drought were likely due to changes in soil VWC. We did not find any relationship between root length density or root mass density and soil CO_2 efflux, before or after precipitation events, suggesting that in our system the root component of soil CO_2 efflux is not very large and is unresponsive to soil water content, at least during the spring and summer period. Soil VWC may have influenced soil CO_2 efflux directly through drought water limitation stress on plant and microbes and indirectly through plant productivity and C allocation, and there may be a plant and microbial specific response to drying and rewetting within the oak savannah system. This leads to a broad range of 'near' optimum soil VWC and/or drought tolerance above and belowground where changes in soil VWC have limited effect, if any, on soil CO_2 efflux, as our data suggests. Thus, soil CO_2 efflux rates in post-oak savannah are governed predominantly by species composition and the response of these species to VWC.

CHAPTER IV
RELATIVE IMPORTANCE OF ROOT AND MICROBIAL RESPIRATION IN RESPONSE TO PLANT SPECIES, SEASON, AND SOIL WATER AVAILABILITY IN A POST OAK SAVANNAH

Introduction

Climate change, fragmentation of the landscape, and altered land management practices, coupled with fire suppression have resulted in invasion and expansion of *Juniperus* (L.) spp. Into grassland and savannah systems of North America (Briggs *et al.*, 2002; Briggs *et al.*, 2005). Climate change and shifting dominance from herbaceous to woody vegetation may have major, if uncertain, implications for terrestrial ecosystem carbon (C) storage (Jackson *et al.*, 2002). Total C stocks will likely shift both in size and in distribution above and below ground with woody plant encroachment and displacement of herbaceous species, complicating projections of terrestrial ecosystem C storage.

Soil carbon dioxide (CO_2) efflux is the major pathway for C exiting terrestrial ecosystems (Schimel, 1995; Schlesinger & Andrews, 2000), and is the cumulative result of root, fungal, and bacterial respiration, making modelling and interpretation complex (Ryan & Law, 2005). Changes in plant productivity and species composition may alter below ground physical and chemical conditions, the supply of C to the soil, and the structure and activity of microbial communities, and thus C release from the soil (Bardgett *et al.*, 2008). The size of the microbial pool is largely dependent on the availability and composition of substrates (Trumbore, 2000), while activity of root and microbes is strongly affected by temperature, provided adequate moisture is available (Hanson *et al.*, 2000).

Projected increases in global surface temperatures and variability of precipitation and drought events in response to global warming (Bates *et al.*, 2008), may potentially differentially affect root and microbial respiration (Hanson *et al.*, 2000), depending on vegetation and climate (Raich & Schlesinger, 1992; Raich & Tufekcioglu, 2000). Any stimulation of CO_2 efflux may potentially increase atmospheric CO_2 levels, and provide a positive feedback to global warming (Cox *et al.*, 2000; Friedlingstein *et al.*, 2006). Thus, disentangling climatic conditions, plant species effects, and the relative contribution of root and microbial respiration to soil CO_2 efflux

remains a key challenge in understanding the response of terrestrial ecosystems and the global C cycle to climate change drivers.

Fungal respiration may be closely tied to mycorrhizal hyphae and associated roots. In that, root and associated mycorrhizal respiration are dependent on current photosynthates for substrate supply (Hogberg *et al.*, 2001), but stored carbohydrates may be temporarily utilized when environmental conditions are unfavourable for photosynthesis (Ryan & Law, 2005). Separating root and mycorrhizal respiration rate is practically impossible without interfering with the symbiotic exchange of carbohydrates, water, and nutrients, which in turn would probably affect respiration rates. Thus, root respiration is frequently overestimated due to inclusion of the mycorrhizal component. Ectomycorrhizal (EM) fungi are suggested to be a larger component of soil respiration when compared to arbuscular mycorrhizal (AM) fungi (Phillips & Fahey, 2005). Mycorrhizal fungi may potentially influence soil and ecosystem level C dynamics by controlling the release of C to the soil microbial community (Hogberg & Read, 2006).

The broad objective of this study was to determine the effects of plant species composition, increased intensity of summer drought, and the amount of cool season precipitation on the root and microbial component of soil CO_2 efflux in post oak savannah. Post oak savannah in the south-central United States are dominated by three contrasting plant functional types: *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) a C_4 grass, *Quercus stellata* Wangenh. (post oak) a C_3 deciduous tree, and *Juniperus virginiana* L. (eastern redcedar) a C_3 evergreen tree. We collected soil CO_2 efflux data, soil volumetric water content (VWC), and soil temperature, approximately every 5-6 weeks from July 2008 – April 2010. The goal was to separate and quantify root, fungal, and bacterial components of soil CO_2 efflux, and to explore the effects of plant species composition (tree and grass), and increased intensity of summer drought and the amount of cool season precipitation on root and microbial CO_2 efflux rates between the *J.* virginiana and *S. scoparium*. We hypothesised that: (i) the relative contribution of roots, fungi, and bacteria to soil CO_2 efflux rates would stay relatively stable as all three are likely to respond more or less equally to environmental conditions, in that we expect a standard seasonal pattern of soil CO_2 efflux rates, with the highest rates in the spring and the lowest rates in both the cooler winter season and at the end of the dry summer period, (ii) root and microbial CO_2 efflux rates would be higher in *S. scoparium* dominated plots, since *S. scoparium* were expected to have greater root length density, greater root turnover rates, and greater above

ground litter inputs which would provide more substrate to the microbes than *J. virginiana* inputs, and (iii) decreased water availability during the summer would negatively affect microbial CO_2 efflux rates, and that fungal respiration would be most affected, then microbial respiration, and then root respiration.

Materials and Methods

EXPERIMENTAL SITE AND INFRASTRUCTURE

The Texas warming and rainfall manipulation experiment (Texas WaRM Experiment) was located on a remnant post oak savannah site (30°34 N 96°21 W) near Texas A&M University, College Station, Texas. This facility was constructed in 2003 to investigate the combined effects of altered precipitation distribution and warming on tree grass dominants of southern oak savannah. The research infrastructure included eight permanent 18 × 9 × 4.5 m (L × W × H) rainout shelters covered with clear polypropylene film. The side walls below 1.5 m were open to maintain microclimate conditions as near ambient as possible, but effectively exclude precipitation (Fay *et al.*, 2000; Weltzin & McPherson, 2003). A fine mesh shade cloth, matching the radiation attenuation of the film (70% transmittance), excludes windblown precipitation from entering two 4.5 m high open ends of each shelter. Sheet metal flashing 40 cm in height, was inserted 30 cm into the soil penetrating the clay hardpan, to isolate each shelter from surface and subsurface water flow.

Ten 2 × 2 m plots with five species combinations were located beneath each shelter in the native soil (Volder *et al.*, 2010). Soil consisted of a shallow layer (< 20 cm) of Boonville fine sandy loam, with a thick clay pan below (Chervenka, 2003). An overhead irrigation system (17 pressure regulated spray nozzles per shelter) simulated precipitation regimes by supplying reverse osmosis (RO) treated ground water, from four 11,500 L holding tanks, to each shelter. A weather station (EZ Mount GroWeather, Davies Instruments, Hayward, CA) on site recorded precipitation, air temperature, and humidity. Solar radiation (total PPFD), air temperature, and relative humidity were continuously monitored in each shelter and control plots using data loggers (Hobo U12, Onset Company Corp., Bourne, MA). Soil water content was measured twice weekly for each plot using permanently installed time domain reflectometry (TDR) probes (Soil Moisture Corp., Santa Barbara, CA) which were inserted vertically to give an integrated measure of soil VWC in the top 20 cm of the soil profile. The rainout shelter design preserves

natural variation in the microenvironment that is for the most part similar to ambient conditions (Fay *et al.*, 2000). Mean daily temperature in the shelters were on average 0.3 °C higher, RH values were 2% lower, and PPFD levels were 30% lower than ambient.

PRECIPITATION AND WARMING TREATMENT

Simulated precipitation regimes included two patterns that varied in season distribution and event size, but not in total annual precipitation (1018 mm) or total number of events. The long-term (50 yr) precipitation events were also simulated from the regional long-term precipitation record. The frequency and intensity (amount) of precipitation events were also simulated from the regional long-term precipitation record (Figure 4.1a). Precipitation redistribution treatment imposed beneath the other four shelters had 40% of the summer (May – September) precipitation withheld from each event and evenly redistributed to the preceding spring (March and April) and autumn (October and November). The redistribution treatment effectively increased the intensity of the summer drought (redistribution dry phase) and the amount of precipitation that occurred during the cooler season of the year (redistributed wet phase). Each precipitation regime was replicated within four rainout shelters. Precipitation regimes were initiated in March 2004.

One half of the experimental plots beneath each shelter were continuously warmed (24 h per day) with overhead infrared lamps (models MRM 1208L, Kalglo Electronic, Bethlehem, PA) that output 400 W (100 W m^{-2}) of radiant energy from a height of 1.5 m above the soil surface (Figure 4.1b) (Harte *et al.*, 1995; Shaw & Harte, 2001; Wan *et al.*, 2002). Due to increasing height of both *J. virginiana* and *Q. stellata*, all heaters were raised to 2 m (from 1.5 m) in February 2008, while output of heaters was doubled from 400 W to 800 W.

PLANT SPECIES COMBINATIONS

Two sets of five species combinations were grown in 2 × 2 m plots beneath each of the rainout shelters and two unsheltered controls. One set of plots was warmed with overhead infrared lamps while the other set was fitted with dummy lamps. *S. scoparium*, *Q. stellata* and *J. virginiana* were each grown in monoculture (25 plants per plot). In addition, each of the tree species was grown with the grass in separate mixed species plots (13 trees and 12 grasses) to investigate tree grass interactions.

The plots were established in 2003 one year prior to the start of experiment treatments (March 2004) from local transplants of *S. scoparium*, 1-yr-old containerized *Q. stellata*, and

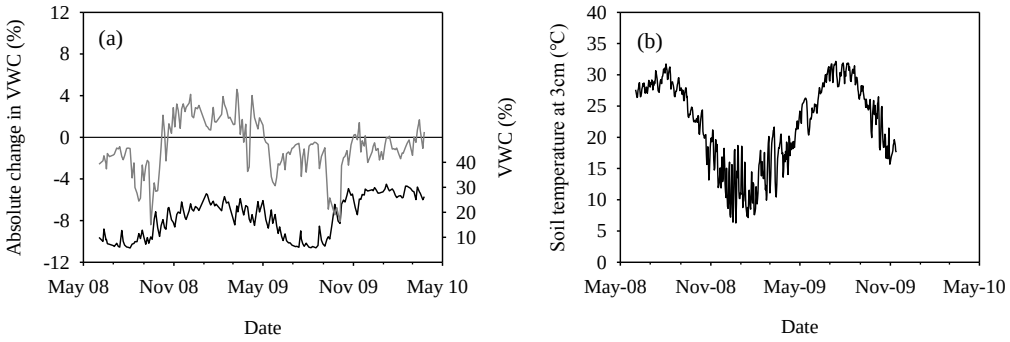

Figure 4.1. Effect of (a) precipitation treatment on soil volumetric water content (VWC) over time averaged across plant species mixture. The grey line depicts absolute changes in soil VWC due to the precipitation redistribution treatment and the black line depicts the seasonal soil VWC pattern. Seasonal mean daily soil temperature pattern at 3 cm depth averaged across plant species mixture and precipitation treatment (b).

J. virginiana grown from native, regional seed sources. Monocultures of *J. virginiana* were thinned in December 2007. Twelve trees were removed from each monoculture plot. The remaining trees had the same spacing as the trees in the mixture plots (stem/trunk of each tree that were left were now 0.8 m apart, instead of 0.4 m).

SOIL CO_2 EFFLUX MEASUREMENTS

Three collars (10 cm diameter, 24 cm high, ~1885 cm^3 volume, with three drain holes at soil surface) were inserted 20 cm into the soil (volume of soil in collar ~1571 cm^3) into the soil in June 2008. To reduce the number of measurements involved, collars were only installed in unwarmed *S. scoparium* monoculture, *J. virginiana* monoculture and *S. scoparium – J.virginiana* mixture plots (72 collars total). The collar concept was modified from that proposed by Johnson *et al.* (2001). Collars were inserted directly into the soil, thus limiting disturbance caused by removal of soil, burying of collar, and refilling with sieved soil. Each collar had eight circular (5 cm diameter) windows, arranged in two off set ranks of four windows (~25% of surface area of each collar in the soil was a window). Each plot contained three different exclusion collar treatments; 1) a coarse nylon mesh (2.5 cm openings) which allowed roots, fungal, and bacterial access (collar A), 2) a 30 µm nylon mesh (NORMESH Ltd., Oldham, Gtr. Manchester, UK), which excluded roots, and allowed fungal and bacterial access (collar B), and 3) a 1 µm nylon mesh (NORMESH Ltd.), which excluded both root and fungal, and allowed bacterial access (collar C) (Johnson *et al.*, 2001; Heinemeyer *et al.*, 2006; Heinemeyer *et al.*, 2007). These collars were used to calculate the relative contribution of root, fungal, and bacterial respiration to total soil CO_2 efflux. The CO_2 fluxes were partitioned as follows: bacterial flux is flux from collar C, hyphal flux is collar B – collar C, and root flux is collar A – collar B.

Collars were weeded when required, 48 h prior to measurement being taken and drain holes were plugged during measurements. Soil CO_2 efflux was measured approximately every 5-6 weeks from July 2008 to April 2010, and every 3 h during two intensive 24 h campaigns, on the 14-15 and 17-18 May 2009. Soil CO_2 efflux was measured using a soil chamber (LI6400, LI-COR Inc., Nebraska) connected to a portable photosynthesis system (LI-6400, LI COR Inc.). Soil temperature was measured at 5 cm depth with a hand held temperature probe (model no. SC-GG-K-30-36-PP Thermocouple and model no. HH309 Data Logger OMEGA Engineering, Inc., Stamford, CT).

FINAL SOIL CORE PROCESSING

At termination of the experiment in April 2010, one soil core (5 cm diameter × 20 cm length; AMS soil core sampler kit, AMS Inc., American Falls, ID) was collected from each collar. Cores were sealed in plastic bags and refrigerated at ~5°C until processed (within 2 weeks). Soil cores were checked for roots and carefully separated from the bulk soil. Roots were carefully separated from the bulk soil, rinsed in nanopure water, and sorted where applicable by species, into fine (< 1 mm diameter) and coarse (> 1 mm diameter) and root fresh mass (Model CX 301, Laboratory Balance, Citizen Scale Inc., Edison, NJ) and length (WinRHIZO, Régent Instruments Inc., Québec City, Québec, Canada) were determined. Soil pH (Model B-213, Compact pH Meter, HORBIA Ltd., Kyoto, Japan) was also determined at this time. Soil pH was 5.49±0.05, 5.53±0.06, and 5.56±0.07 for the *S. scoparium* monoculture, *J. virginiana* monoculture, and mixture, respectively. Collars were carefully removed from each plot and condition of mesh screens was assessed. All mesh collars were intact, except one (a collar B) which had a slight tear/puncture in one window.

Soil microbial biomass was determined for each collar based on comparison of formation of total dissolved organic carbon (DOC) in chloroform fumigated and nonfumigated soil (Brookes *et al.*, 1985; Beck *et al.*, 1997). Procedure was modified as follows: four 8 g samples of root free soil were weighed into appropriately labelled centrifuge tubes. Non fumigated samples were extracted immediately with 24 ml of 0.5M K_2SO_4 (Mallinckrodt Baker, Inc., Phillipsburgh, NJ), tubes were securely capped, vortexed (VWR® Mini Vortexer, VWR International, West Chester, PA) for ~30 seconds, shaken (Model No. 3590, Lab-Line Orbit Shaker, Lab-Line Instruments Inc., Melrose Park, IL) at 3 rpm for 1 h, and centrifuged (Model 5810, Eppendorf Centrifuge, Eppendorf North America, Hauppauge, NY) at 3200 rpm for 5 minutes. Samples were then filtered through 0.5M K_2SO_4 pre-leached and rinsed, oven dried, filter paper (No. 1 Whatman® Filter Paper, Whatman plc., Maidstone, Kent, UK), and frozen for later analysis. Fumigated sample centrifuge tubes were placed in a hood and plugged with two cotton wool balls. Four ml of chloroform (Mallinckrodt Baker, Inc.) was carefully added to each cotton ball, care was taken to ensure that chloroform did not leak onto soil sample, and tubes were securely closed, and kept in the dark for 7 days. Tubes were then uncapped in the hood, cotton balls were carefully removed, and samples were vortexed for 30 seconds approximately every hour for 3 h to enhance chloroform removal. Fumigated samples were then extracted with K_2SO_4, vortexed, shaken, centrifuged, filtered, and stored as described previously for the non

fumigated samples. Dissolved organic carbon (DOC) was measured using high temperature platinum-catalyzed combustion with a Shimadzu TOC-VCSH measuring unit (Shimadzu Corp., Houston, TX). Organic C was measured as non-purgeable C using USEPA method 415.1 which entails acidifying the sample and sparging for 4 minutes with C-free air. Microbial carbon was calculated by subtracting non-fumigated samples from fumigated samples and dividing by 0.45 to convert the chloroform-labile C pool to the microbial biomass C (Brookes *et al.*, 1985; Beck *et al.*, 1997), which was then expressed as microbial DOC ($\mu g\ g^{-1}$ dry soil).

STATISTICAL DESIGN

Effects of precipitation redistribution, warming and species mixture on respiration rates were be analyzed using a mixed model with precipitation treatment, warming, and species mixture as fixed effects and between shelter variation as a random effect. The precipitation and species treatments were arranged as a split-plot factorial in a completely randomized design. The precipitation regime constituted the whole-plot factor (with four replications), while the species combinations were assigned as within-plot factors. Precipitation effects were tested over the 'between shelter' error, and species mixture effect and treatment interactions were tested over the residual error. All analyses were conducted with statistical analysis software (JMP 7.02, SAS Institute, Cary, NC).

Results

RELATIONSHIP BETWEEN YEAR AND SOIL CO_2 EFFLUX

Partitioning of root, fungal, and bacterial respiration demonstrated the substantial contribution of bacterial respiration to soil CO_2 efflux (at least $\geq 45\%$) throughout the study for all species, regardless of precipitation treatment (Table 4.1, Figure 4.2 - Figure 4.4; see also Appendix). The contribution of fungal and root respiration varied over the course of the study. Contribution of fungal respiration was in general equal or higher than root respiration for all species, except for *S. scoparium* in control precipitation treatment where root contribution was greater than the fungal contribution (Figure 4.2 – Figure 4.4).

Table 4.1. Probability values (*P*-values) and F-ratios determined using ANOVA for soil CO_2 efflux, volumetric soil water content (VWC), and soil temperature from July 2008 – April 2010.

	Soil CO_2 efflux		Volumetric water content[z]		Soil temperature	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.29	0.608	0.08	0.782	0.09	0.778
Mixture (M)	4.87	**0.008**	140.1	**<0.001**	18.9	**<0.001**
P × M	0.44	0.644	3.17	**0.043**	1.48	0.228
Respiration Component (RC)	278.5	**<0.001**	-	-	1.56	0.210
RC × P	11.6	**<0.001**	-	-	0.33	0.716
RC × M	6.00	**<0.001**	-	-	0.27	0.898
RC × P × M	3.89	**0.004**	-	-	0.97	0.424
Date (D)	14.8	**<0.001**	278.0	**<0.001**	834.4	**<0.001**
P × D	0.72	0.741	17.1	**<0.001**	1.61	0.077
M × D	2.02	**0.002**	8.27	**<0.001**	1.11	0.325
P × M × D	0.37	0.999	1.56	0.043	0.69	0.875
RC × D	4.01	**<0.001**	-	-	0.52	0.978
P × RC × D	1.21	0.214	-	-	0.17	1.000
M × RC × D	0.90	0.681	-	-	0.39	1.000
P × M × RC × D	1.00	0.481	-	-	0.38	1.000

P-values ≤ 0.05 are printed in bold.

[z] Soil VWC was collected by plot (i.e. one probe per plot, not by collar). Therefore, these values were not applicable (-).

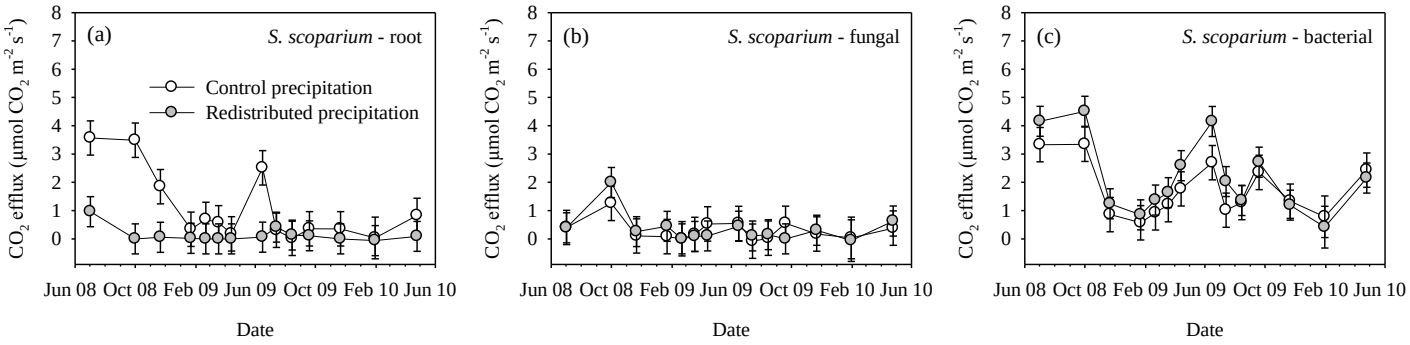

Figure 4.2. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time for (a) root respiration of *Schizachyrium scoparium* monoculture, (b) fungal respiration of *S. scoparium* monoculture, (c) bacterial respiration of *S. scoparium* monoculture (LSMeans ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

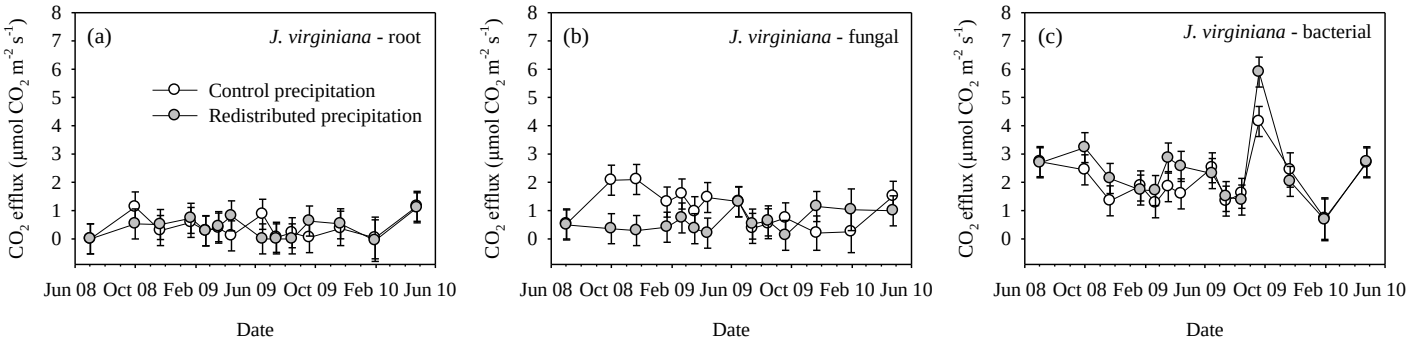

Figure 4.3. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time for (a) root respiration of *Juniperus virginiana* monoculture, (b) fungal respiration of *J. virginiana* monoculture, (c) bacterial respiration of *J. virginiana* monoculture (LSMeans ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

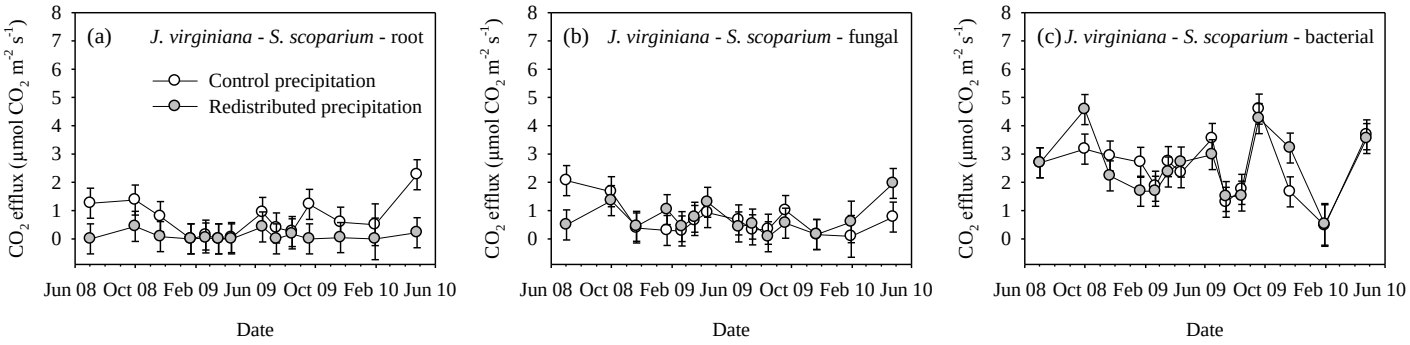

Figure 4.4. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time for (a) root respiration of *Juniperus virginiana* grown with *Schizachyrium scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (LSMeans ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

EFFECT OF ENVIRONMENTAL CONDITIONS ON ROOT, FUNGAL, AND BACTERIAL CONTRIBUTION TO SOIL CO_2 EFFLUX

Schizachyrium scoparium monoculture root respiration was greater in control precipitation treatment when compared to redistribution treatment regardless of soil VWC (precipitation effect, P =0.046, Figure 4.5a). *Juniperus virginiana* were not affected by precipitation treatments (Figure 4.6). *Juniperus virginiana – S. scoparium* mixture fungal respiration was optimal at moderate soil VWC and was lower at the extremes (high and low) soil VWC (soil VWC effect, P =0.027; Figure 4.7b). *Juniperus virginiana – S. scoparium* mixture bacterial respiration decreased with increasing soil VWC (precipitation × VWC interaction, P = 0.028; Figure 4.7c).

Schizachyrium scoparium monoculture root respiration was greater in control precipitation treatment when compared to redistributed precipitation treatment with increasing soil temperature (precipitation effect, P = 0.046; Figure 4.8a). *Juniperus virginiana* were not affected by precipitation treatments (Figure 4.9). *Juniperus virginiana – S. scoparium* mixture root respiration increased with increasing soil temperature (temperature effect, P =0.047; Figure 4.10a). *Juniperus virginiana – S. scoparium* mixture fungal respiration increased with increasing soil temperature for control precipitation treatment and peaked at moderate soil temperature and was lower at extremes in temperature (highs and lows) for redistributed precipitation treatment (precipitation × temperature effect, P = 0.028; Figure 4.10c).

DIURNAL ROOT, FUNGAL, AND BACTERIAL CONTRIBUTION TO SOIL CO_2 EFFLUX

Percentage contribution did not alter over time and no clear diurnal pattern for component contribution was detected during either campaign. Respiration rates were not different for precipitation treatments during each 24 hour survey on the 14 and 17 May in the *S. scoparium* monoculture and mixture root and bacteria component contribution and *J. virginiana* root, fungal, and bacterial component contribution (Figure 4.11 – Figure 4.13). *Schizachyrium scoparium* monoculture fungal respiration was greater in the control precipitation treatment when compared to the redistributed precipitation treatment on the 14 May (Figure 4.11b). *Juniperus virginiana – S. scoparium* mixture fungal respiration was greater in the redistributed precipitation treatment when compared to the control precipitation treatment on the 17 May (Figure 4.13b).

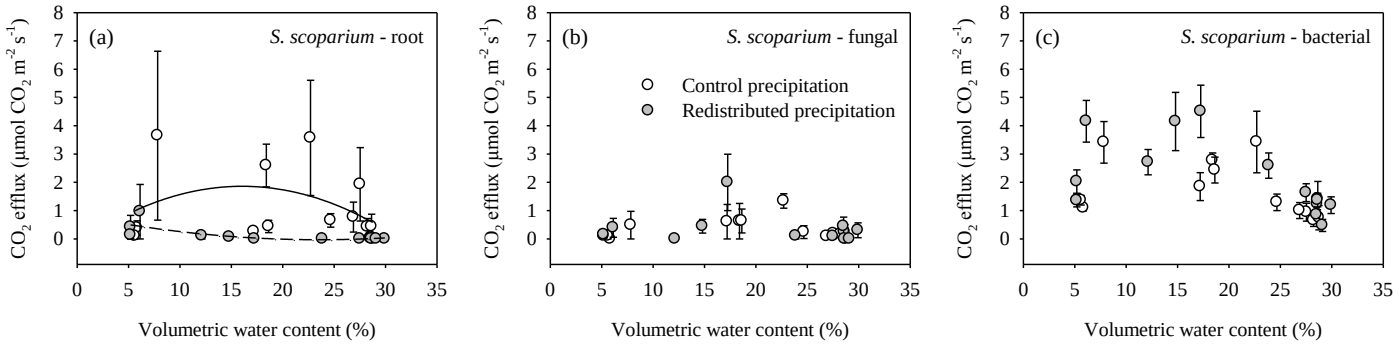

Figure 4.5. Effect of soil volumetric water content (%) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Schizachyrium scoparium* monoculture, (b) fungal respiration of *S. scoparium* monoculture, (c) bacterial respiration of *S. scoparium* monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation. Statistically significant regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (a) control precipitation root CO_2 efflux, $r^2 = 0.125$; redistributed precipitation root CO_2 efflux, $r^2 = 0.537$.

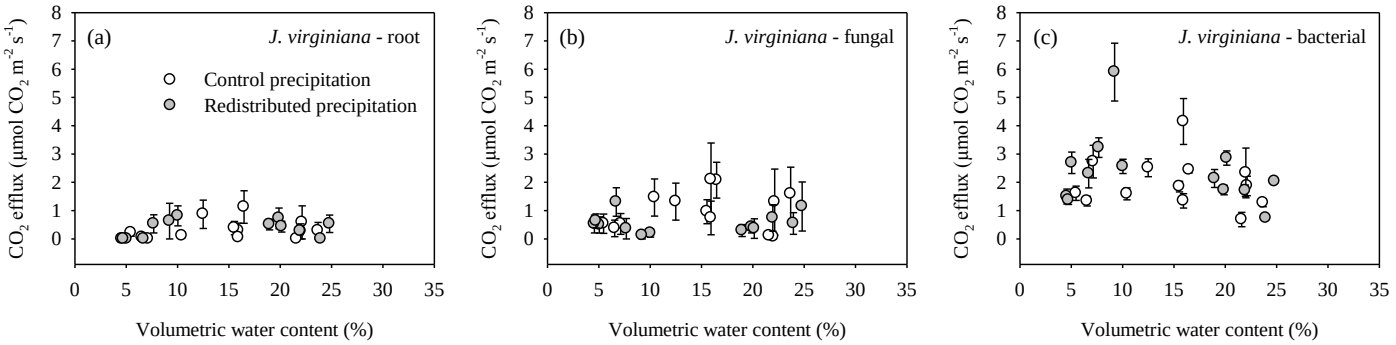

Figure 4.6. Effect of soil volumetric water content (%) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Juniperus virginiana* monoculture, (b) fungal respiration of *J. virginiana* monoculture, (c) bacterial respiration of *J. virginiana* monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

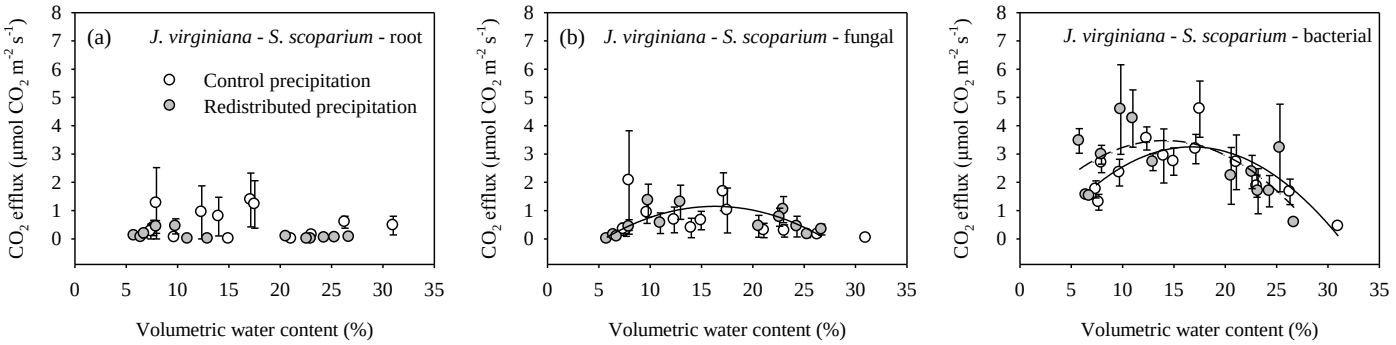

Figure 4.7. Effect of soil volumetric water content (%) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Juniperus virginiana* grown with *Schizachyrium scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means ± SE). Statistically significant regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (c) *J. virginiana – S. scoparium* control precipitation bacterial CO_2 efflux, $r^2 = 0.695$; redistributed precipitation bacterial CO_2 efflux, $r^2 = 0.354$. Single lines depict significant trends for (b) fungal CO_2 efflux, $r^2 = 0.558$.

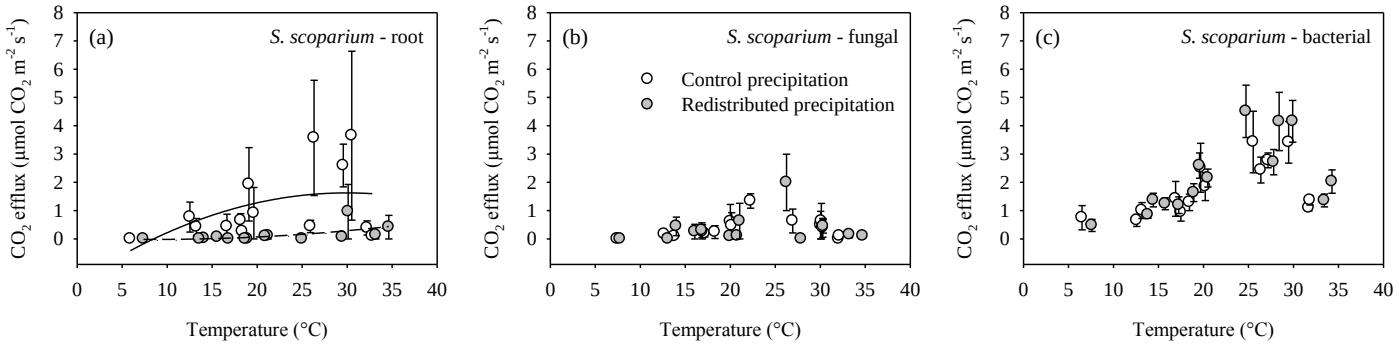

Figure 4.8. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Schizachyrium scoparium* monoculture, (b) fungal respiration of *S. scoparium* monoculture, (c) bacterial respiration of *S. scoparium* monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation. Significant regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (a) *S. scoparium* control precipitation root CO_2 efflux, $r^2 = 0.211$; redistributed precipitation root CO_2 efflux, $r^2 = 0.341$.

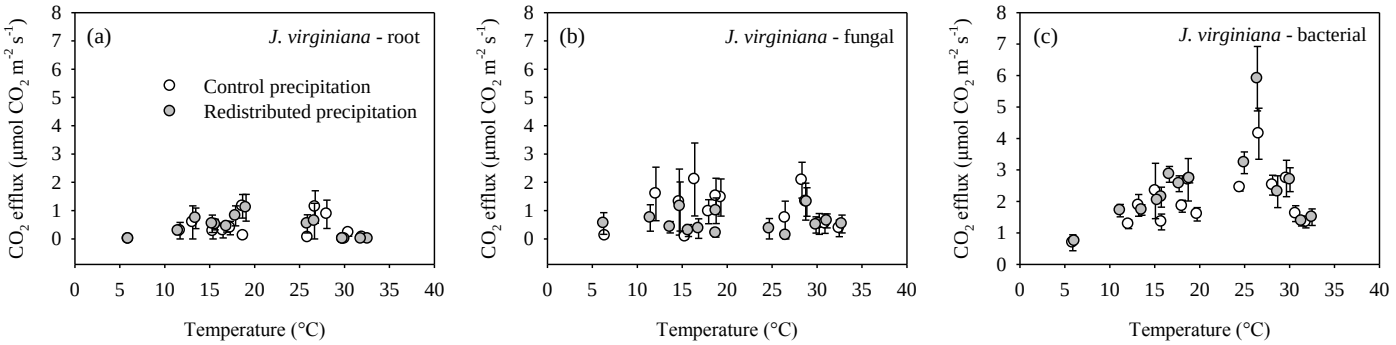

Figure 4.9. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Juniperus virginiana* monoculture, (b) fungal respiration of *J. virginiana* monoculture, (c) bacterial respiration of *J. virginiana* monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

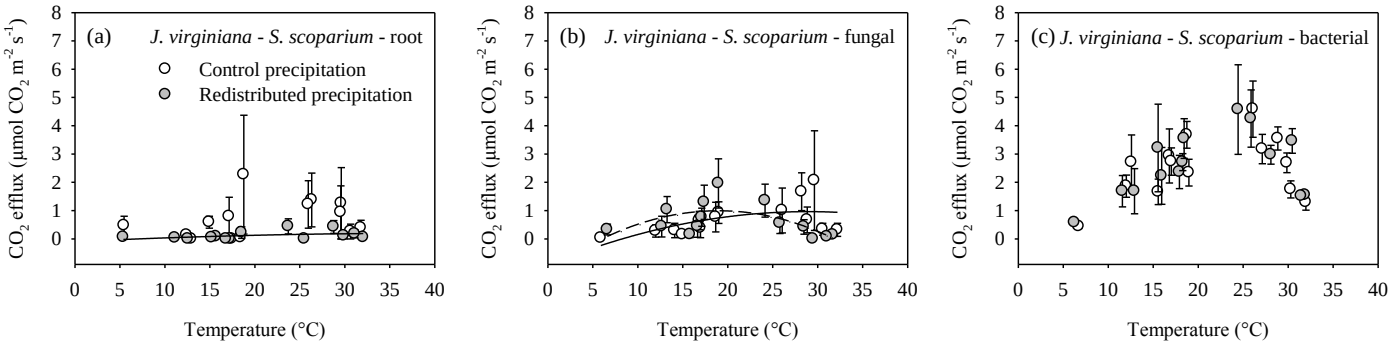

Figure 4.10. Effect of soil temperature (°C) on respiration components on soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Juniperus virginiana* grown with *Schizachyrium scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation. Significant regression relationships are depicted for control precipitation (solid line) and redistributed precipitation (dashed line); (b) *J. virginiana* – *S. scoparium* control precipitation fungal CO_2 efflux, $r^2 = 0.342$; redistributed precipitation fungal CO_2 efflux, $r^2 = 0.397$. Single lines depict significant trends for (a) root CO_2 efflux, $r^2 = 0.174$.

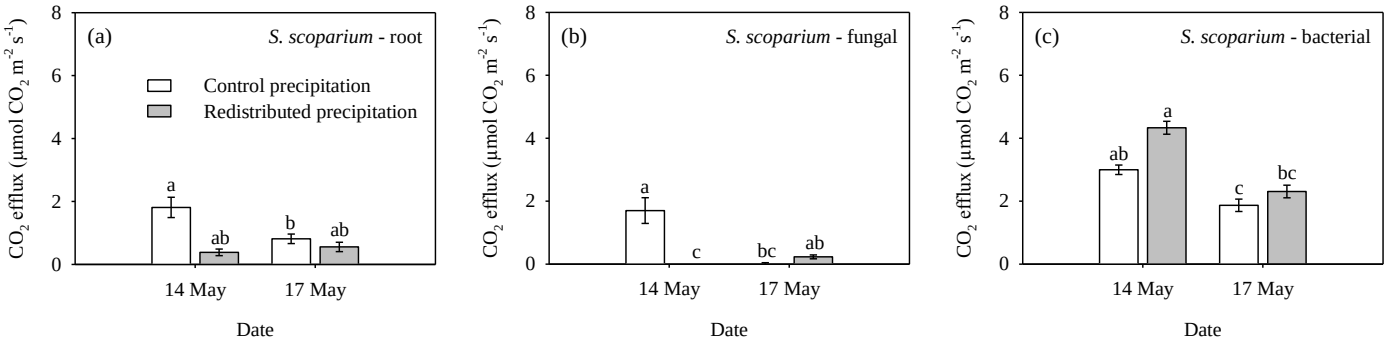

Figure 4.11. Effect of precipitation event on components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Schizachyrium scoparium* monoculture, (b) fungal respiration of *S. scoparium* monoculture, (c) bacterial respiration of *S. scoparium* monoculture before the precipitation event (14 May 2009) and after the precipitation event (17 May 2009) (mean ± SE). Unfilled bars represent control precipitation and filled bars redistributed precipitation. Letters indicate significant ($P \leq 0.05$) differences in response for precipitation treatment and date.

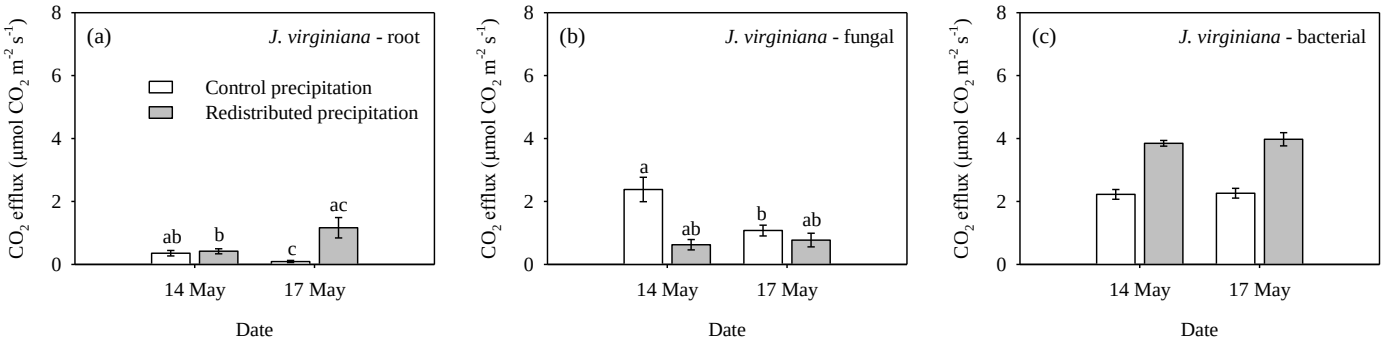

Figure 4.12. Effect of precipitation event on components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Juniperus virginiana* monoculture, (b) fungal respiration of *J. virginiana* monoculture, (c) bacterial respiration of *J. virginiana* monoculture before the precipitation event (14 May 2009) and after the precipitation event (17 May 2009 24) (mean ± SE). Unfilled bars represent control precipitation and filled bars redistributed precipitation. Letters indicate significant ($P \leq 0.05$) differences in response for precipitation treatment and date.

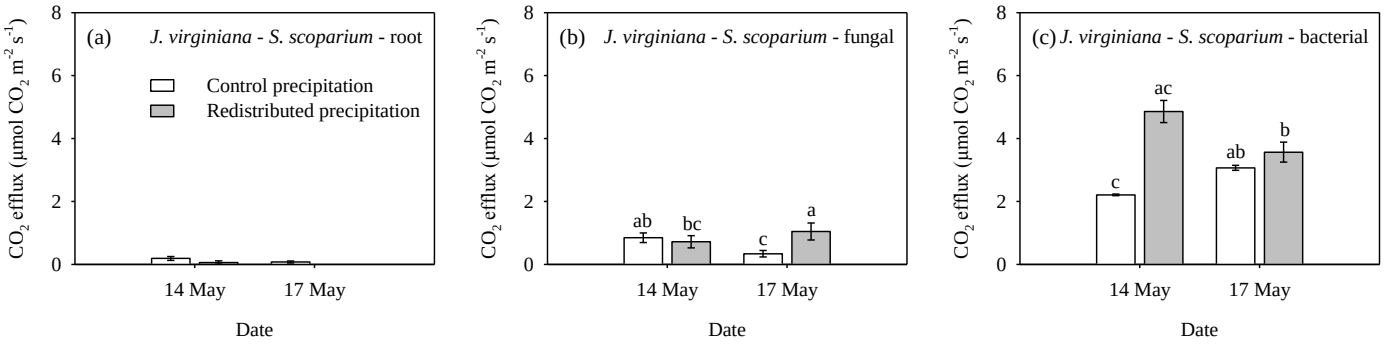

Figure 4.13. Effect of precipitation event on components on soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Juniperus virginiana* grown with *Schizachyrium scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* before precipitation event (14 May 2009) and after precipitation event (17 May 2009) (means ± SE). Unfilled bars represent control precipitation and filled bars redistributed precipitation. Letters indicate significant ($P \leq 0.05$) differences in response for precipitation treatment and date.

QUANTIFICATION OF ROOT AND MICROBIAL CONTRIBUTION TO SOIL CO_2 EFFLUX

There was no relationship between total root length and microbial DOC for any plant species (Figure 4.14). Microbial DOC was not affected by collar treatment or precipitation treatment in the *S. scoparium* monoculture and mixture (Figure 4.15). Microbial DOC was not affected within collar by precipitation treatment in *J. virginiana* monoculture, but was greater in collar C (which excluded both root and fungal, and allowed bacterial access), when compared to collar A (which allowed root, fungal, and bacterial access) and collar B (which excluded roots, and allowed fungal and bacterial access) collars in the control precipitation treatment (precipitation × collar interaction, $P = 0.026$; Figure 4.15b). Soil respiration increased with increasing total root length in *J. virginiana* monoculture (Figure 4.16b). Microbial DOC and soil CO_2 efflux were not correlated for any of the plant species (Figure 4.17).

Fine and total root length was greater in the collar A when compared to the other collars for all treatments (Table 4.2; Figure 4.18 – Figure 4.20). Fine and total root length were greater in the redistributed precipitation treatment when compared to the control precipitation treatment in the *J. virginiana* monoculture, regardless of collar (Table 4.2; Figure 4.19a and c). Coarse root length was greater in the *J. virginiana* mixture redistributed precipitation treatment collar A when compared to other collar and precipitation treatments (Table 4.2; Figure 4.20b).

Discussion

Partitioning of root, fungal, and bacterial respiration demonstrated the substantial contribution of bacterial respiration to soil CO_2 efflux throughout the study for all plant species, regardless of precipitation treatment, suggesting that in our system the root and fungal component of soil CO_2 efflux are not very large. Component contribution to soil CO_2 efflux in this study was within ranges reported in the literature (as reviewed by Hanson *et al.*, 2000; Raich & Tufekcioglu, 2000). Greater microbial (bacterial and fungal) respiration may reflect the ability of microbes to adapt to a wide range of environmental conditions (as reviewed by Harris, . 1981). Bacteria are physically protected from desiccation in the soil pore spaces, while fungal hyphae are generally found on the exterior of soil aggregates and may be more prone to water stress (Frey *et al.*, 1999).

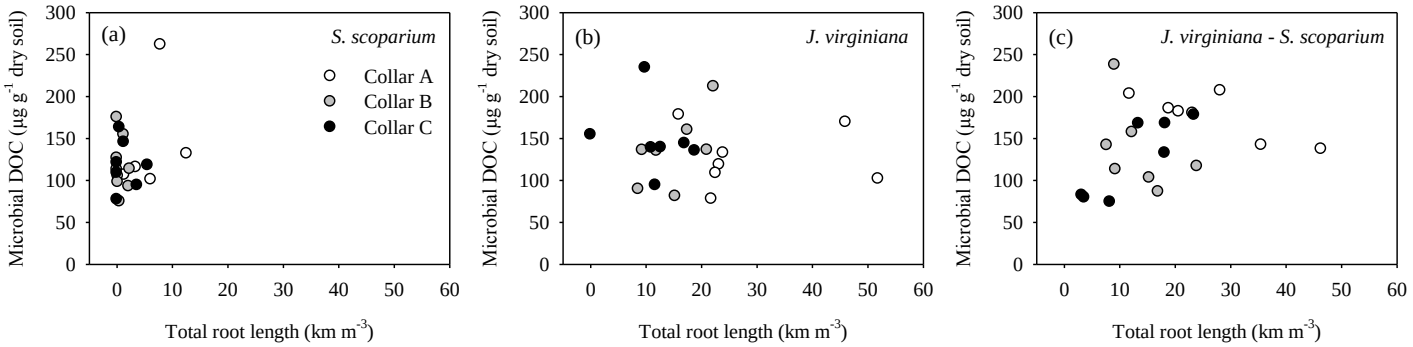

Figure 4.14. Relationship between total root length (km m^{-3}) and microbial dissolved organic carbon (DOC) (µg g^{-1} dry soil) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010). Unfilled circles represent collars which allowed roots, fungi, and bacteria access (collar A), grey filled circles represent collars which allowed fungi and bacteria access (collar B), and black filled circles represent collars which allowed bacteria only access (collar C).

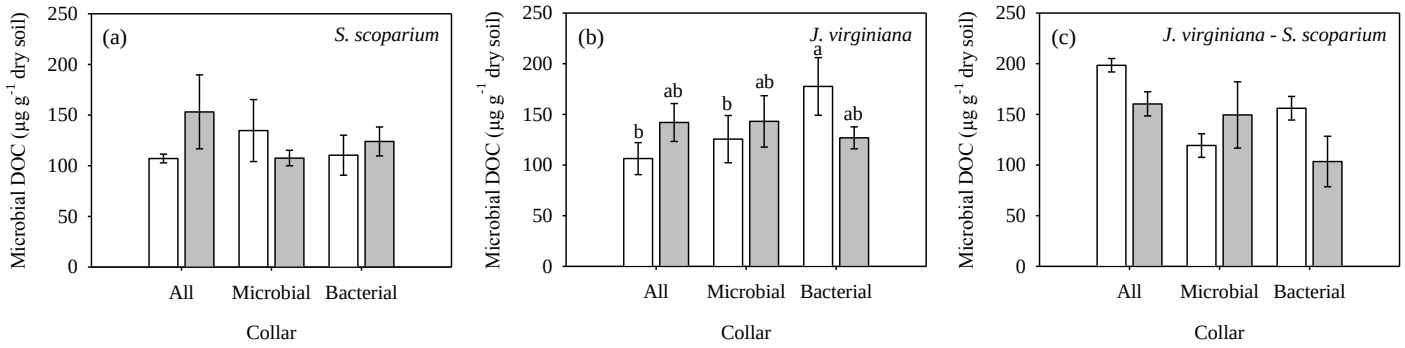

Figure 4.15. Effect of collar treatment on microbial dissolved organic carbon (DOC) (µg g^{-1} dry soil) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means ± SE). 'All' allowed roots, fungi, and bacteria access (collar A), 'microbial' allowed fungi and bacteria access (collar B), and 'bacterial' allowed only bacterial access (collar C). Unfilled bar represents control precipitation treatment and filled bar represents redistributed precipitation.

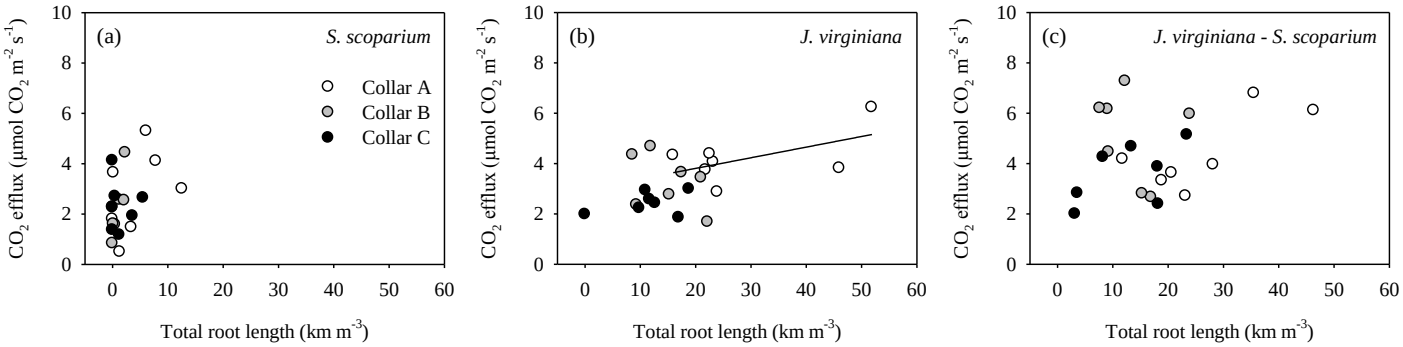

Figure 4.16. Effect of total standing root length (km m^{-3}) on CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) . Unfilled circles represent collars which allowed roots, fungi, and bacteria access (collar A), grey filled circles represent collars which allowed fungi and bacteria access (collar B), and black filled circles represent collars which allowed bacteria access (collar C). Solid line indicates relationship between CO_2 efflux and root length for collar A, $r^2 = 0.321$; $P = 0.008$.

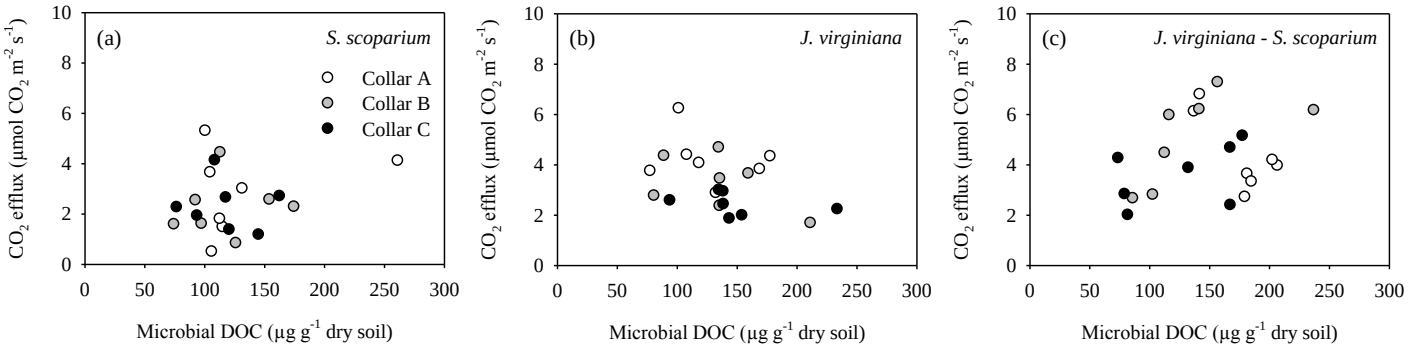

Figure 4.17. Effect of microbial dissolved organic carbon (DOC) (µg g^{-1} dry soil) on CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010). Unfilled circles represent collars which allowed roots, fungi, and bacteria access (collar A), grey filled circles represent collars which allowed fungi and bacteria access (collar B), and black filled circles represent collars which allowed bacteria access (collar C).

Table 4.2. Probability values (*P*-values) and F-ratios determined using ANOVA for root length (km m^{-3}) by species mixture for 25 April 2010.

	Schizachyrium scoparium		*Juniperus virginiana*		*J. virginiana – S. scoparium*	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
			Fine root length			
Precipitation (P)	0.38	0.562	8.21	**0.029**	1.12	0.330
Collar (C)	8.09	**0.006**	6.75	**0.011**	9.74	**0.003**
P × C	0.32	0.735	0.51	0.614	2.80	0.100
			Coarse root length			
Precipitation (P)	0.66	0.449	0.18	0.685	0.16	0.701
Collar (C)	2.62	0.113	1.77	0.213	6.62	**0.012**
P × C	0.32	0.731	0.18	0.840	5.15	**0.024**
			Total root length			
Precipitation (P)	0.26	0.626	7.66	**0.033**	1.08	0.339
Collar (C)	8.29	**0.006**	7.13	**0.009**	10.5	**0.002**
P × C	0.24	0.792	0.49	0.624	3.14	0.080

P-values ≤ 0.05 are printed in bold.

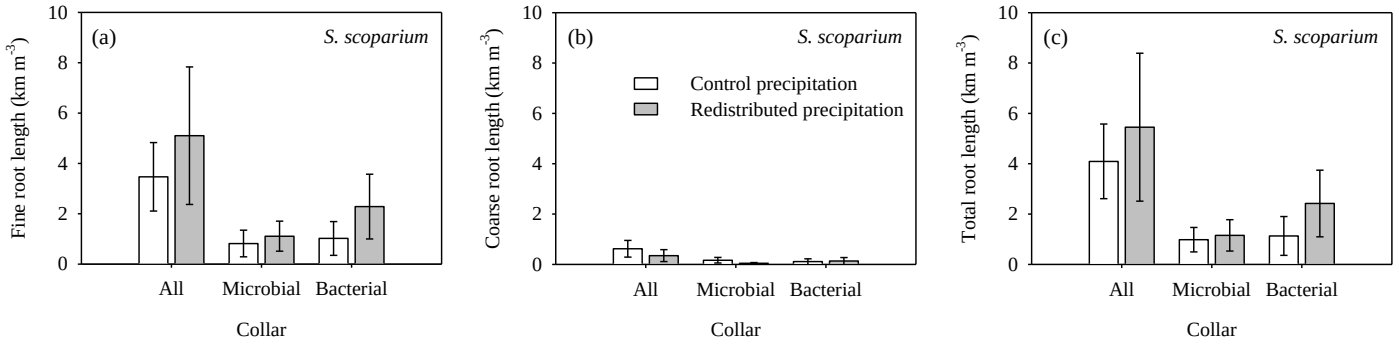

Figure 4.18. Effect of collar treatment on recovered (a) fine, (b) coarse, and (c) total root length (km m^{-3}) for *Schizachyrium scoparium* monoculture (means ± SE) at the termination of the experiment (25 April 2010). 'All' allowed roots, fungi, and bacteria access (collar A), 'microbial' allowed fungi and bacteria access (collar B), and 'bacterial' allowed bacteria access only (collar C). Unfilled bars represent control precipitation treatment and filled bars represent redistributed precipitation treatment.

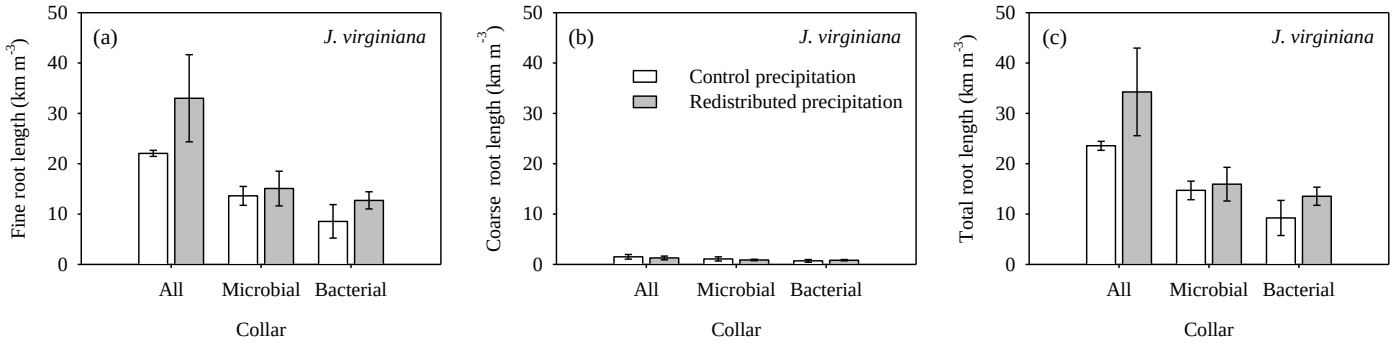

Figure 4.19. Effect of collar treatment on recovered (a) fine, (b) coarse, and (c) total root length (km m^{-3}) for *Juniperus virginiana* monoculture (means ± SE) at the termination of the experiment (25 April 2010). 'All' allowed roots, fungi, and bacteria access (collar A), 'microbial' allowed fungi and bacteria access (collar B), and 'bacterial' allowed bacteria access only (collar C). Unfilled bars represent control precipitation treatment and filled bars represent redistributed precipitation treatment.

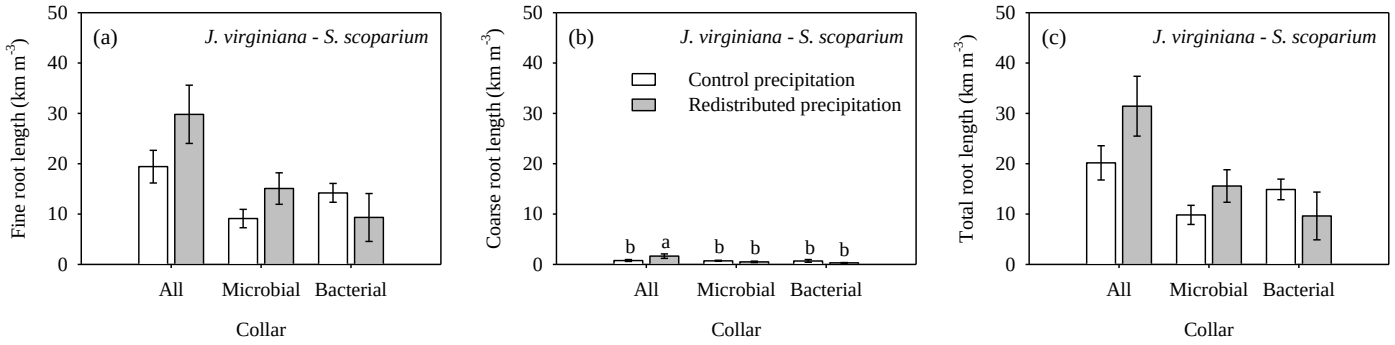

Figure 4.20. Effect of collar treatment on recovered (a) fine, (b) coarse, and (c) total root length (km m^{-3}) for *Juniperus virginiana* grown with *Schizachyrium scoparium* (means ± SE) at the termination of the experiment (25 April 2010). 'All' allowed roots, fungi, and bacteria access (collar A), 'microbial' allowed fungi and bacteria access (collar B), and 'bacterial' allowed bacteria access only (collar C). Unfilled bars represent control precipitation treatment and filled bars represent redistributed precipitation treatment.

Individual components of soil CO_2 efflux in this study varied with seasonal changes in soil VWC and temperature, with higher respiration rates in the spring and lower rates in both the cooler winter season and at the end of the dry summer period (Hanson *et al.*, 2000; Ryan & Law, 2005). However, no clear inter annual or diurnal pattern of relative component contribution was detected. Seasonal variations in component contribution to CO_2 efflux in our study may reflect the distinct seasonal differences in *J. virginiana* (a C_3 evergreen tree) and *S. scoparium* (a C_4 grass) leaf structure and longevity, quality of litter inputs, and root growth and turnover. In that, plant species within a plant community that provide resources of contrasting quality and quantity and/or in pulses are likely to exert temporal effects on below ground organisms and processes (Wardle *et al.*, 2004; Yang *et al.*, 2008). The lack of variation in diurnal component contribution to soil CO_2 efflux and total soil CO_2 efflux during the May 2009 pre- and post- precipitation event campaigns may have been due to a high night time humidity and lack of a diurnal pattern in soil temperature at the study site on those dates (Davidson *et al.*, 2000).

Root-related CO_2 efflux, while low, was in general higher in the control precipitation treatment when compared to the redistributed precipitation treatment in *S. scoparium* monoculture and mixture, where root contribution to soil CO_2 efflux was frequently nonexistent. Greater root related CO_2 efflux rates in the *S. scoparium* monoculture in particular are not due to greater standing root length density (RLD) in the *S. scoparium* monocultures since RLD was much reduced in the *S. scoparium* monocultures compared to *J. virginiana* monoculture plots. Greater root related CO_2 efflux in the *S. scoparium* monoculture plots may reflect higher turnover of *S. scoparium* roots compared to *J. virginiana* roots, resulting in a lower average root age. A younger root population would lead to higher CO_2 efflux rates due to higher respiratory activity of young roots (Volder *et al.*, 2005).

Reduced root respiration rates in the redistributed precipitation treatment may be due to drought conditions (Burton *et al.*, 1996; Bryla *et al.*, 1997), especially in warmed soils (Bryla *et al.*, 2001), during the summer and higher soil VWC conditions during the cool seasons, which may have reduced oxygen availability and restricted root growth and activity (Kozlowski & Pallardy, 2002). Root respiration in the *S. scoparium* monoculture plots and *S. scoparium* – *J. virginiana* mixture plots in the control precipitation distribution treatment showed a distinct seasonal pattern with higher respiration rates in June. Seasonal changes in root respiration may reflect changes in root production (Bahn *et al.*, 2006). The root component of soil respiration is suggested to be largely in sync with periods of high root production, with generally a peak

production rate of roots during early spring (e.g, Eissenstat & Caldwell, 1988; Zogg *et al.*, 1996; Jarvis *et al.*, 1997; Fitter *et al.*, 1999).Young roots are suggested to have higher respiration rates than older roots, potentially reflecting their higher metabolic activity and turnover rates (Bouma *et al.*, 2001; Volder *et al.*, 2005). In addition, during periods of unfavourable environmental conditions, decreased photosynthetic activity may result in the use of stored carbohydrates to maintain living tissue and a decoupling of root respiration from aboveground photosynthetic activity (Hogberg *et al.*, 2001), which may explain the lack of root activity in general, particularly in the redistributed precipitation treatments.

Juniperus virginiana – S. scoparium mixture fungal respiration was greater at moderate soil VWC and was lower at the extremes (high and low) soil VWC. *Juniperus virginiana – S. scoparium* mixture fungal respiration increased with increasing soil temperature for the control precipitation treatment and peaked at moderate soil temperature and was lower at extremes in temperature (highs and lows) for the redistributed precipitation treatment. Greater extremes in the drying and rewetting cycles in the redistributed precipitation treatment may have resulted anoxic conditions during the cool seasons and periods of intense drought during the summer months. Reflecting that fungal respiration in our study, may be closely affiliated with root respiration (Pendall *et al.*, 2004) which is reduced during extreme drought conditions (Bryla *et al.*, 1997; Burton *et al.*, 1998), especially in warmed soils (Bryla *et al.*, 2001), and under anoxic conditions (Drew, 1997).

Bacterial respiration was, in general, greater in redistributed precipitation treatments when compared to control precipitation treatments for tree and grass monocultures. *Juniperus virginiana – S. scoparium* mixture bacterial respiration decreased with increasing soil VWC. Bacterial communities which regularly experience drought and rewetting events, as in the redistributed precipitation treatment in this study, may well have acclimated to these conditions over time, resulting in selection of tolerant bacteria within the microbial community (Fierer *et al.*, 2003). Therefore, we suggest that in our study, there has been a selection for microbes that can tolerate more extreme VWC conditions in the redistributed precipitation treatment. In addition, rather than a total shift in microbial community, it is more likely that in our study, the bacterial community comprised of slow growing drought tolerant gram-positive bacteria and fast growing drought sensitive gram-negative bacteria, which alternately proliferate as conditions change (Vangestel *et al.*, 1993). Bacteria may acclimate to stress within our system by altering resource allocation from growth to survival mechanisms (Schimel *et al.*, 2007).

Plant productivity and microbial biomass are reported to be positively related across a wide range of soils (Schimel, 1986; Burke, 1989). In that, root exudates represent a major flux of C into the soil and are an important resource for soil microbes. However, the microbial biomass was not correlated with standing root length for plant species or plant species combination in our study, suggesting that standing root length density is not a good predictor of total microbial biomass. This lack of a relationship is surprising, as we expected that standing root length density would influence the quantity and quality of substrates available to the microbial community.

The lack of correlation between standing root length and microbial biomass may reflect the variety of substrates used by the microbial community i.e., shifting back and forth from polysaccharides that are readily used by microorganisms as energy sources to C compounds such as those with aromatic ring structures that are much more difficult for the microbes to use. In that, microbial respiration/community may mineralize the labile soil organic matter first (Trumbore, 2000; de Graaff *et al.*, 2010) but may also use substrate with older more recalcitrant C (Waldrop & Firestone, 2004; Kramer & Gleixner, 2006). This shift from using labile to more recalcitrant older C sources may reflect changes in root exudation due to changes in climatic conditions, as imposed during our study, and/or changes in microbial community composition and enzyme activity (Waldrop & Firestone, 2004). Addition of organic C from root exudates may stimulate microbial decomposition of more recalcitrant soil C (Pendall *et al.*, 2003; Fontaine *et al.*, 2004; Fontaine *et al.*, 2007). Litter from coniferous species generally decomposes more slowly than from woody angiosperm species, which in turn breakdown more slowly than from herbaceous species (Cornelissen, 1996).

Microbial DOC was not affected by mesh size or precipitation treatment in the *S. scoparium* monoculture and mixture suggesting a high level of available microbial substrate in the soil and/or a shift in substrate used to more recalcitrant forms of soil C. We expected that collars which limit root growth would have a reduction in available substrate, and, as most microbial respiration is from recently produced material (Trumbore, 2000), thus result in reduced microbial respiration (Hogberg & Hogberg, 2002). Microbial DOC was greater in the bacteria only collars than in the open collars and fungal + bacteria collars in the control precipitation treatment for *J. virginiana* plots. This was surprising because we expected a smaller amount of microbial DOC in collars lacking roots and fungi due to potentially higher amounts of easily decomposable substrates being provided by roots and fungi. It is possible that the microbial

community in the *J. virginiana* plots is actively suppressed by the presence of exudates from *J. virginiana* roots and/or associated fungi. Thus, by reducing the amount of roots, microbial growth may have been stimulated by reducing the amount of anti-microbial compounds exudated by *J. virginiana* roots. *Juniperus ashei* J. Buchholz (Ashe juniper) has been shown to have allelopathic effects on neighbouring species (Young & Bush, 2009) and thus it is possible that the presence of *J. virginiana* has similar belowground effects.

Alternatively, *J. virginiana* roots and associated mycorrhizal fungi may limit resources in sufficient quantities to reduce the amounts of available C to the microbial community and thus reduce microbial activity when roots are present. Furthermore, microbial activity in the rhizosphere is limited by N availability, thus root uptake of N may increase the competition for nutrients and decrease microbial growth and metabolism (Hu *et al.*, 2001). Foliar litter inputs and root inputs from either exudates or root turnover are the main source of soil C and N (McClaugherty *et al.*, 1982). Norris *et al.* (2001b) reported C:N ratios of ~100:1and high lignin content in *J. virginiana* fine roots, which may immobilize N in cores where *J. virginiana* roots are present and thus limit N availability for microbial growth.

Microbial DOC was not affected by collar treatment or precipitation treatment in the *S. scoparium* monoculture and mixture suggesting a high level of available microbial substrate in the soil. We expected that collars which limit/exclude root growth would have a reduction in substrate, and thus result in reduced microbial biomass and respiration (Hogberg & Hogberg, 2002). Microbial DOC and soil CO_2 efflux were not correlated for any of the plant species, suggesting a disconnect between microbial abundance and soil CO_2 efflux.

Carbon flux to both the roots and microbes may also be affected by soil water conditions. Drought events may lead to a decoupling of root growth and respiration from aboveground photosynthetic activity and root growth and respiration may become more dependent on stored carbohydrate reserves (Hogberg *et al.*, 2001). Reduced photosynthetic activity can reduce the flow of C into the roots and rhizosphere, and thus induce soil microbe dormancy or mortality, resulting in reduced microbial growth and activity and reduced microbial CO_2 efflux.

Soil CO_2 efflux increased with increasing standing total root length in *J. virginiana* monoculture. Fine and total root length was greater in the collar that allowed root, fungal, and bacterial access when compared to the other collars, suggesting that the collar treatment worked. Fine and total root length were greater in the redistributed precipitation treatment when

compared to the control precipitation treatment in the *J. virginiana* monoculture, thus *J. virginiana* root production was more prolific under dry summers and wet springs and winters.

Current understanding of microbial biodiversity and response to environmental conditions (drying and rewetting) in the soil is limited. Drying-rewetting cycles have been reported to increase fungal and decrease bacterial dominance (Cosentino *et al.*, 2006), increase bacterial and decrease fungal dominance (Denef *et al.*, 2001; Gordon *et al.*, 2008), and have limited effect on dominance of fungal or bacterial component (Hamer *et al.*, 2007). However, the potential underlying mechanism for bacterial to fungal dominance in component contribution to soil CO_2 efflux remains unclear in this study, and may reflect high fungivore/macrophage activity at the study site, differential fungal-bacterial response to drying and rewetting cycles, and/or shift in substrate supply (Strickland & Rousk, 2010). The effect of increased C flux from roots to soil for microbial communities and C exchange are difficult to predict as these effects are influenced by a range of factors including plant cover, soil VWC, and to a lesser extend soil temperature.

Some of our findings may have been affected by the mesh collar system utilized. In short, in our study we have assumed that 1) ingrowth of roots and hyphae was quick (< 1 month); 2) CO_2 influx from the surrounding soil profile was negligible; 3) the mesh collar system did not change microbial activity, 4) installation disturbance was negligible, and 5) contribution of macro- and micro-fauna was negligible. We were unable to completely eliminate *J. virginiana* root growth, from below and up into our collars and thus some root exclusion collars had small amounts of root material in them (Figure 4.10), potentially leading to underestimation of the root component of soil CO_2 flux. In addition, since the collars were designed to allow free water movement, the collar design also allows for the possible diffusion of CO_2 from surrounding soil through the mesh windows and thus may overestimate fungal and bacterial contribution. This is a potential artefact that has not been adequately studied in earlier experiments (Johnson *et al.*, 2001; Heinemeyer *et al.*, 2007). The short time periods between insertion of collars in June 2008 and start of data collection in July 2008 may have led to some initially very high soil CO_2 fluxes due to disturbance effects, particularly in the *S. scoparium* monocultures.

Conclusion

Given the structural, physiological, and phylogenetic differences between grasses and gymnosperms and the relatively small respiration differences observed in this study, suggests that the components (root, fungal, and bacterial) of soil CO_2 efflux were affected more by climatic and inherent soil conditions with plant species causing a secondary effect. Accurate modelling of soil CO_2 efflux within the juniper-grass savannah system is dependent on consideration of individual component response to environmental conditions. Our results strongly indicate the substantial contribution (45-100%) of bacterial respiration to soil CO_2 efflux within this system. Low soil VWC may have influenced soil CO_2 efflux directly through drought stress on roots and microbes and indirectly through reduced plant productivity and C allocation. High VWC likely limited soil CO_2 efflux by reducing CO_2 diffusion through the soil and through the generation of anoxic conditions that limited microbial and root activity. There may be a plant and microbial specific response to drying and rewetting within the system. Potentially reflecting a broad range of 'near' optimum soil VWC where changes in soil VWC have limited effect, if any, on soil CO_2 efflux.

CHAPTER V
EFFECT OF WARMING AND PRECIPITATION DISTRIBUTION ON MYCORRHIZAL COLONIZATION POTENTIAL OF YOUNG ROOTS IN POST OAK SAVANNAH

Introduction

Mycorrhizal fungi are an integral part of terrestrial ecosystems (Read, 1991; van der Heijden *et al.*, 1998; Allen *et al.*, 2003) and are an important component of belowground response to climate change due to their key position at the plant-soil interface. Mycorrhizal fungi exist in symbiotic (mutually beneficial) associations with fine roots of most higher plants. The plant supplies the fungus with carbon (C) (from photosynthesis) while the mycorrhizal fungi enhance plant nutrient and water uptake and help alleviate environmental stresses (Smith & Read, 2008). Increasing concentrations of greenhouse gasses are projected to elevate global surface temperatures and potentially increase the variability of precipitation and drought events (Bates *et al.*, 2008) and will likely have a strong effect on mycorrhizal fungi (Staddon *et al.*, 2003b).

Precipitation redistribution and drought events may adversely affect mycorrhizal abundance (Allen *et al.*, 1987; Allen *et al.*, 1989b; Shi *et al.*, 2002). More intense flooding and drought events may eliminate some mycorrhizal species that are not able to tolerate the more 'extreme' conditions (Stenstrom, 1991; Miller & Bever, 1999; Robertson *et al.*, 2006) or may restrict some mycorrhizal associations to less extreme portions of the year (Apple *et al.*, 2005; Escudero & Mendoza, 2005). Climate warming may increase mycorrhizal abundance (Rillig *et al.*, 2002; Gavito *et al.*, 2005) depending on host plant (Entry *et al.*, 2002; Heinemeyer & Fitter, 2004). Warming may directly affect mycorrhizal establishment and growth (Koske, 1987; Malcolm *et al.*, 2008) and indirectly through enhanced host plant biomass and growth (Heinemeyer & Fitter, 2004), increased allocation of photosynthates (Hawkes *et al.*, 2008), reduced soil volumetric water content (VWC) availability and altered soil nutrient mineralization and immobilization processes (Fitter *et al.*, 1999). Warming may also eliminate some mycorrhizal species that are not able to tolerate higher soil temperatures and/or restrict mycorrhizal associations to specific, less extreme/cooler seasons of the year (Bentivenga & Hetrick, 1992; Heinemeyer & Fitter, 2004).

In the southern United States, intensification of summer drought coupled with increased variability in size and intensity of precipitation events in spring and autumn is projected to be more probable than a substantial change in the mean annual precipitation (Groisman *et al.*, 2005; Groisman & Knight, 2008). Climate change, fragmentation of the landscape, and altered land management practices, coupled with fire suppression have resulted in invasion and expansion of woody plants into grassland and savannah systems of North America (Van Auken, 2000; Heisler *et al.*, 2003). Post oak savannah in the south-central United States are dominated by three contrasting plant functional types: *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) a C_4 grass, *Quercus stellata* Wangenh. (post oak), a C_3 deciduous tree, and increasingly *Juniperus virginiana* L. (eastern redcedar) a C_3 evergreen tree. In the past 50 years, *J. virginiana* has strongly increased its presence, often at the expense of *S. scoparium* and, to a lesser extent, *Q. stellata* (Briggs *et al.*, 2002; Briggs *et al.*, 2005). *Schizachyrium scoparium* commonly form symbiotic associations with AM fungi and are frequently considered to be obligate mycotrophs (Dhillion *et al.*, 1988; Anderson & Liberta, 1992; Dhillion, 1992; Meredith & Anderson, 1992; Anderson *et al.*, 1994). Most *Quercus* spp. usually form associations with EM mycorrhizae (Mitchell *et al.*, 1984; Daughtridge *et al.*, 1986; Bakker *et al.*, 2000; Dickie *et al.*, 2001; Egerton-Warburton & Allen, 2001; Pregitzer *et al.*, 2002). Some *Quercus* spp. will form associations with both EM and AM fungi (Grand, 1969; Rothwell *et al.*, 1983; Dickie *et al.*, 2001). *Juniperus* spp. have been reported to form associations with ectomycorrhizal (EM) fungi (Thomas, 1943) and arbuscular mycorrhizal (AM) fungi (Reinsvold & Reeves, 1986; Pregitzer *et al.*, 2002; Caravaca *et al.*, 2006; Wubet *et al.*, 2006).

Mycorrhizal associations with the roots of woody and herbaceious species in post oak savannah may be a key component of the structure and function of this system, and may play an important role in tree-grass competition and community dynamics. The broad objective of this study was to determine the effects of warming and precipitation redistribution on mycorrhizal abundance of *J. virginiana* and *S. scoparium* in southern post oak savannah. The goal was to quantify the effects of plant species composition, warming, increased intensity of summer drought, and the increased amount of cool season precipitation on mycorrhizal abundance in southern post oak savannah. We hypothesised that: (i) climate warming and rainfall redistribution both independently and in combination will adversely affect mycorrhizal colonization potential of young roots, and (ii) the effect of warming and rainfall redistribution

both independently and in combination on mycorrhizal colonization potential of young roots is mediated by plant species interaction.

Materials and Methods

EXPERIMENTAL SITE AND INFRASTRUCTURE

The Texas warming and rainfall manipulation experiment (Texas WaRM Experiment) is located on a remnant post oak savannah site (30°34 N 96°21 W) near Texas A&M University, College Station, Texas. This facility was constructed in 2003 to investigate the combined effects of altered precipitation distribution and warming on tree grass dominants of southern oak savannah. The research infrastructure included eight permanent 18 × 9 × 4.5 m (L × W × H) rainout shelters covered with clear polypropylene film. The side walls below 1.5 m were open to maintain microclimate conditions as near ambient as possible, but effectively exclude precipitation (Fay *et al.*, 2000; Weltzin & McPherson, 2003). A fine mesh shade cloth, matching the radiation attenuation of the film (70% transmittance), excludes windblown precipitation from entering two 4.5 m high open ends of each shelter. Sheet metal flashing 40 cm in height, was inserted 30 cm into the soil, penetrating the clay hardpan, to isolate each shelter from surface and subsurface water flow.

Ten 2 × 2 m plots with five species combinations were located beneath each shelter in the native soil (Volder *et al.*, 2010). Soil consisted of a shallow layer (< 20 cm) of Boonville fine sandy loam, with a thick clay pan below (Chervenka, 2003). An overhead irrigation system (17 pressure regulated spray nozzles per shelter) simulated precipitation regimes by supplying reverse osmosis (RO) treated ground water, from four 11,500 L holding tanks, to each shelter. A weather station (EZ Mount GroWeather, Davies Instruments, Hayward, CA) on site recorded precipitation, air temperature, and humidity. Solar radiation (total PPFD), air temperature, and relative humidity were continuously monitored in each shelter and control plots using data loggers (Hobo U12, Onset Company Corp., Bourne, MA). Soil water content was measured twice weekly for each plot using permanently installed time domain reflectometry (TDR) probes (Soil Moisture Corp., Santa Barbara, CA) which were inserted vertically to give an integrated measure of soil volumetric water content (VWC) in the top 20 cm of the soil profile. The rainout shelter design preserves natural variation in the microenvironment that is for the most part similar to ambient conditions (Fay *et al.*, 2000). Mean daily temperature in the shelters were on

average 0.3 °C higher, RH values were 2% lower, and PPFD levels were 30% lower than ambient.

PRECIPITATION AND WARMING TREATMENT

Simulated precipitation regimes included two patterns that varied in season distribution and event size, but not in total annual precipitation (1018 mm) or total number of events. The long-term (50 yr) precipitation events were also simulated from the regional long-term precipitation record. The frequency and intensity (amount) of precipitation events were also simulated from the regional long-term precipitation record. Precipitation redistribution treatment beneath the other four shelters had 40% of the summer (May – September) precipitation withheld from each event and evenly redistributed to the preceding spring (March and April) and autumn (October and November) (Figure 5.1a). The redistribution treatment effectively increased the intensity of the summer drought (redistribution dry phase) and the amount of precipitation that occurred during the cooler season of the year (redistributed wet phase). Each precipitation regime was replicated within four rainout shelters. Precipitation regimes were initiated in March 2004.

One half of the experimental plots beneath each shelter were continuously warmed (24 h per day) with overhead infrared lamps (models MRM 1208L, Kalglo Electronic, Bethlehem, PA) that output 400 W (100 W m^{-2}) of radiant energy from a height of 1.5 m above the soil surface (Figure 5.1b) (Harte *et al.*, 1995; Shaw & Harte, 2001; Wan *et al.*, 2002). Due to increasing height of both *J. virginiana* and *Q. stellata*, all heaters were raised to 2 m (from 1.5 m) in February 2008, while output of heaters was doubled from 400 W to 800 W.

PLANT SPECIES COMBINATIONS

Two sets of five species combinations were grown in 2 × 2 m plots beneath each of the rainout shelters and two unsheltered controls. One set of plots was warmed with overhead infrared lamps while the other set was fitted with dummy lamps. *Schizachyrium scoparium*, *Q. stellata* and *J. virginiana* were each grown in monoculture (25 plants per plot). In addition, each of the tree species were each grown with *S. scoparium* in separate mixed species plots (13 trees and 12 grasses) to investigate tree-grass interactions.

The plots were established in 2003 one year prior to the start of experiment treatments (March 2004) from local transplants of *S. scoparium*, 1-yr-old bare root containerized *Q. stellata*, and *J. virginiana* grown from native, regional seed sources. Monocultures of *J. virginiana* were

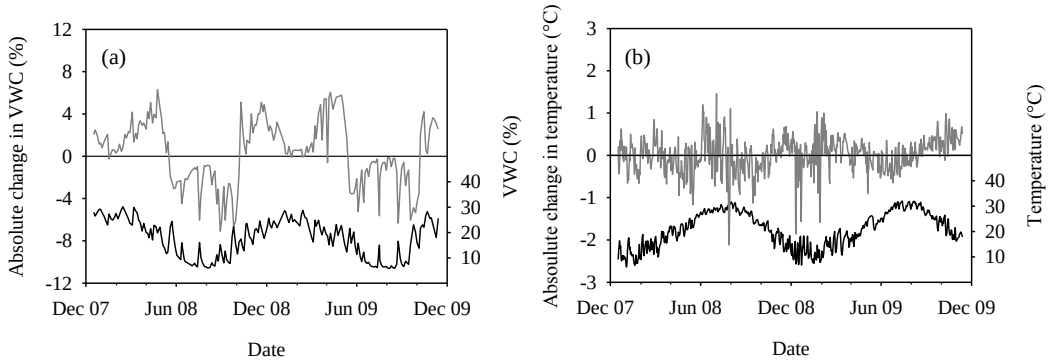

Figure 5.1. Effect of (a) precipitation treatment on soil volumetric water content (VWC) over time averaged across plant species mixture and warming treatment. The grey line depicts absolute change in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal soil VWC pattern. Effect of (b) warming treatment on soil temperature at 3 cm depth averaged across plant species mixture and precipitation distribution treatment. The grey line depicts absolute change in soil temperature due to the warming treatment and the black line depicts the seasonal soil temperature pattern.

thinned in December 2007. Twelve trees were removed from each monoculture plot. The remaining trees had the same spacing as the trees in the mixture plots (stem/trunk of each tree that were left were now 0.8 m apart, instead of 0.4 m). One-year-old transplant/replacement bare root *Q. stellata* seedlings were replanted as necessary in February 2008.

MYCORRHIZAL ABUNDANCE

Three soil in-growth cores (5 cm diameter × 20 cm length; AMS soil core sampler kit, AMS Inc., American Falls, ID) were collected from each plot (n=4) at the end of each watering treatment phase (February, May, and September) from February 2008 – September 2009 (240 cores per collection, 3 times per year) and refilled with sieved soil to allow for new root growth to occur. This allowed us to know during which precipitation distribution period each root grew into the core and the mycorrhizal colonization potential of the young roots within this system. Cores were sealed in plastic bags and refrigerated at ~5°C until processed (up to 2 weeks). Roots were carefully separated from the bulk soil, rinsed with nanopure water, sorted where applicable by species, into fine (≤ 1 mm diameter) and coarse (> 1 mm diameter). A random subsample of fine roots (~25 cm length) was then separated from the bulk roots collected, stored in 70% ETOH, and examined for EM and AM colonization.

Ectomycorrhizal colonization was determined with a dissecting microscope (Cole Parmer, Vernon Hills, IL) at × 10. We employed a point intersection method to estimate the root length, EM root length, and EM root tips (Brundrett *et al.*, 1996). Roots were then cleared with KOH, stained with CBE (Chlorazol Black E, Thermo Scientific Inc., NJ), and mounted on microscope slide (Brundrett *et al.*, 1996). Arbuscular mycorrhizal colonization was assessed using a compound microscope (Vista Vision, West Chester, PA) fitted with a cross haired graticule at × 200. Fungal structures were verified at × 400. A minimum of 150 intersections was assessed per plot (McGonigle *et al.*, 1990). We were able to distinguish two morphological groups of AM hyphae, a fine endophyte (FE) hyphae (~1-2 μm) and coarse AM hyphae (~3-10 μm) from non mycorrhizal hyphae (Rillig *et al.*, 1999). Non-mycorrhizal colonization was also determined at this time. Mycorrhizal abundance was not determined for *Q. stellata* roots due to poor root recovery and low number.

STATISTICAL DESIGN

Effects of precipitation redistribution, warming and species mixture on mycorrhizal infection

rate was analyzed using a mixed model with precipitation treatment, warming, and species mixture as fixed effects, and between shelter variation as a random effect. Precipitation treatment, warming, and species treatments were arranged as a split-plot factorial in a completely randomized design. The precipitation regime constituted the whole-plot factor (with four replications), while the warming and species combinations were assigned as within-plot factors. Precipitation effects were tested over the 'between shelter' error and warming and species mixture effects and treatment interactions were tested over the residual error. All analyses were conducted with statistical analysis software (JMP 7.02, SAS Institute, Cary, NC).

Results

JUNIPERUS VIRGINIANA ECTOMYCORRHIZAL FUNGI COLONIZATION

Ectomycorrhizal colonization was observed on *J. virginiana* roots. The mantle appeared swollen and was dark brown in color, resembling the root itself. No attempt was made to identify the ectomycorrhizal symbiont to the species level. *Juniperus virginiana* root length colonized by EM was affected by the treatments on only one out of the six dates (Table 5.1 and Table 5.2). In September 2009, root length colonized by EM was higher in monocultures when compared to mixtures with *S. scoparium*, regardless of warming and precipitation treatment (Table 5.2). The total number of colonized root tips was higher in monocultures than in mixtures in February 2008 and 2009 (Table 5.1 and Table 5.2), while warming reduced the total number of root tips colonized in September 2008.

Of the six dates analyzed, root tip number per root length (tips m^{-1} root) was greater in *J. virginiana* mixture in redistributed precipitation treatment when compared to *J. virginiana* monoculture in redistributed precipitation treatment and *J. virginiana* mixture in control precipitation treatment in September 2008 only (Table 5.1). Ectomycorrhizal colonization (tips colonized m^{-1} root) was higher in the control precipitation treatment when compared to the redistributed precipitation treatment in February 2008 (Table 5.1). Ectomycorrhizal colonization (tips colonized m^{-1} root) was greater in monocultures in the control precipitation treatment when compared to monocultures in the redistributed precipitation treatment and mixtures in control precipitation treatment in September 2008 (Table 5.1).

Table 5.1. Probability values (*P*-values) and F-ratios determined using ANOVA for ectomycorrhizal (EM) colonization and total tip number of *Juniperus virginiana* roots in 2008.

	EM root length		EM root tips		EM colonization		Total tips	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
				February 2008				
Precipitation (P)	0.94	0.369	3.35	0.117	6.67	**0.042**	0.01	0.939
Warming (W)	0.16	0.695	0.05	0.831	0.40	0.536	1.59	0.223
P × W	0.00	0.965	1.15	0.298	0.01	0.909	2.43	0.136
Mixture (M)	2.17	0.158	5.64	**0.029**	2.67	0.120	0.27	0.610
P × M	0.11	0.742	0.23	0.640	0.10	0.761	0.02	0.895
W × M	0.75	0.397	0.32	0.580	0.59	0.454	0.22	0.648
P × W × M	2.42	0.137	4.05	0.059	1.89	0.186	0.21	0.654
				May 2008				
Precipitation (P)	2.62	0.157	0.08	0.790	4.00	0.093	3.02	0.133
Warming (W)	6.04	0.240	2.92	0.105	1.64	0.217	0.01	0.920
P × W	0.43	0.520	1.25	0.279	0.00	0.982	1.08	0.313
Mixture (M)	2.00	0.175	0.02	0.887	0.64	0.433	0.91	0.353
P × M	0.53	0.477	0.50	0.489	0.04	0.837	0.92	0.349
W × M	0.18	0.676	0.05	0.827	0.51	0.486	1.40	0.253
P × W × M	0.30	0.593	0.06	0.813	0.16	0.695	0.60	0.450
				September 2008				
Precipitation (P)	0.03	0.871	4.19	0.083	0.30	0.615	6.02	0.063
Warming (W)	4.07	0.060	6.09	**0.024**	4.32	0.055	0.03	0.858
P × W	0.07	0.798	0.15	0.703	1.72	0.209	1.71	0.209
Mixture (M)	0.00	0.968	0.78	0.389	0.34	0.571	0.01	0.929
P × M	3.99	0.062	0.08	0.781	7.65	**0.014**	11.5	**0.004**
W × M	0.88	0.362	0.24	0.633	0.43	0.522	1.75	0.205
P × W × M	0.21	0.653	0.21	0.651	0.44	0.515	1.89	0.188

P-values ≤ 0.05 are printed in bold.
Data were log transformed.

Table 5.2. Probability values (*P*-values) and F-ratios determined using ANOVA for ectomycorrhizal (EM) colonization and total tip number of *Juniperus virginiana* roots in 2009.

	EM root length		EM root tips		EM colonization		Total tips	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
				February 2009				
Precipitation (P)	1.12	0.331	1.35	0.289	0.69	0.437	0.35	0.575
Warming (W)	0.27	0.613	3.53	0.077	0.29	0.597	2.98	0.101
P × W	0.95	0.344	3.33	0.085	1.21	0.286	0.03	0.857
Mixture (M)	1.41	0.251	11.1	**0.004**	0.98	0.336	0.69	0.416
P × M	2.70	0.117	0.23	0.635	2.81	0.111	2.68	0.119
W × M	0.01	0.936	2.50	0.131	0.01	0.931	1.07	0.315
P × W × M	1.94	0.181	0.03	0.865	0.97	0.339	1.51	0.235
				May 2009				
Precipitation (P)	0.39	0.553	0.03	0.867	0.56	0.486	0.25	0.636
Warming (W)	0.05	0.827	0.03	0.862	0.09	0.772	0.46	0.506
P × W	2.00	0.174	0.44	0.515	2.71	0.119	2.46	0.136
Mixture (M)	0.09	0.763	0.77	0.394	0.56	0.466	0.02	0.889
P × M	0.35	0.559	0.01	0.914	0.76	0.395	1.45	0.247
W × M	0.16	0.697	0.30	0.593	0.01	0.910	0.64	0.435
P × W × M	0.29	0.597	0.97	0.339	0.33	0.576	2.10	0.166
				September 2009				
Precipitation (P)	2.32	0.177	0.26	0.630	0.48	0.521	0.22	0.658
Warming (W)	0.09	0.764	0.68	0.423	0.80	0.385	0.22	0.645
P × W	0.98	0.335	0.00	0.972	0.02	0.888	0.11	0.739
Mixture (M)	15.6	**0.001**	0.09	0.767	0.06	0.805	0.01	0.938
P × M	3.94	0.063	3.82	0.067	3.74	0.071	0.14	0.717
W × M	0.44	0.517	0.01	0.925	0.01	0.924	0.23	0.636
P × W × M	2.10	0.165	0.14	0.717	0.24	0.628	0.21	0.649

P-values ≤ 0.05 are printed in bold.
Data were log transformed.

Table 5.3. Probability values (*P*-values) and F-ratios determined using ANOVA for fine (1-2 µm diameter), coarse (3-10 µm diameter), and total arbuscular mycorrhizal (AM) hyphal percentage colonization, vesicles percentage colonization, and non-mycorrhizal percentage colonization of *Juniperus virginiana* roots in 2008.

	Fine AM		Coarse AM		Total AM		Vesicles		Non-mycorrhizal	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
					February 2008					
Precipitation (P)	0.83	0.398	1.06	0.342	0.24	0.640	0.11	0.748	0.21	0.659
Warming (W)	0.12	0.733	1.39	0.253	1.35	0.260	0.01	0.923	0.47	0.503
P × W	0.34	0.569	0.16	0.694	0.02	0.894	0.28	0.601	1.04	0.321
Mixture (M)	41.7	**<0.001**	12.8	**0.002**	46.6	**<0.001**	0.54	0.474	0.18	0.681
P × M	2.30	0.147	1.96	0.178	0.03	0.862	0.54	0.472	0.37	0.552
W × M	1.72	0.206	0.01	0.926	0.39	0.541	0.18	0.677	0.27	0.610
P × W × M	0.05	0.832	0.31	0.584	0.04	0.846	0.05	0.833	1.98	0.177
					May 2008					
Precipitation (P)	0.02	0.880	3.67	0.104	1.18	0.319	0.00	0.991	0.20	0.667
Warming (W)	1.13	0.302	0.00	0.959	0.42	0.526	0.71	0.409	0.10	0.759
P × W	0.01	0.928	2.62	0.123	0.65	0.430	0.41	0.530	0.85	0.368
Mixture (M)	3.04	0.098	16.3	**<0.001**	8.74	**0.009**	0.41	0.532	23.8	**<0.001**
P × M	0.15	0.705	0.05	0.826	0.15	0.703	0.30	0.593	0.74	0.400
W × M	0.30	0.592	0.67	0.423	0.02	0.888	0.03	0.868	0.00	0.969
P × W × M	0.21	0.654	0.03	0.868	0.02	0.879	1.65	0.215	0.06	0.816
					September 2008					
Precipitation (P)	0.27	0.624	1.13	0.330	0.64	0.455	0.57	0.479	0.18	0.686
Warming (W)	0.00	0.980	0.39	0.540	0.06	0.812	0.46	0.507	0.61	0.447
P × W	0.14	0.713	0.40	0.533	0.07	0.799	4.30	0.053	0.10	0.758
Mixture (M)	1.63	0.218	1.95	0.180	6.13	**0.024**	0.35	0.564	4.15	0.058
P × M	2.72	0.117	0.18	0.680	0.00	0.962	0.35	0.565	0.29	0.595
W × M	0.06	0.810	0.43	0.520	0.26	0.619	2.88	0.107	0.88	0.362
P × W × M	0.21	0.650	0.06	0.811	0.06	0.834	1.17	0.294	0.45	0.514

P-values ≤ 0.05 are printed in bold.

Data were log transformed.

No arbuscles were observed in *J. virginiana* roots in 2008.

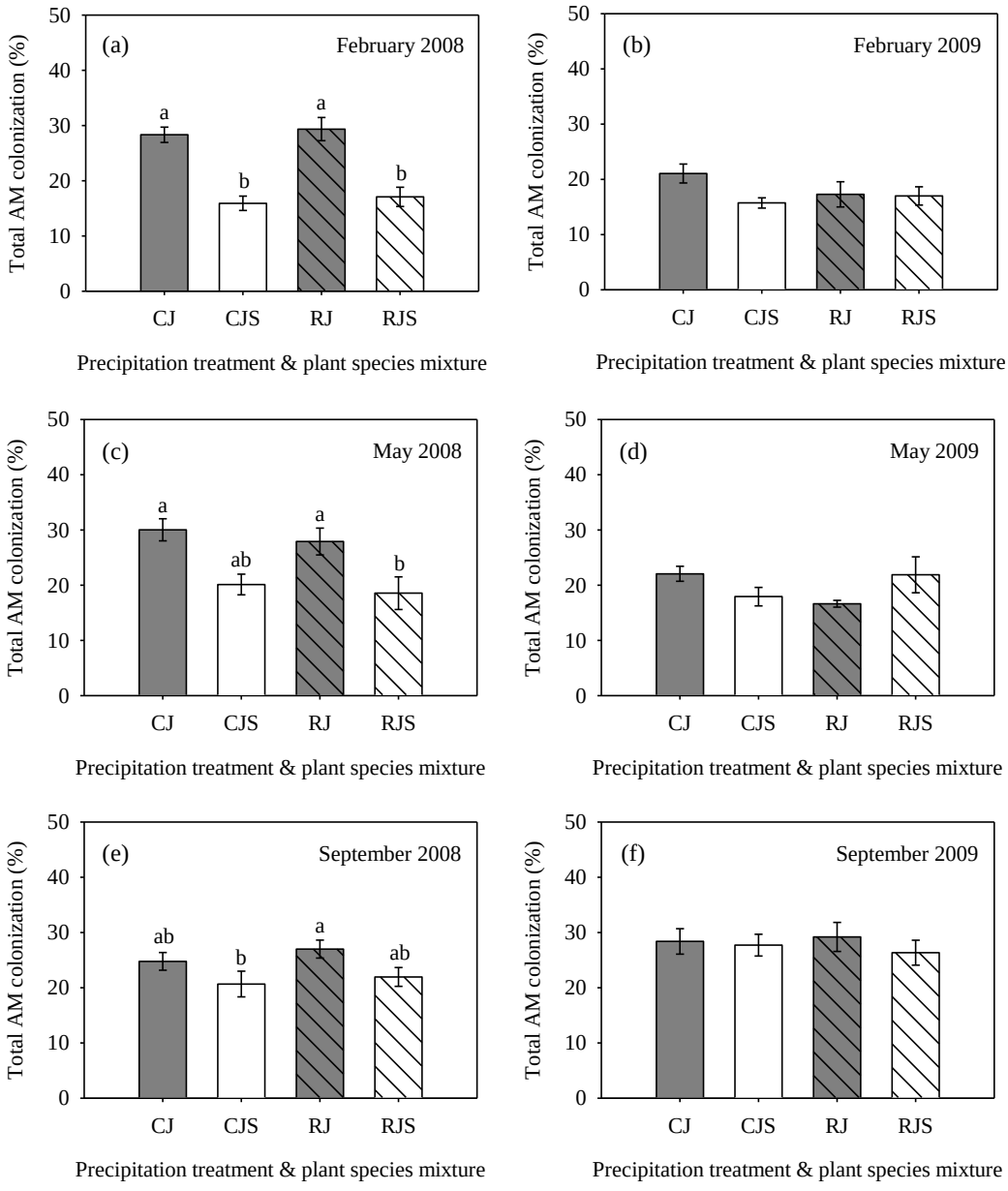

Figure 5.2. Effect of precipitation distribution treatment on percent total arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across warming treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

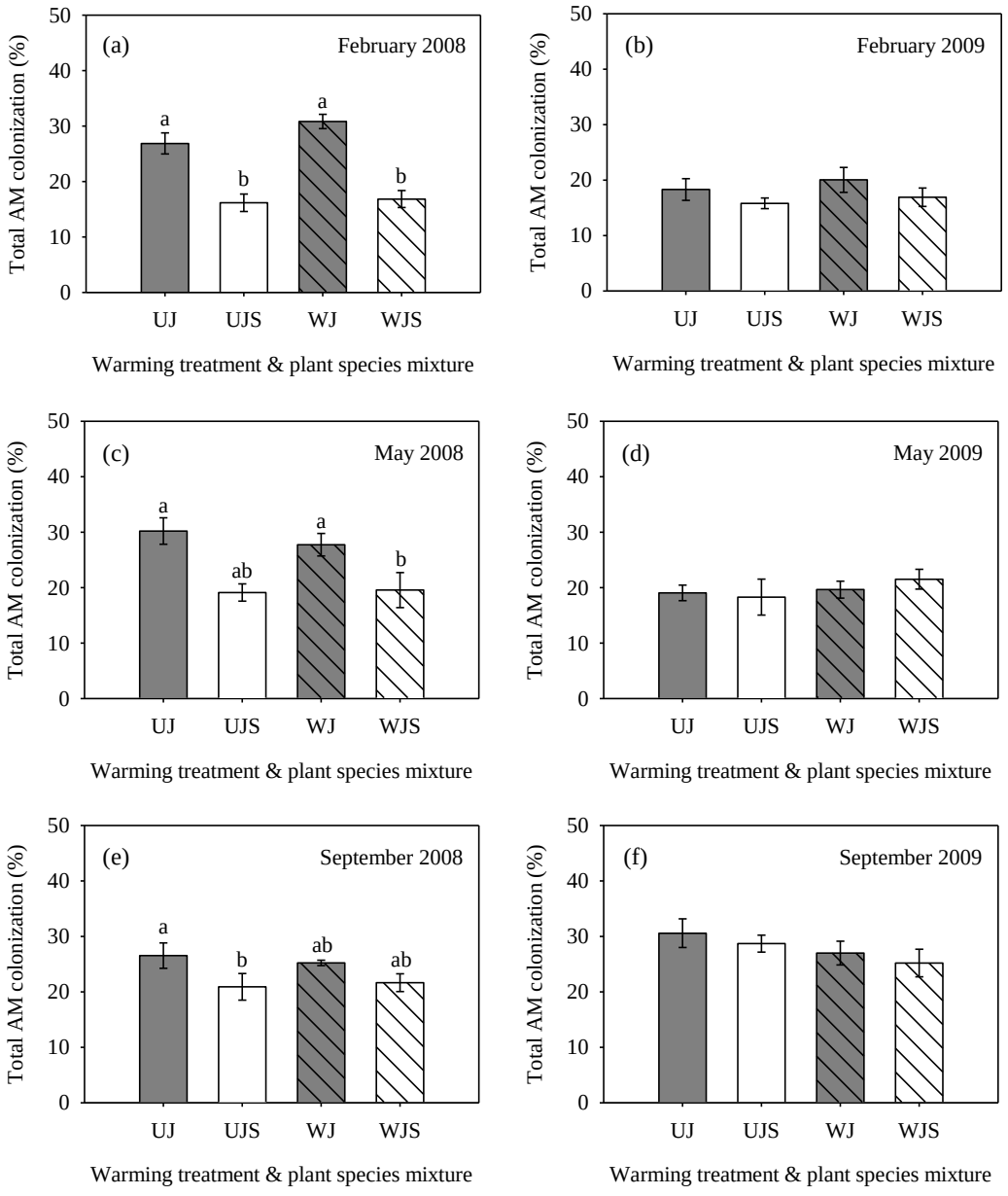

Figure 5.3. Effect of warming on percent total arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

Table 5.4. Probability values (*P*-values) and F-ratios determined using ANOVA for fine (1-2 µm diameter), coarse (3-10 µm diameter), and total arbuscular mycorrhizal (AM) hyphal percentage colonization, vesicles percentage colonization, and non-mycorrhizal percentage colonization of *Juniperus virginiana* roots in 2009.

	Fine AM		Coarse AM		Total AM		Vesicles		Non-mycorrhizal	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
					February 2009					
Precipitation (P)	0.23	0.650	0.04	0.845	0.46	0.525	0.03	0.870	1.94	0.213
Warming (W)	0.03	0.871	0.16	0.691	0.65	0.430	0.51	0.483	4.12	0.057
P × W	0.06	0.809	0.86	0.366	0.00	0.970	0.08	0.781	0.02	0.901
Mixture (M)	0.40	0.536	1.70	0.208	2.67	0.120	0.52	0.479	46.2	**<0.001**
P × M	1.07	0.315	0.46	0.507	2.78	0.113	0.93	0.347	0.00	0.959
W × M	1.02	0.327	0.68	0.422	0.07	0.792	0.55	0.466	1.83	0.193
P × W × M	3.21	0.090	0.82	0.377	0.51	0.483	1.85	0.191	1.05	0.318
					May 2009					
Precipitation (P)	0.39	0.555	0.07	0.806	0.35	0.576	1.13	0.330	2.80	0.145
Warming (W)	3.09	0.096	0.45	0.511	1.64	0.217	0.68	0.422	4.61	**0.046**
P × W	2.57	0.126	0.90	0.354	0.01	0.931	0.02	0.885	0.96	0.340
Mixture (M)	7.86	**0.012**	9.85	**0.006**	0.02	0.893	1.23	0.283	20.3	**<0.001**
P × M	6.44	**0.021**	1.27	0.275	4.54	**0.047**	0.84	0.373	8.94	**0.008**
W × M	0.67	0.424	6.15	**0.023**	0.98	0.335	0.21	0.654	0.16	0.691
P × W × M	4.66	**0.045**	5.94	**0.025**	0.02	0.890	0.08	0.779	0.22	0.643
					September 2009					
Precipitation (P)	0.13	0.743	0.25	0.633	0.13	0.734	0.38	0.559	2.15	0.203
Warming (W)	1.04	0.324	0.09	0.770	3.59	0.075	0.00	0.959	2.27	0.152
P × W	0.15	0.700	6.96	**0.017**	7.36	**0.015**	0.22	0.642	0.07	0.796
Mixture (M)	1.97	0.181	0.23	0.635	0.75	0.398	0.91	0.354	0.17	0.683
P × M	4.51	0.051	1.15	0.297	0.37	0.553	0.63	0.438	0.31	0.588
W × M	1.45	0.248	1.61	0.221	0.06	0.817	0.08	0.776	5.56	**0.031**
P × W × M	0.47	0.503	0.18	0.676	0.01	0.921	0.06	0.813	3.06	0.100

P-values ≤ 0.05 are printed in bold.

Data was log transformed.

No arbuscles were observed in *J. virginiana* roots in 2009.

***JUNIPERUS VIRGINIANA* ARBUSCULAR MYCORRHIZAL FUNGI COLONIZATION**

Total AM colonization was greater (42%, 32%, and 16% in February, May, and September 2008, respectively) in *J. virginiana* monoculture when compared to *J. virginiana* mixture in 2008 (Table 5.3, Figures 5.2a, c, and e, and 5.3a, c, and e). Fine and coarse AM colonization followed a similar trend in February 2008 and May 2009, and February 2008, May of 2008, and May 2009, respectively (Table 5.3 and Table 5.4). Total AM colonization was greater in control precipitation treatment when compared to redistributed precipitation treatment in *J. virginiana* monoculture in May 2009 (Table 5.4). Fine AM colonization was only affected in the redistributed precipitation treatment, where fine AM colonization was greater in *J. virginiana* mixture when compared to *J. virginiana* monoculture in May 2009 (Table 5.4). Coarse AM colonization was only affected in the unwarmed treatment, where coarse AM colonization was greater in *J. virginiana* monoculture when compared to *J. virginiana* mixture in May 2009 (Table 5. 4). Fine AM colonization was only affected by warming treatment and species mixture in redistributed precipitation treatment, where fine AM colonization was greater in warmed *J. virginiana* mixture when compared to unwarmed *J. virginiana* monoculture in May 2009 (Table 5.4). Coarse AM colonization was greater in *J. virginiana* monoculture in the unwarmed redistributed precipitation treatment when compared to *J. virginiana* monoculture and *J. virginiana* mixture in the warmed redistributed treatment and *J. virginiana* mixture in the warmed and unwarmed control precipitation treatments in May 2009 (Table 5.4). Total AM colonization was only affected in the redistributed precipitation treatment, where total AM colonization was greater in the unwarmed treatment when compared to the warmed treatment in September 2009 (Table 5.4). Coarse AM colonization was greater in the warmed control precipitation treatment when compared to the unwarmed control precipitation treatment and warmed redistributed precipitation treatment in September 2009 (Table 5.4). No arbuscules were observed in *J. virginiana* roots during 2008 and 2009.

Non-mycorrhizal colonization was greater in *J. virginiana* monoculture when compared to *J. virginiana* mixture in May of 2008, February 2009, and May 2009 (Table 5.3 and Table 5.4). Non-mycorrhizal colonization was greater in *J. virginiana* monoculture in redistributed precipitation treatment when compared to *J. virginiana* mixture in control and redistributed precipitation treatments in May 2009 (Table 5.4). Non-mycorrhizal colonization was only affected by warming treatments in *J. virginiana* mixture, where non-mycorrhizal colonization was greater in unwarmed treatments when compared to warmed treatment in September 2009

Table 5.5. Probability values (*P*-values) and F-ratios determined using ANOVA for fine (1-2 µm diameter), coarse (3-10 µm diameter), and total arbuscular mycorrhizal (AM) hyphal percentage colonization, vesicles percentage colonization, arbuscules, and non-mycorrhizal colonization percentage colonization of *Schizachyrium scoparium* roots in 2008.

	Fine AM		Coarse AM		Total AM		Vesicles		Arbuscules		Non-mycorrhizal	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
						February 2008						
Precipitation (P)	11.2	**0.018**	2.57	0.157	0.02	0.888	0.01	0.911	0.19	0.682	0.60	0.470
Warming (W)	0.58	0.452	0.00	0.997	0.23	0.632	0.28	0.599	0.06	0.813	1.03	0.320
P × W	0.31	0.580	0.40	0.530	0.32	0.573	0.18	0.671	0.27	0.609	1.17	0.290
Mixture (M)	6.21	**0.006**	1.97	0.158	10.5	**<0.001**	2.60	0.092	7.03	**0.003**	3.77	**0.036**
P × M	0.40	0.677	0.49	0.618	0.65	0.530	2.48	0.101	0.16	0.857	0.37	0.695
W × M	1.06	0.362	0.19	0.831	0.17	0.847	0.06	0.942	0.02	0.983	0.38	0.689
P × W × M	2.34	0.116	0.47	0.632	0.65	0.530	0.90	0.418	0.46	0.639	1.75	0.193
						May 2008[z]						
Precipitation (P)	0.02	0.905	0.07	0.793	4.11	0.053	0.87	0.386	0.47	0.521	1.18	0.327
Warming (W)	-	-	-	-	-	-	-	-	-	-	-	-
P × W	-	-	-	-	-	-	-	-	-	-	-	-
Mixture (M)	3.32	0.055	3.37	0.051	1.86	0.178	3.81	**0.037**	3.99	**0.033**	0.01	0.989
P × M	0.60	0.555	0.19	0.827	1.76	0.194	1.33	0.283	0.44	0.649	1.57	0.230
W × M	-	-	-	-	-	-	-	-	-	-	-	-
P × W × M	-	-	-	-	-	-	-	-	-	-	-	-
						September 2008						
Precipitation (P)	1.40	0.329	0.33	0.629	0.17	0.738	0.18	0.684	0.00	0.982	0.55	0.490
Warming (W)	0.25	0.624	0.80	0.379	1.08	0.308	0.07	0.788	0.17	0.686	0.08	0.785
P × W	0.19	0.666	0.68	0.416	0.13	0.717	0.81	0.379	0.48	0.497	0.04	0.852
Mixture (M)	4.36	**0.027**	1.02	0.374	3.25	0.056	5.21	**0.015**	6.74	**0.005**	0.50	0.615
P × M	2.36	0.121	0.06	0.945	2.14	0.139	2.17	0.140	0.02	0.981	0.90	0.421
W × M	0.63	0.542	0.35	0.708	0.39	0.679	0.37	0.697	0.06	0.938	0.28	0.758
P × W × M	0.71	0.506	0.34	0.714	0.54	0.536	1.90	0.176	0.62	0.547	0.32	0.727

P-values ≤ 0.05 are printed in bold.

Data were log transformed.

[z] Insufficient *S. scoparium* roots recovered from warming treatments in May 2008.

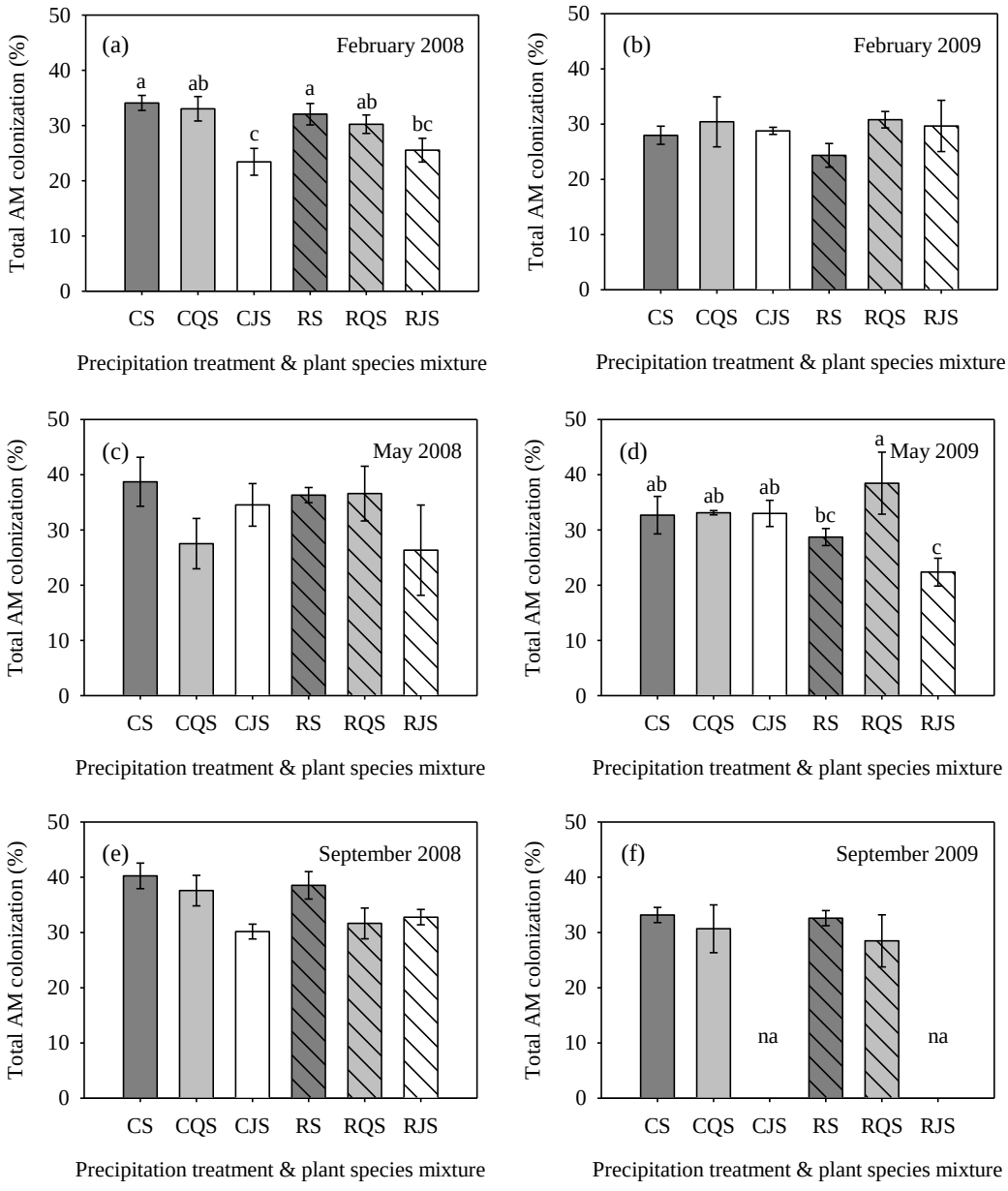

Figure 5.4. Percent total arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across warming treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* grown in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoparium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

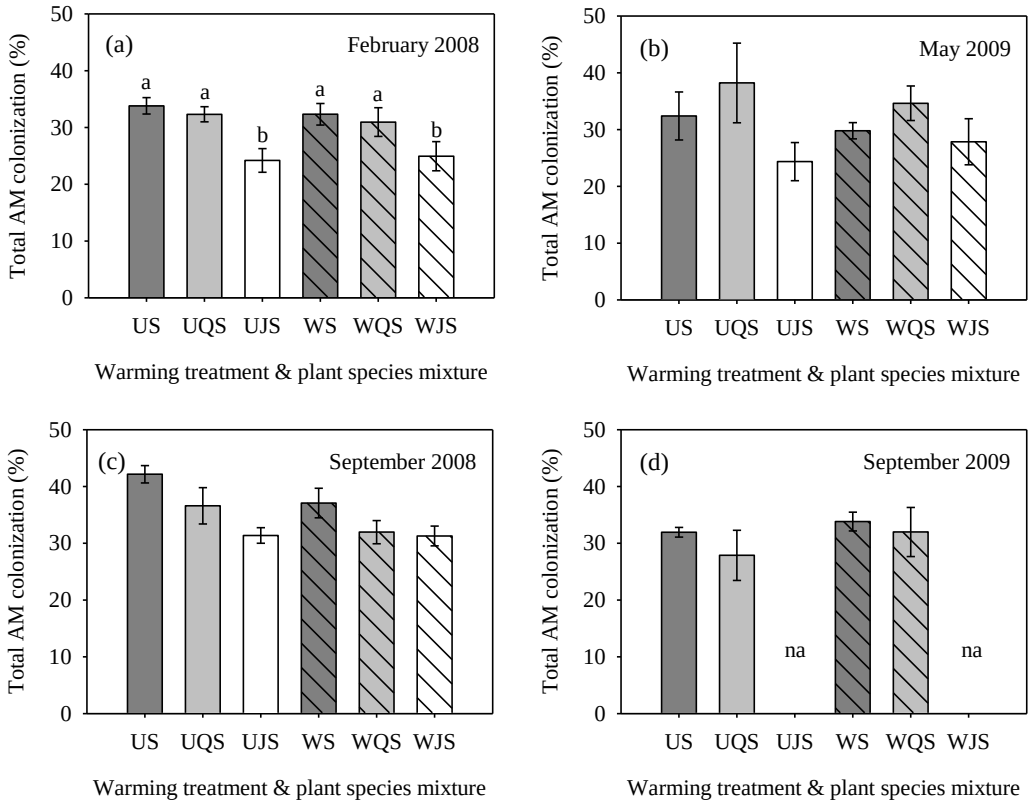

Figure 5.5.Percent total arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across precipitation treatments in (a) February 2008, (b) May 2009, (c) September 2008, and (d) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* grown in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoparium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate warming treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from warming treatments in May 2008, February 2009, and from JS in September 2009 (na).

Table 5.6. Probability values (*P*-values) and F-ratios determined using ANOVA for fine (1-2 µm diameter), coarse (3-10 µm diameter), and total arbuscular mycorrhizal (AM) hyphal percentage colonization, vesicles percentage colonization, arbuscules, and non-mycorrhizal percentage colonization of *Schizachyrium scoparium* roots in 2009.

	Fine AM		Coarse AM		Total AM		Vesicles		Arbuscules		Non-mycorrhizal	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
						February 2009[z]						
Precipitation (P)	0.06	0.815	0.84	0.389	0.11	0.746	2.85	0.127	0.05	0.842	0.13	0.728
Warming (W)	-	-	-	-	-	-	-	-	-	-	-	-
P × W	-	-	-	-	-	-	-	-	-	-	-	-
Mixture (M)	2.55	0.104	0.47	0.633	1.78	0.193	18.2	**<0.001**	2.36	0.117	0.28	0.759
P × M	0.10	0.907	1.76	0.196	0.73	0.493	0.28	0.756	0.05	0.954	1.03	0.374
W × M	-	-	-	-	-	-	-	-	-	-	-	-
P × W × M	-	-	-	-	-	-	-	-	-	-	-	-
						May 2009						
Precipitation (P)	0.54	0.502	0.28	0.620	1.22	0.316	0.69	0.867	0.03	0.864	0.66	0.446
Warming (W)	0.09	0.775	0.01	0.939	0.23	0.639	0.97	0.281	1.27	0.292	0.44	0.518
P × W	0.10	0.759	0.13	0.728	0.21	0.657	4.20	0.162	0.03	0.864	0.07	0.795
Mixture (M)	3.86	**0.050**	0.17	0.850	2.85	0.106	5.77	0.272	1.43	0.296	1.86	0.197
P × M	0.01	0.989	7.40	**0.012**	4.98	**0.032**	3.33	0.315	0.04	0.966	0.85	0.452
W × M	0.12	0.890	2.13	0.174	2.22	0.160	0.52	0.831	1.43	0.296	3.08	0.082
P × W × M	1.28	0.312	2.81	0.111	0.25	0.781	0.37	0.973	0.04	0.266	0.94	0.415
						September 2009[y, x]						
Precipitation (P)	0.12	0.739	0.03	0.871	0.00	0.967	0.06	0.811	-	-	2.40	0.182
Warming (W)	0.00	0.951	0.21	0.655	1.48	0.245	0.08	0.777	-	-	3.21	0.093
P × W	0.06	0.811	0.27	0.612	0.02	0.894	0.21	0.658	-	-	1.75	0.206
Mixture (M)	28.9	**<0.001**	2.61	0.129	2.47	0.141	0.76	0.400	-	-	0.31	0.587
P × M	1.08	0.316	0.70	0.419	0.02	0.886	0.28	0.606	-	-	0.20	0.661
W × M	1.32	0.268	1.29	0.273	0.40	0.537	0.13	0.720	-	-	2.25	0.154
P × W × M	1.10	0.310	2.46	0.138	0.94	0.350	0.30	0.593	-	-	0.01	0.913

P-values ≤ 0.05 are printed in bold.

Data were log transformed.

[z] Insufficient *S. scoparium* roots recovered from warming treatments in February 2009.

[y] Insufficient *S. scoparium* roots recovered from *J. virginiana* grown with *S. scoparium* in September 2009.

[x] Arbuscles were only observed in *S. scoparium* in monoculture in redistributed precipitation treatment in September 2009.

(Table 5.4). Non-mycorrhizal colonization of *J. virginiana* roots was greater in unwarmed treatment when compared to warmed treatment in May 2009 (Table 5.4).

SCHIZACHYRIUM SCOPARIUM ARBUSCULAR MYCORRHIZAL FUNGI COLONIZATION

Total AM colonization was greater (27%) in *S. scoparium* monoculture when compared to *S. scoparium* grown with *J. virginiana* in February 2008 (Table 5.5, Figures 5.4a and 5.5a). Fine AM colonization was greater in *S. scoparium* grown with *Q. stellata* and lower in *S. scoparium* grown with *J. virginiana* in February 2008 (Table 5.5). Fine AM colonization was greater in *S. scoparium* grown with *Q. stellata* and lower in *S. scoparium* monoculture and when grown with *J. virginiana* in May 2009 (Table 5.6). Fine AM colonization was greater in *S. scoparium* monoculture when compared with *S. scoparium* grown with *J. virginiana* and *S. scoparium* grown with *Q. stellata* in September of 2008 and 2009, respectively (Table 5.5 and Table 5.6). Vesicle colonization was greater in *S. scoparium* grown with *J. virginiana* when compared to *S. scoparium* grown with *Q. stellata* and *S. scoparium* monoculture in May and September of 2008, respectively (Table 5.5). Vesicle colonization was greater in *S. scoparium* monoculture when compared to *S. scoparium* grown with either tree species in February 2009 (Table 5.6). Arbuscular colonization was greater in *S. scoparium* monoculture when compared to *S. scoparium* grown with either tree species in February, May, and September of 2008 (Table 5.5). There was a mixture effect in the redistributed precipitation treatment, where total AM colonization was greater in *S. scoparium* grown with *Q. stellata* when compared to *S. scoparium* monoculture and *S. scoparium* grown with *J. virginiana* and coarse AM colonization was greater in *S. scoparium* grown with *Q. stellata* when compared to *S. scoparium* grown with *J. virginiana* in May 2009 (Table 5.6). Fine AM colonization was greater in control precipitation when compared to redistributed precipitation treatment in February 2008 (Table 5.5). Non-mycorrhizal colonization was greater in *S. scoparium* monoculture when compared to *S. scoparium* grown with *J. virginiana* in February 2008 (Table 5.5).

Discussion

EFFECT OF WARMING AND RAINFALL DISTRIBUTION ON MYCORRHIZAL ABUNDANCE

Juniperus virginiana roots can form both EM (Thomas, 1943) and AM associations (Reinsvold & Reeves, 1986; Pregitzer *et al.*, 2002; Caravaca *et al.*, 2006; Wubet *et al.*, 2006), however AM associations appear to be more common which is in agreement with our findings. The formation of EM associations with *Juniperus* spp. May be facultative rather than symbiotic (Meyer, . 1973). This co-dominant mycorrhizal association (AM & EM) may give the host species a competitive advantage (Lapeyrie & Chilvers, 1985) and may in part explain the expansion of *J. virginiana* into grassland and savannah systems. Co-dominant mycorrhizal associations may differentially benefit the host plant (van der Heijden, 2001) depending on environmental conditions. Arbuscular mycorrhizal fungi are able to maintain beneficial activity under less favorable environmental conditions and have a lower C cost than EM, while under more favorable environmental conditions EM have a higher C cost (Leake *et al.*, 2004) but maybe more effective at nutrient uptake when compared to AM (Jones *et al.*, 1998; van der Heijden & Kuyper, 2001). Thus, fluctuations in EM colonization due to seasonal fluctuations in temperature and moisture may be beneficial to plants growing in nutrient poor sites and/or drought conditions (Meyer, 1973). It is important to note that mycorrhizae may deliver the greatest benefit to one plant species, but grow better on another, thus presence and/or abundance do not necessarily reflect mycorrhizal effectiveness (Bever, 2002; Bever, 2003). Lodge and Wentworth (1990) found that under moist soil conditions, EM fungi appeared to displace AM fungi but not under either drier or wetter conditions. Thus, we had expected that extremes of soil water availability that lead to stressful conditions for the host plant (i.e. drought and flooding) would negatively affect abundance of EM and to a lesser degree AM fungi (Allen *et al.*, 1987; Allen *et al.*, 1989b; Shi *et al.*, 2002), however this was not observed in our experiment. We found that ectomycorrhizal colonization in *J. virginiana* was generally not affected by warming or precipitation distribution, while colonization was inconsistently affected across season and years. Overall, approximately 43% of the observed *J. virginiana* root tips were infected with EM while AM colonization of both plant species was not strongly affected by warming and precipitation treatment.

Precipitation redistribution and warming reduced AM mycorrhizal abundance on only two dates for *J. virginiana* and one date for *S. scoparium*. This is surprising because warming is frequently reported to increase AM abundance under a variety of settings (field and laboratory) (Graham *et al.*, 1982; Baon *et al.*, 1994; Rillig *et al.*, 2002; Staddon *et al.*, 2003b; Heinemeyer & Fitter, 2004; Heinemeyer *et al.*, 2004; Staddon *et al.*, 2004; Gavito *et al.*, 2005; Heinemeyer *et al.*, 2006; Hawkes *et al.*, 2008). Shifts in AM mycorrhizal structure abundance have been reported in response to warming (Hawkes *et al.*, 2008), drought stress (Staddon *et al.*, 2003a), and waterlogging (Mendoza *et al.*, 2005) and may help the fungus to survive in adverse conditions. However, we did not observe a precipitation or warming effect on abundance of vesicles and arbuscules.

Experimental limitations may have contributed to the lack of temperature response that we observed. The warming treatment, which was applied with overhead infrared heaters, did not consistently 'warm' the soil rather it warmed the canopy (Volder *et al.* Unpublished), and thus potentially affected above ground growth more than below ground growth. The lack of effect of temperature and moisture on colonization may also reflect the sampling method employed, as soil temperature and soil VWC measurements may not have been an accurate representation of the range (extremes) of conditions experienced by the mycorrhizal fungi between sampling dates; for example the extra wet conditions in May and the extra dry conditions in September in redistributed precipitation treatments.

EFFECT OF WARMING AND PRECIPITATION DISTRIBUTION ON MYCORRHIZAL ABUNDANCE IS MEDIATED BY PLANT SPECIES INTERACTION

Although we documented few warming and precipitation distribution treatment responses in the monocultures, growing both species in the same plot did reduce (≥16%) AM mycorrhizal abundance (either fine, coarse or total) on four out of six dates for both species, suggesting that both species actively suppress AM abundance on each others' roots. Competition between the two hosts may have affected the C balance of both species, potentially reducing the C flow to the symbiont (Bever, 2002; Bever, 2003; McHugh & Gehring, 2006). Competition for light may reduce photosynthetic activity, and limit mycorrhizal C availability (Heinemeyer & Fitter, 2004). *Schizachyrium scoparium* was shaded by *J. virginiana* during the measurement period, likely reducing its C availability for symbiosis in the mixture plots compared to *S. scoparium* monocultures. Ectomycorrhizal colonization of *J. virginiana* roots was reduced when grown

with AM colonized *S. scoparium.* One possible mechanism could be that *J. virginiana* root exudates may have increased in quantity and/or quality in response to the presence of *S. scoparium* roots which may have had an adverse effect on EM colonization (Kraus *et al.*, 2003; Bais *et al.*, 2006).

Little is known about EM in plant competition, however there is a suggestion that they influence plant-plant interactions (Perry *et al.*, 1989) and that the interactions between EM species may vary depending on species and environmental conditions (Kennedy *et al.*, 2007). Arbuscular mycorrhizal fungi may alter the competitiveness of plants by enhancing the availability of soil resources (Hodge, 2003) and/or promoting growth of one species while inhibiting a second species (Allen *et al.*, 1989a). In addition, competition between EM colonized *J. virginiana* and AM colonized *S. scoparium* for soil resources may reduce EM colonization (Haskins & Gehring, 2005). We did not find any change in *J. virginiana* root morphology (root tips m^{-1}) when grown with *S. scoparium*, suggesting that differences in EM colonization between *J. virginiana* in monoculture and *J. virginiana* grown with *S. scoparium* was not due to reduced lateral root growth/number of root tips.

Conclusion

Warming and precipitation distribution did not have a strong effect on EM or AM colonization in *J. virginiana* and *S. scoparium* roots, four and five years after commencement of the treatments, suggesting that mycorrhizal species may acclimate to climatic conditions overtime. Growing both species in the same plot did reduce AM mycorrhizal abundance (either fine, coarse or total) on four out of six dates for both species, suggesting that both species actively suppress AM abundance on each others' roots. While we acknowledge that we may have missed some of the 'initial' mycorrhizal responses to warming and moisture, our data does suggest that in the longer term, the effect of host species and potential competitive interactions may be more important in determining future mycorrhizal abundance than climate fluctuations. These findings are important because changes in growth of mycorrhizal fungi may potentially influence soil and ecosystem level C dynamics by controlling the release of C to the soil microbial community (Hogberg & Read, 2006) and by enhancing the stabilization of soil organic C through the promotion of soil aggregation (Rillig & Mummey, 2006; De Deyn *et al.*, 2008; Wilson *et al.*, 2009).

CHAPTER VI
CONCLUSION

Overview

Terrestrial ecosystems play a major role in climate feedback because they release and absorb carbon dioxide (CO_2), while storing large quantities of carbon (C) and acting as a significant global C sink (Heimann & Reichstein, 2008; Chapin *et al.*, 2009). Global climate change and the feedback between plant communities and the belowground subsystem have the potential to drive ecosystem processes which influence ecosystem C flux (Wardle *et al.*, 2004; Cornelissen *et al.*, 2007; Chapin *et al.*, 2009). There is considerable concern that global warming will increase the liberation of CO_2 from soil to the atmosphere due to enhanced microbial breakdown of soil organic matter (Jenkinson *et al.*, 1991; Davidson & Janssens, 2006). This acceleration of C loss may significantly exacerbate the soil C cycle feedback (Cox *et al.*, 2000; Friedlingstein *et al.*, 2006). However, the potential for acclimation and adjustment of the system to climate change questions the validity of this and other projections.

Climate change may influence soil CO_2 efflux via shifts in the functional composition and diversity of the vegetation. Expansion of woody plant material into grassland and savannah systems may have important consequences above and belowground. Plant species within a plant community that provide resources of contrasting quality and quantity and/or in pulses are likely to exert temporal effects on belowground organisms and processes (Wardle *et al.*, 2004; Yang *et al.*, 2008). Leaf litter quality, decomposition, and nutrient mineralization may vary within and between species depending on environmental conditions (Gartner & Cardon, 2004) and/or among individuals or groups of individuals of a single species (Madritch & Hunter, 2002). Litter from coniferous species generally decomposes more slowly when compared to material from woody angiosperm species, which in turn break down more slowly than material from herbaceous species (Cornelissen, 1996). Changes in plant productivity and species composition may alter below ground physical and chemical conditions, and the supply of C to the soil, and the structure and activity of microbial communities, and thus C release from the soil (Bardgett *et al.*, 2008). Increased C flux from roots to soil for microbial communities and C exchange are difficult to predict as these effects are influenced by a range of factors including plant cover, soil volumetric water content (VWC), and to a lesser extent soil temperature. Increased belowground

allocation of C to roots and its transfer from roots to soil may stimulate microbial biomass and enhance mineralization of both recent and old soil organic C (Fontaine & Barot, 2005).

Oak savannah in the south-central United States is dominated by three contrasting plant functional types: *Schizachyrium scoparium* (Michx.) Nash. (little bluestem) a C_4 grass, *Quercus stellata* Wangenh. (post oak) a C_3 deciduous tree, and *Juniperus virginiana* L. (eastern redcedar) a C_3 evergreen tree. Increasing woody plant encroachment has been observed in these ecosystems in the last decades (McPherson, 1997; Scholes & Archer, 1997). The oak-savannah ecosystem is an ecotone where the grasslands of the west meet the deciduous forests of the east, and thus represents a unique ecosystem where species composition may be especially sensitive to changes in temperature and soil water availability. Climate change models project an increase in the intensity and variability of summer drought and precipitation events in the United States (Groisman *et al.*, 2005; Groisman & Knight, 2008).

A major concern is whether changes in species composition within the oak savannah system may lead to enhanced release of CO_2 from the soil. In general, soil CO_2 efflux rates are dependent on soil conditions such as temperature, moisture, and chemical and biological properties, as well as species composition, and seasonal changes in climate (Raich & Schlesinger, 1992; Raich & Tufekcioglu, 2000; Ryan & Law, 2005). Seasonal changes in climate affect soil CO_2 efflux directly through soil water availability and temperature effects on both microbial and root respiration and indirectly as new root production and C supply to the roots vary seasonally (Raich & Potter, 1995). Mycorrhizal fungi may potentially influence soil and ecosystem level C dynamics by controlling the release of C to the soil microbial community (Ames *et al.*, 1984; Hogberg & Read, 2006). Rates of soil CO_2 efflux are associated with the size of both the root and microbial pool and the activity of each pool (Hanson *et al.*, 2000).
Here we focused on four main questions: 1) what are the effects of changes in plant species and species mixture on CO_2 efflux from the soil, 2) how are these processes affected by climate change drivers, 3) how are the three components of soil CO_2 efflux (root, fungal, bacterial) affected by plant species and climate change drivers and 4) how are mycorrhizal type and presence altered by plant species and the climate change drivers.

Summary of Findings

In this study we observed inter-annual variability in soil CO_2 efflux, probably as a result of

climatic variation, changes in soil temperature and soil moisture content, and/or duration of growing season, and subsequent changes in plant carbon allocation (Chapter II). Surprisingly, over time annual soil CO_2 efflux decreased in the *S. scoparium* monoculture and mixtures and remained at a steady state in the tree monocultures, even though standing aboveground biomass in the plots increased as plants became established. This suggests a stabilization of the belowground system irrespective of above ground biomass. Soil CO_2 efflux in this study varied with seasonal changes in soil volumetric water content (VWC) and temperature, with higher respiration rates in the spring and lower rates in both the cooler winter season and at the end of the dry summer period. Overall, the effect of plant species combination was greater than that of either treatment, although the effect was not as large as the seasonal variations in soil CO_2 efflux. Total soil CO_2 efflux was strongly affected by plant species; plots with *S. scoparium* generally had the higher soil CO_2 efflux rates in the early years of the study, while plots dominated by *J. virginiana* had the higher soil CO_2 efflux rates at the end of the five-year study period (Chapter II). Differences in soil CO_2 efflux rates between plant communities growing on the same soil type and within the same climatic conditions were likely due to differences in specific root respiration and root turnover, rather than differences in standing root length and microbial biomass (Chapters III and IV). Plant species effects on microclimate and changes in microbial activity and composition may also play a role (Chapter IV).

Soil CO_2 efflux response to intensified summer drought was species-dependent (Chapter III). We did not find any relationship between root length density or root mass density and soil CO_2 efflux, before or after precipitation events, suggesting that in our system the root component of soil CO_2 efflux is not determined by standing root mass or length and is unresponsive to rapid changes in soil water content, at least during the spring and summer period. We found a broad range of 'near' optimum soil VWC where changes in VWC had limited effect, if any, on soil CO_2 efflux (Chapters II, III, and IV). Thus, soil CO_2 efflux rates in post-oak savannah appear to be governed predominantly by species composition and the response of these species to VWC extremes. These findings suggest that soil CO_2 efflux in oak savannah will likely respond more to changes in species composition and associated species specific responses to extreme precipitation or drought events.

Accurate modelling of soil CO_2 efflux within this system is dependent on consideration of individual soil CO_2 efflux component responses to environmental conditions. We were able to test this in the *S. scoparium* monoculture and *J. virginiana* monoculture and mixture in the

precipitation distribution treatment (Chapter IV). However, while partitioning of the components contribution to soil CO_2 efflux within this system is highly relevant, we need to acknowledge the complexity of the belowground system and the profound conceptual and experimental challenge of separating out plant, mycorrhizal, and microbial contribution to soil CO_2 efflux and our inherent inability to do this satisfactorily. In short we present an oversimplification and snap shot of a portion of a complex web of interdependent physical, chemical, and biological interactions intrinsically linked above and belowground.

Our results strongly indicate the substantial contribution of bacterial respiration to soil CO_2 efflux within this system (*J. virginiana*-dominated grassland) (Chapter IV). However, given the structural, physiological, and phylogenetic differences between grasses and gymnosperms and the relatively small respiration differences due to plant species mixture in this study, we conclude that components (root, fungal, and bacterial) of soil CO_2 efflux were affected more by seasonal fluctuations (e.g., plant activity, VWC, temperature) than plant species or precipitation redistribution. What remains unclear is whether more frequent long term moisture limiting conditions in the summer months will result in a negative feedback on microbial activity and respiration (Henry *et al.*, 2005). In this five-year study, we found no evidence for a decline in overall soil CO_2 efflux except in the plots planted with *S. scoparium*, but it is possible that in the tree plots a decline in microbial activity was matched with an increase in root CO_2 efflux. The root exclusion study, however, suggests that this was not the case for the *S. scoparium* and *J. virginiana* monocultures or the *S. scoparium – J. virginiana* mixture.

Furthermore the effect and response of the plant and microbial community to warming (not tested here) needs to be considered. The temperature sensitivity and acclimation ability of the plant and microbial components of soil CO_2 may occur at differing temporal scales (Atkin *et al.*, 2005). The temperature dependence of decomposition of plant litter of differing quality and quantity remains unclear (Davidson & Janssens, 2006). It is uncertain whether short term increases in C mineralization, which are commonly observed in warming experiments in the field (Melillo *et al.*, 2002; Bradford *et al.*, 2008), will be sustained due to depletion and/or substrate availability and/or acclimation of soil communities to higher temperatures (Kirschbaum, 2004; Bradford *et al.*, 2008).

Warming and precipitation distribution did not have a strong effect on ectomycorrhizal (EM) or arbuscular mycorrhizal (AM) colonization in *J. virginiana* and *S. scoparium* roots, four and five years after commencement of the treatments, suggesting that mycorrhizal species may

acclimate to climatic conditions overtime (Chapter V). Growing both species in the same plot did reduce AM mycorrhizal abundance (either fine, coarse or total) on four out of six dates for both species, suggesting that both species actively suppress AM abundance on each others' roots. While we acknowledge that we may have missed some of the 'initial' mycorrhizal responses to warming and moisture, our data does suggest that in the longer term, the effect of host species and potential competitive interactions may be more important in determining future mycorrhizal abundance than climate fluctuations. These findings are important because changes in growth of mycorrhizal fungi may potentially influence soil and ecosystem level C dynamics by controlling the release of C to the soil microbial community (Ames *et al.*, 1984; Hogberg & Read, 2006) and by enhancing the stabilization of soil organic C through the promotion of soil aggregation (Rillig & Mummey, 2006; De Deyn *et al.*, 2008; Wilson *et al.*, 2009). In that, mycorrhiza may contribute some of the most recalcitrant C compounds to soil (i.e. chitin and glomalin), thus changes in abundance and/or growth may have major implications for soil C dynamics (Rillig & Allen, 1999; Langley *et al.*, 2006).

Conclusion

In this study we assessed the response of a range of factors that contribute to soil CO_2 efflux to community composition, seasonal climatic changes, precipitation distribution pattern and warming. Total soil CO_2 efflux was strongly affected by plant species; plots with *S. scoparium* generally had the higher soil CO_2 efflux rates in the early years of the study, while plots dominated by *J. virginiana* had the higher soil CO_2 efflux rates at the end of the five-year study period (Chapter II). While aboveground standing mass of the trees increased nine-fold for *J. virginiana* and 115-fold for *Q. stellata*, there was no difference in mean annual soil CO_2 efflux between 2005 and 2009, even though one could reasonably expect a strong increase in standing root length density over this period. More detailed analyses confirmed this finding, showing that there was no relationship between standing root length (or mass) density and soil CO_2 efflux for measurements collected in early summer (chapter III). There also was no relationship between microbial biomass [(microbial dissolved organic carbon (DOC)] and soil CO_2 efflux, or root length (or mass) density and microbial biomass (Chapter IV). This suggests that species and climatic effects on root and microbial activity drive soil CO_2 efflux.

Of the underlying components of soil CO_2 efflux, we found that neither bacterial nor root and mycorrhizal respiration were strongly affected by climate warming or precipitation redistribution. However, the underlying components of soil CO_2 efflux are affected by plant species and seasonal climatic changes. Both the root and hyphal component of soil CO_2 efflux were generally small, with the vast majority of soil CO_2 efflux originating from bacterial respiration.

Expansion of *J. virginiana* into grassland and savannah systems of the southern United States will affect soil CO_2 efflux, but it seems likely that components within this system will acclimate/adjust to climate change drivers and thus not experience a substantial acceleration of carbon loss, at least in the short term. We suggest that ultimately the net effect of climate change on our system will depend on seasonal changes in soil VWC and the occurrence of extreme precipitation events, as soil CO_2 efflux *per se* was negatively affected by conditions of high VWC and to a lesser extent very low VWC. However, climate change drivers may have strong indirect effects on species competition and plant carbon balance. The seasonal signal in our measurements indicates that soil CO_2 efflux is high during periods of high plant activity (Spring), regardless of soil VWC and temperature. Thus, drivers that reduce plant production (such as warming in the oak monoculture plots) were found to reduce soil CO_2 efflux, even at the same soil VWC and soil temperature. A climate change driven shift in plant species dominance as a result of differential response to warming and precipitation distribution (Prentice *et al.*, 1992; Woodward *et al.*, 2004) will also affect soil CO_2 efflux. Plant species within this system differ in their association with microbial communities and mycorrhizal fungi, thus climate driven shifts in vegetation composition may affect the capacity of microbes to decompose plant litter (positive or negative) and will also affect litter quality, which in turn may alter the nutrient competition between plants and soil microbes with possible consequences for ecosystem nutrient cycling and thus soil CO_2 efflux in the long term. Thus, shifts in vegetation cover and growth need to be considered in the context of long term warming and precipitation effects on soil C dynamics and CO_2 efflux.

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APPENDIX

Table A-2.1. Probability values (*P*-values) and F-ratios determined using ANCOVA for annual soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}).

	Soil CO_2 efflux	
Treatment	F-ratio	*P*-value
Precipitation (P)	0.18	0.675
Warming (W)	0.16	0.687
P × W	0.63	0.430
Mixture (M)	1.10	0.359
P × M	0.58	0.680
W × M	1.31	0.268
P × W × M	2.56	**0.041**
Year (Y)	2.63	0.052
Y × P	1.31	0.272
Y × W	0.25	0.862
Y × P × W	0.02	0.996
Y × M	0.24	0.996
Y × P × M	0.53	0.890
Y × W × M	0.59	0.851
Y × P × W × M	0.57	0.861
VWC[z]	0.27	0.601
Y × VWC	0.24	0.870
P × VWC	1.37	0.244
Y × P × VWC	0.13	0.940
W × VWC	0.01	0.931
Y × W × VWC	0.41	0.745
P × W × VWC	0.83	0.363
Y × P × W × VWC	0.56	0.646
M × VWC	0.33	0.855
Y × M × VWC	0.16	0.999
P × M × VWC	1.55	0.191
Y × P × M × VWC	0.75	0.703
W × M × VWC	0.57	0.682
Y × W × M × VWC	0.43	0.949
P × W × M × VWC	0.96	0.430
Y × P × W × M × VWC	0.36	0.976

P-values ≤ 0.05 are printed in bold.

[z] Soil volumetric water content (VWC).

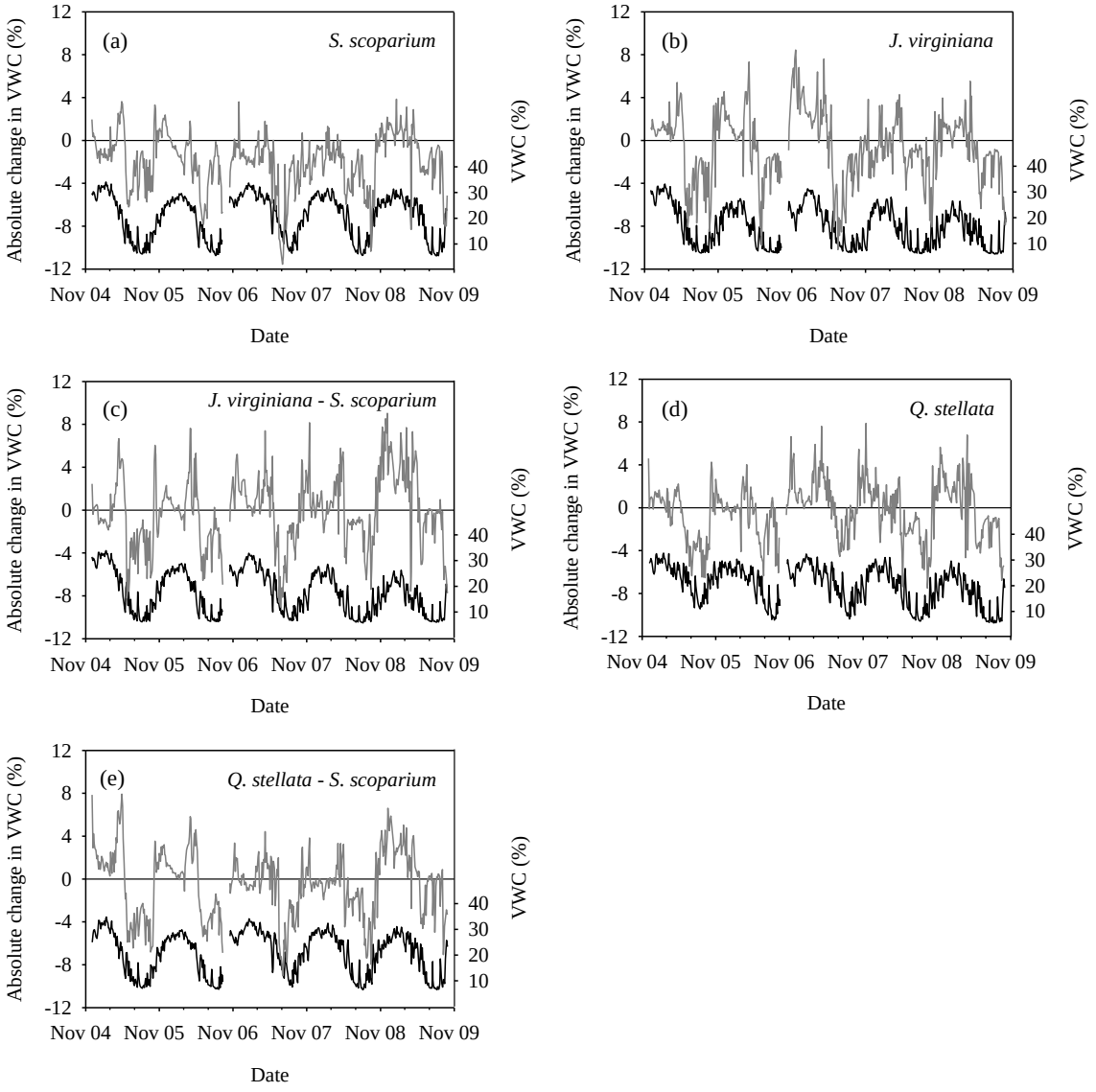

Figure A-2.1. Effect of precipitation treatment on soil volumetric water content (VWC) over time averaged across warming treatment for (a) *Schizachyrium scoparium* in monoculture, (b) *Juniperus virginiana* grown in monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* in monoculture, and (e) *Q. stellata* grown with *S. scoparium*. The grey line depicts absolute changes in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal VWC pattern.

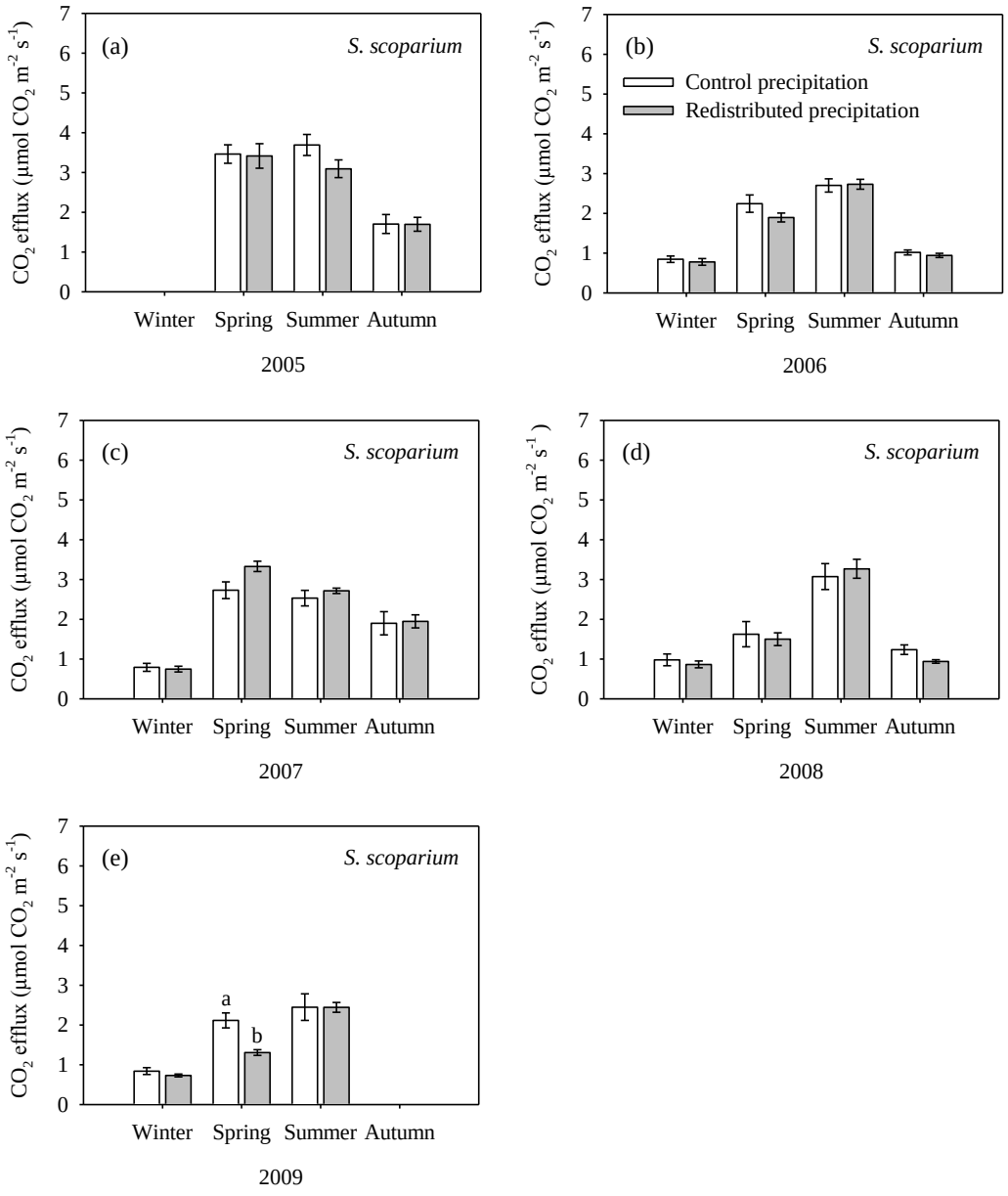

Figure A-2.2. Effect of season on soil CO_2 efflux (μmol CO_2 $m^{-2}s^{-1}$) averaged across warming treatment for control precipitation (unfilled bar) and redistributed precipitation (filled bar) in *Schizachyrium scoparium* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

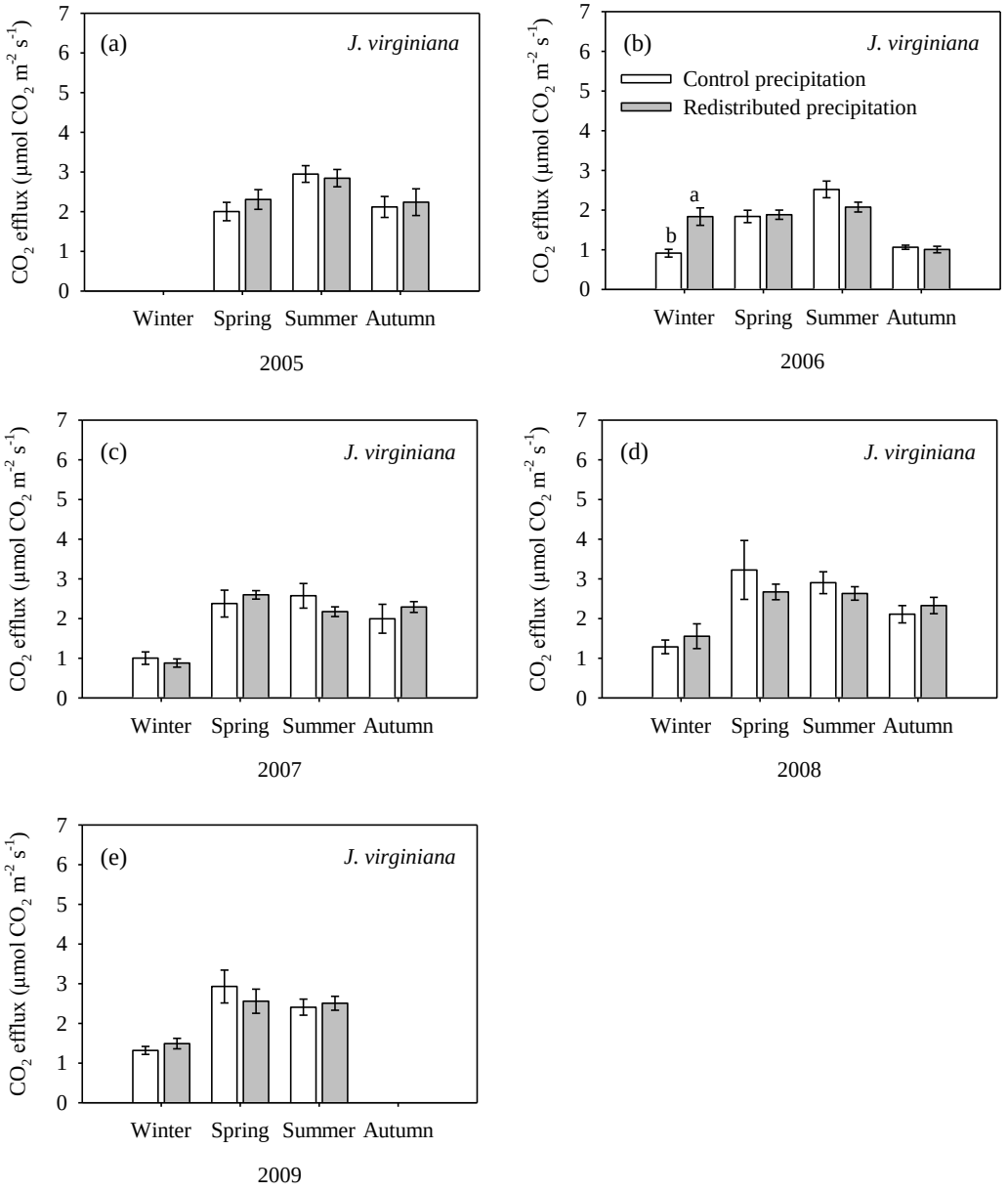

Figure A-2.3. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across warming treatment for control precipitation (unfilled bar) and redistributed precipitation (filled bar) in *Juniperus virginiana* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

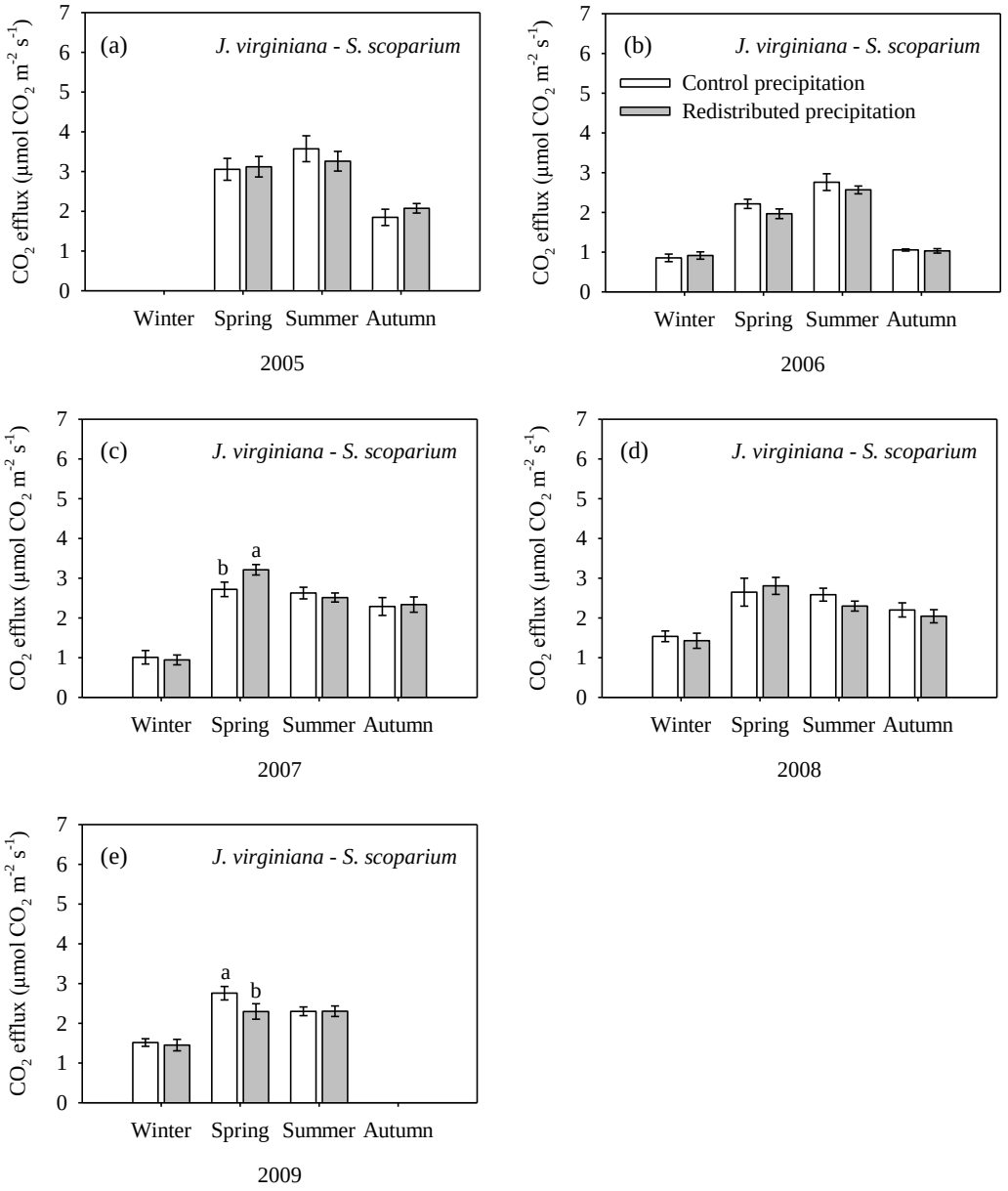

Figure A-2.4. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across warming treatment for control precipitation (unfilled bar) and redistributed precipitation (filled bar) in *J. virginiana* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

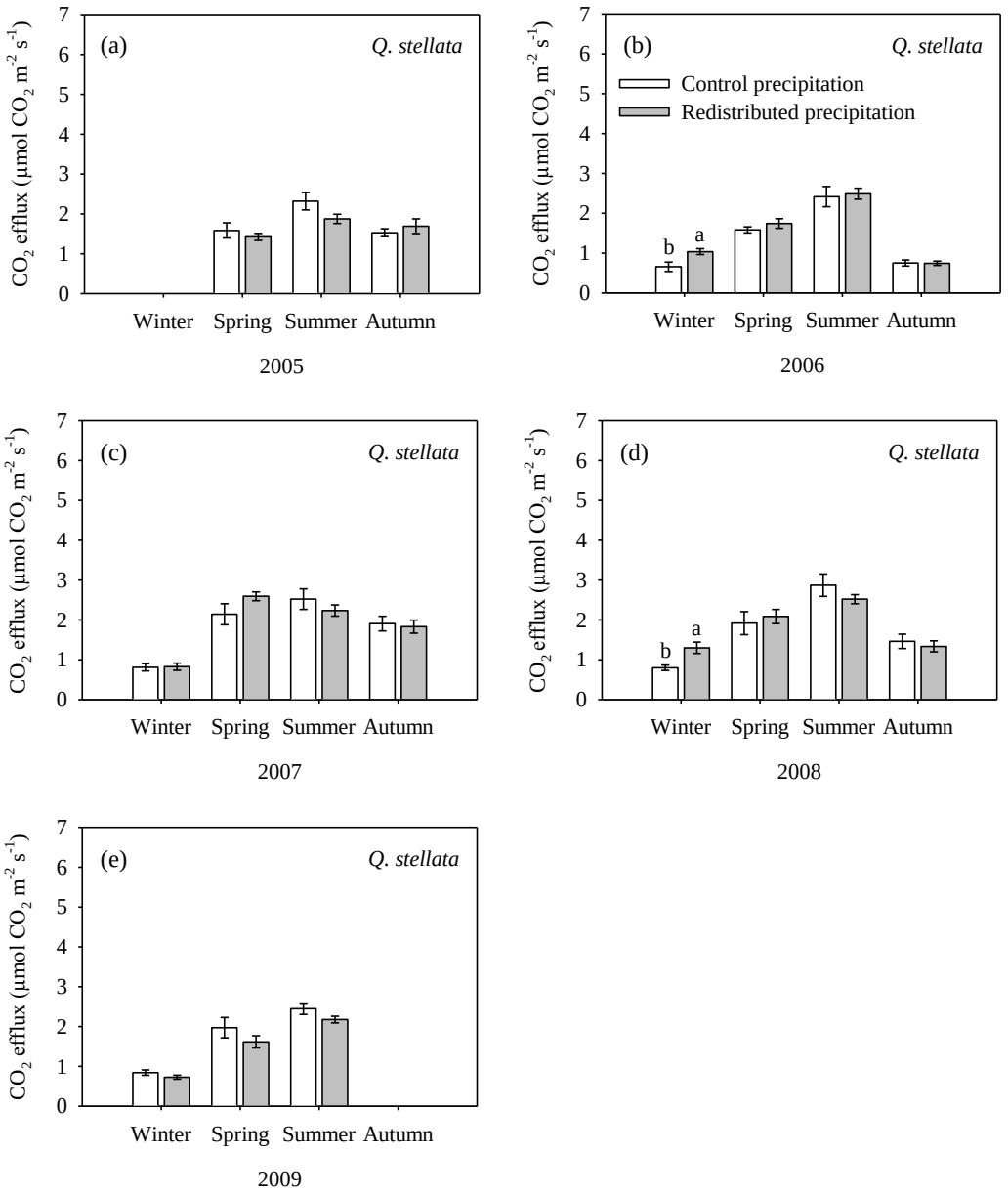

Figure A-2.5. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across warming treatment for control precipitation (unfilled bar) and redistributed precipitation (filled bar) in *Quercus stellata* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

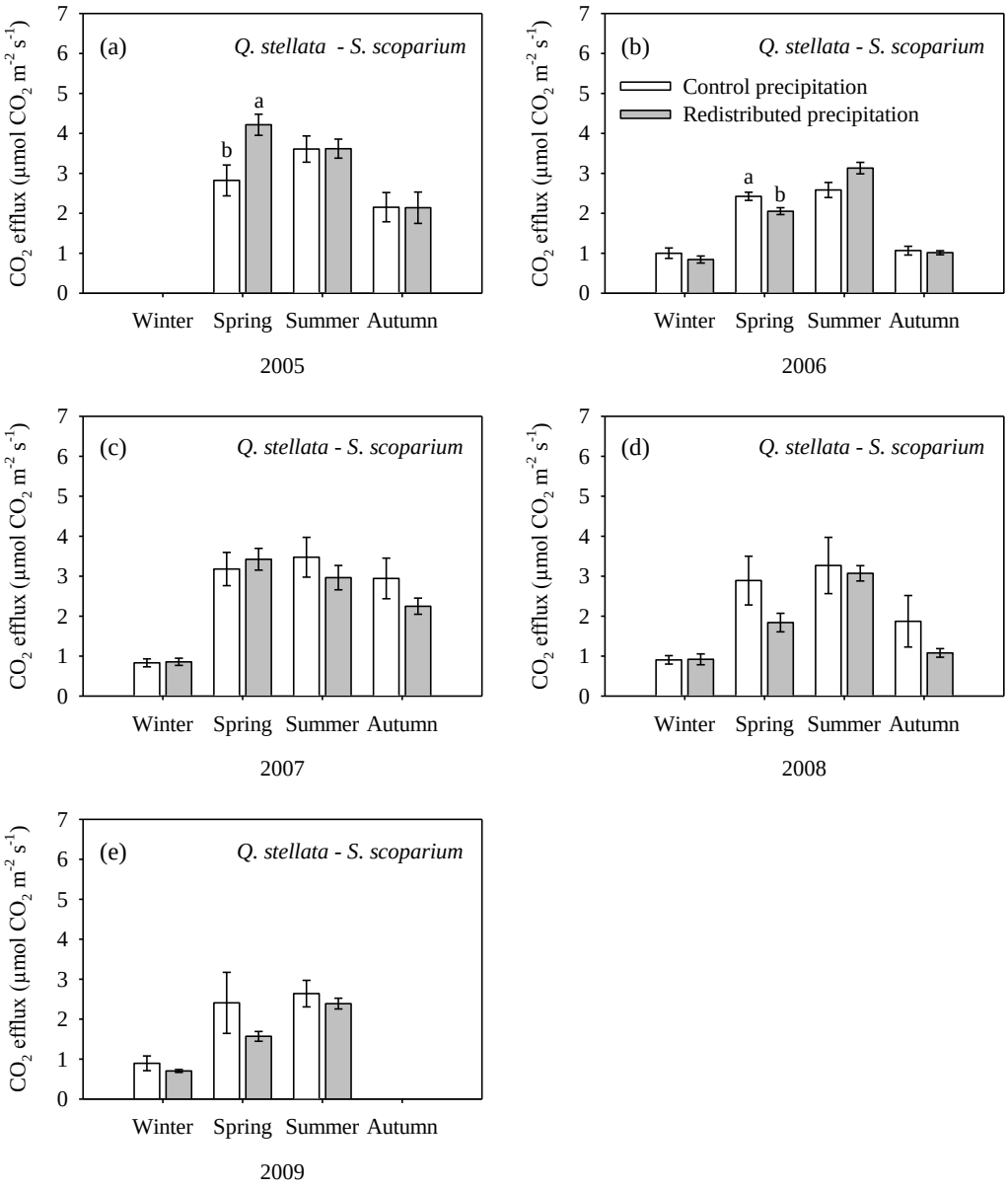

Figure A-2.6. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across warming treatment for control precipitation (unfilled bar) and redistributed precipitation (filled bar) in *Q. stellata* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

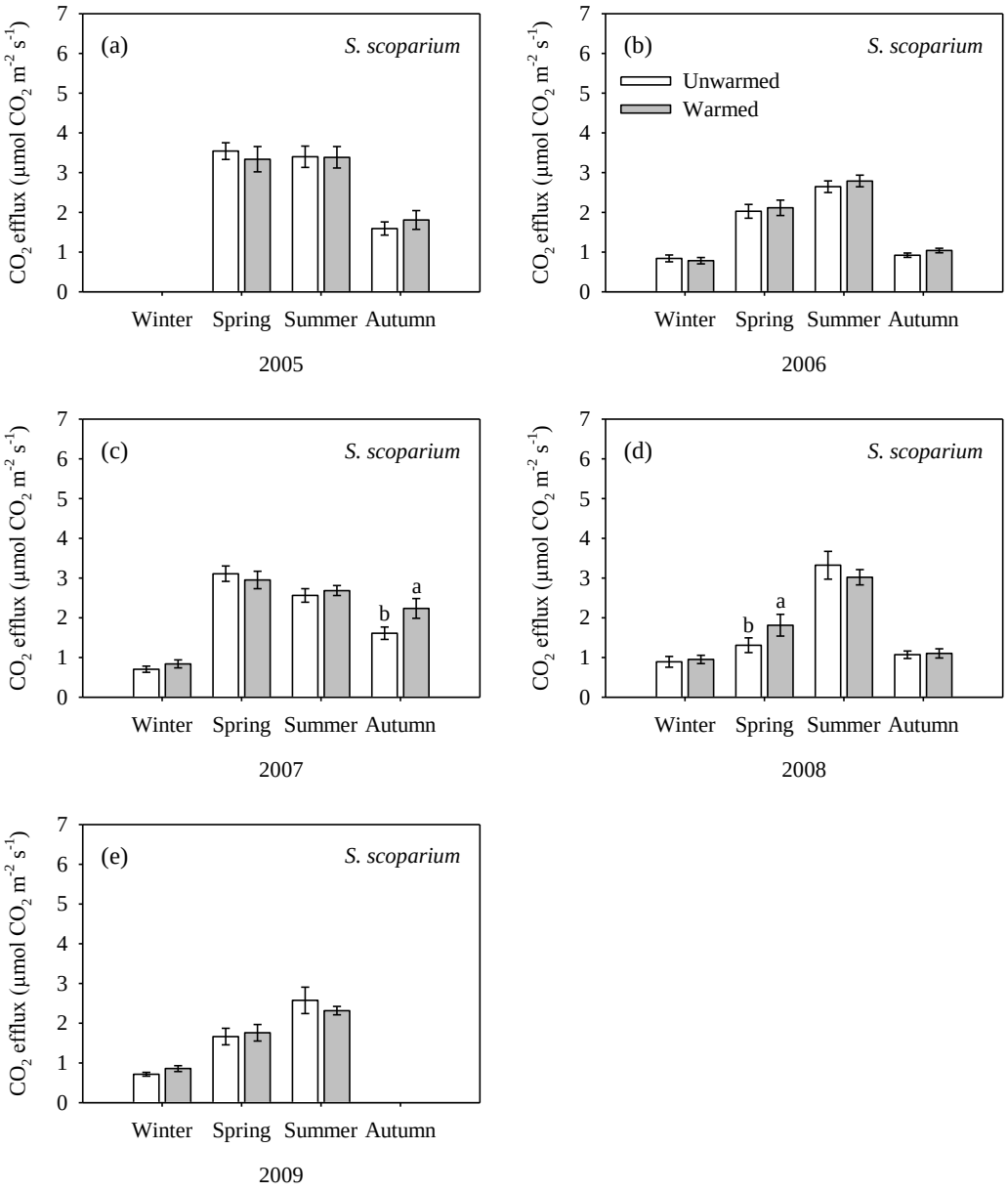

Figure A-2.7. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across precipitation treatment for unwarmed (unfilled bar) and warmed (filled bar) treatments in *Schizachyrium scoparium* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

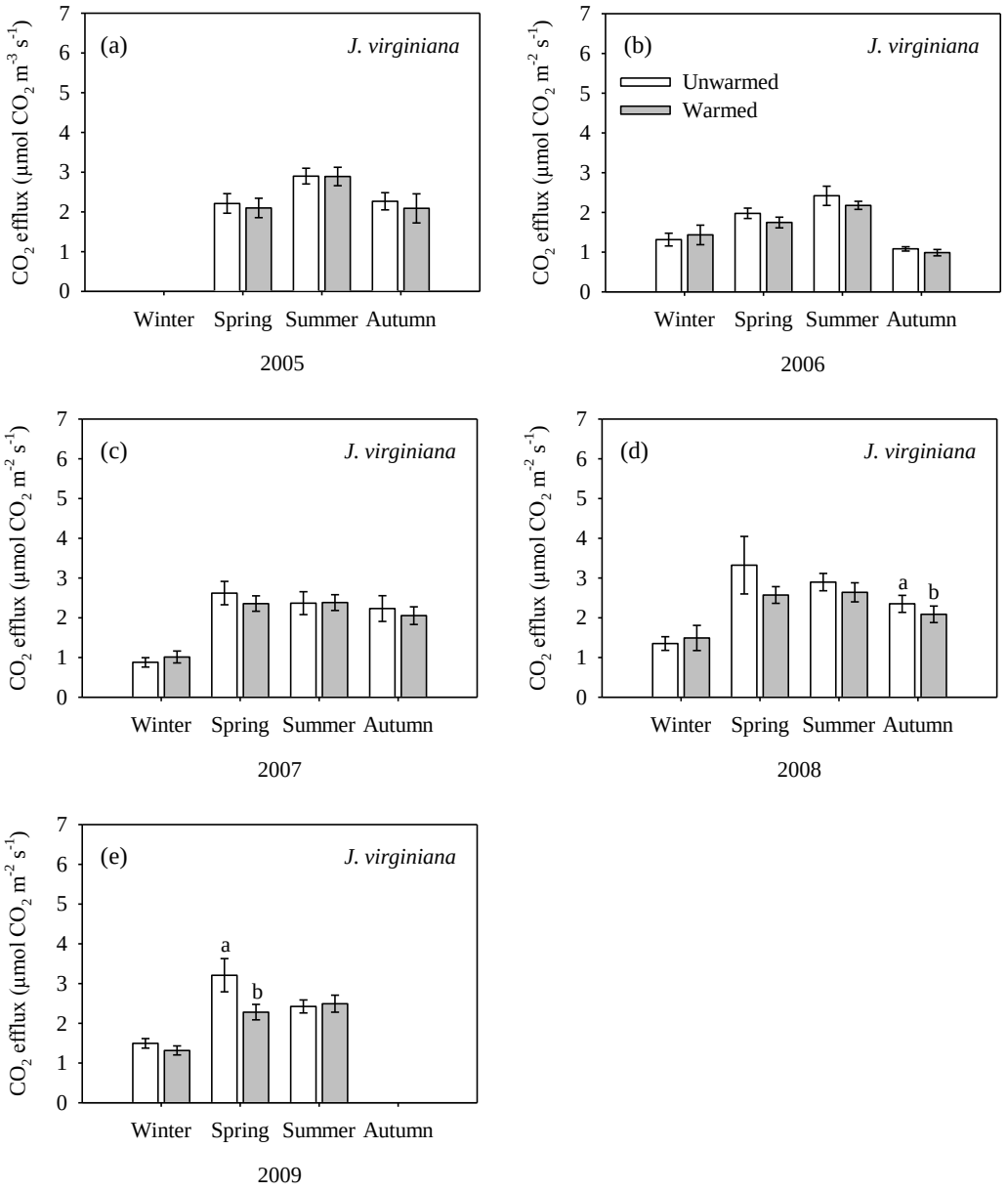

Figure A-2.8. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across precipitation treatment for unwarmed (unfilled bar) and warmed (filled bar) treatments in *Juniperus virginiana* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

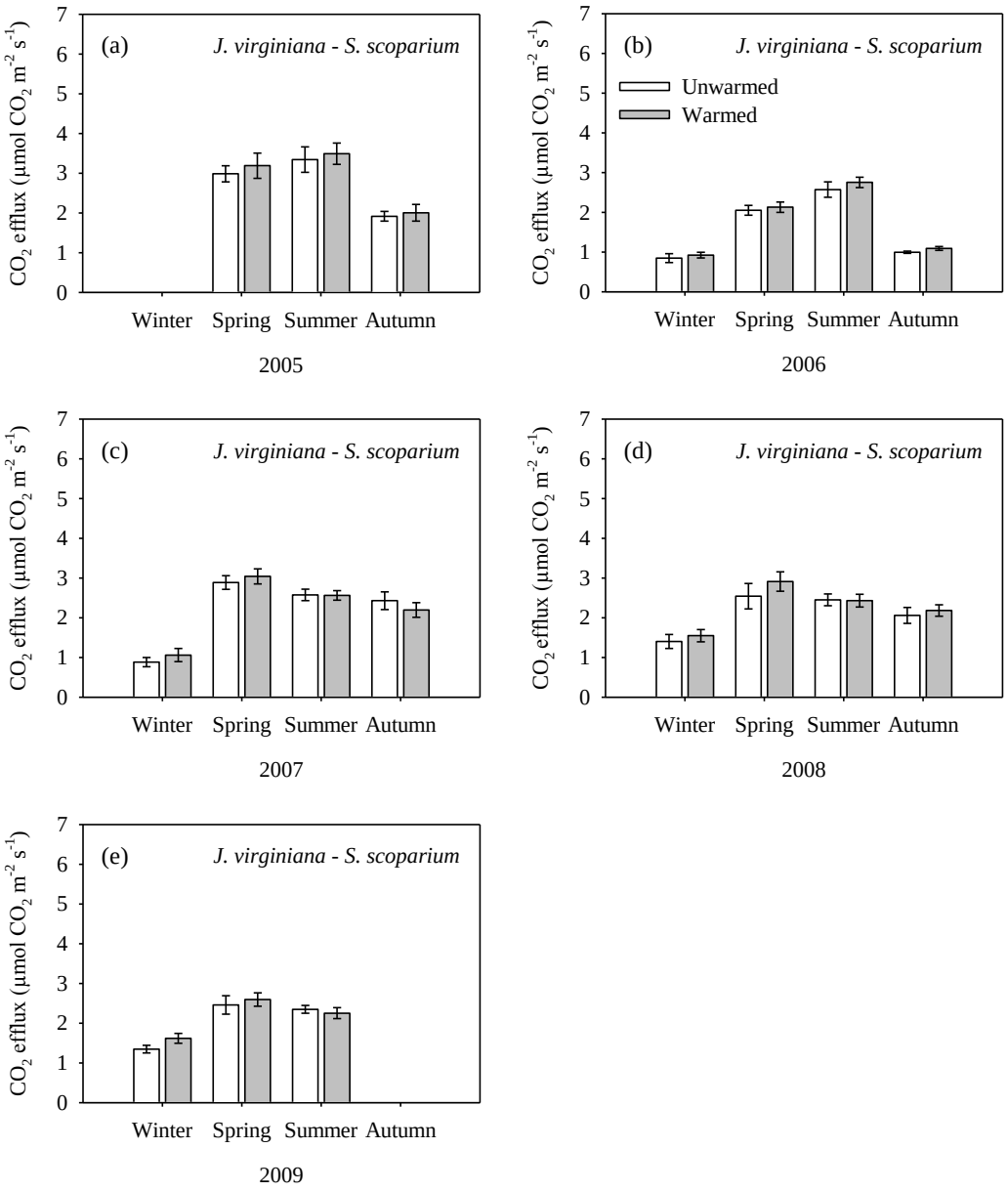

Figure A-2.9. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across precipitation treatment for unwarmed (unfilled bar) and warmed (filled bar) treatments in *J. virginiana* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

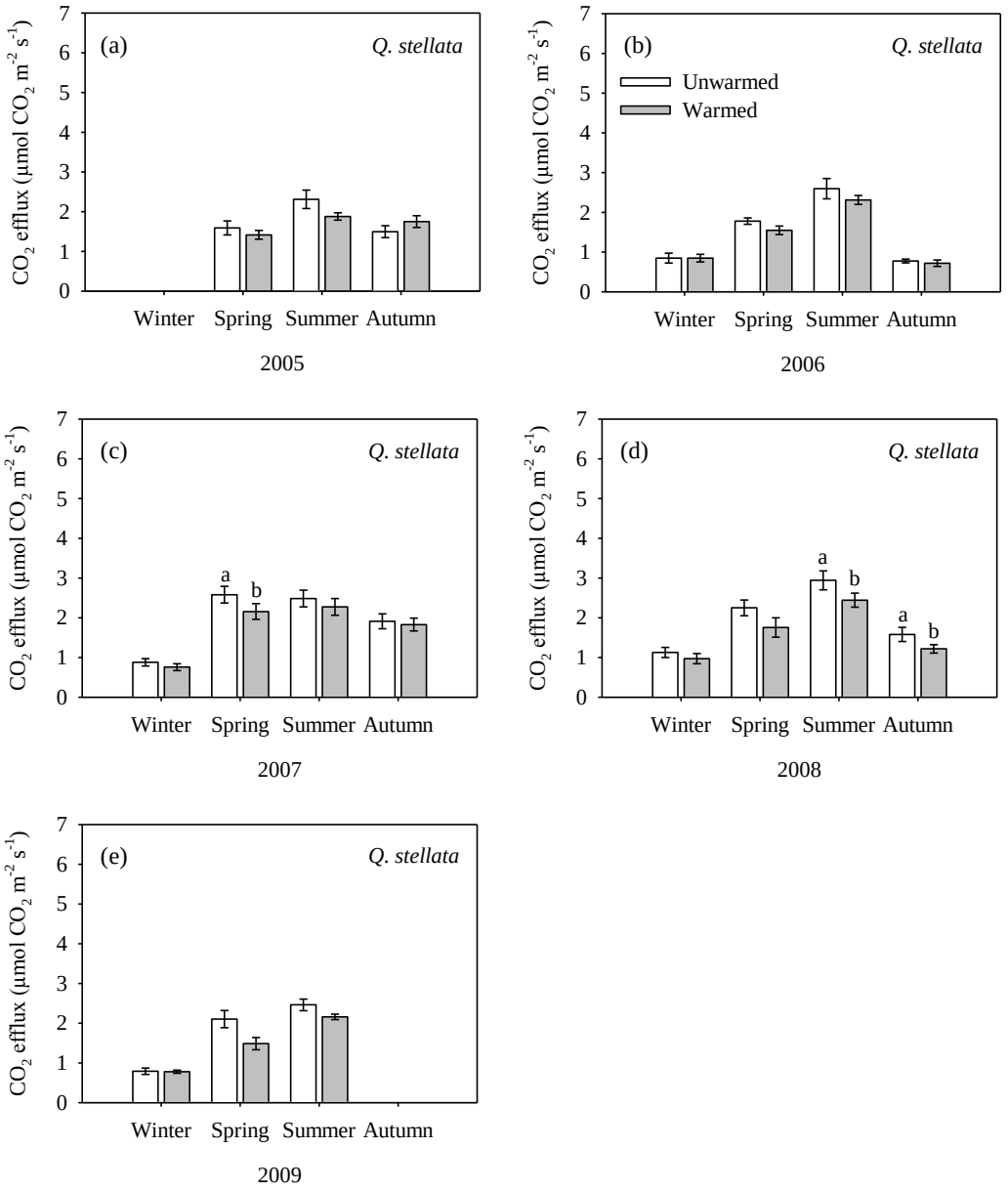

Figure A-2.10. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across precipitation treatment for unwarmed (unfilled bar) and warmed (filled bar) treatments in *Quercus stellata* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

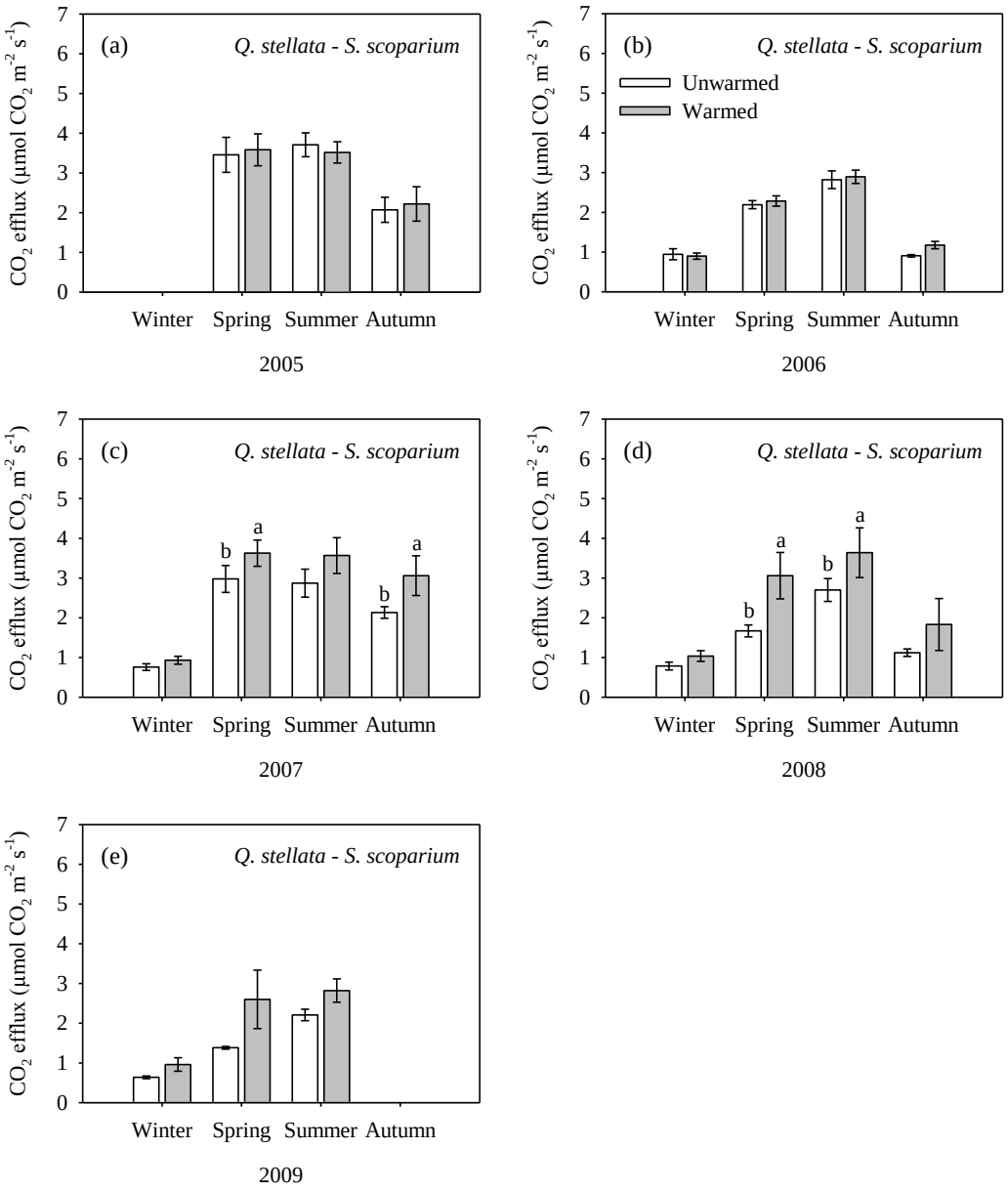

Figure A-2.11. Effect of season on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across precipitation treatment for unwarmed (unfilled bar) and warmed (filled bar) treatments in *Q. stellata* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE). Treatments with different letters were significantly different according to Student's t-test ($P \leq 0.05$).

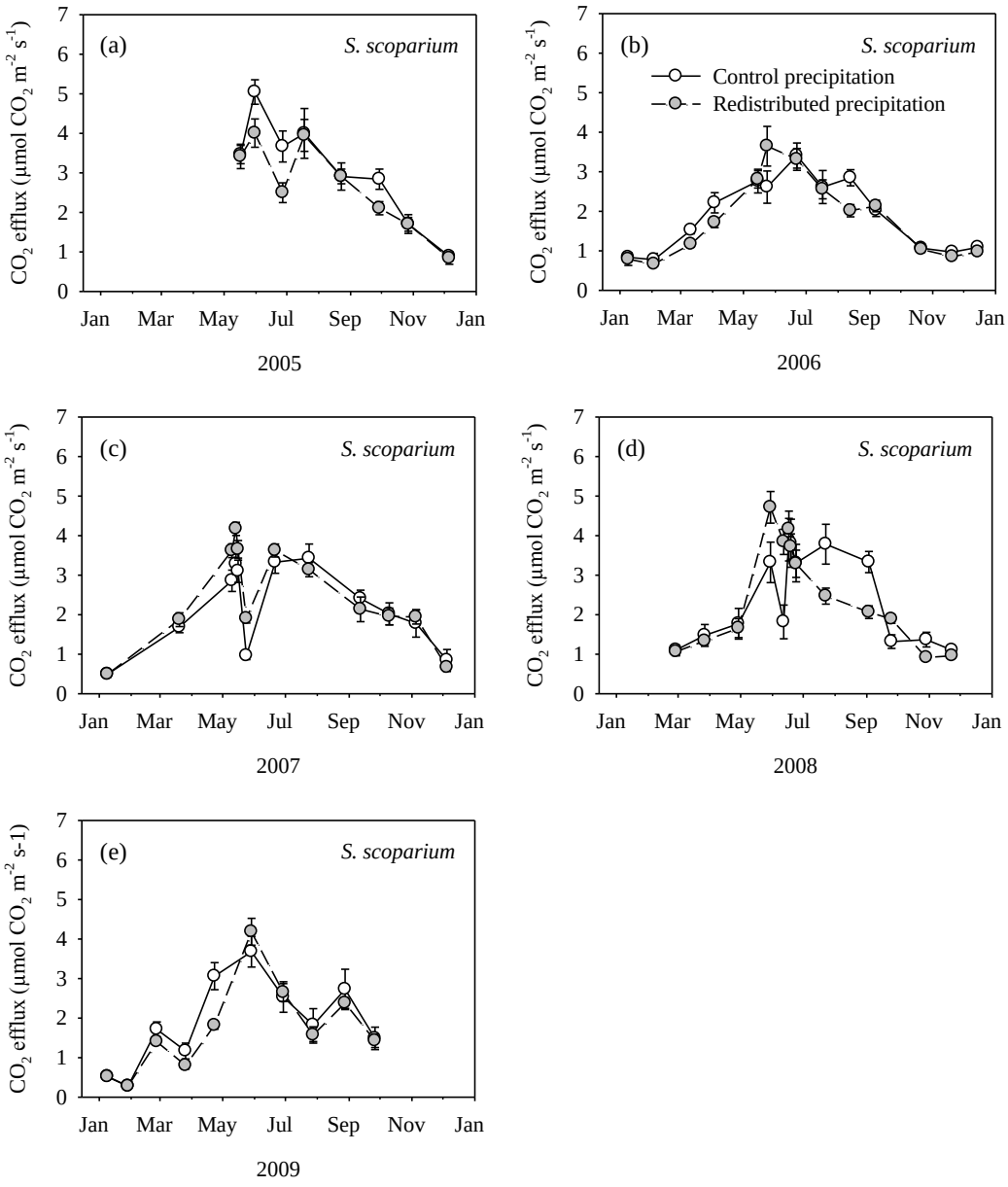

Figure A-2.12. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across warming treatment for control precipitation (unfilled circle) and redistributed precipitation (filled circle) in *Schizachyrium scoparium* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

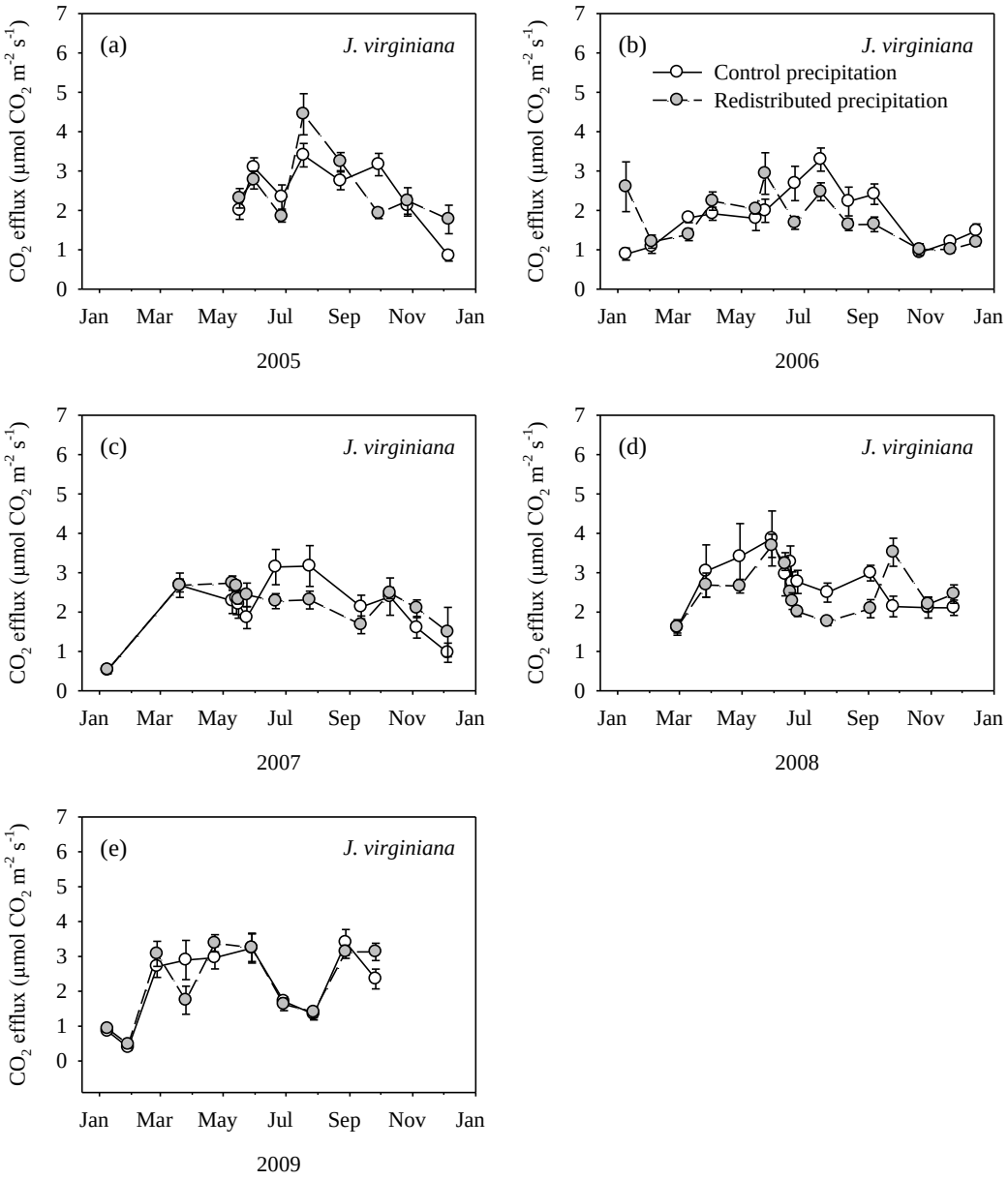

Figure A-2.13. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across warming treatment for control precipitation (unfilled circle) and redistributed precipitation (filled circle) in *Juniperus virginiana* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

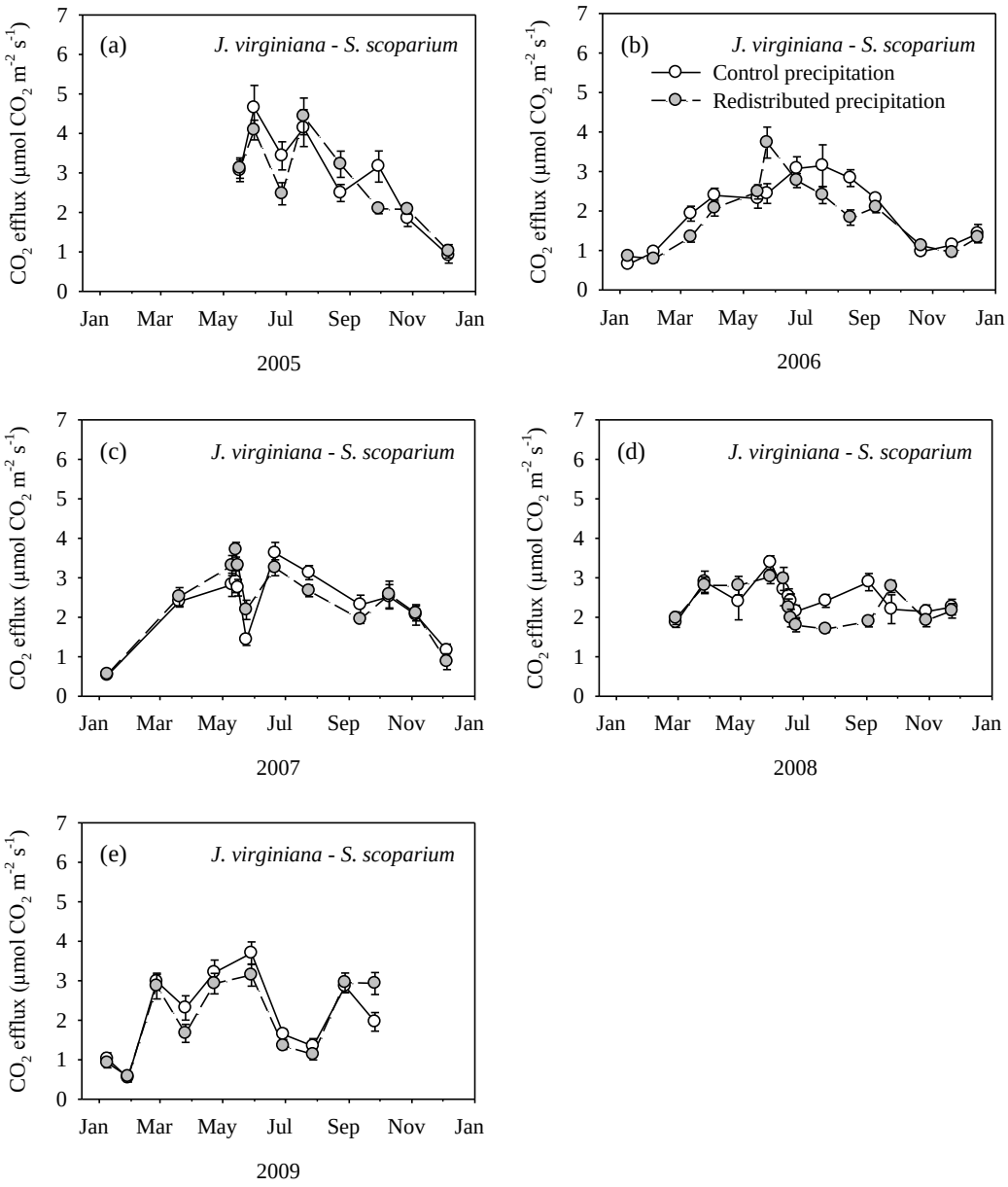

Figure A-2.14. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across warming treatment for control precipitation (unfilled circle) and redistributed precipitation (filled circle) in *J. virginiana* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

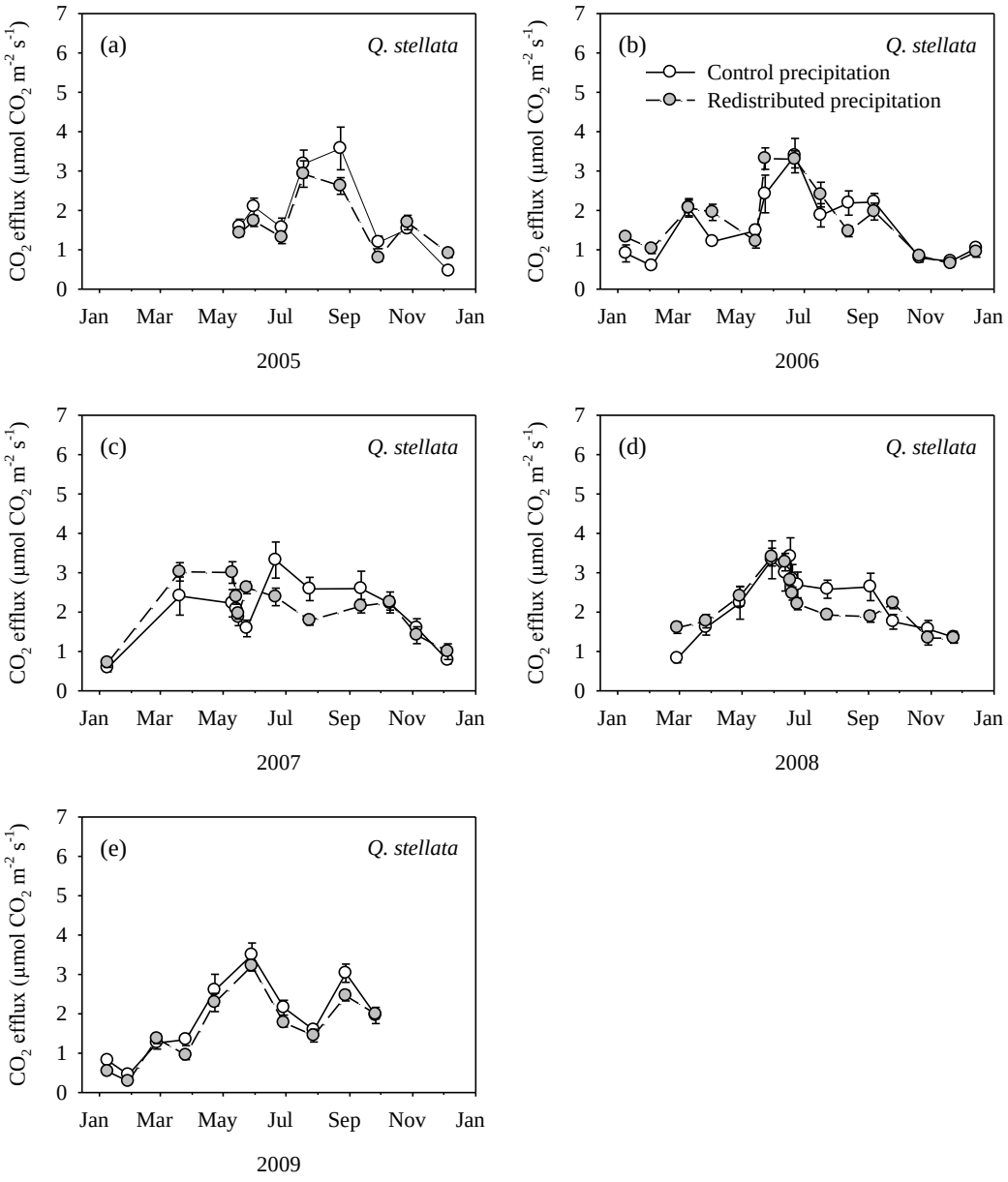

Figure A-2.15. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across warming treatment for control precipitation (unfilled circle) and redistributed precipitation (filled circle) in *Quercus stellata* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

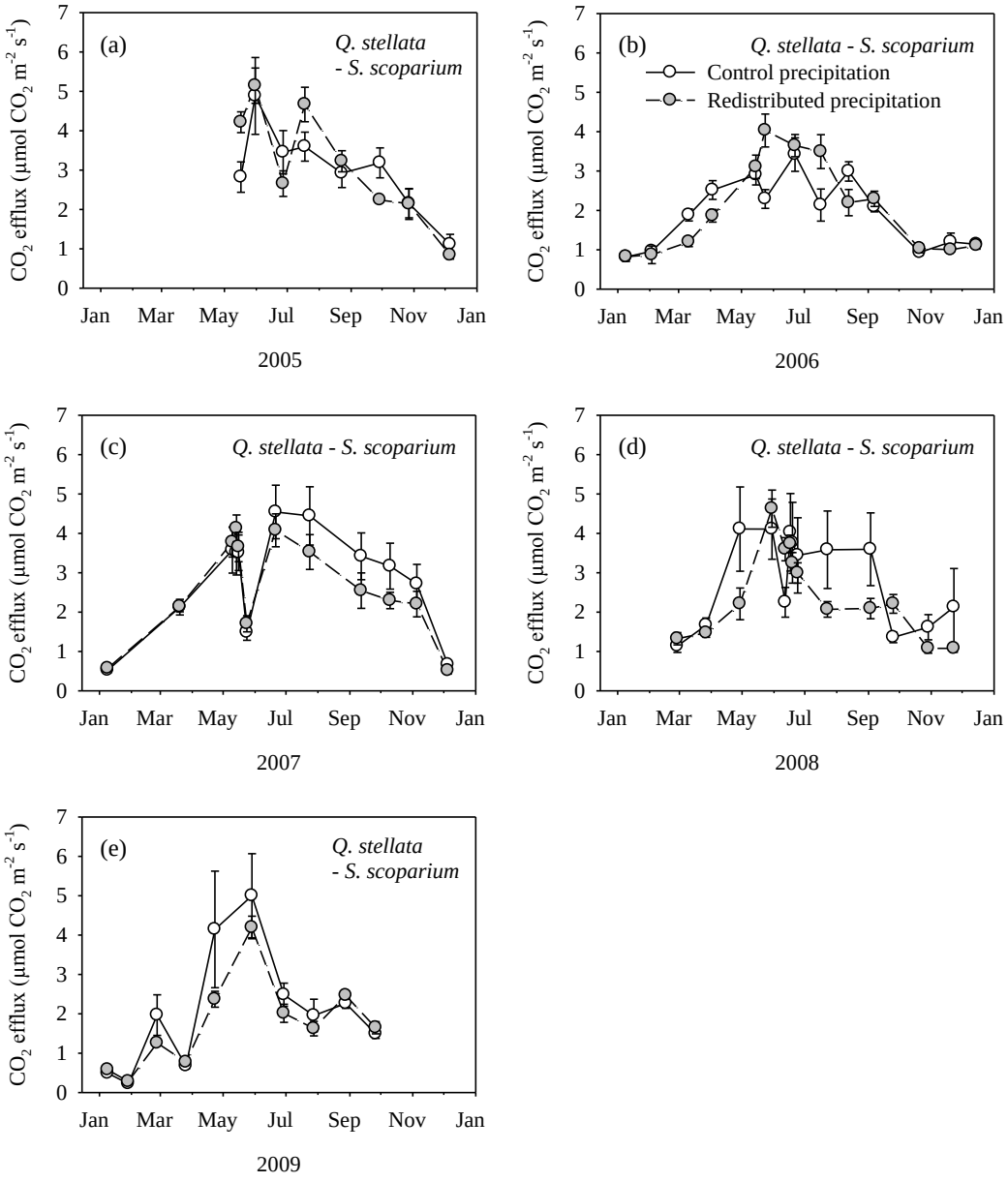

Figure A-2.16. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across warming treatment for control precipitation (unfilled circle) and redistributed precipitation (filled circle) in *Q. stellata* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

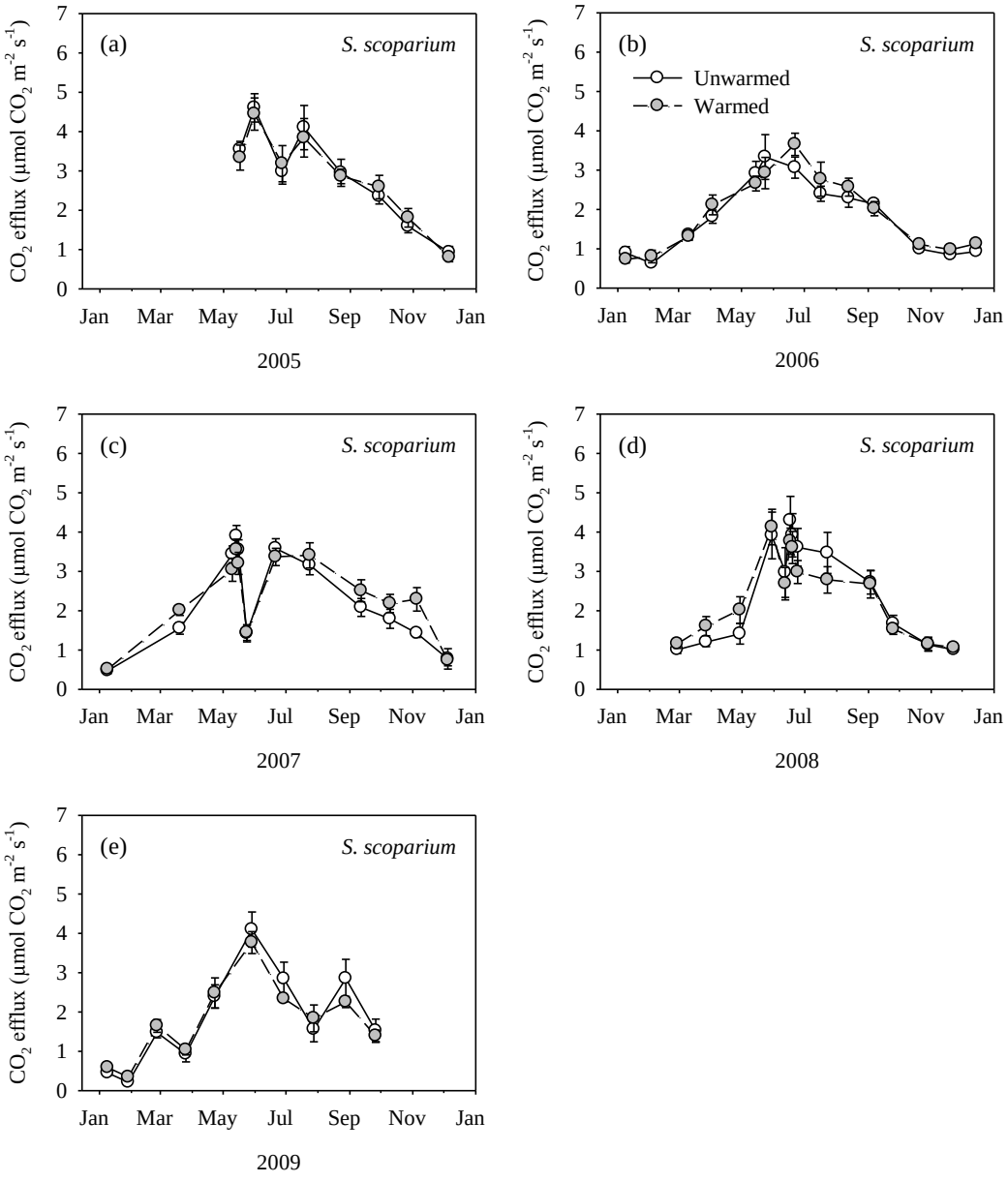

Figure A-2.17. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across precipitation treatment for unwamed (unfilled circle) and warmed (filled circle) in *Schizachyrium scoparium* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

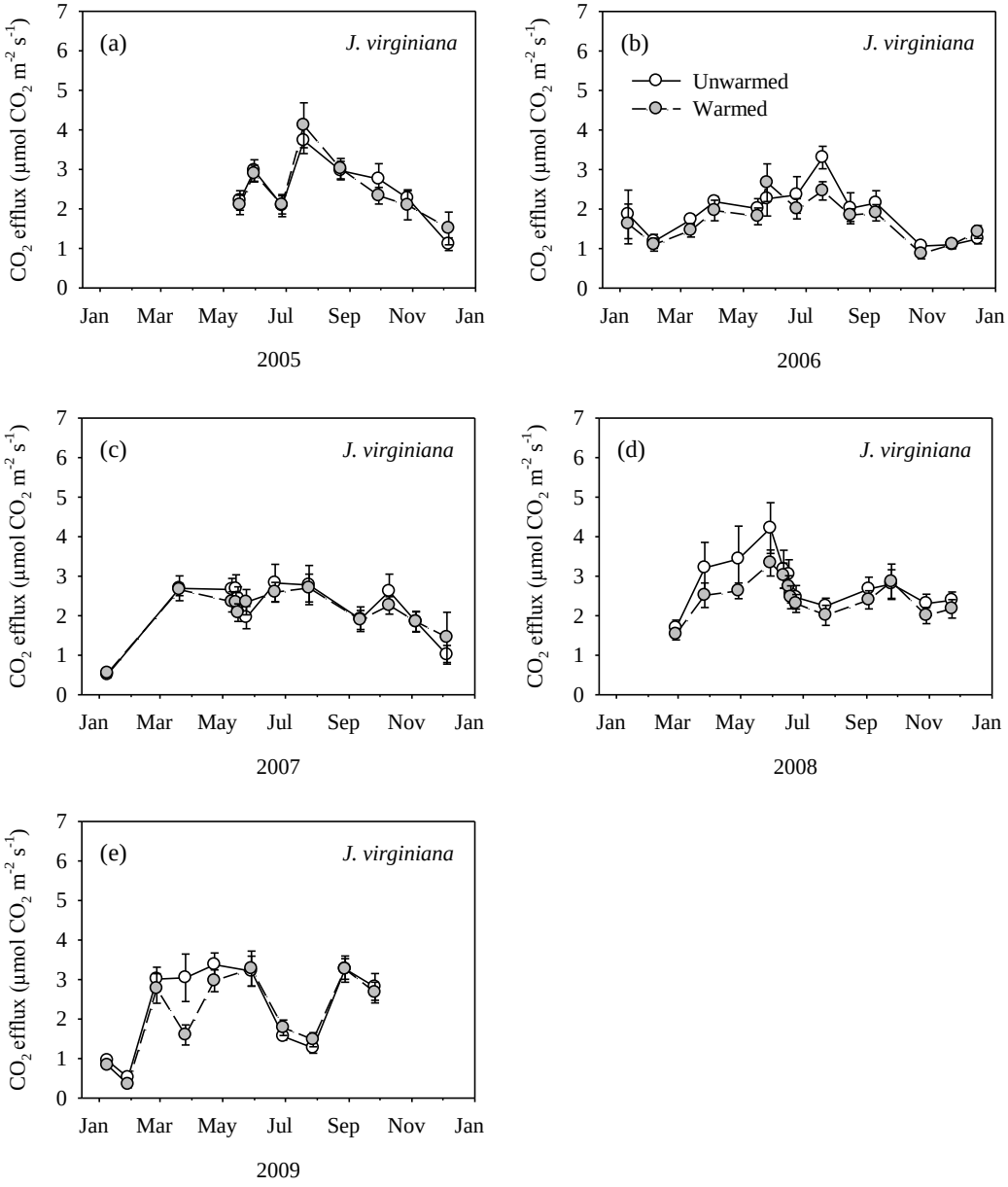

Figure A-2.18. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across precipitation treatment for unwarmed (unfilled circle) and warmed (filled circle) in *Juniperus virginiana* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

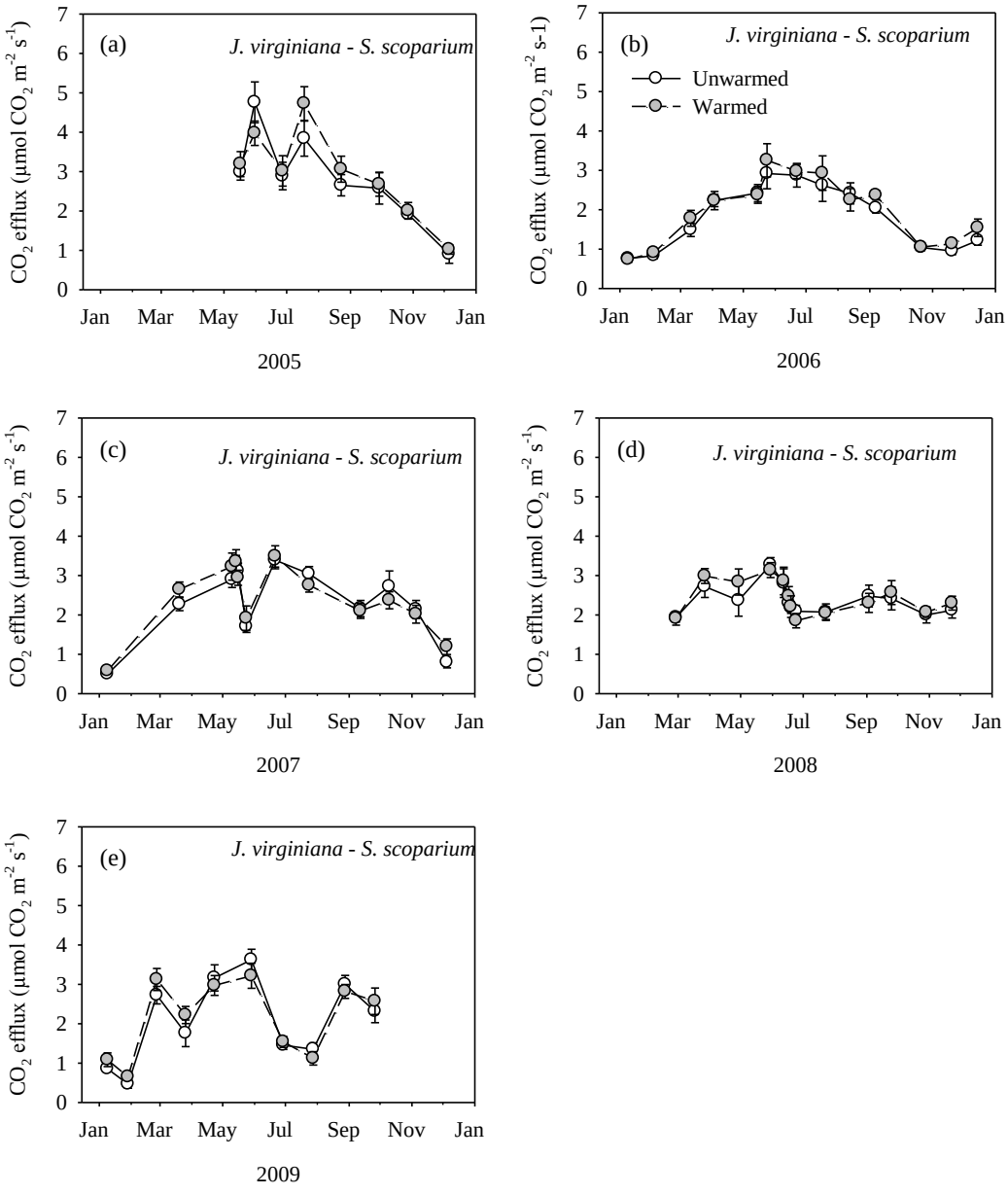

Figure A-2.19. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across precipitation treatment for unwarmed (unfilled circle) and warmed (filled circle) in *J. virginiana* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

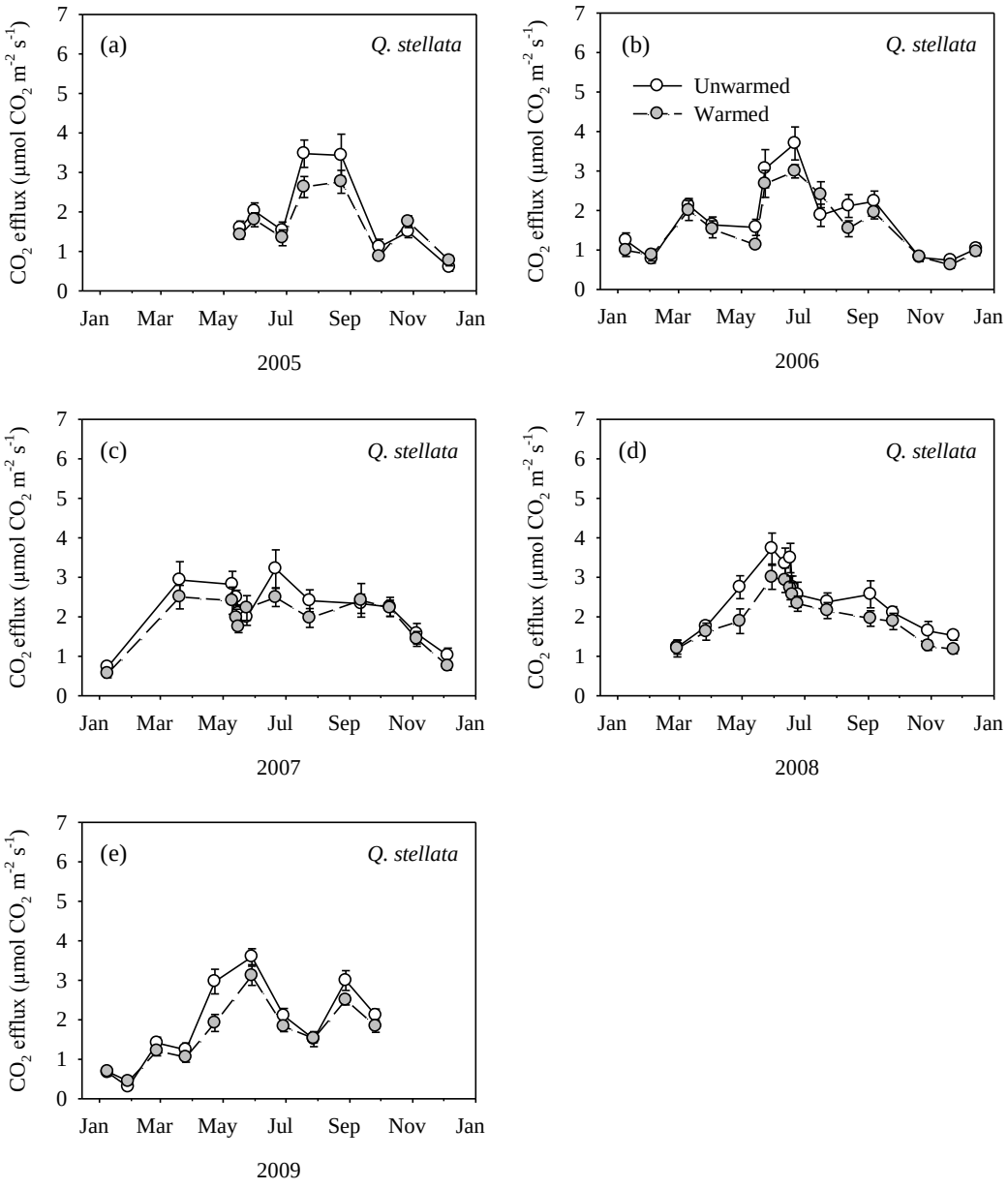

Figure A-2.20. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across precipitation treatment for unwarmed (unfilled circle) and warmed (filled circle) in *Quercus stellata* monoculture during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

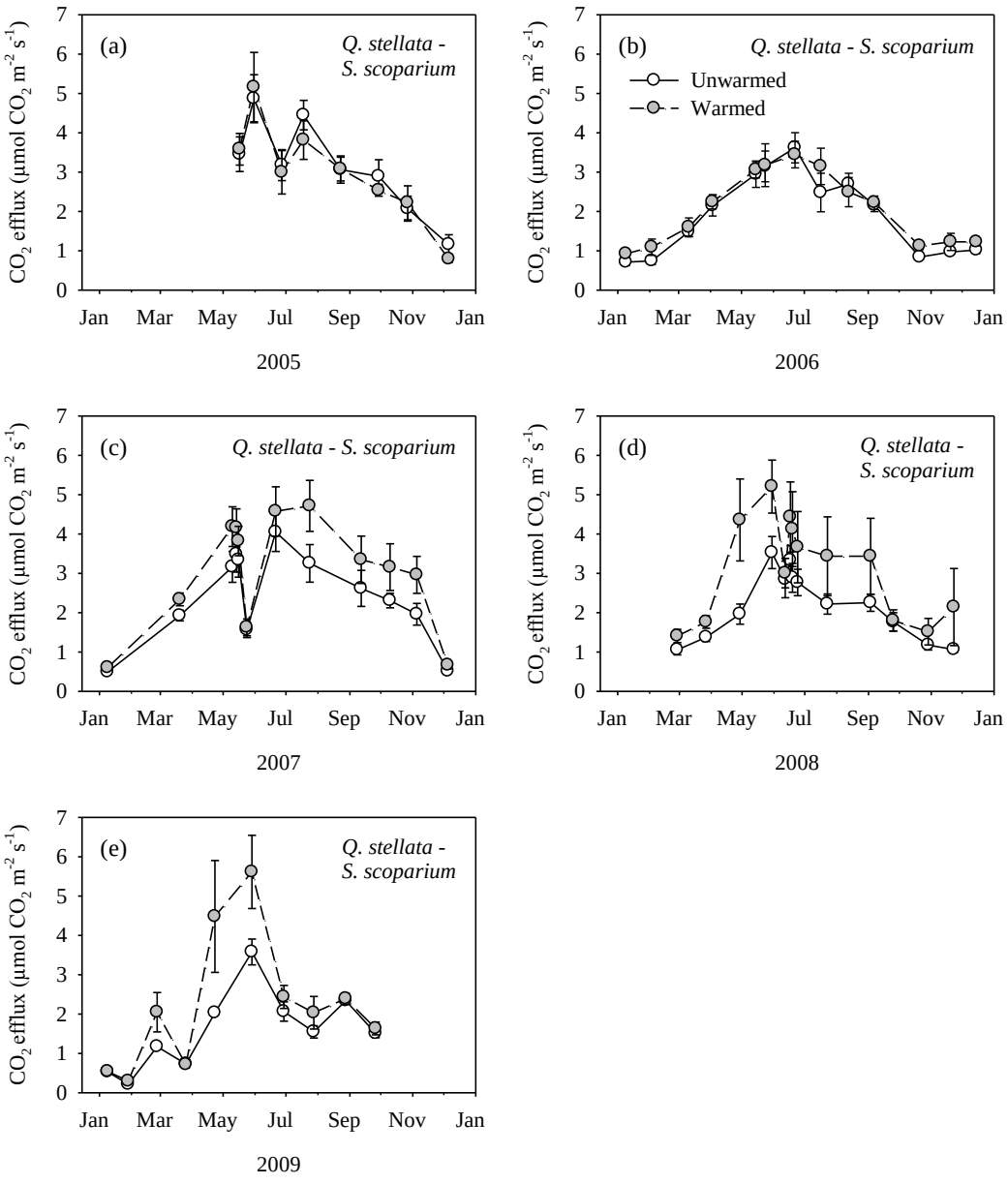

Figure A-2.21. Soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) through time averaged across precipitation treatment for control precipitation (unfilled circle) and redistributed precipitation (filled circle) in *Q. stellata* grown with *S. scoparium* during (a) 2005, (b) 2006, (c) 2007, (d) 2008, and (e) 2009 (means ± SE).

Table A-3.1. Probability values (*P*-values) and F-ratios determined using ANOVA for soil volumetric water content (VWC) during the May 2006, May 2007, and June 2008 campaigns.

	Soil volumetric water content					
	May 2006		May 2007		June 2008	
	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	7.90	**0.030**	5.42	0.059	16.7	**0.006**
Warming (W)	0.47	0.493	1.90	0.170	4.41	**0.037**
W × P	1.06	0.306	0.15	0.698	0.03	0.858
Mixture (M)	15.3	**<0.001**	13.0	**<0.001**	21.5	**<0.001**
P × M	0.64	0.636	3.60	**0.007**	2.31	0.058
W × M	0.88	0.481	0.79	0.533	2.10	0.082
P × W × M	0.59	0.667	1.52	0.197	1.44	0.221
Date (D)	158.8	**<0.001**	149.3	**<0.001**	99.8	**<0.001**
P × D	5.69	**0.019**	11.4	**<0.001**	2.32	0.075
W × D	0.34	0.562	0.52	0.667	0.06	0.983
P × W × D	0.11	0.742	3.61	0.616	0.10	0.962
M × D	0.67	0.614	0.60	**<0.001**	1.07	0.382
P × M × D	0.33	0.858	0.80	0.649	0.32	0.984
W ×M ×D	0.11	0.979	0.75	0.701	0.27	0.993
P × W × M ×D	0.67	0.614	1.05	0.407	0.84	0.614

P-values ≤0.05 are printed in bold.

[z] Soil volumetric water content.

Table A-3.2. Probability values (*P*-values) and F-ratios determined using ANCOVA for soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) during the May 2006, May 2007, and June 2008 campaigns.

	Soil CO_2 efflux					
	May 2006		May 2007		June 2008	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.52	0.474	0.06	0.815	0.73	0.420
Warming (W)	0.23	0.631	0.23	0.636	0.02	0.892
W × P	0.21	0.650	0.023	0.879	0.02	0.879
Mixture (M)	1.74	0.151	1.10	0.364	5.09	0.001
P × M	0.38	0.824	0.20	0.939	1.10	0.357
W × M	0.18	0.948	0.25	0.906	3.29	0.012
P × W × M	0.30	0.877	1.52	0.207	7.73	<0.001
VWC[z]	0.02	0.900	0.02	0.884	5.34	0.022
P × VWC	0.46	0.933	2.42	0.240	3.14	0.001
W × VWC	0.01	0.472	1.41	0.374	10.8	0.672
M × VWC	0.44	0.764	0.58	0.057	1.15	0.015
P × W ×VWC	0.52	0.579	0.80	0.230	0.18	0.701
M × P × VWC	1.21	0.777	0.57	0.675	0.17	0.332
M × W ×VWC	0.31	0.313	1.47	0.682	0.15	0.952
M × P × W × VWC	0.34	0.853	0.10	0.415	0.74	0.566
Root length density (RLD)	0.48	0.489	0.10	0.759	[y]-	[y]-
M × RLD	0.61	0.660	1.13	0.349	-	-
P × RLD	0.72	0.400	0.13	0.719	-	-
M × P × RLD	1.44	0.230	0.33	0.856	-	-
W × RLD	0.23	0.636	0.34	0.560	-	-
M × W × RLD	0.58	0.675	0.5	0.715	-	-
P × W × RLD	0.27	0.606	0.0	0.847	-	-
M × P × W × RLD	0.39	0.817	1.01	0.411	-	-
VWC × RLD	0.02	0.878	0.61	0.437	-	-
M × VWC × RLD	0.60	0.666	0.61	0.658	-	-
P × VWC × RLD	0.00	0.991	1.68	0.199	-	-
M × P × VWC × RLD	0.34	0.848	0.75	0.564	-	-
W × VWC × RLD	0.57	0.451	0.86	0.358	-	-
M × W × VWC × RLD	0.56	0.692	1.10	0.364	-	-
P × W × VWC × RLD	0.44	0.510	1.11	0.296	-	-
M × P × W × VWC × RLD	0.34	0.850	0.47	0.758	-	-

P-values ≤0.05 are printed in bold.

[z] Soil volumetric water content (VWC).

[y] Insuffiicient *Q. stellat* root recovered for June 2008 campaign to allow running of RLD as a covariate.

Table A-3.3. Probability values (*P*-values) and F-ratios determined using ANOVA for root length density (km m^{-3}), mass density (kg m^{-3}) during May 2006, May 2007, and June 2008 campaigns.

	May 2006 Campaign				May 2007 Campaign				June 2008 Campaign			
	Root length density		Root mass density		Root length density		Root mass density		Root length density		Root mass density	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.17	0.689	0.05	0.830	1.10	0.335	2.43	0.170	4.94	0.064	0.77	0.412
Warming (W)	0.00	0.977	0.00	0.996	2.90	0.092	0.10	0.320	1.10	0.296	0.78	0.379
P × W	0.86	0.355	0.50	0.481	0.08	0.774	1.31	0.255	7.43	**0.007**	9.48	**0.003**
Mixture (M)	29.1	**<0.001**	46.3	**<0.001**	51.8	**<0.001**	88.2	**<0.001**	26.7	**<0.001**	110.6	**<0.001**
M × P	0.29	0.886	0.18	0.948	5.91	**<0.001**	5.07	**<0.001**	2.34	0.059	10.7	**<0.001**
M × W	2.44	**0.049**	2.25	0.066	0.58	0.676	2.25	0.067	1.69	0.156	1.48	0.213
M ×W × P	0.73	0.570	0.88	0.478	1.96	0.105	2.69	**0.034**	5.47	**<0.001**	10.8	**<0.001**

P-values ≤0.05 are printed in bold.
Data was log transformed.

Table A-3.4. Probability values (*P*-values) and F-ratios determined using ANCOVA for soil CO_2 efflux during the May 2006, May 2007, and June 2008 campaigns.

	Plant species mixture									
	S. scoparium		*J. virginiana*		*J. virginiana – S. scoparium*		*Q. stellata*		*Q. stellata – S. scoparium*	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
					May 2006					
Precipitation (P)	1.08	0.339	2.97	0.131	7.66	**0.042**	1.14	0.331	9.44	**0.028**
VWC[z]	0.44	0.515	5.52	**0.029**	3.59	0.070	19.1	**<0.001**	0.62	0.437
P × VWC	0.68	0.417	1.38	0.253	0.04	0.836	2.30	0.143	0.52	0.477
Warming (W)	0.84	0.369	0.72	0.407	0.50	0.487	1.29	0.270	0.12	0.735
W × VWC	1.31	0.266	0.01	0.935	3.33	0.082	1.38	0.253	0.15	0.699
					May 2007					
Precipitation (P)	5.24	0.063	1.15	0.325	23.8	**0.008**	5.17	**0.062**	0.79	0.408
VWC[z]	30.2	**<0.001**	3.43	0.070	9.80	**0.003**	0.26	0.615	13.9	**<0.001**
P × VWC	0.51	0.480	1.14	0.289	0.60	0.444	3.19	0.080	0.57	0.454
Warming (W)	0.62	0.435	1.38	0.245	0.11	0.747	3.22	0.079	2.64	0.110
W × VWC	0.04	0.837	1.19	0.280	0.07	0.786	3.34	0.073	0.03	0.857
					June 2008					
Precipitation (P)	0.70	0.431	0.05	0.823	0.01	0.919	0.59	0.478	0.07	0.807
VWC[z]	0.18	0.675	18.7	**<0.001**	8.94	**0.004**	7.53	**0.008**	0.69	0.408
P × VWC	7.42	**0.009**	12.0	**0.001**	2.26	0.139	1.54	0.219	0.06	0.810
Warming (W)	1.54	0.220	3.70	0.060	0.65	0.425	3.86	0.055	4.34	**0.042**
W × VWC	0.49	0.486	3.44	0.069	0.16	0.690	1.19	0.279	0.29	0.593

P-values ≤ 0.05 are printed in bold.

[z]Soil volumetric water content (VWC).

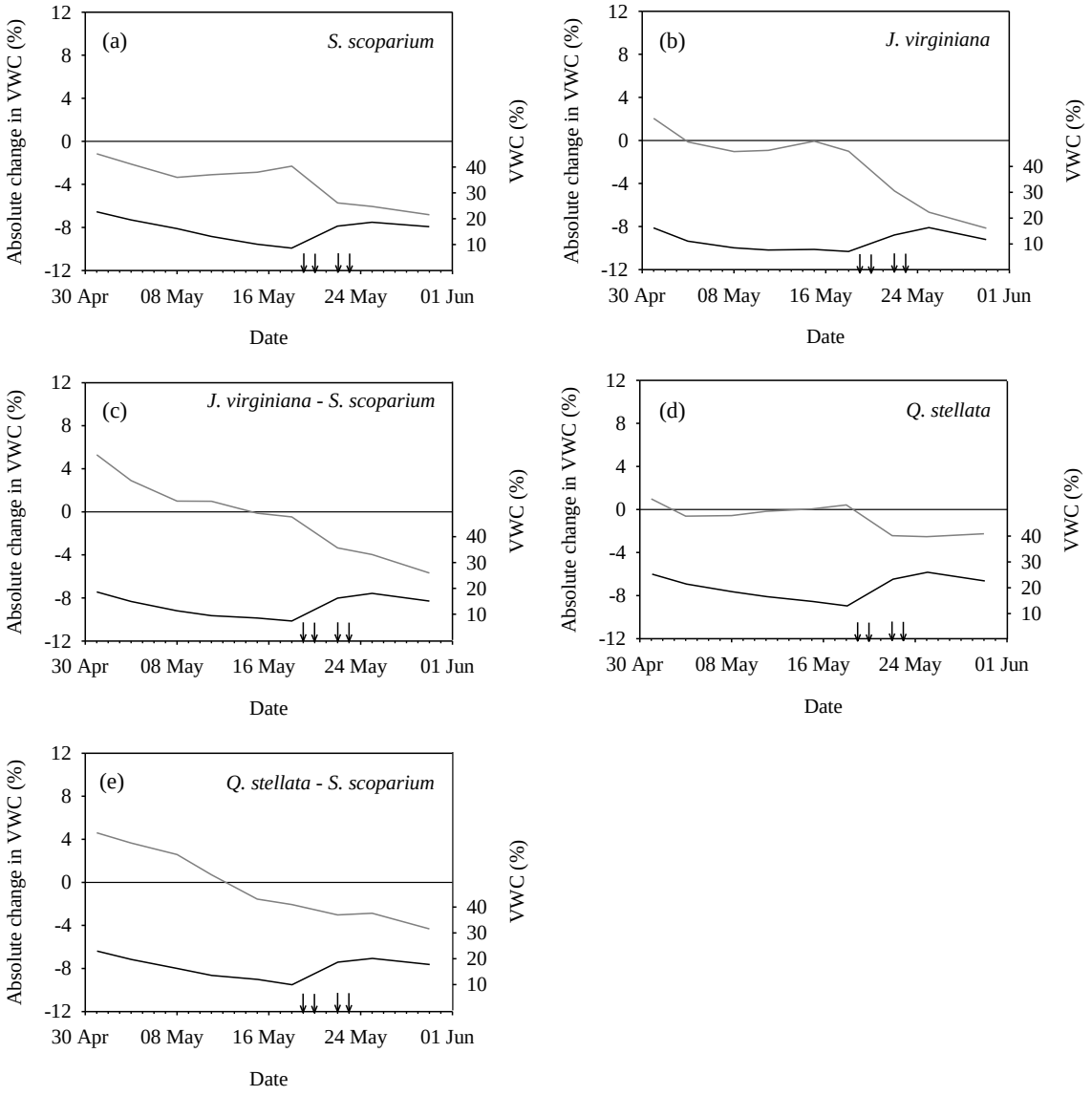

Figure A-3.1. Effect of precipitation on soil volumetric water content (VWC) (%) over time averaged across warming treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2006 campaign. The grey line depicts absolute change in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal soil VWC pattern. Arrows denote precipitation events. Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2006 and 2007 campaigns. Precipitation event size for the control treatment were 9.7 and 29.7, and redistributed treatment were 5.8 and 17.8, on 10 and 11 June, respectively, for the 2008 campaign.

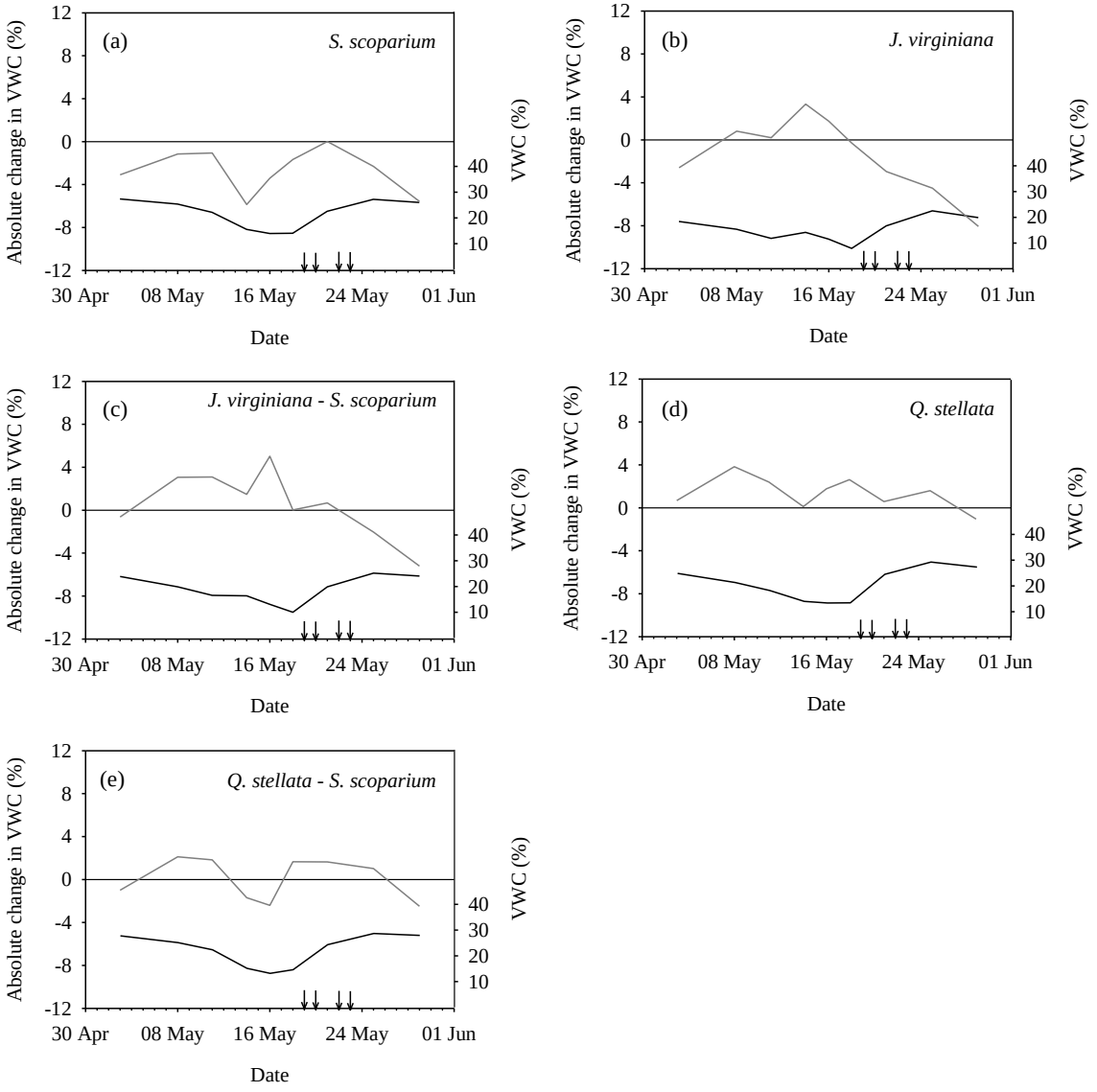

Figure A-3.2. Effect of precipitation on soil volumetric water content (VWC) (%) over time averaged across warming treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2007 campaign. The grey line depicts absolute change in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal soil VWC pattern. Arrows denote precipitation events. Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2006 and 2007 campaigns. Precipitation event size for the control treatment were 9.7 and 29.7, and redistributed treatment were 5.8 and 17.8, on 10 and 11 June, respectively, for the 2008 campaign.

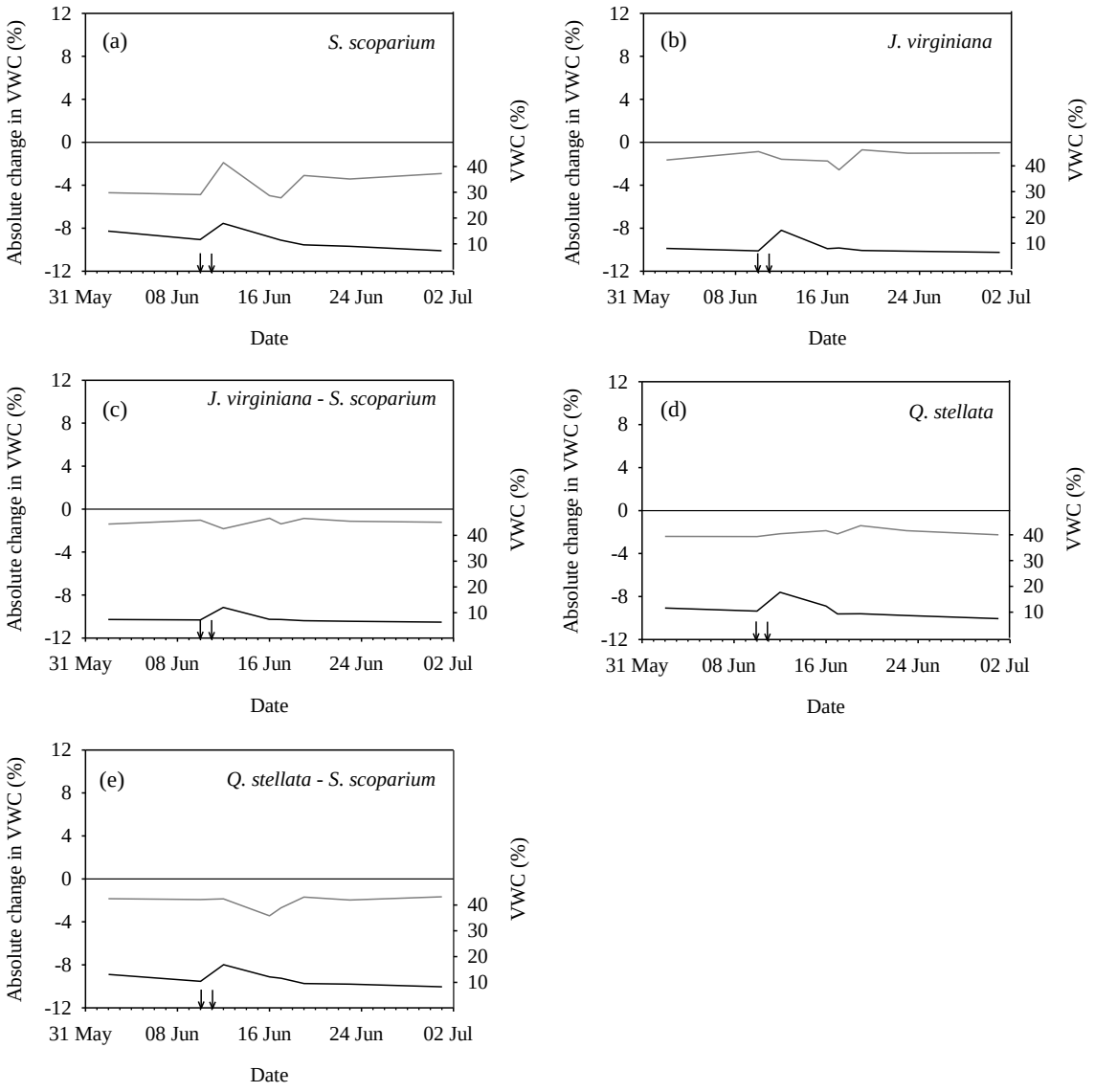

Figure A-3.3. Effect of precipitation on soil volumetric water content (VWC) (%) over time averaged across warming treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the June 2008 campaign. The grey line depicts absolute change in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal soil VWC pattern. Arrows denote precipitation events. Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2006 and 2007 campaigns. Precipitation event size for the control treatment were 9.7 and 29.7, and redistributed treatment were 5.8 and 17.8, on 10 and 11 June, respectively, for the 2008 campaign.

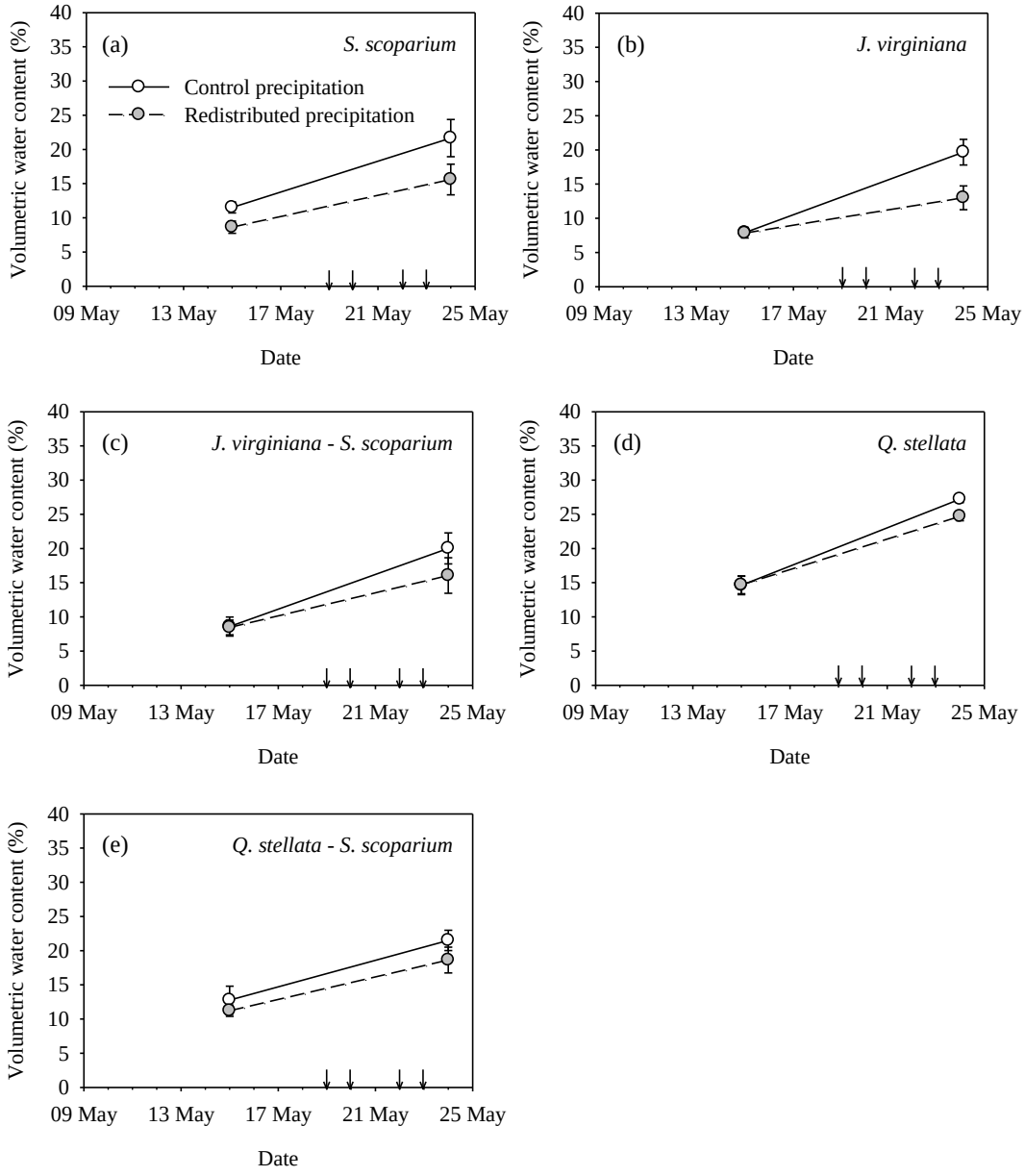

Figure A-3.4. Effect of precipitation treatment on soil volumetric water content (%) averaged across warming treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2006 campaign (means ± SE). Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2006 campaign. Filled symbols depict redistributed precipitation treatment and unfilled symbols depict control precipitation treatment. Arrows denote precipitation events.

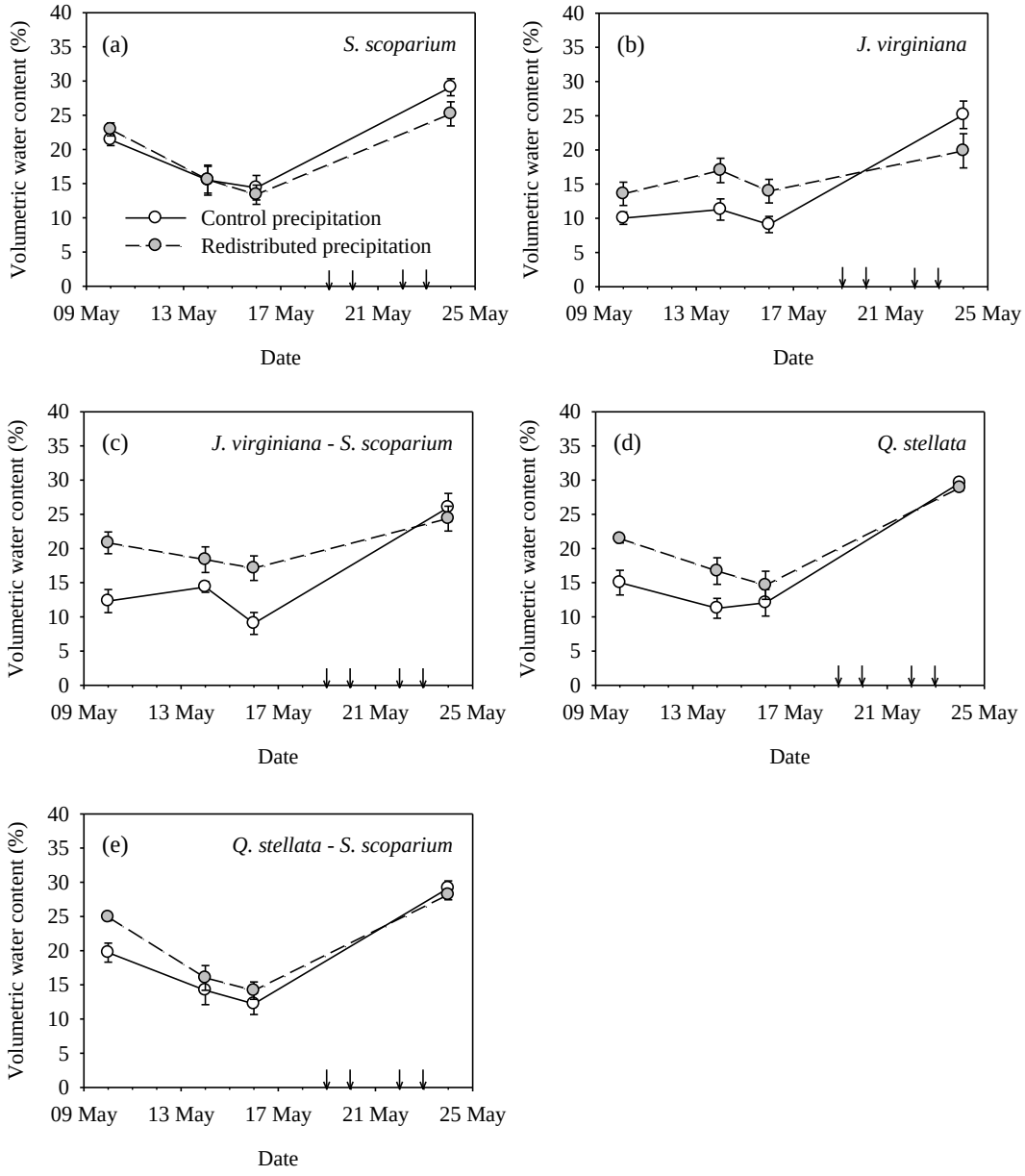

Figure A-3.5. Effect of precipitation treatment on soil volumetric water content (%) averaged across warming treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2007 campaign (means ± SE). Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2007 campaigns. Filled symbols depict redistributed precipitation treatment and unfilled symbols depict control precipitation treatment. Arrows denote precipitation events.

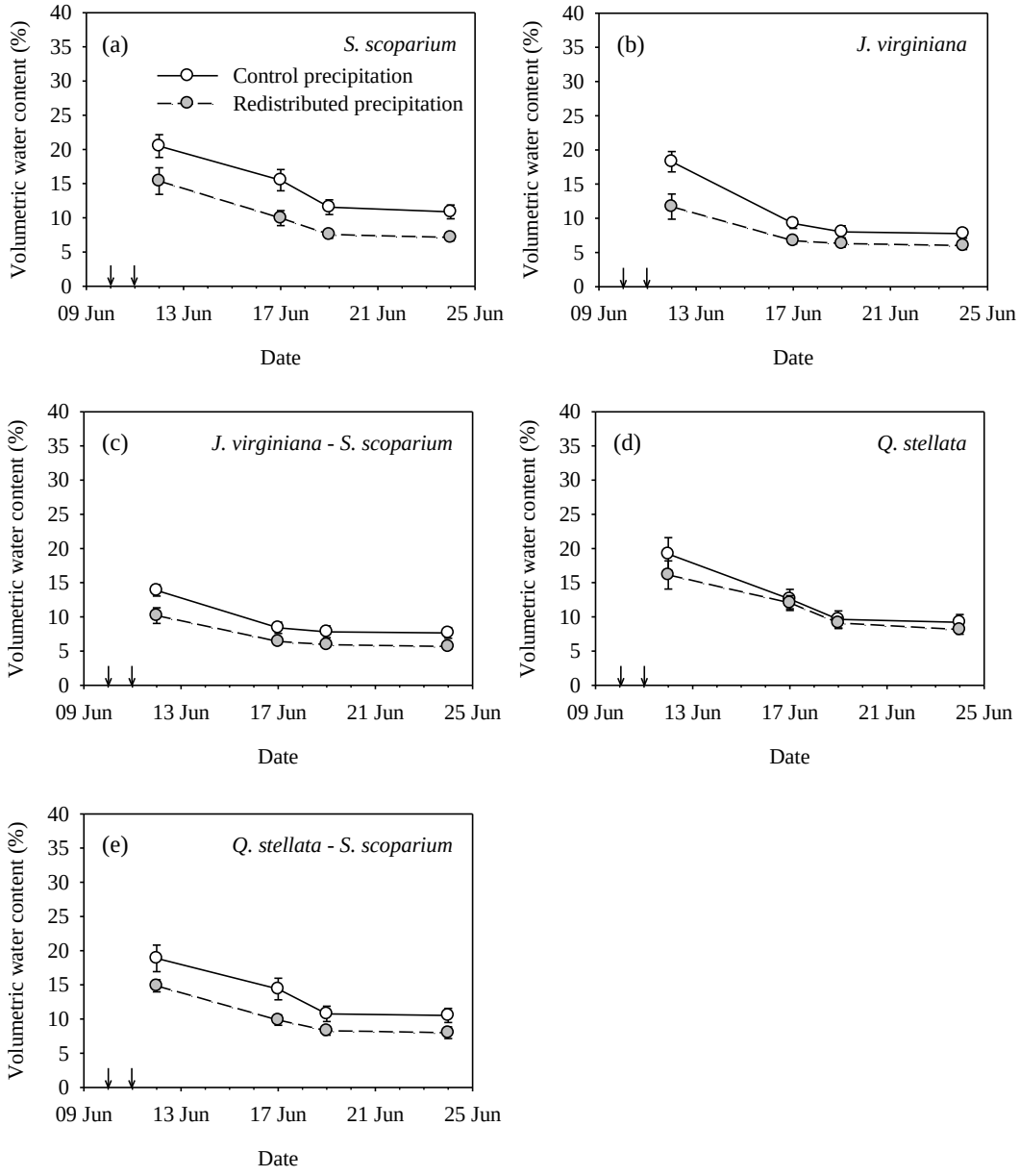

Figure A-3.6. Effect of precipitation treatment on soil volumetric water content (%) averaged across warming treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the June 2008 campaign (means ± SE). Precipitation event size for the control treatment were 9.7 and 29.7, and redistributed treatment were 5.8 and 17.8, on 10 and 11 June, respectively, for the 2008 campaign. Filled symbols depict redistributed precipitation treatment and unfilled symbols depict control precipitation treatment. Arrows denote precipitation events.

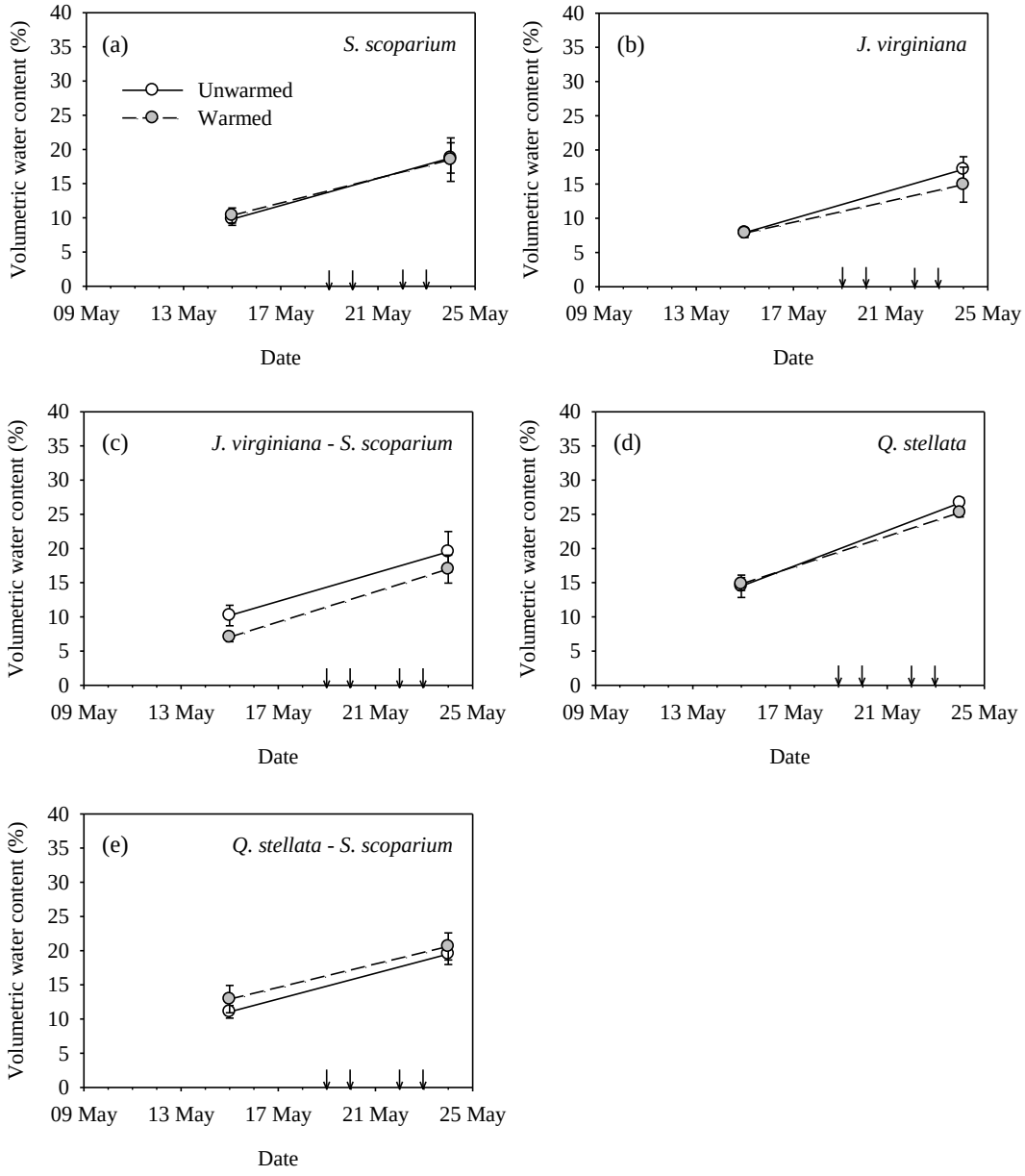

Figure A-3.7. Effect of warming on soil volumetric water content (%) averaged across precipitation treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2006 campaign (means ± SE). Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2006 campaign. Filled symbols depict warmed treatment (IR lamp 100 W m^{-2}) and unfilled symbols depict unwarmed treatment. Arrows denote precipitation events.

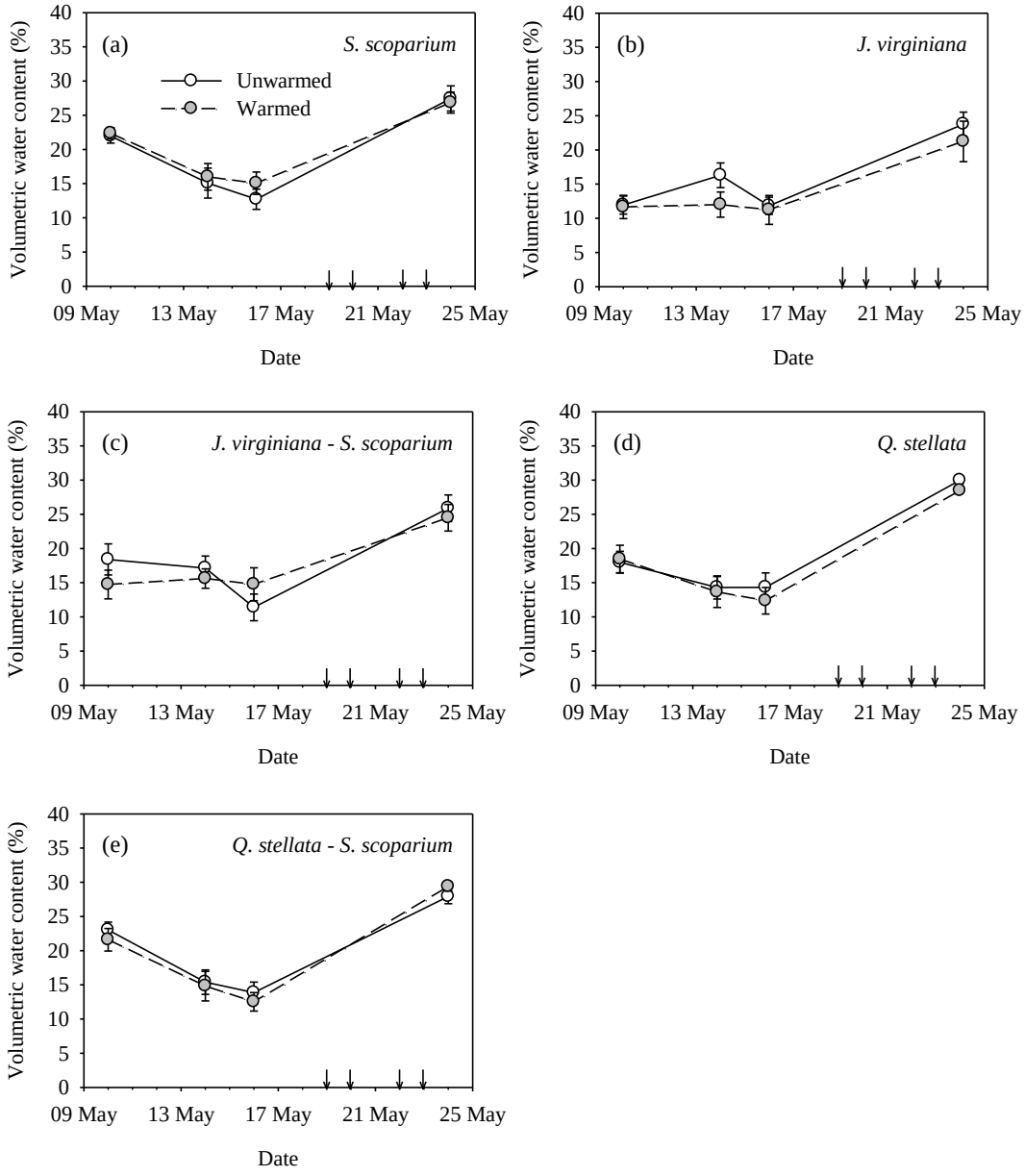

Figure A-3.8. Effect of warming on soil volumetric water content (%) averaged across precipitation treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2007 campaign (means ± SE). Precipitation event size for control treatment were 34.1, 30.9, 29.8, and 20.5 mm, and redistributed treatment were 20.5, 18.5, 17.9, and 12.3 mm on 19, 20, 22, and 23 May, respectively, for the 2007 campaign. Filled symbols depict warmed treatment (IR lamp 100 W m^{-2}) and unfilled symbols depict unwarmed treatment. Arrows denote precipitation events.

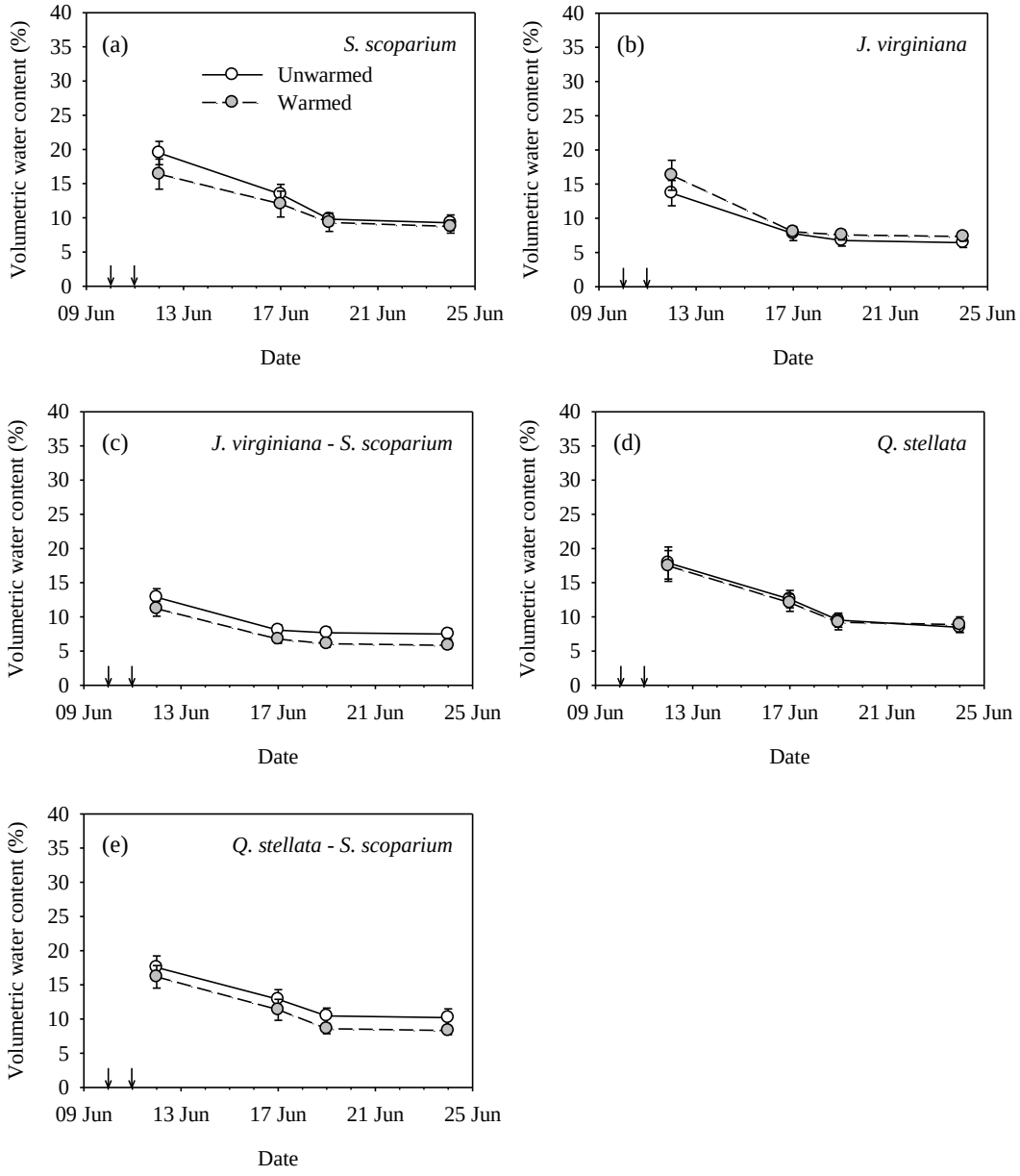

Figure A-3.9. Effect of warming on soil volumetric water content (%) averaged across precipitation treatment for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the June 2008 campaign (means ± SE). Precipitation event size for the control treatment were 9.7 and 29.7, and redistributed treatment were 5.8 and 17.8, on 10 and 11 June, respectively, for the 2008 campaign. Filled symbols depict warmed treatment (IR lamp 100 W m^{-2}) and unfilled symbols depict unwarmed treatment. Arrows denote precipitation events.

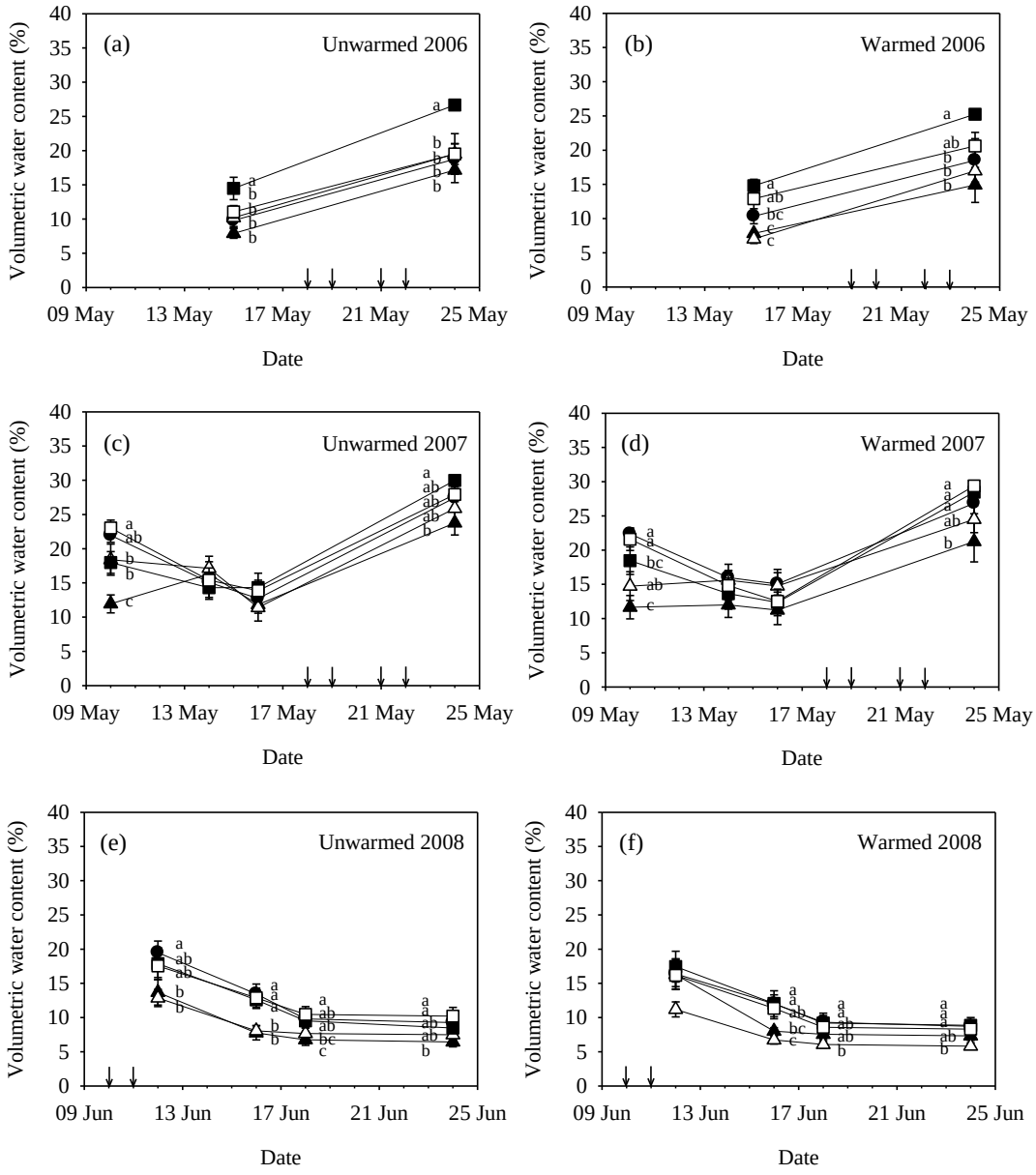

Figure A-3.10. Effect of species mixture on soil volumetric water content (%) averaged across precipitation treatment for (a) unwarmed, (b) warmed during the May 2006 campaign, (c) unwarmed, (d) warmed during the May 2007 campaign, (e) unwarmed, and (f) warmed during the June 2008 campaign (means ± SE). Arrows denote precipitation events. The symbols depict the species as follows: filled circles *Schizachyrium scoparium* monoculture, filled triangles *Juniperus virginiana* monoculture, unfilled triangles *J. virginiana* grown with *S. scoparium*, filled squares *Quercus stellata* monoculture, unfilled squares *Q. stellata* grown with *S. scoparium*. Letters indicate significant ($P \leq 0.05$) differences in response for a species within date measured according to student's t-test.

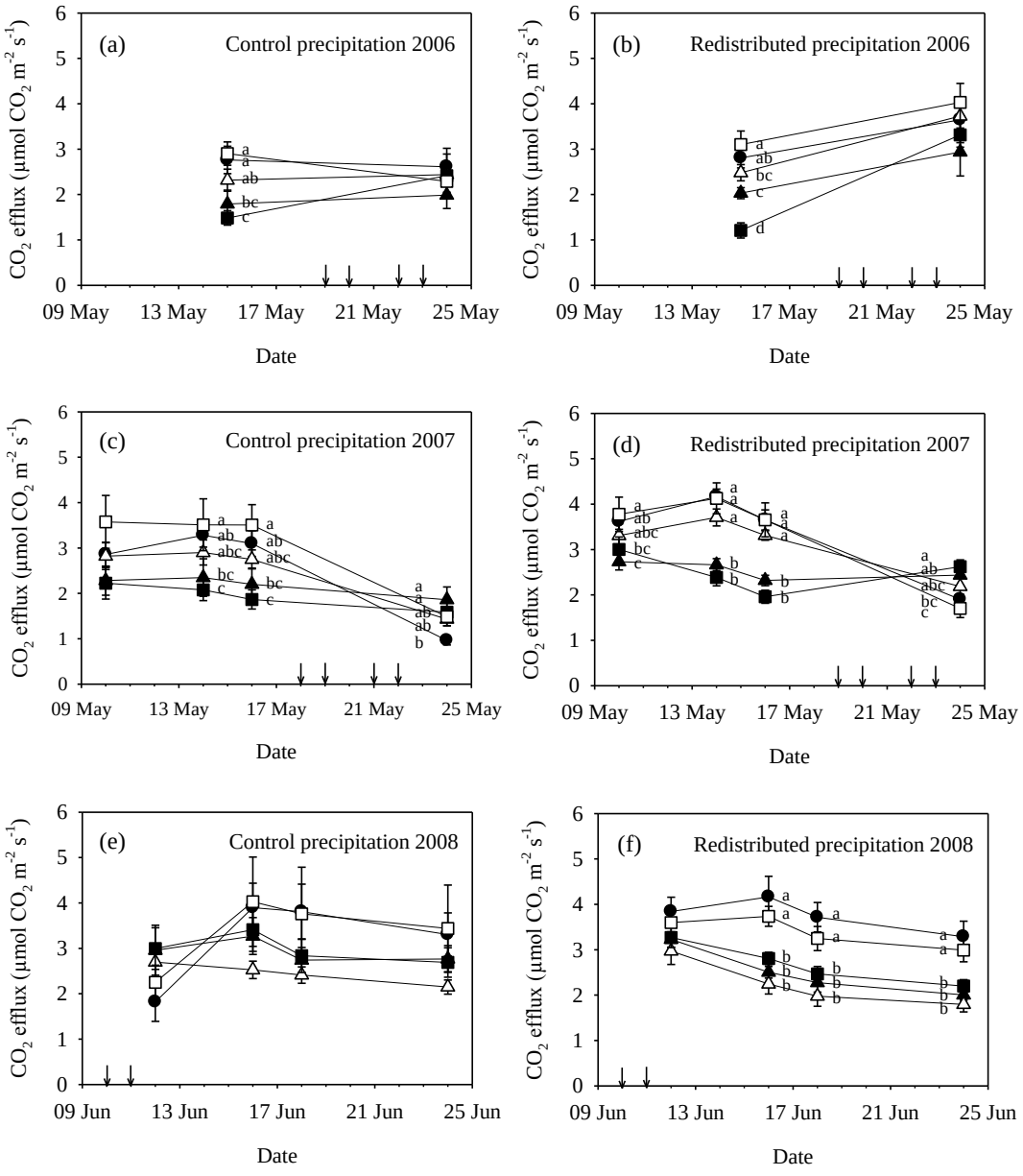

Figure A-3.11. Effect of species mixture on soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) averaged across warming treatment for (a) control precipitation, (b) redistributed precipitation during the May 2006 campaign, (c) control precipitation, (d) redistributed precipitation during the May 2007 campaign, (e) control precipitation, and (f) redistributed precipitation during the June 2008 campaign (means ± SE). Arrows denote precipitation events. The symbols depict the species as follows: filled circles *Schizachyrium scoparium* monoculture, filled triangles *Juniperus virginiana* monoculture, unfilled triangles *J. virginiana* grown with *S. scoparium*, filled squares *Quercus stellata* monoculture, unfilled squares *Q. stellata* grown with *S. scoparium*. Letters indicate significant ($P \leq 0.05$) differences in response for a species within date measured according to student's t-test.

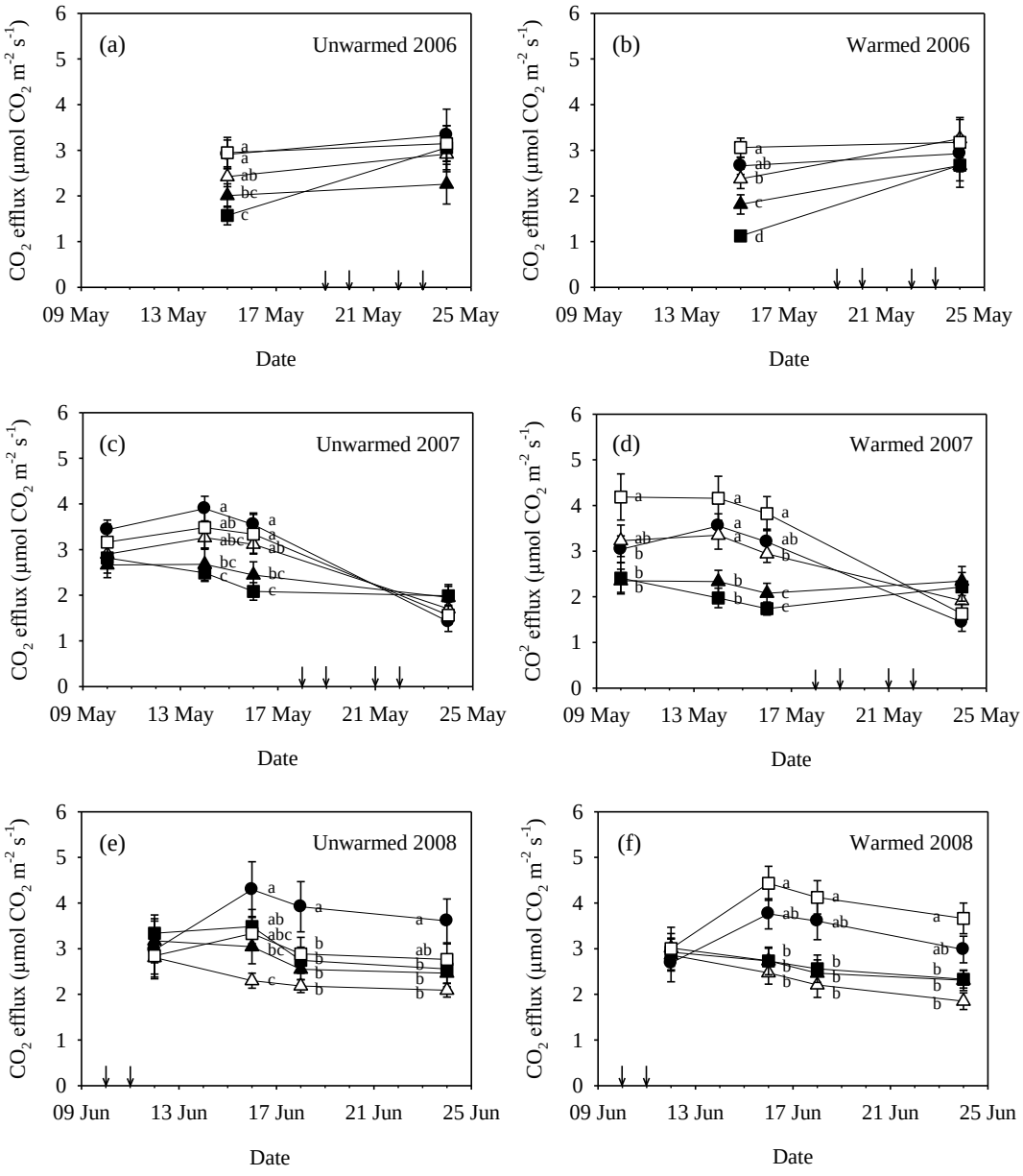

Figure A-3.12. Effect of species mixture on soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) averaged across precipitation treatment for (a) unwarmed, (b) warmed during the May 2006 campaign, (c) unwarmed, (d) warmed during the May 2007 campaign, (e) unwarmed, and (f) warmed during the June 2008 campaign. Arrows denote precipitation events (means ± SE). The symbols depict the species as follows: filled circles *Schizachyrium scoparium* monoculture, filled triangle *Juniperus virginiana* monoculture, unfilled triangles *J. virginiana* grown with *S. scoparium*, filled square *Quercus stellata* monoculture, unfilled squares *Q. stellata* grown with *S. scoparium*. Letters indicate significant ($P \leq 0.05$) differences in response for a species within date measured according to student's t-test.

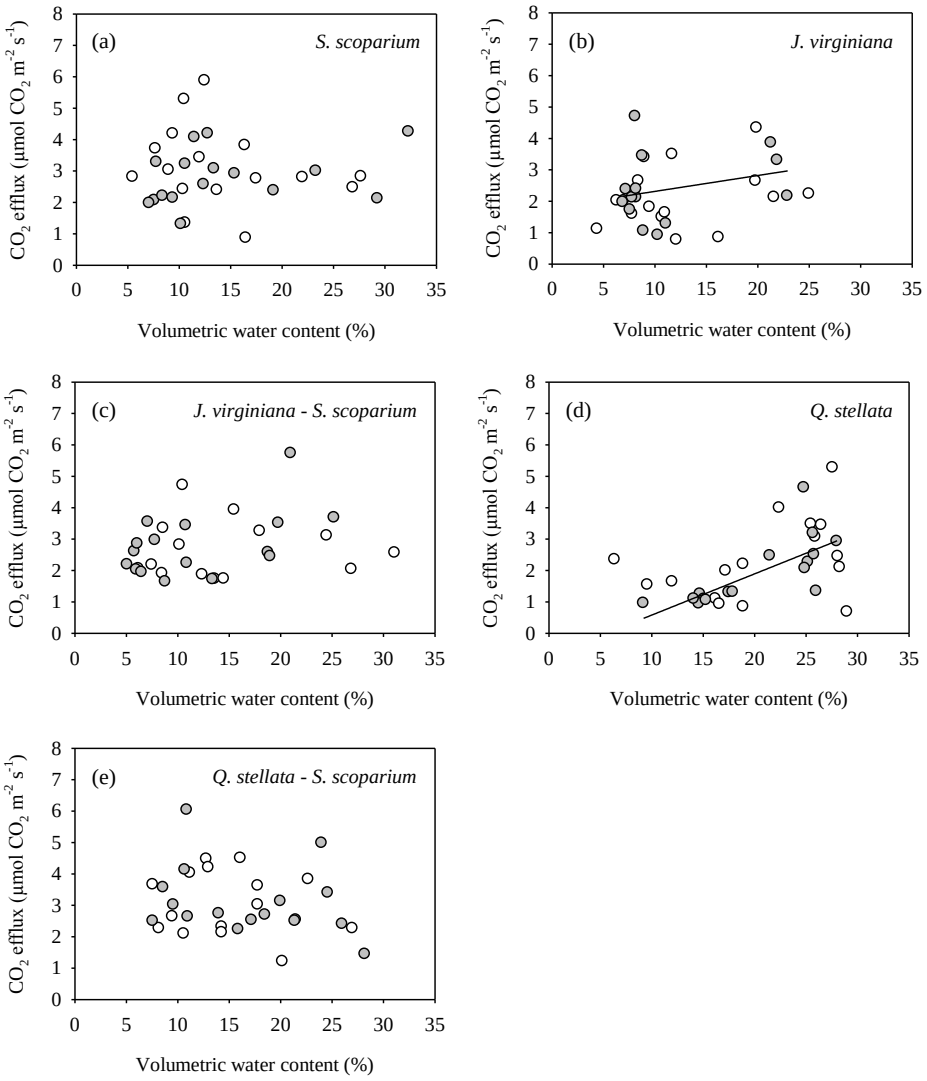

Figure A-3.13. Effect of volumetric water content (%) on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* in a monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2006 campaign. Filled symbols depict warmed treatment (IR lamp 100 W m^{-2}) and unfilled symbols depict unwarmed treatment. For the following significant regression relationships are depicted across warming treatments; (b) *J. virginiana* CO_2 efflux = 1.8086 + 0.0506*VWC, r^2 = 0.0749, and (d) *Q. stellata* CO_2 efflux = -0.7320 + 0.1313*VWC, r^2 = 0.5357.

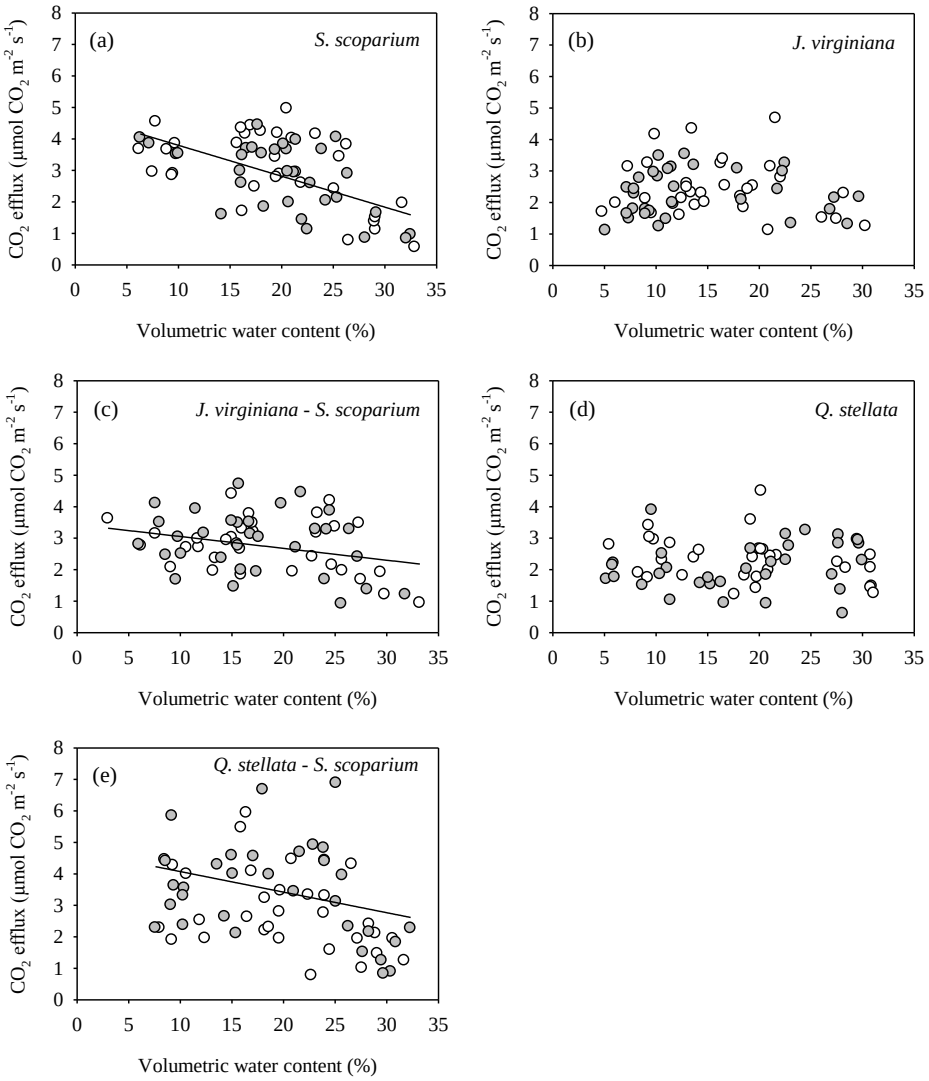

Figure A-3.14. Effect of volumetric water content (%) on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the May 2007 campaign (means). Filled symbols depict warmed treatment (IR lamp 100 W m^{-2}) and unfilled symbols depict unwarmed treatment. For the following significant regression relationships are depicted across warming treatments; (a) *S. scoparium* CO_2 efflux = 4.7795 – 0.0982*VWC, r^2 = 0.3369, (c) *J. virginiana – S. scoparium* CO_2 efflux = 3.4292 – 0.0377*VWC, r^2 = 0.1152, and (e) *Q. stellata – S. scoparium* CO_2 efflux = 4.7262 – 0.0653*VWC, r^2 = 0.1113.

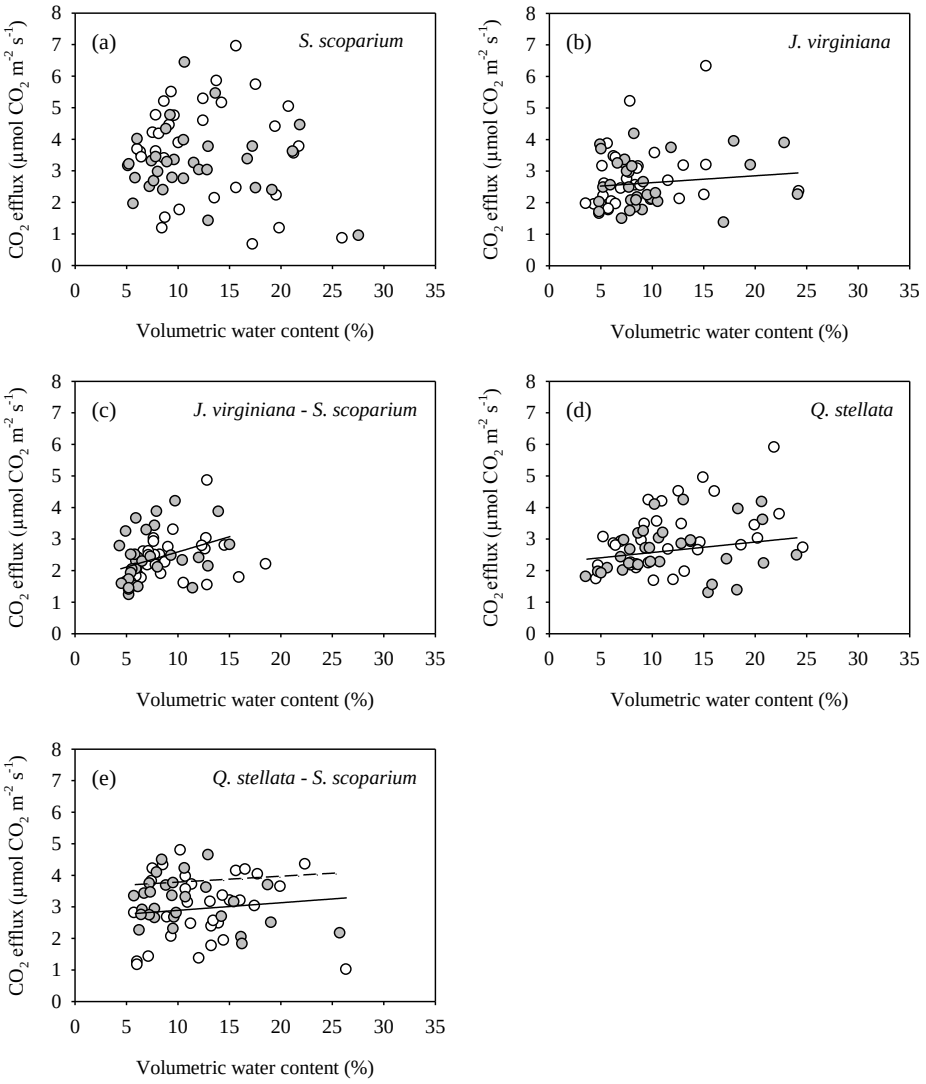

Figure A-3.15. Effect of volumetric water content (%) and soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* monoculture, and (e) *Q. stellata* grown with *S. scoparium* during the June 2008 campaign (means). Filled symbols depict warmed treatment (IR lamp 100 W m^{-2}) and unfilled symbols depict unwarmed treatment. For (e) *Q. stellata* grown with *S. scoparium* the following statistically significant regression relationships are depicted for unwarmed treatment (solid line) and warmed treatment (dashed line); unwarmed CO_2 efflux = 2.6484 + 0.0241*VWC, r^2 = 0.0117; warmed CO_2 efflux = 3.596 + 0.0188*VWC, r^2 =0.0015. For the following statistically significant regression relationships are depicted across warming treatments (b) *J. virginiana* CO_2 efflux = 2.4169 + 0.0217*VWC, r^2 = 0.0187, (c) *J. virginiana* – *S. scoparium* CO_2 efflux = 1.6312 + 0.0960*VWC, r^2 = 0.1183, and (d) *Q. stellata* CO_2 efflux = 2.2409 + 0.0332*VWC, r^2 = 0.0514.

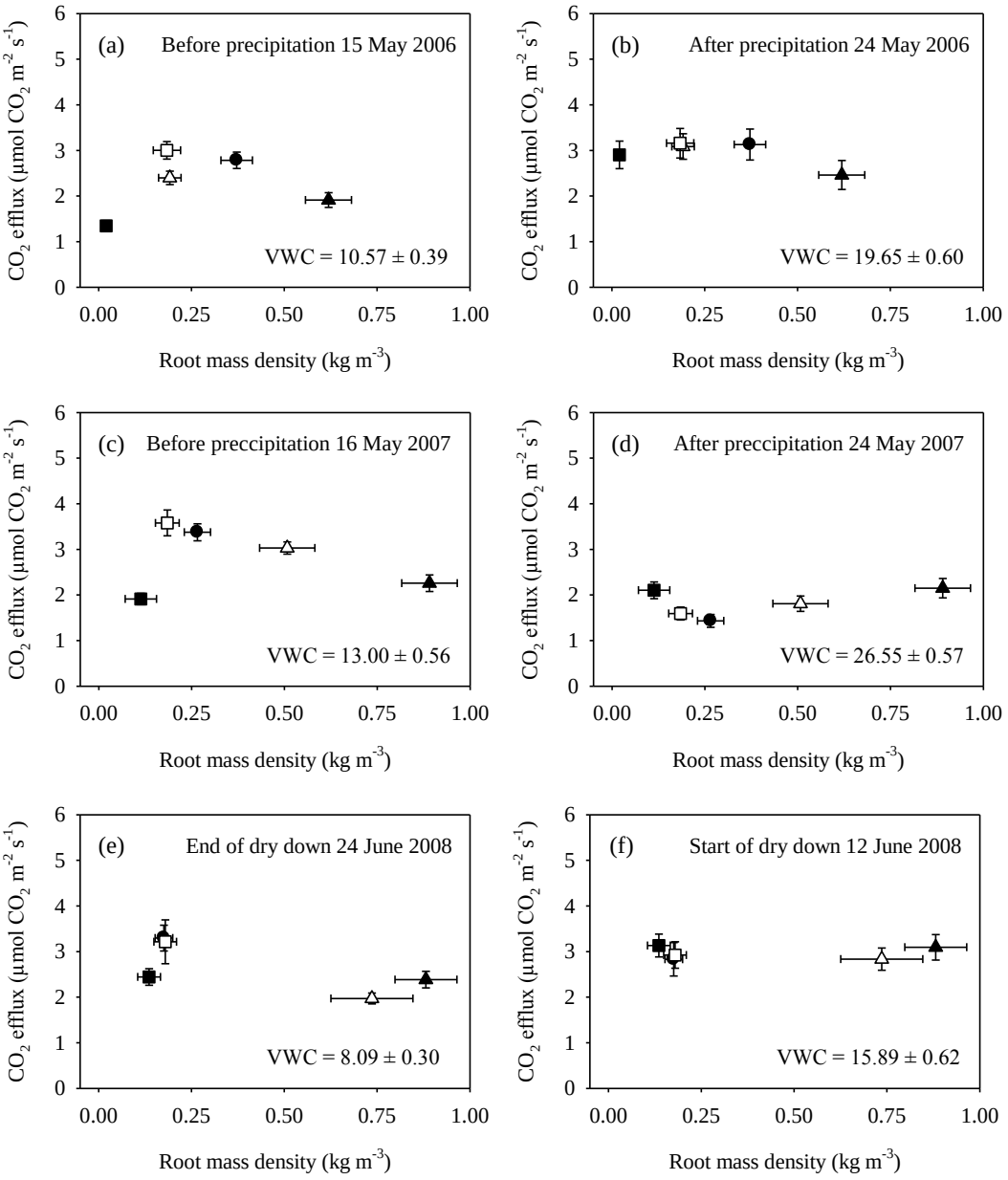

Figure A-3.16. Effect of root mass density (kg m^{-3}) on soil CO_2 efflux (µmol CO_2 $m^{-2}s^{-1}$) averaged across averaged, warming, and precipitation treatments for (a) before precipitation event 15 May 2006, (b) after precipitation event 24 May 2006, (c) before precipitation event 16 May 2007, (d) after precipitation event 24 May 2007, (e) end of dry down 24 June 2008, and (f) start of dry down 12 June 2008 (means ± bi-directional SE). The symbols depict the species as follows: filled circles *Schizachyrium scoparium* in a monoculture, filled triangle *Juniperus virginiana* in a monoculture, unfilled triangles *J. virginiana* grown with *S. scoparium*, filled square *Quercus stellata* in a monoculture, unfilled squares *Q. stellata* grown with *S. scoparium*.

Table A-4.1. Probability values (*P*-values) and F-ratios determined using ANCOVA for CO_2 efflux component contribution by plant species mixture from July 2008 – April 2010.

	Schizachyrium scoparium						*Juniperus virginiana*						*J. virginiana – S. scoparium*					
	Root		Fungal		Bacterial		Root		Fungal		Bacterial		Root		Fungal		Bacterial	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	7.46	**0.046**	0.00	0.973	0.87	0.394	010	0.774	0.96	0.367	2.75	0.210	1.77	0.248	0.24	0.646	0.02	0.894
VWC[z]	0.10	0.753	0.02	0.884	0.14	0.711	5.67	0.062	0.77	0.383	0.12	0.733	1.34	0.251	5.06	**0.027**	1.35	0.248
P × VWC	0.14	0.711	0.12	0.734	0.601	0.442	0.16	0.703	0.37	0.544	0.03	0.874	1.26	0.264	0.70	0.406	4.98	**0.028**
Temperature (T)[y]	0.44	0.510	0.08	0.782	2.29	0.134	4.09	0.056	2.08	0.152	2.96	0.091	4.05	0.047	2.51	0.117	0.00	0.943
P × T	0.55	0.461	0.09	0.769	0.10	0.749	2.36	0.140	0.00	0.944	0.00	0.948	2.22	0.140	4.98	**0.028**	2.80	0.098

P-values ≤ 0.05 are printed in bold.

[z] Soil volumetric water content.

[y] Soil temperature collected with collar.

Table A-4.2. Probability values (*P*-values) and F-ratios determined using ANOVA for CO_2 efflux component contribution by plant species mixture for 14 May and 17 May 2009 24 hour campaigns.

	Schizachyrium scoparium						*Juniperus virginiana*						*J. virginiana – S. scoparium*					
	Root		Fungal		Bacterial		Root		Fungal		Bacterial		Root		Fungal		Bacterial	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	1.31	0.381	0.84	0.476	1.64	0.352	0.53	0.548	0.71	0.492	6.23	0.135	0.52	0.516	0.02	0.880	1.82	0.314
Date (D)	1.60	**0.006**	5.52	**<0.001**	42.5	**<0.001**	0.21	0.238	8.02	**<0.001**	0.72	0.470	3.67	**0.022**	4.90	**0.003**	3.42	0.470
P × D	3.14	**<0.001**	14.8	**<0.001**	2.16	**<0.018**	5.24	**<0.001**	12.8	**<0.001**	0.23	0.898	0.72	0.435	20.4	**<0.001**	88.7	**<0.001**

P-values ≤ 0.05 are printed in bold.
Data was log transformed.

Table A-4.3. Probability values (*P*-values) and F-ratios determined using ANOVA for microbial dissolved organic carbon (DOC) (μg g^{-1} dry soil) by plant species mixture for 25 April 2010.

	Schizachyrium scoparium		*Juniperus virginiana*		*J. virginiana – S. scoparium*	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.43	0.539	0.00	0.976	2.38	0.184
Collar (C)	0.15	0.864	2.09	0.175	2.64	0.120
P × C	1.14	0.359	5.35	**0.026**	1.72	0.228

P-values ≤ 0.05 are printed in bold.

Table A-4.4. Probability values (*P*-values) and F-ratios determined using ANOVA for CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) by species mixture for 25 April 2010.

	Schizachyrium scoparium		*Juniperus virginiana*		*J. virginiana – S. scoparium*	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
Precipitation (P)	0.30	0.605	2.65	0.165	0.39	0.561
Collar (C)	0.68	0.529	9.19	0.005	3.14	0.088
P × C	0.59	0.574	0.08	0.920	0.65	0.544

P-values ≤ 0.05 are printed in bold.

Table A-4.5. Probability values (*P*-values) and F-ratios determined using ANOVA for root mass (kg m^{-3}) by species mixture for 25 April 2010.

	Schizachyrium scoparium		*Juniperus virginiana*		*J. virginiana – S. scoparium*	
Treatment	F-ratio	*P*-value	F-ratio	*P*-value	F-ratio	*P*-value
			Fine root mass			
Precipitation (P)	1.04	0.347	5.35	0.060	0.38	0.561
Collar (C)	9.91	**0.003**	10.5	**0.002**	9.43	**0.004**
P × C	0.76	0.491	0.36	0.703	1.97	0.183
			Coarse root mass			
Precipitation (P)	0.76	0.417	0.49	0.512	0.31	0.601
Collar (C)	2.76	0.103	2.16	0.159	9.92	**0.003**
P × C	0.10	0.909	2.45	0.131	0.09	0.914
			Total root mass			
Precipitation (P)	0.05	0.824	1.28	0.301	0.12	0.744
Collar (C)	6.40	**0.013**	2.63	0.113	14.4	**0.001**
P × C	0.13	0.881	1.86	0.197	1.33	0.301

P-values ≤ 0.05 are printed in bold.

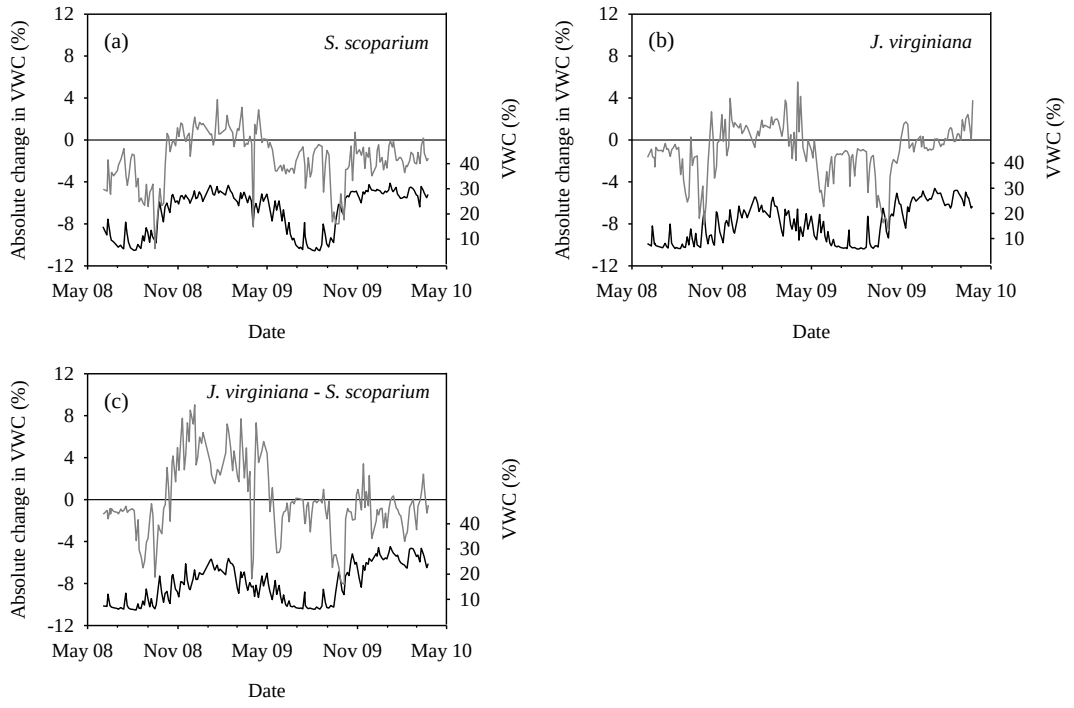

Figure A-4.1. Effect of precipitation treatment on soil volumetric water content (VWC) over time for (a) *Schizachyrium scoparium* in monoculture, (b) *Juniperus virginiana* grown in monoculture, and (c) *J. virginiana* grown with *S. scoparium*. The grey line depicts absolute changes in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal VWC pattern.

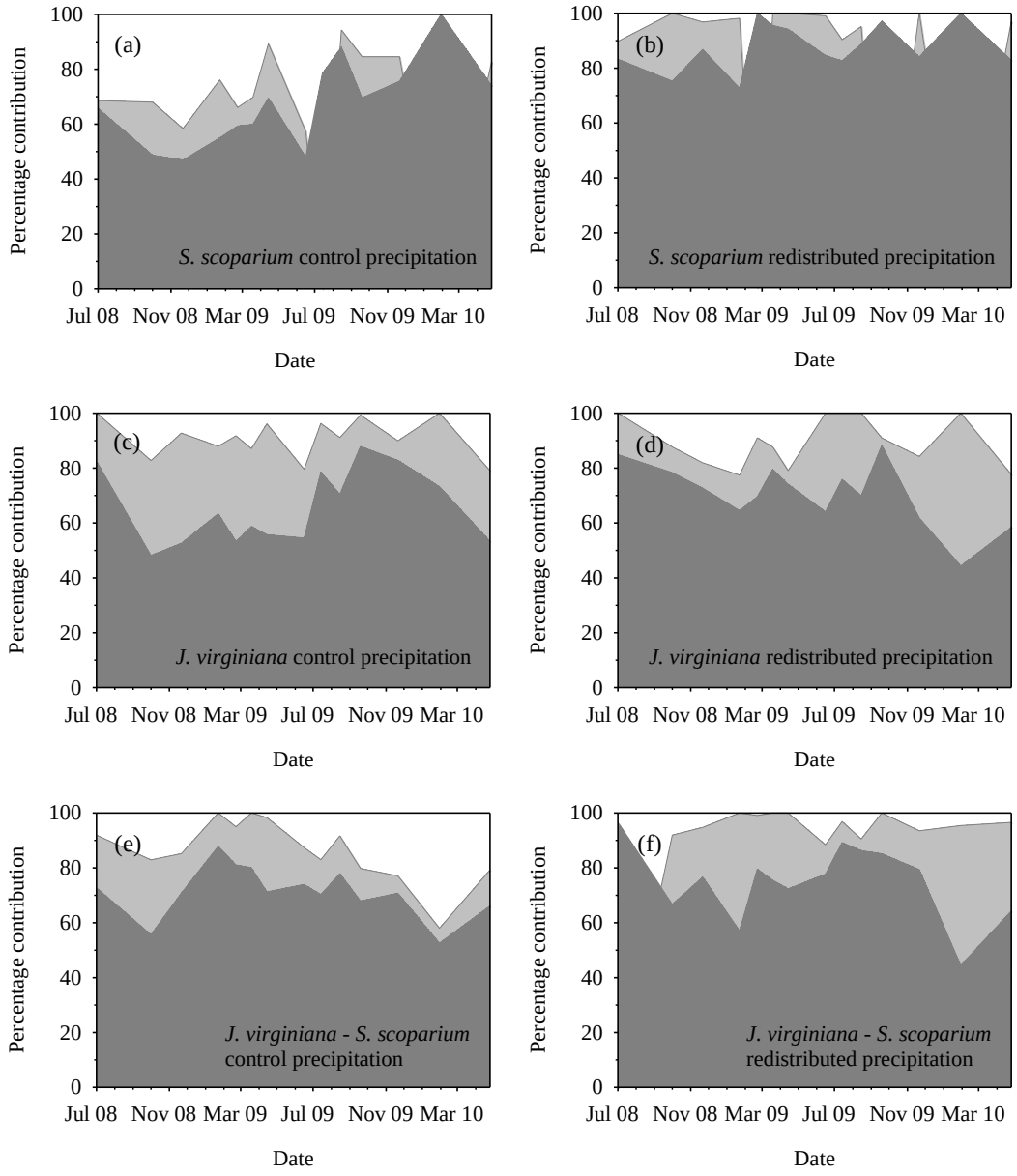

Figure A-4.2. Relationship among date and percentage contribution of root respiration (white fill), hyphal respiration (light grey fill), and bacterial respiration (dark grey fill) for (a) *Schizachyrium scoparium* in a monoculture with control precipitation, (b) *S. scoparium* in a monoculture with redistributed precipation, (c) *Juniperus virginiana* in a monoculture with control precipitation, (d) *J. virginiana* in a monoculture with redistributed precipitation, (e) *J. virginiana* grown with *S. scoparium* with control precipitation, and (f) *J. virginiana* grown with *S. scoparium* with redistributed precipitation (means). (July 2008 – April 2010).

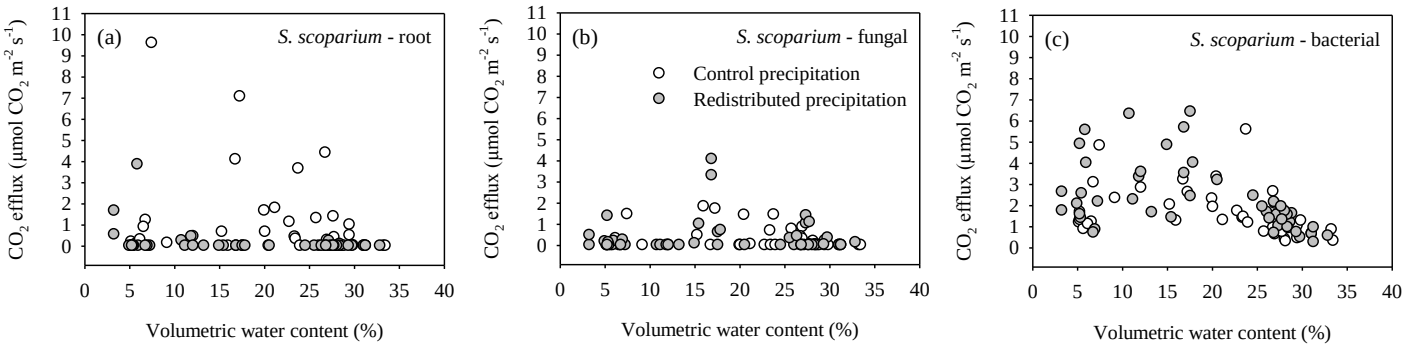

Figure A-4.3. Relationship between soil volumetric water content (%) and soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Schizachyrium scoparium* in a monoculture, (b) fungal respiration of *S. scoparium* in a monoculture, (c) bacterial respiration of *S. scoparium* in a monoculture (means). Unfilled circles represent control precipitation and filled circles redistributed precipitation. (July 08 – April 10).

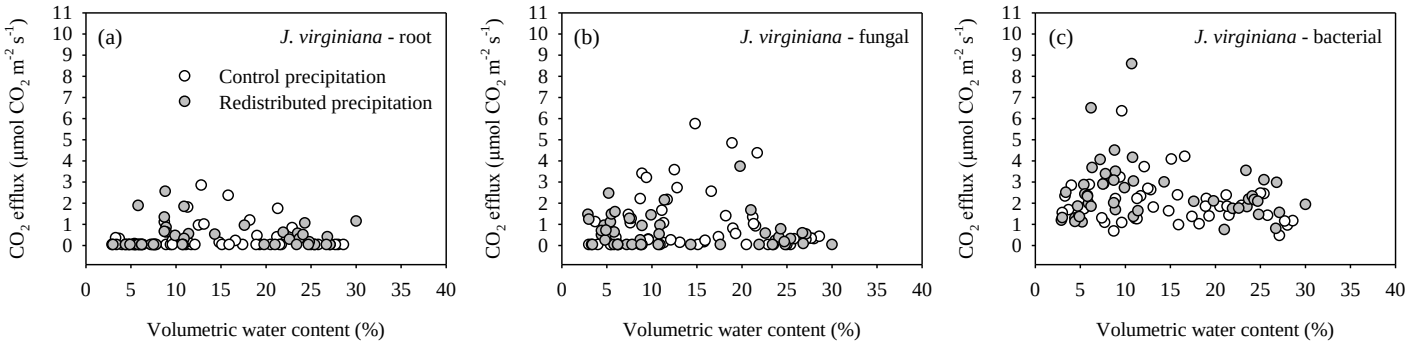

Figure A-4.4. Relationship between soil volumetric water content (%) and soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) (a) root respiration of *Juniperus virginiana* in a monoculture, (b) fungal respiration of *J. virginiana* in a monoculture, (c) bacterial respiration of *J. virginiana* in a monoculture (means). Unfilled circles represent control precipitation and filled circles redistributed precipitation. (July 08 – April 10).

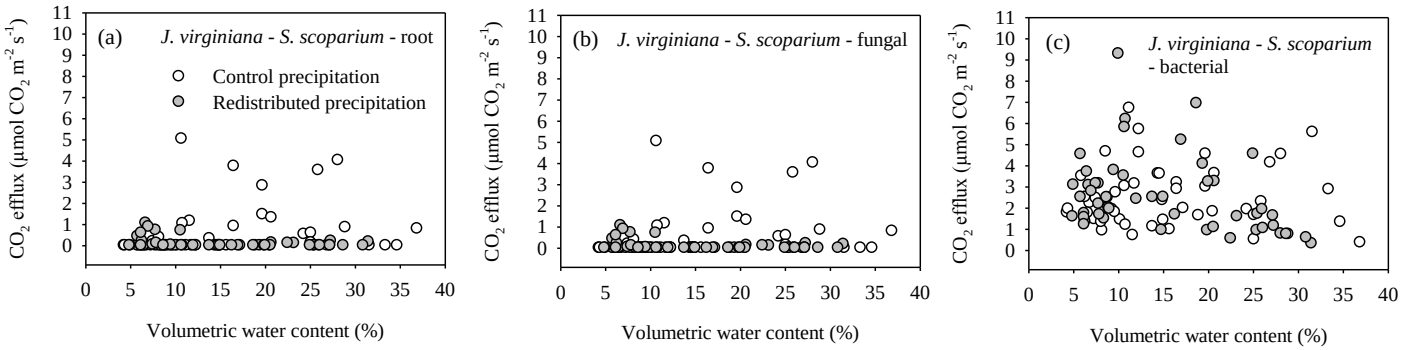

Figure A-4.5. Relationship between soil volumetric water content (%) and soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *J. virginiana* grown with *S. scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means). Unfilled circles represent control precipitation and filled circles redistributed precipitation. (July 08 – April 10).

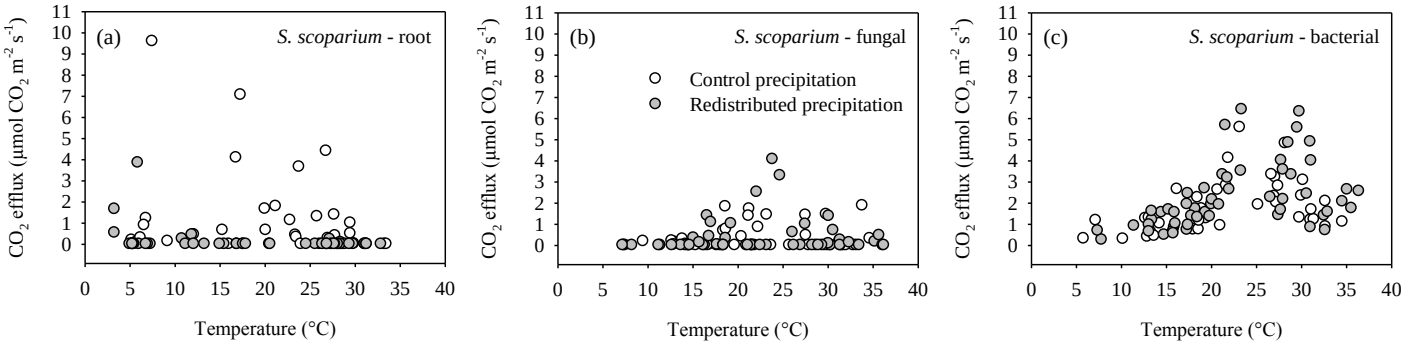

Figure A-4.6. Relationship between soil temperature (°C) and soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Schizachyrium scoparium* in a monoculture, (b) fungal respiration of *S. scoparium* in a monoculture, (c) bacterial respiration of *S. scoparium* in a monoculture (means). Unfilled circles represent control precipitation and filled circles redistributed precipitation. (July 08 – April 10).

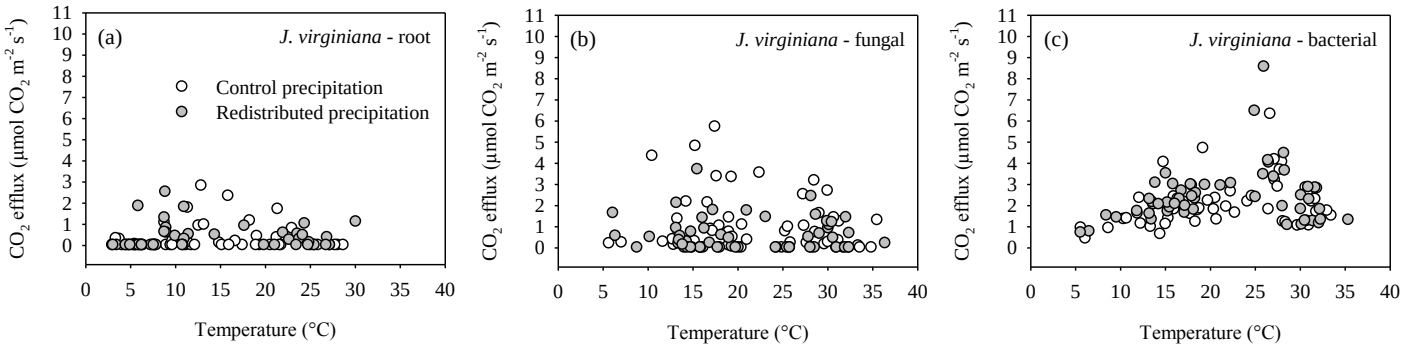

Figure A-4.7. Relationship between soil temperature (°C) and soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *Juniperus virginiana* in a monoculture, (b) fungal respiration of *J. virginiana* in a monoculture, (c) bacterial respiration of *J. virginiana* in a monoculture (means). Unfilled circles represent control precipitation and filled circles redistributed precipitation. (July 08 – April 10).

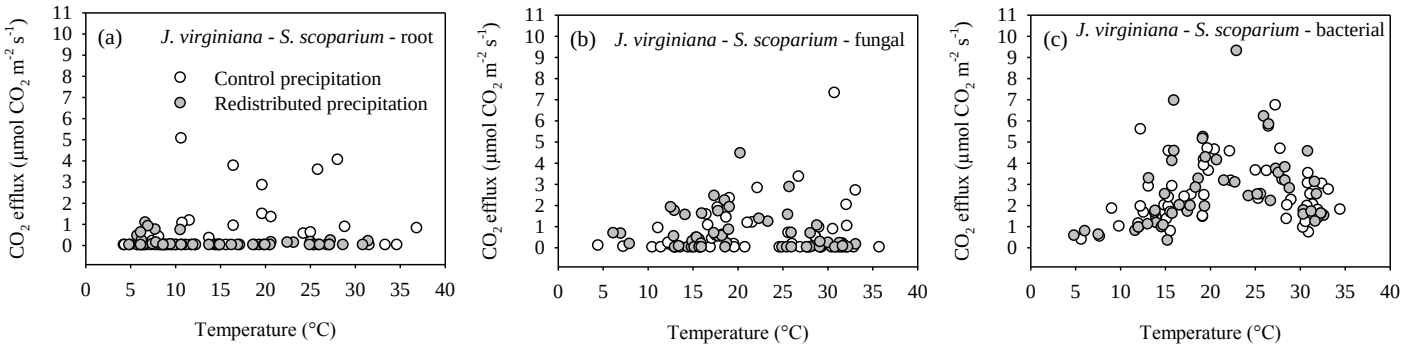

Figure A-4.8. Relationship between soil temperature (°C) and soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) root respiration of *J. virginiana* grown with *S. scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means). Unfilled circles represent control precipitation and filled circles redistributed precipitation. (July 08 – April 10).

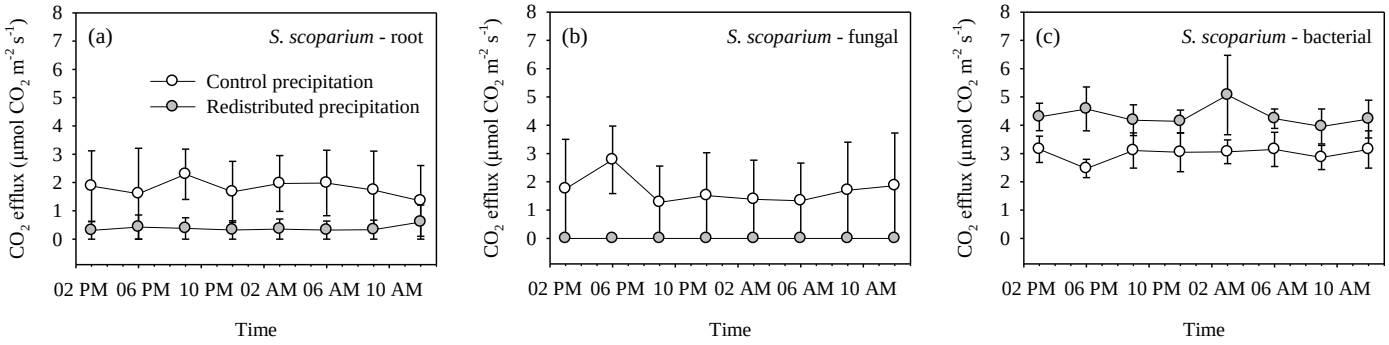

Figure A-4.9. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time during the 24 hour campaign on the 14 – 15 May 2009, for (a) root respiration of *Schizachyrium scoparium* in a monoculture, (b) fungal respiration of *S. scoparium* in a monoculture, (c) bacterial respiration of *S. scoparium* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

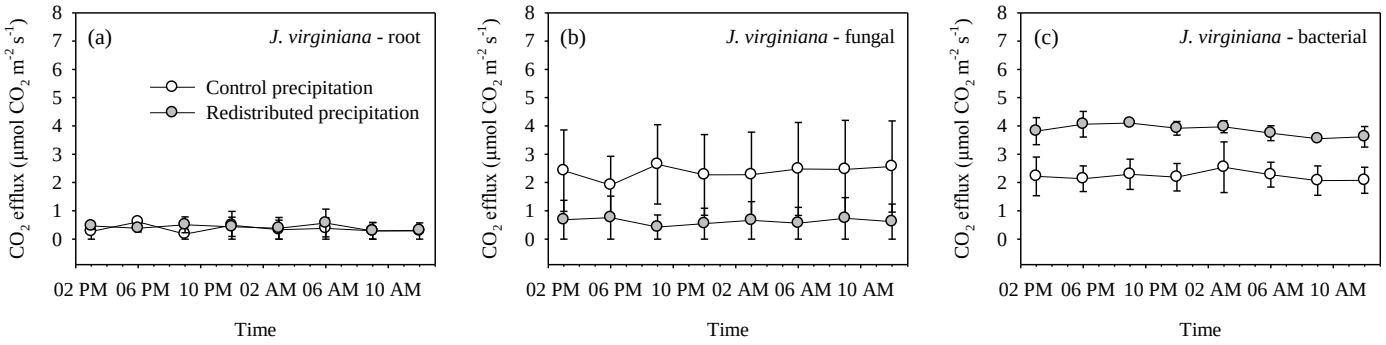

Figure A-4.10. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time during the 24 hour campaign on the 14 – 15 May 2009, for (a) root respiration of *Juniperus virginiana* in a monoculture, (b) fungal respiration of *J. virginiana* in a monoculture, (c) bacterial respiration of *J. virginiana* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

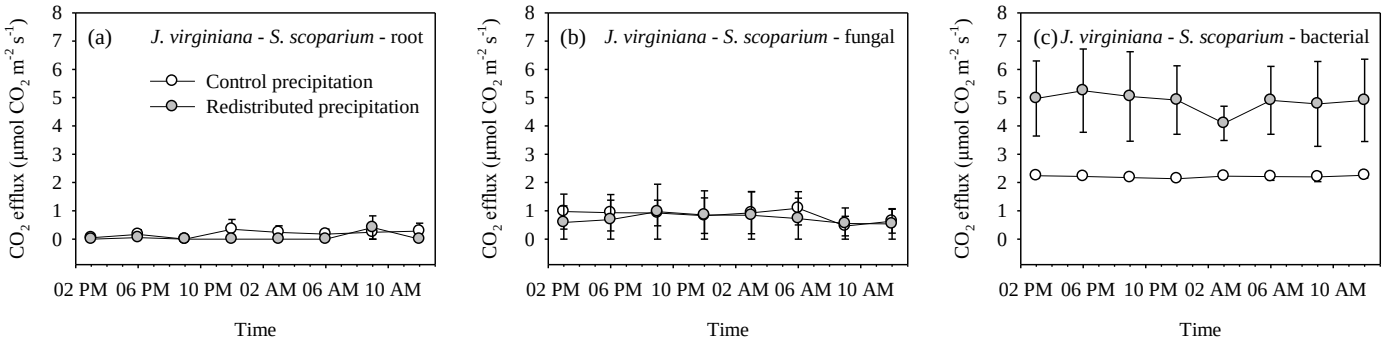

Figure A-4.11. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time during the 14 – 15 May 2009, for (a) root respiration of *J. virginiana* grown with *S. scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

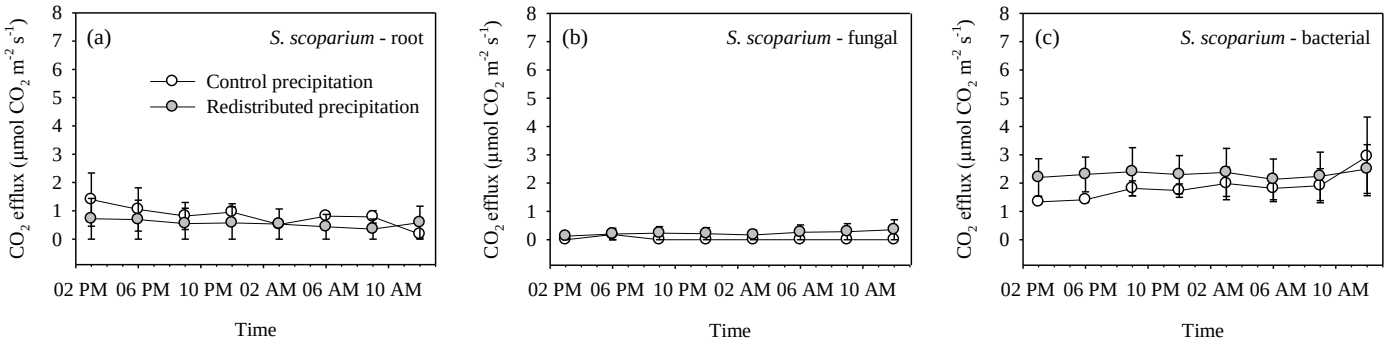

Figure A-4.12. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time during the 17 – 18 May 2009, for (a) root respiration of *Schizachyrium scoparium* in a monoculture, (b) fungal respiration of *S. scoparium* in a monoculture, (c) bacterial respiration of *S. scoparium* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

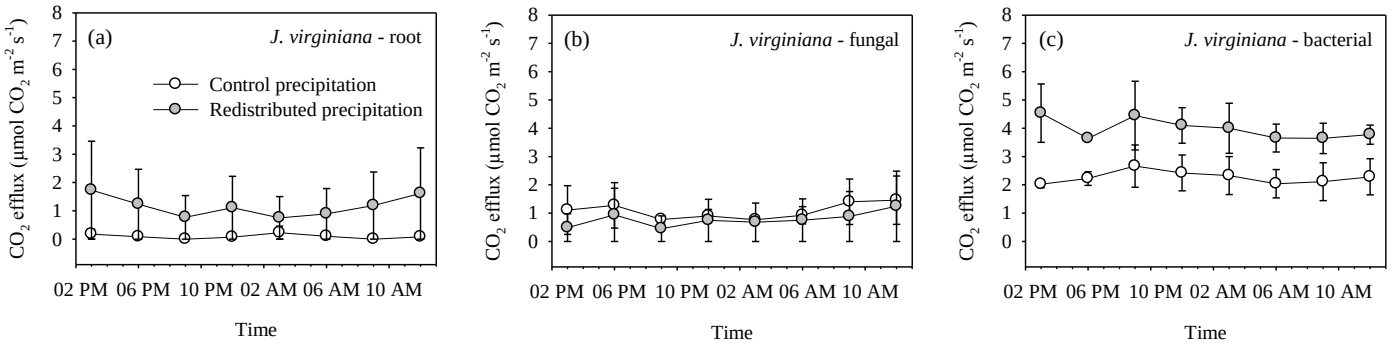

Figure A-4.13. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time during the 17 – 18 May 2009, for (a) root respiration of *Juniperus virginiana* in a monoculture, (b) fungal respiration of *J. virginiana* in a monoculture, (c) bacterial respiration of *J. virginiana* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

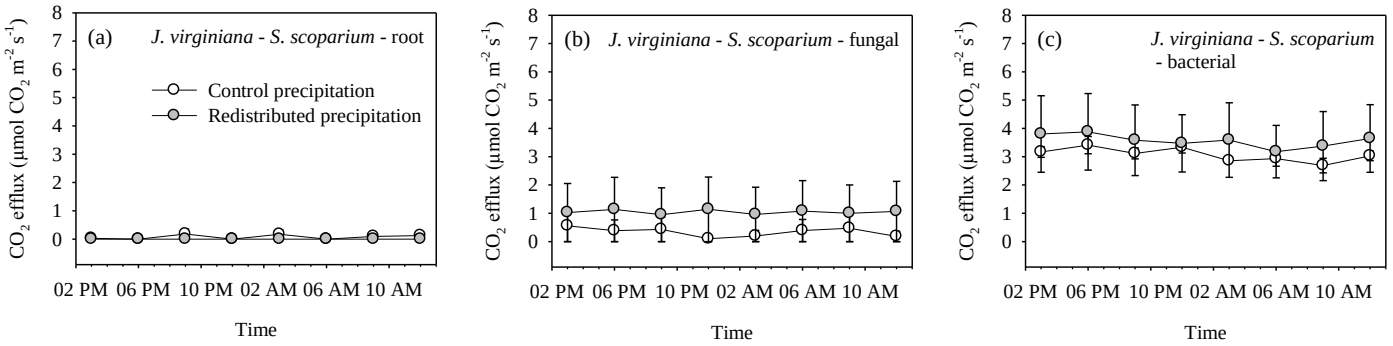

Figure A-4.14. Respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) through time during the 17 – 18 May 2009, for (a) root respiration of *J. virginiana* grown with *S. scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

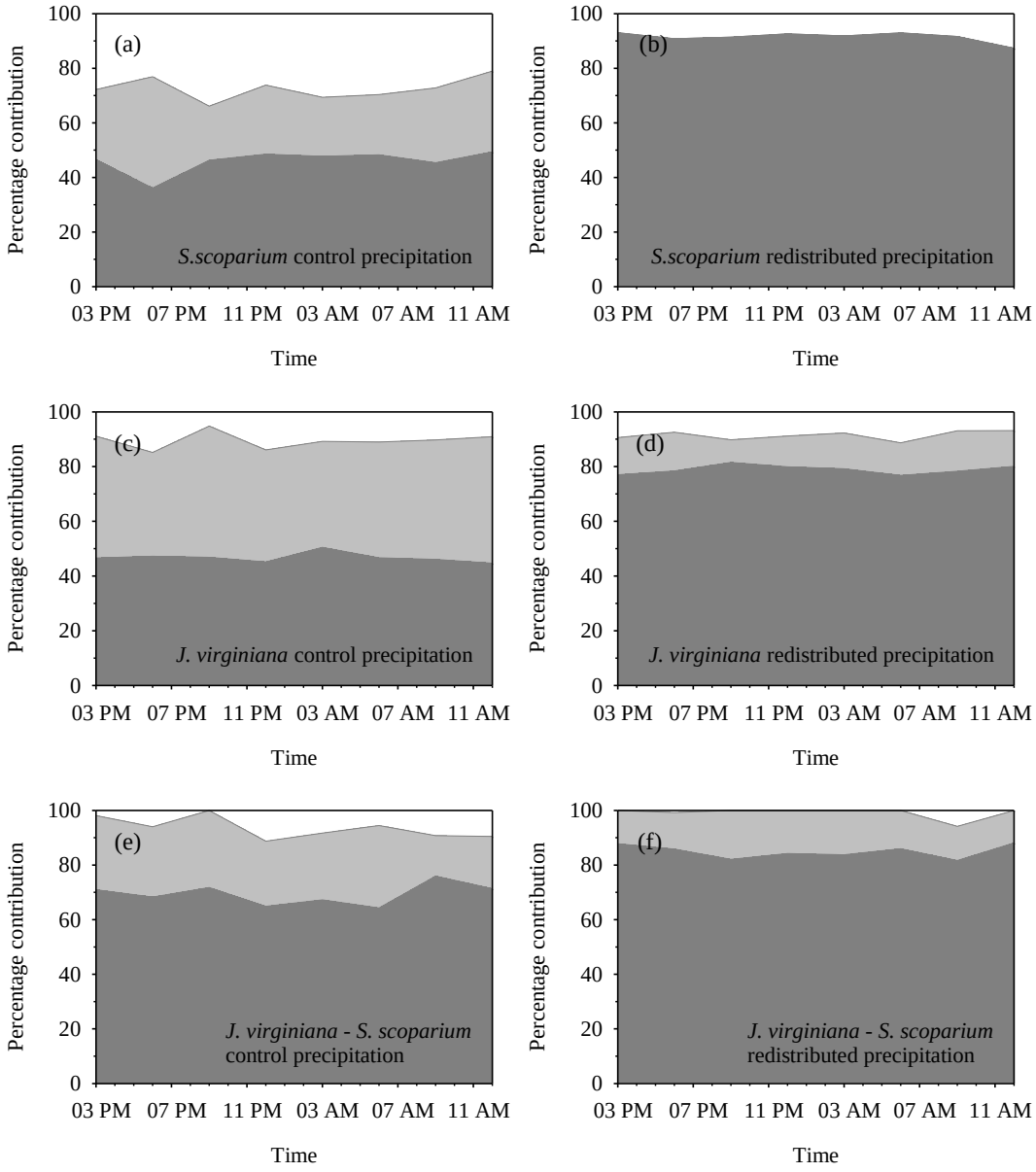

Figure A-4.15. Relationship among time and percentage contribution of root respiration (white fill), hyphal respiration (light grey fill), and bacterial respiration (dark grey fill), during the 24 hour campaign on the 14 – 15 May 2009, for (a) *Schizachyrium scoparium* in a monoculture with control precipitation, (b) *S. scoparium* in a monoculture with redistributed precipation, (c) *Juniperus virginiana* in a monoculture with control precipitation, (d) *J. virginiana* in a monoculture with redistributed precipitation, (e) *J. virginiana* grown with *S. scoparium* with control precipitation, and (f) *J. virginiana* grown with *S. scoparium* with redistributed precipitation (means).

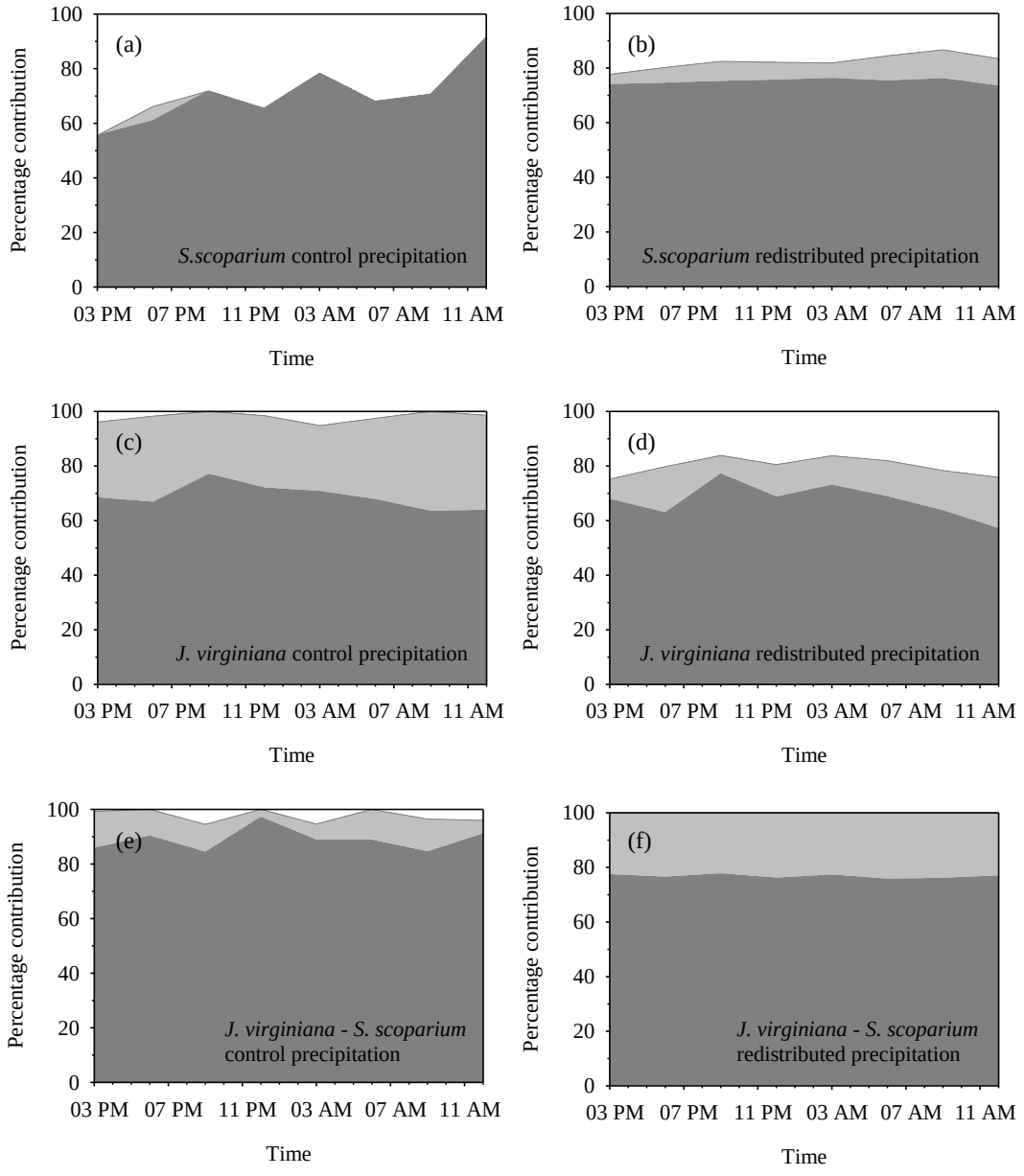

Figure A-4.16. Relationship among time and percentage contribution of root respiration (white fill), hyphal respiration (light grey fill), and bacterial respiration (dark grey fill), during the 24 hour campaign on the 17 – 18 May 2009, for (a) *Schizachyrium scoparium* in a monoculture with control precipitation, (b) *S. scoparium* in a monoculture with redistributed precipation, (c) *Juniperus virginiana* in a monoculture with control precipitation, (d) *J. virginiana* in a monoculture with redistributed precipitation, (e) *J. virginiana* grown with *S. scoparium* with control precipitation, and (f) *J. virginiana* grown with *S. scoparium* with redistributed precipitation (means).

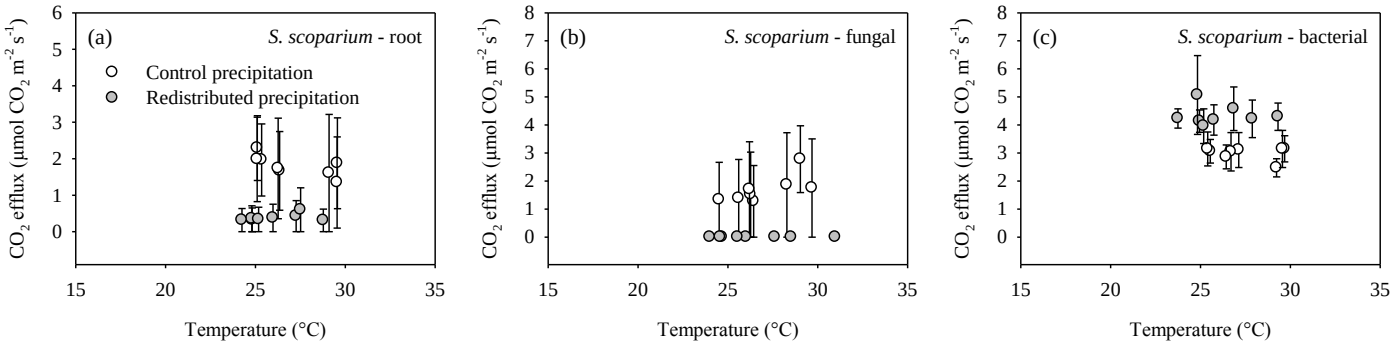

Figure A-4.17. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) during the 24 hour campaign on the 14 – 15 May 2009, for (a) root respiration of *Schizachyrium scoparium* in a monoculture, (b) fungal respiration of *S. scoparium* in a monoculture, (c) bacterial respiration of *S. scoparium* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

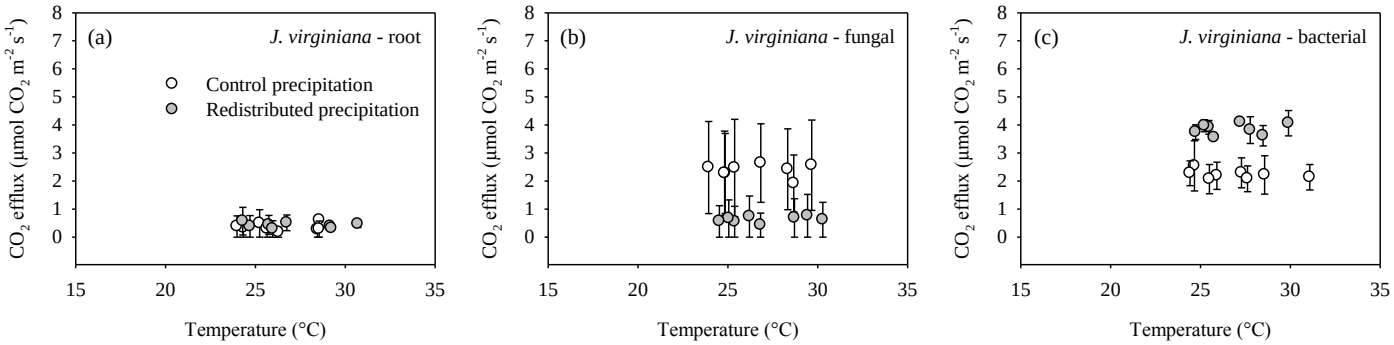

Figure A-4.18. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) during the 24 hour campaign on the 14 – 15 May 2009, for (a) root respiration of *Juniperus virginiana* in a monoculture, (b) fungal respiration of *J. virginiana* in a monoculture, (c) bacterial respiration of *J. virginiana* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

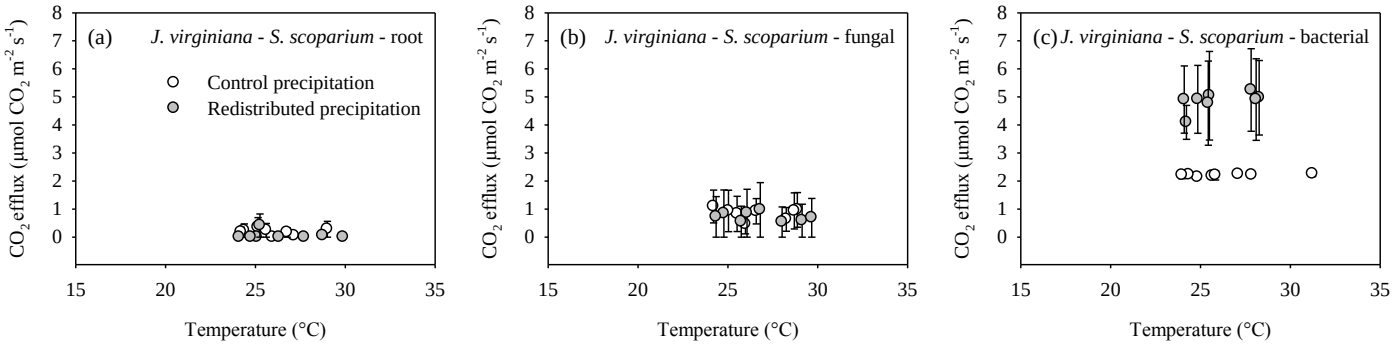

Figure A-4.19. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) during the 24 hour campaign on the 14 – 15 May 2009, for (a) root respiration of *J. virginiana* grown with *S. scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

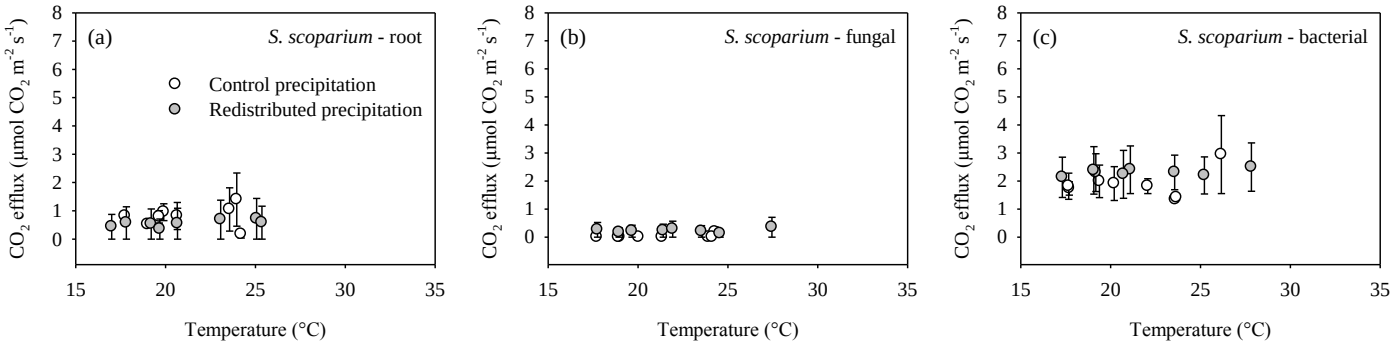

Figure A-4.20. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) during the 24 hour campaign on the 17 – 18 May 2009, for (a) root respiration of *Schizachyrium scoparium* in a monoculture, (b) fungal respiration of *S. scoparium* in a monoculture, (c) bacterial respiration of *S. scoparium* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

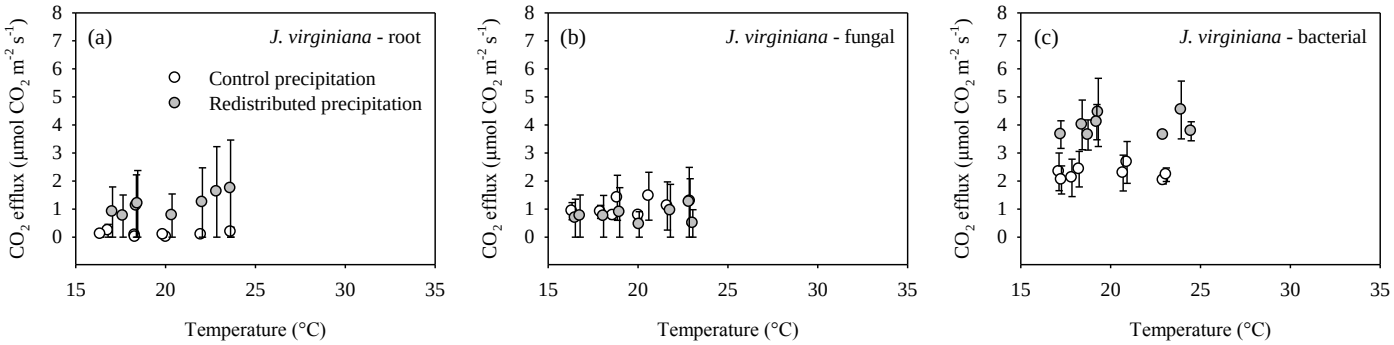

Figure A-4.21. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) during the 24 hour campaign on the 17 – 18 May 2009, for (a) root respiration of *Juniperus virginiana* in a monoculture, (b) fungal respiration of *J. virginiana* in a monoculture, (c) bacterial respiration of *J. virginiana* in a monoculture (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

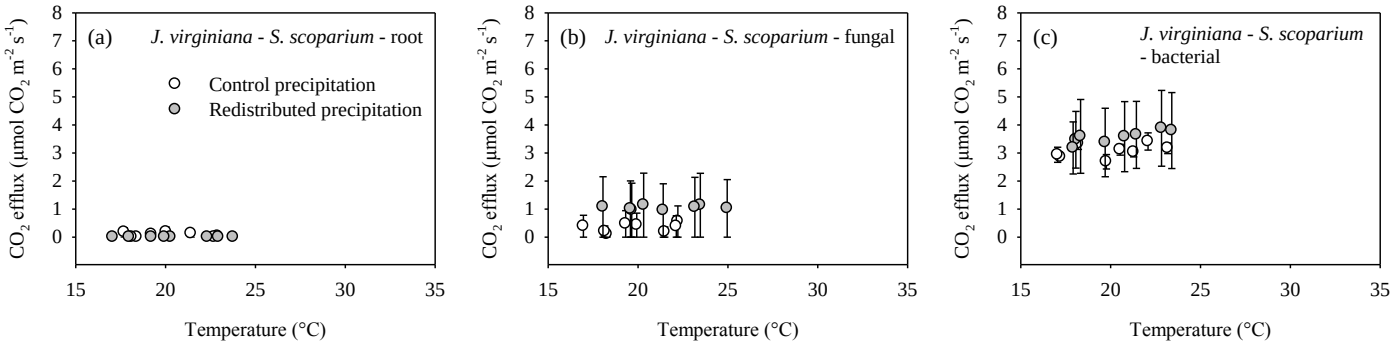

Figure A-4.22. Effect of soil temperature (°C) on respiration components of soil CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) during the24 hour campaign on the 17 – 18 May 2009, for (a) root respiration of *J. virginiana* grown with *S. scoparium*, (b) fungal respiration of *J. virginiana* grown with *S. scoparium*, and (c) bacterial respiration of *J. virginiana* grown with *S. scoparium* (means ± SE). Unfilled circles represent control precipitation and filled circles redistributed precipitation.

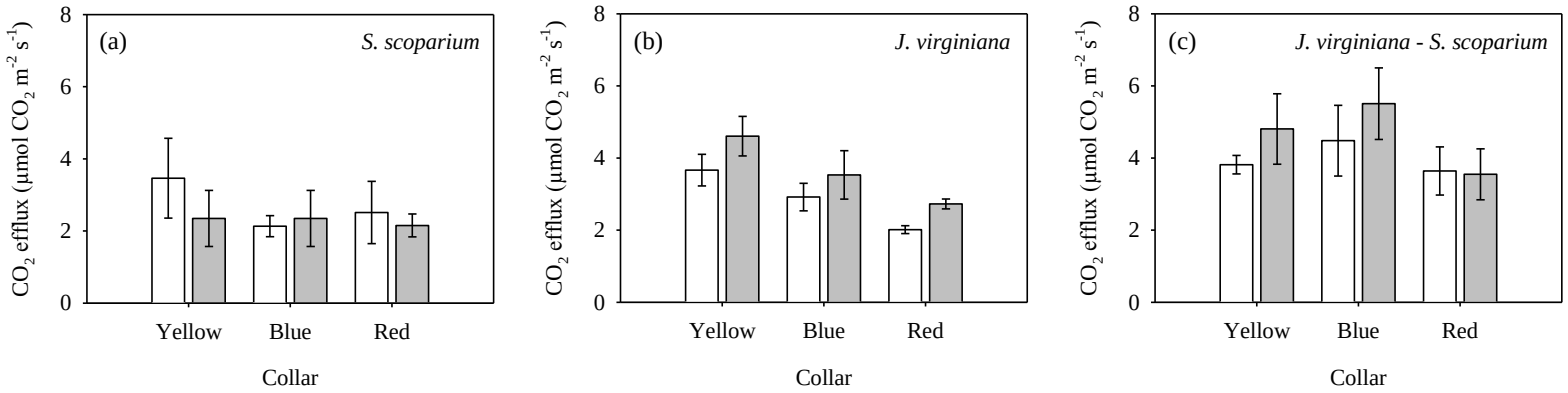

Figure A-4.23. Effect of collar treatment on CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means ± SE). Yellow collar allowed roots, fungi, and bacteria access, blue collar allowed fungi and bacteria access, and red collars allowed bacteria access. Unfilled bars represent control precipitation treatment and filled bars represent redistributed precipitation treatment.

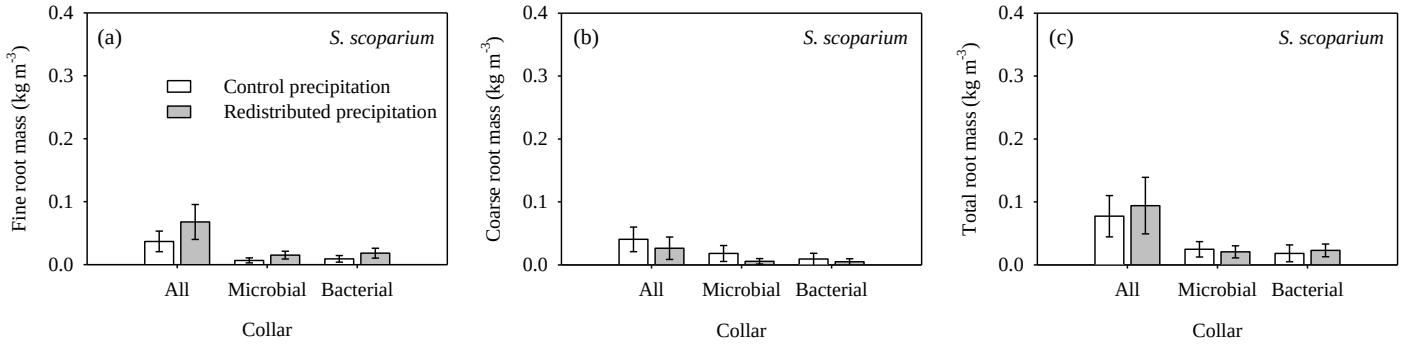

Figure A-4.24. Effect of collar treatment on CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) for (a) fine, (b) coarse, and (c) root mass (kg m^{-3}) for *Schizachyrium scoparium* monoculture at the termination of the experiment (25 April 2010) (mean ± SE). All allowed roots, fungi, and bacteria access (collar A), microbial allowed fungi and bacteria access (collar B), and bacterial allowed bacteria access (collar C). Unfilled bars represent control precipitation treatment and filled bars represent redistributed precipitation treatment.

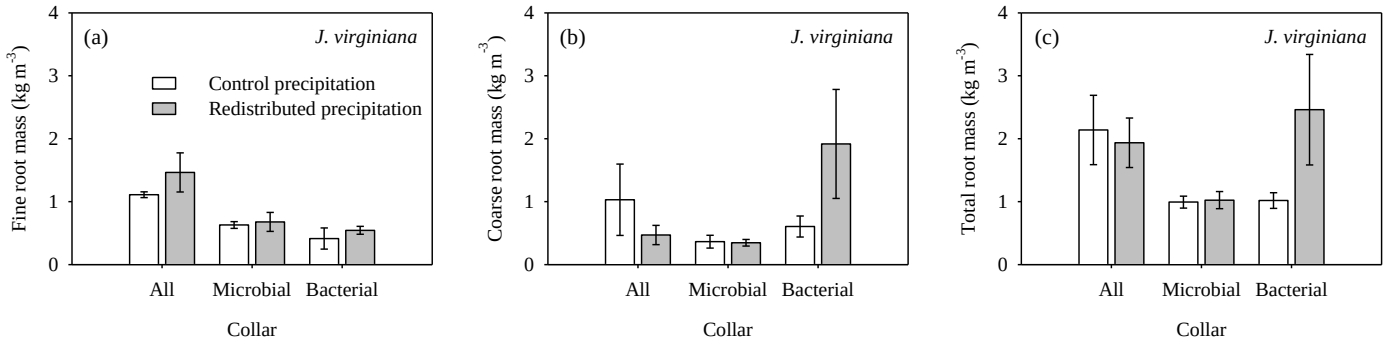

Figure A-4.25. Effect of collar treatment on CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) fine, (b) coarse, and (c) root mass (kg m^{-3}) for *Juniperus virginiana* monoculture at the termination of the experiment (25 April 2010) (means ± SE). All allowed roots, fungi, and bacteria access (collar A), microbial allowed fungi and bacteria access (collar B), and bacterial allowed bacteria access (collar C). Unfilled bars represent control precipitation treatment and filled bars represent redistributed precipitation treatment.

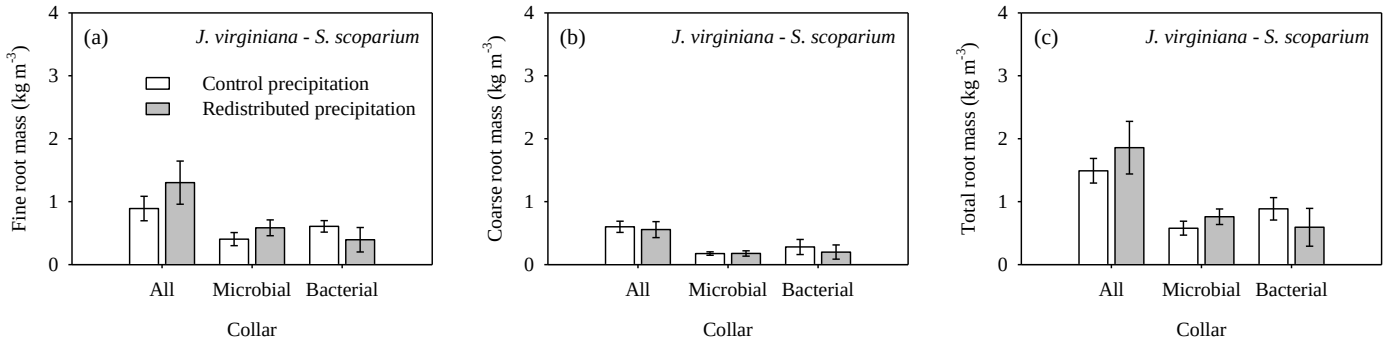

Figure A-4.26. Effect of collar treatment on CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) fine, (b) coarse, and (c) root mass (kg m^{-3})for (a – c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means ± SE). All allowed roots, fungi, and bacteria access (collar A), microbial allowed fungi and bacteria access (collar B), and bacterial allowed bacteria access (collar C). Unfilled bars represent control precipitation treatment and filled bars represent redistributed precipitation treatment.

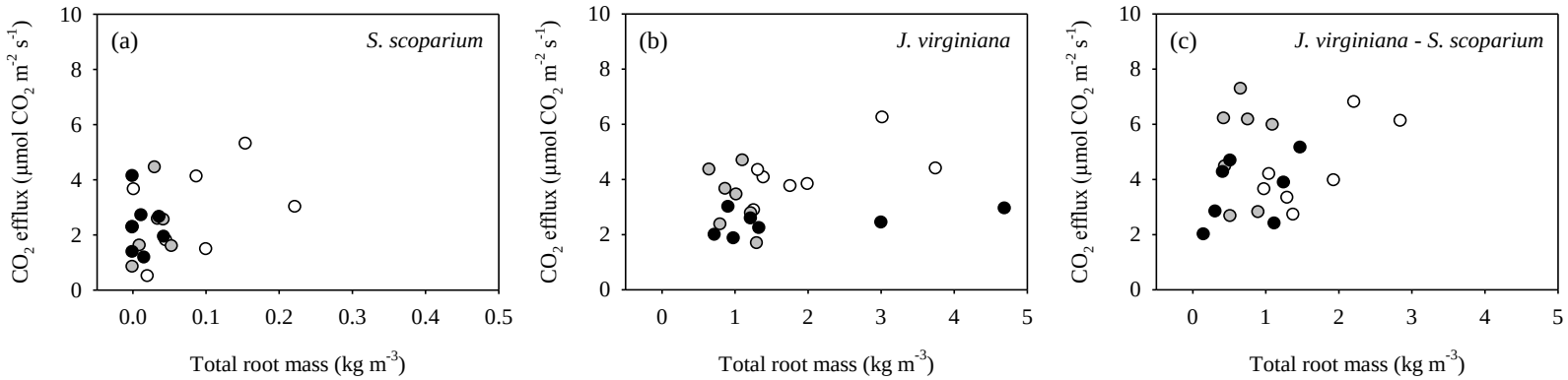

Figure A-4.27. Effect of total root mass (kg m^{-3}) on CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means). Unfilled circles represent collars which allowed roots, fungi, and bacteria access, grey filled circles represent collars which allowed fungi and bacteria access, and black filled circles represent collars which allowed bacteria access.

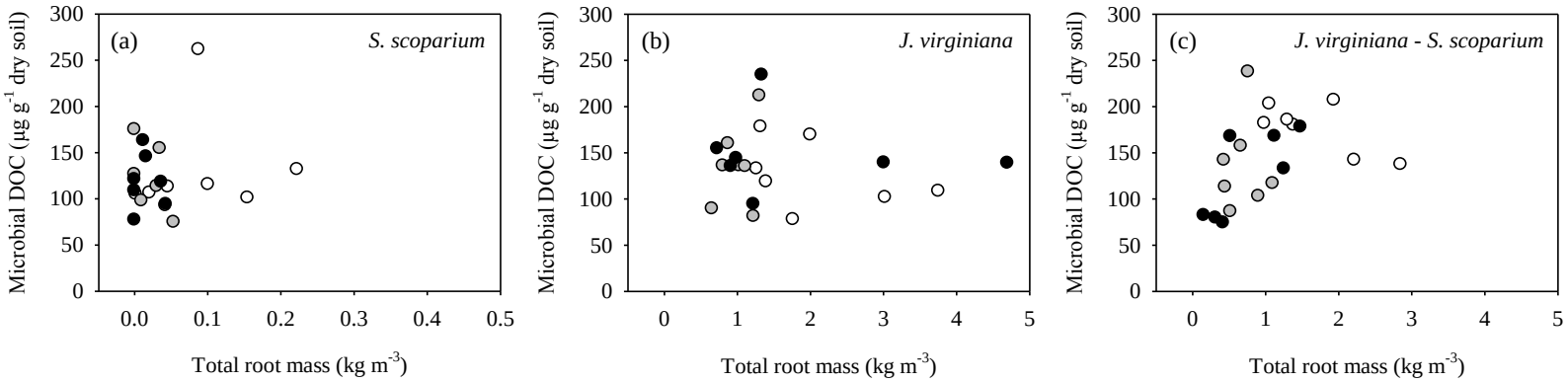

Figure A-4.28. Effect of total root mass (kg m^{-3}) on microbial dissolved organic carbon (DOC) (µg g^{-1} dry soil) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means). Unfilled circles represent collars which allowed roots, fungi, and bacteria access, grey filled circles represent collars which allowed fungi and bacteria access, and black filled circles represent collars which allowed bacteria access.

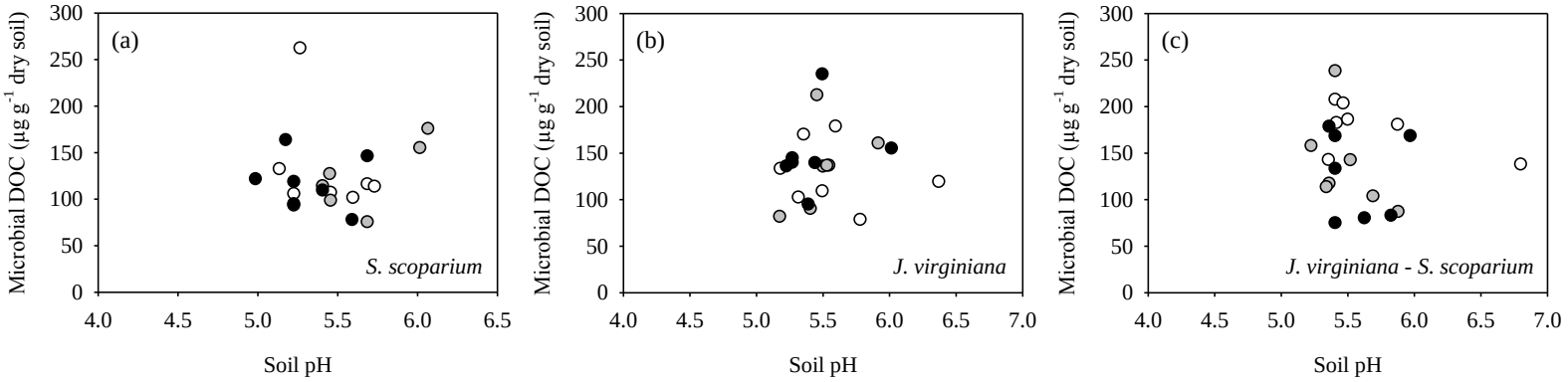

Figure A-4.29. Effect of soil pH on microbial dissolved organic carbon (DOC) (µg g^{-1} dry soil) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means). Unfilled circles represent collars which allowed roots, fungi, and bacteria access, grey filled circles represent collars which allowed fungi and bacteria access, and black filled circles represent collars which allowed bacteria access.

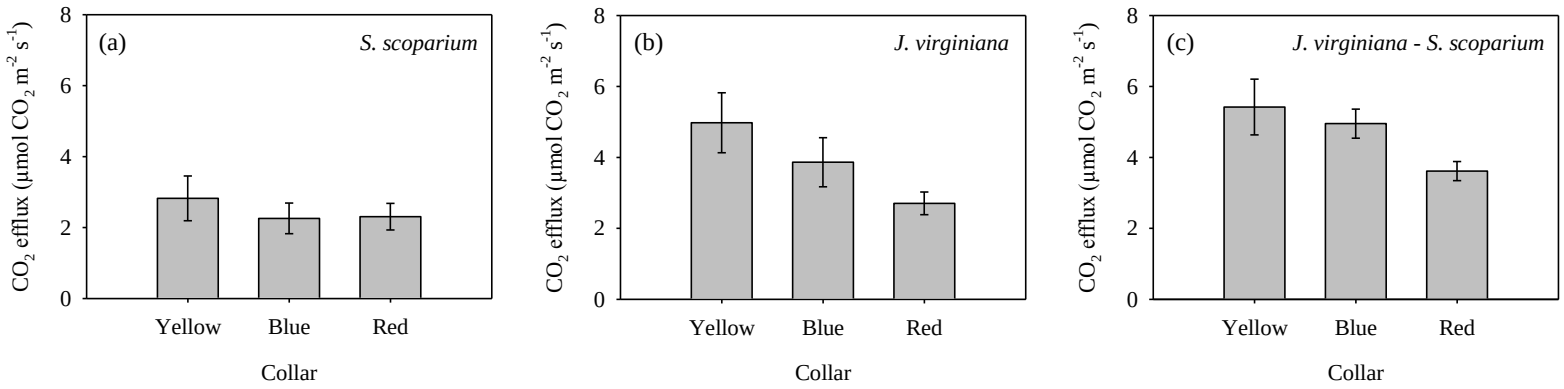

Figure A-4.30. Effect of collar treatment on CO_2 efflux (µmol CO_2 m^{-2} s^{-1}) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means ± SE). Yellow collar allowed roots, fungi, and bacteria access, blue collar allowed fungi and bacteria access, and red collars allowed bacteria access.

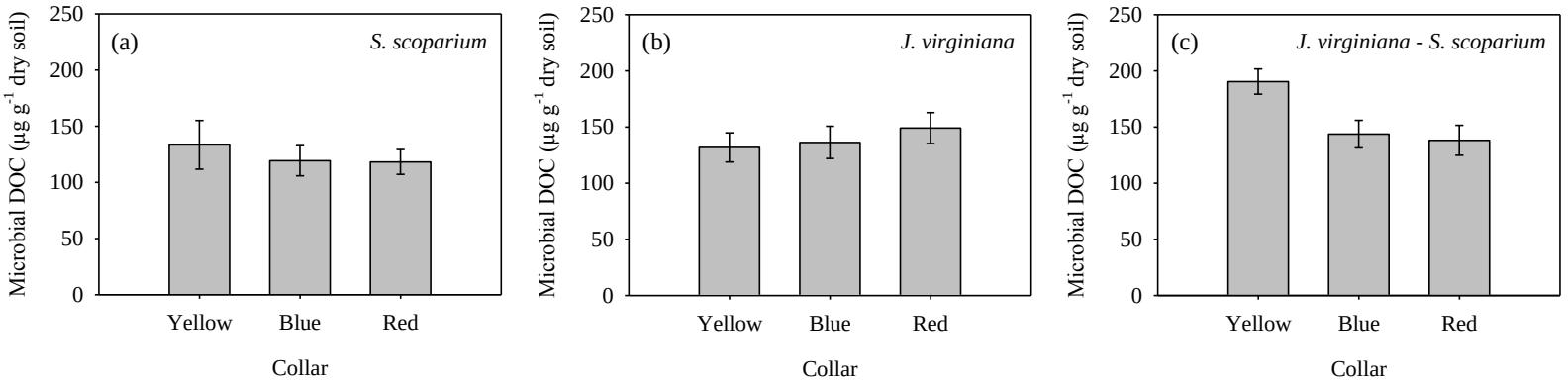

Figure A-4.31. Effect of collar treatment on microbial dissolved organic carbon (DOC) (µg g^{-1} dry soil) for (a) *Schizachyrium scoparium* monoculture, (b) *Juniperus virginiana* monoculture, and (c) *J. virginiana* grown with *S. scoparium* at the termination of the experiment (25 April 2010) (means ± SE). Yellow collar allowed roots, fungi, and bacteria access, blue collar allowed fungi and bacteria access, and red collars allowed bacteria access.

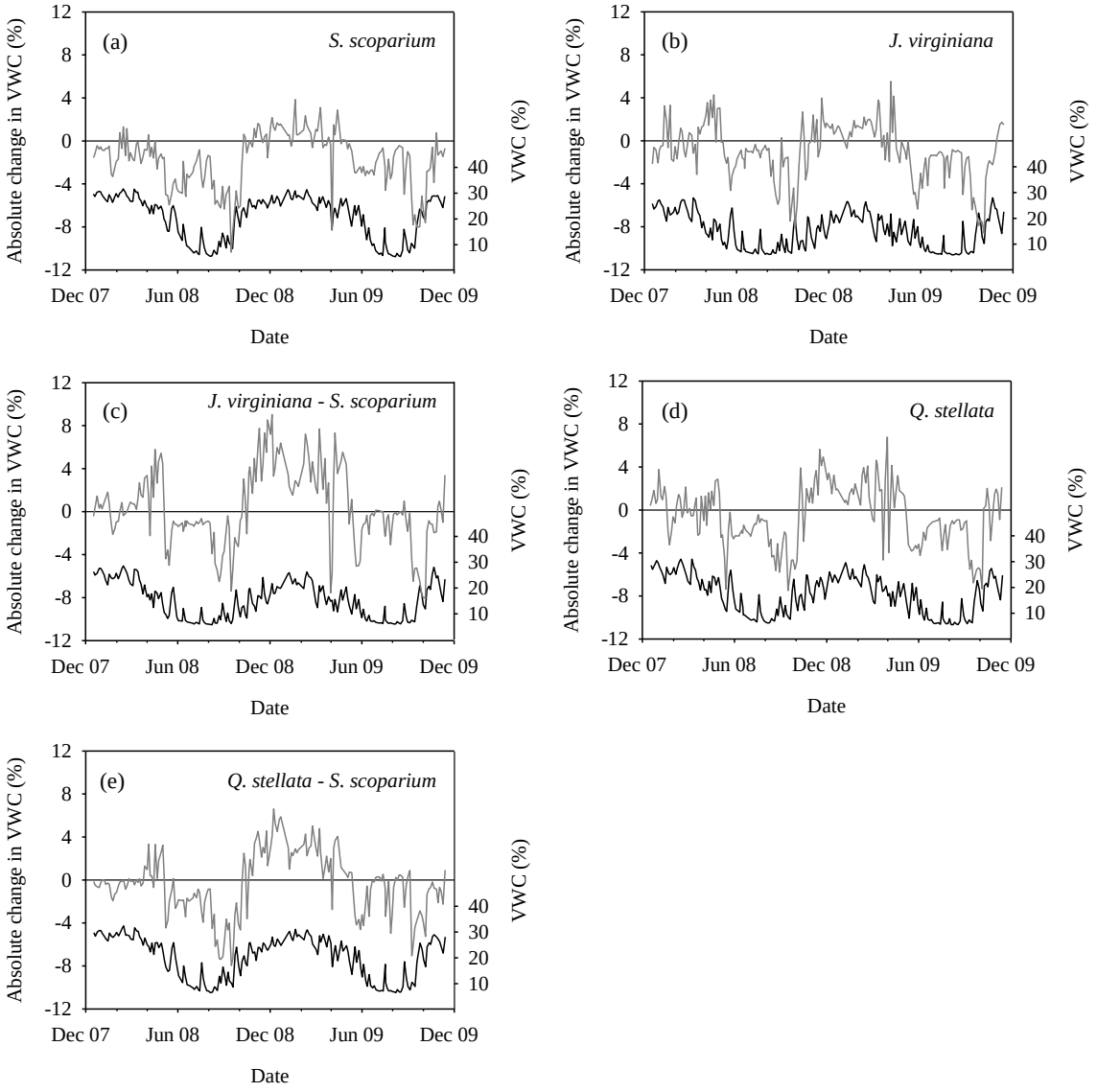

Figure A-5.1. Effect of precipitation treatment on soil volumetric water content (VWC) averaged across warming treatment over time for (a) *Schizachyrium scoparium* in monoculture, (b) *Juniperus virginiana* grown in monoculture, (c) *J. virginiana* grown with *S. scoparium*, (d) *Quercus stellata* in monoculture, and (e) *Q. stellata* grown with *S. scoparium* (means ± SE). The grey line depicts absolute changes in soil VWC due to precipitation redistribution treatment and the black line depicts the seasonal VWC patter.

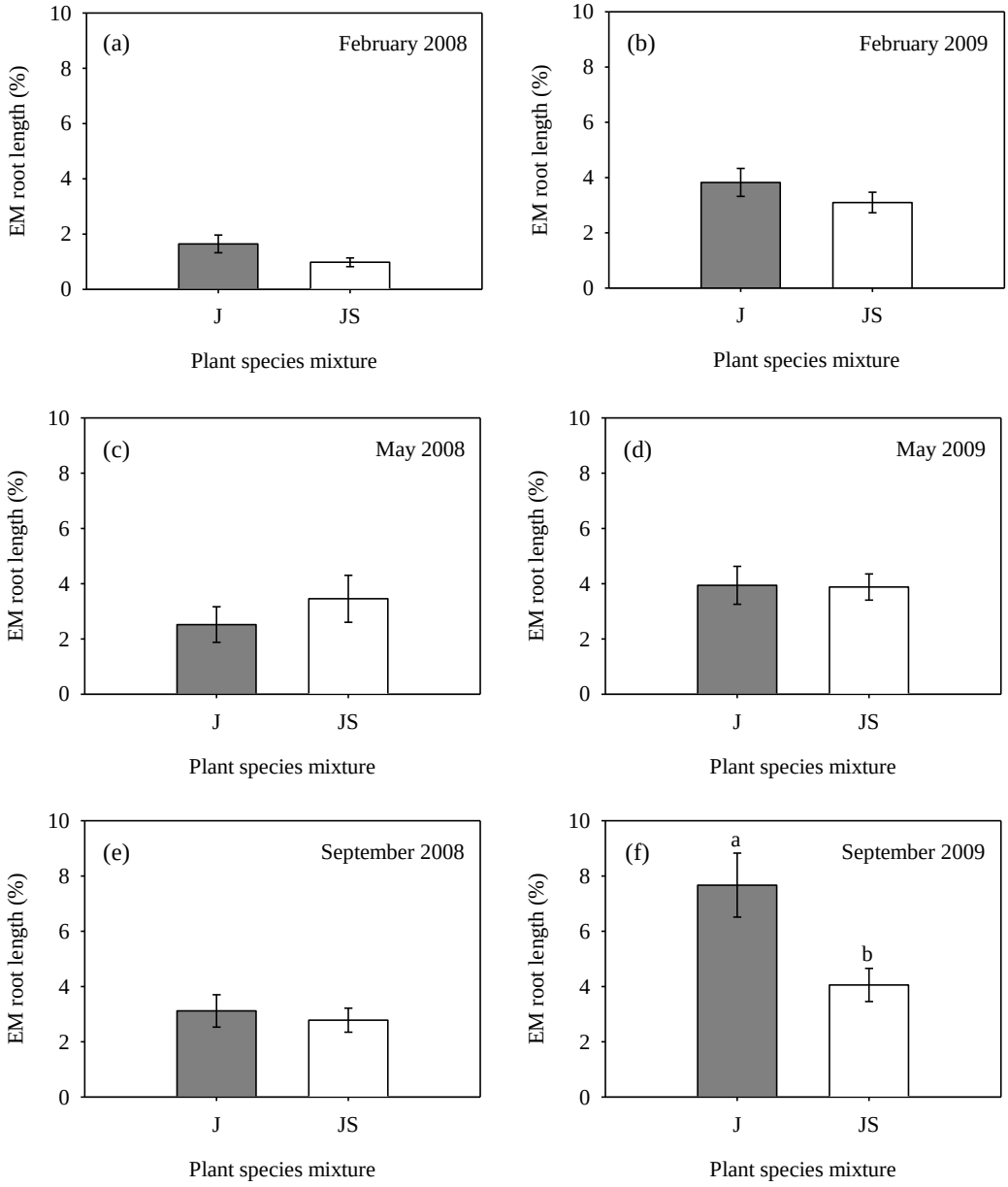

Figure A-5.2. Percent ectomycorrhizal (EM) root length colonization of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

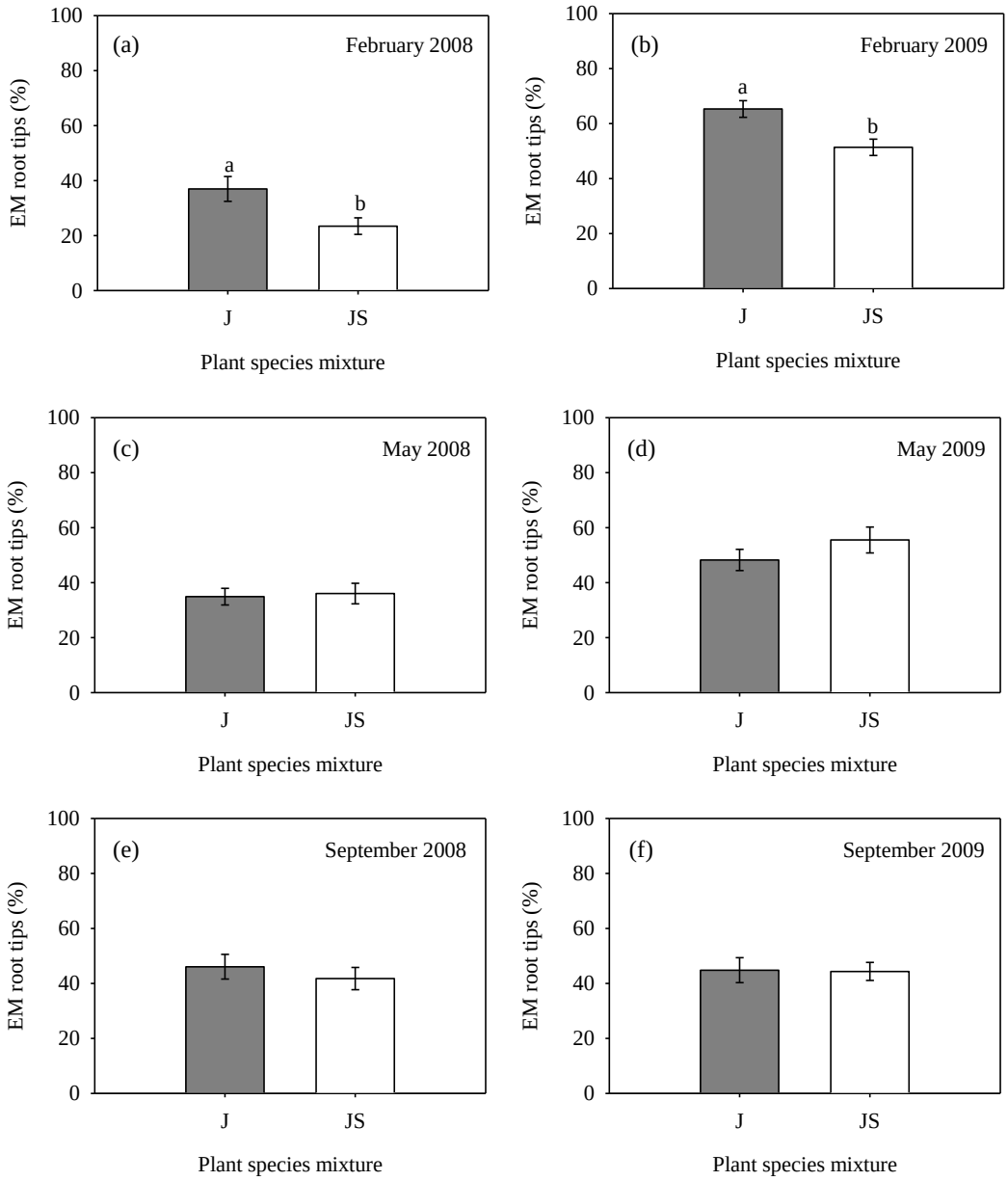

Figure A-5.3. Percent ectomycorrhizal (EM) root tips colonization of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

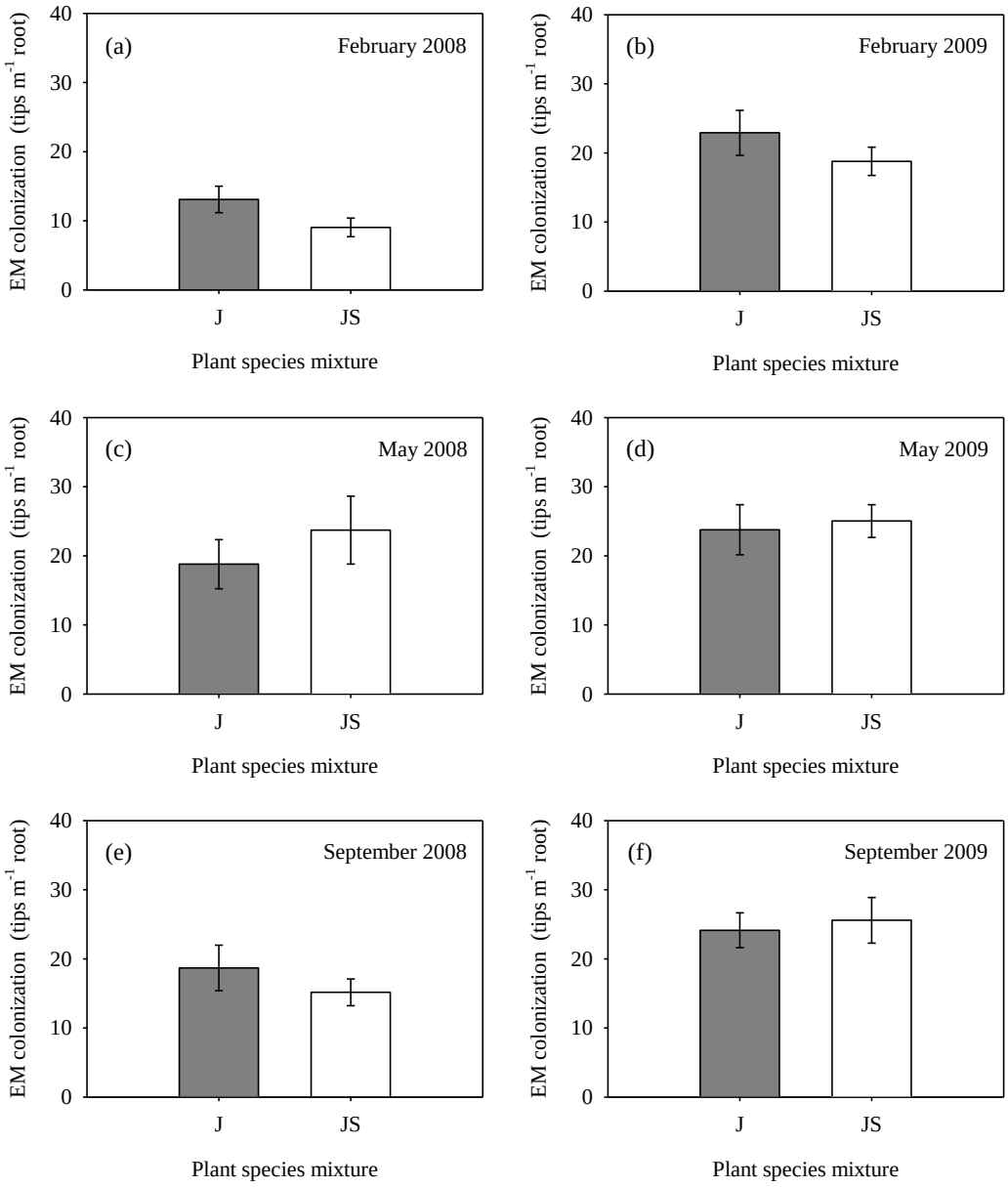

Figure A-5.4. Ectomycorrhizal (EM) colonized root tips (tips m^{-1} root) of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS).

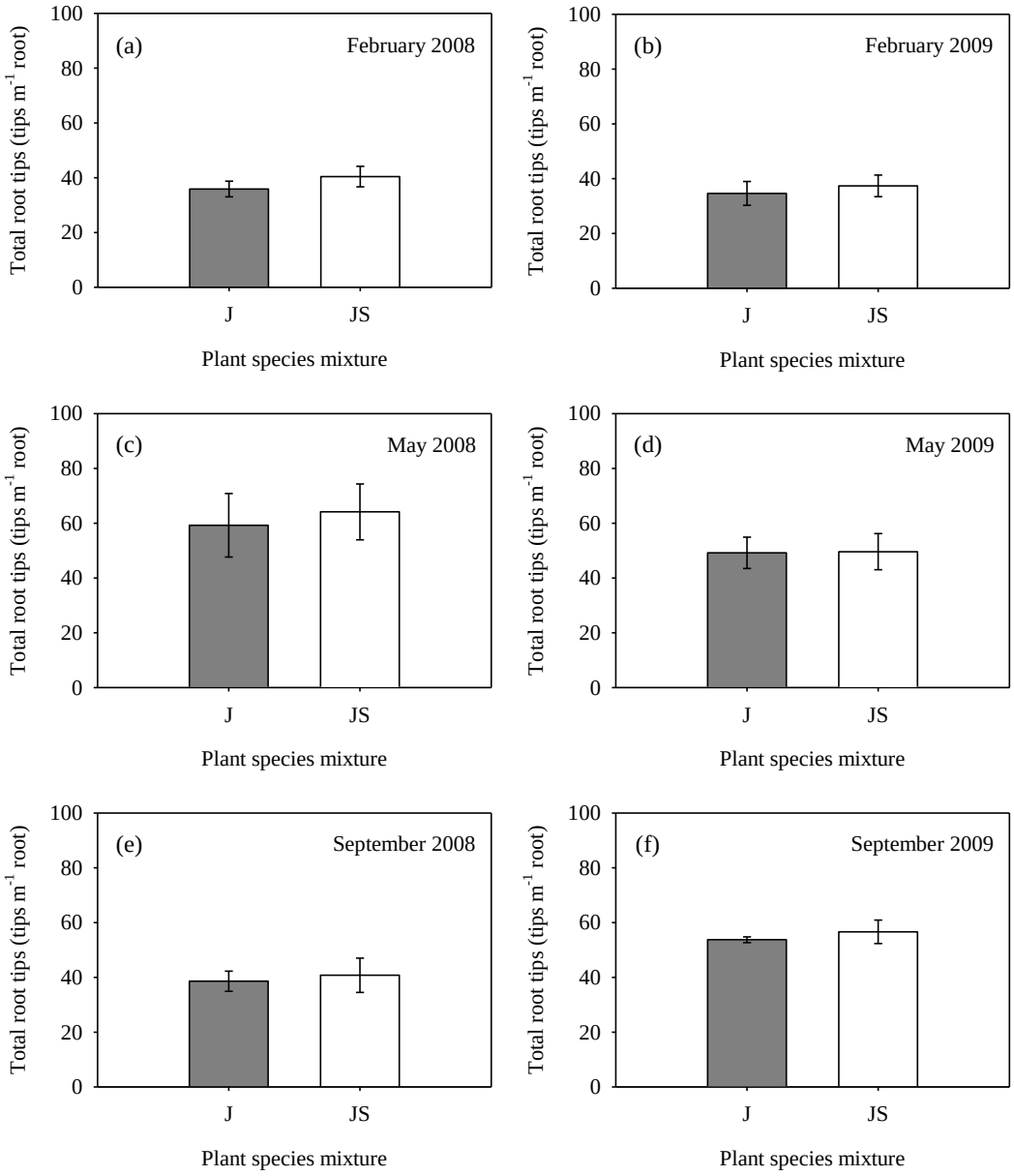

Figure A-5.5. Total root tips per root length (tips m^{-1} root) of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS).

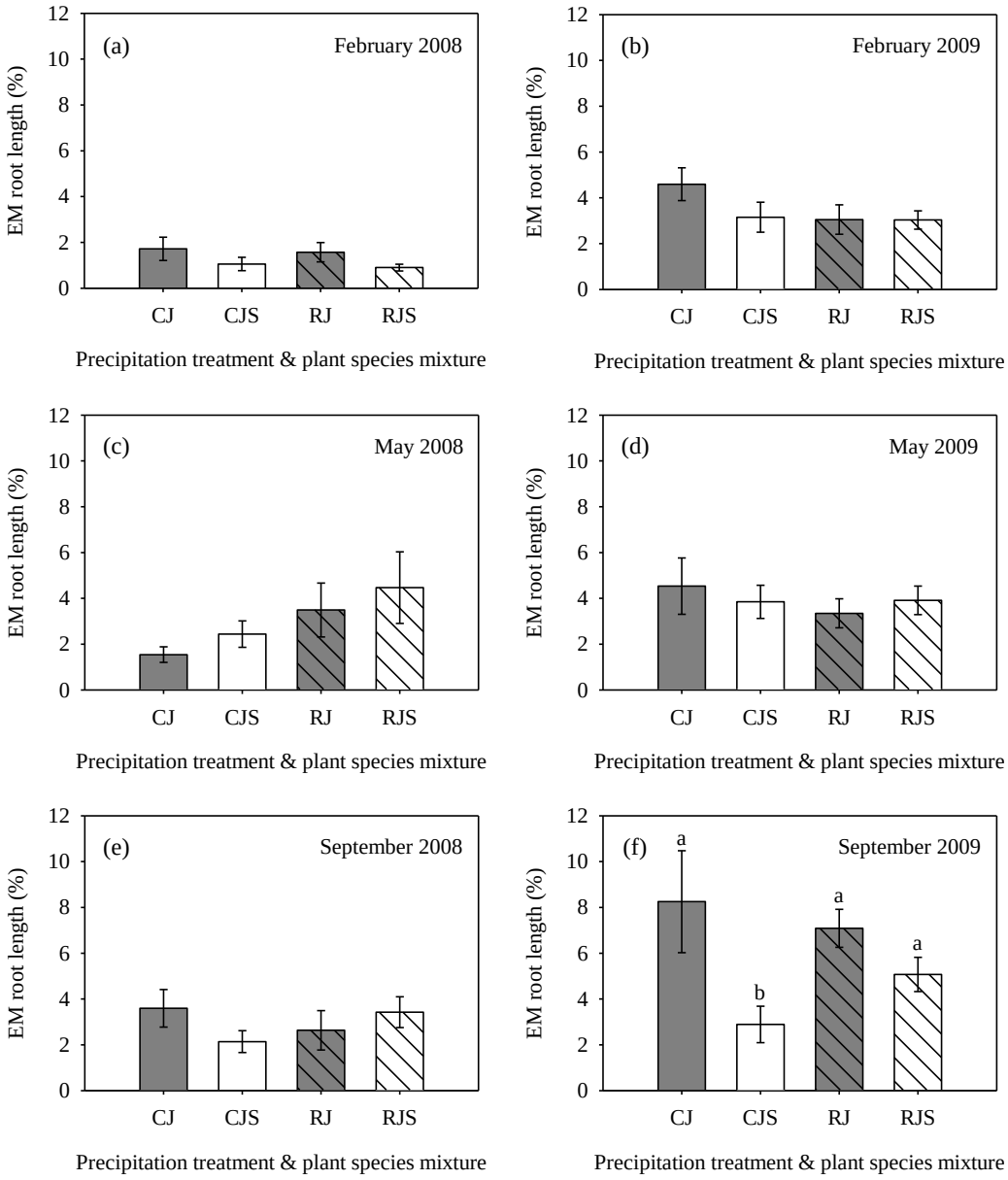

Figure A-5.6. Effect of precipitation distribution treatment on percent ectomycorrhizal (EM) root length colonized of *Juniperus virginiana* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

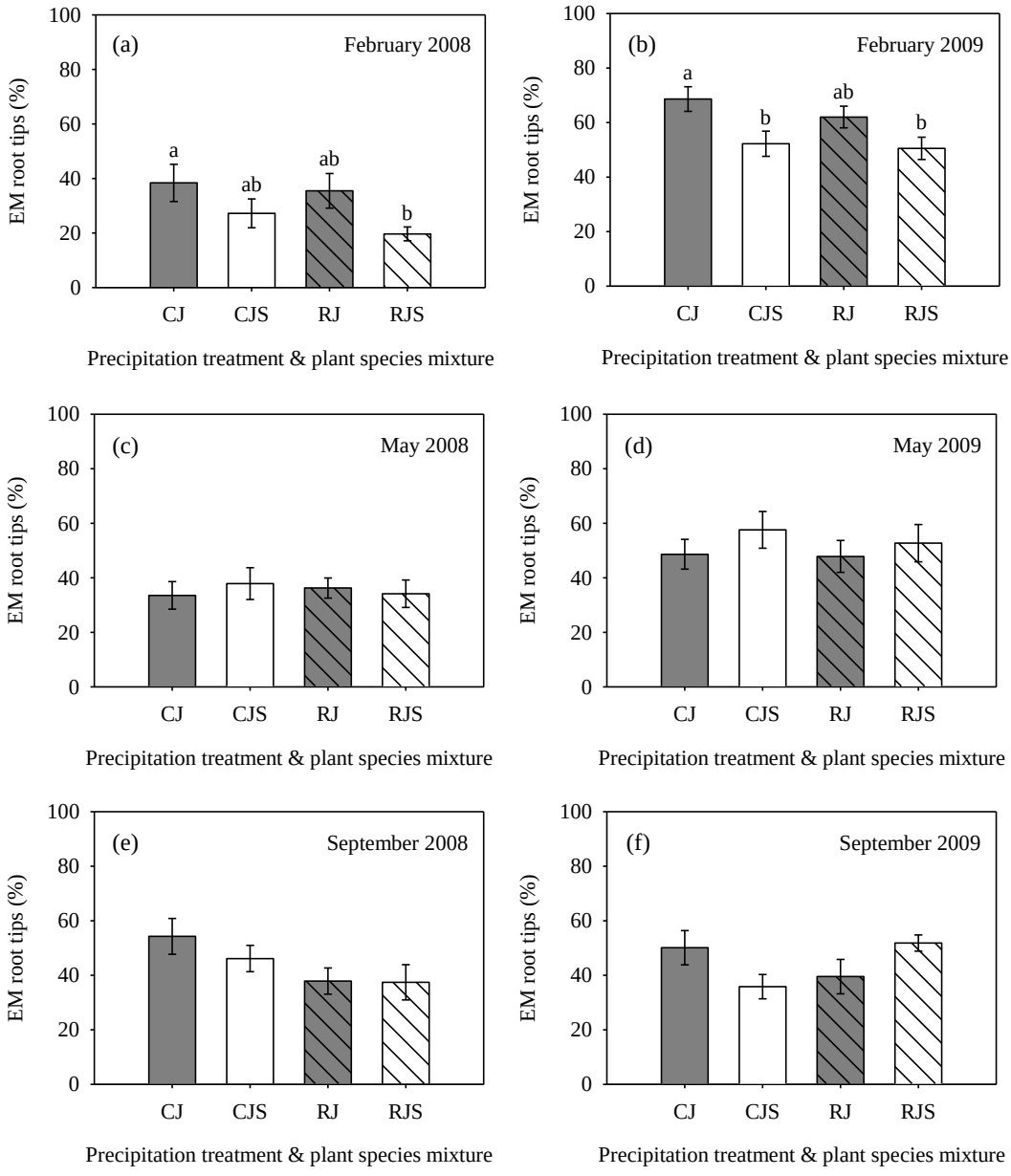

Figure A-5.7. Effect of precipitation distribution on percent ectomycorrhizal (EM) root tips colonized of *Juniperus virginiana* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

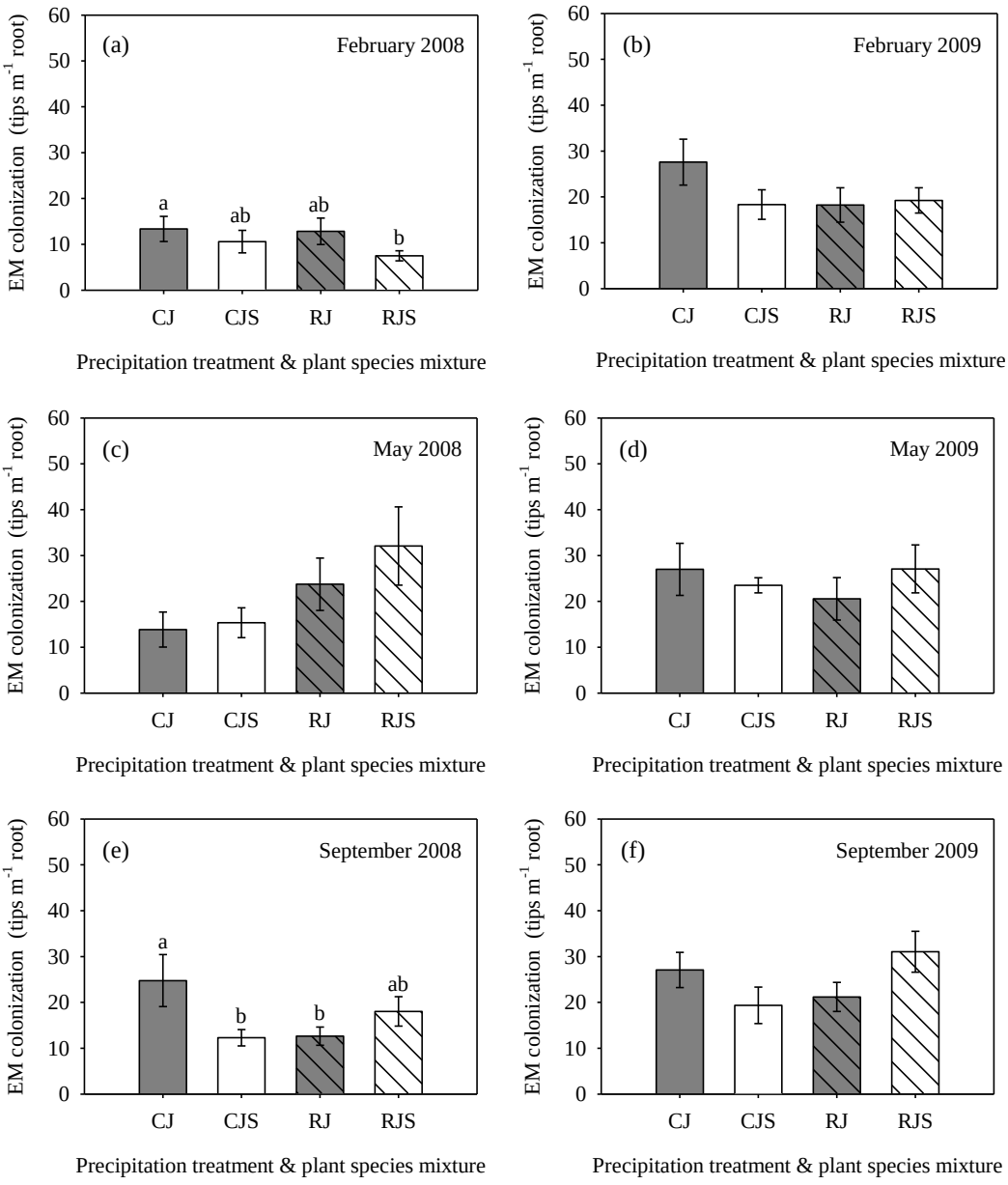

Figure A-5.8. Effect of precipitation on percent ectomycorrhizal (EM) colonized root tips (tips m^{-1} root) of *Juniperus virginiana* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

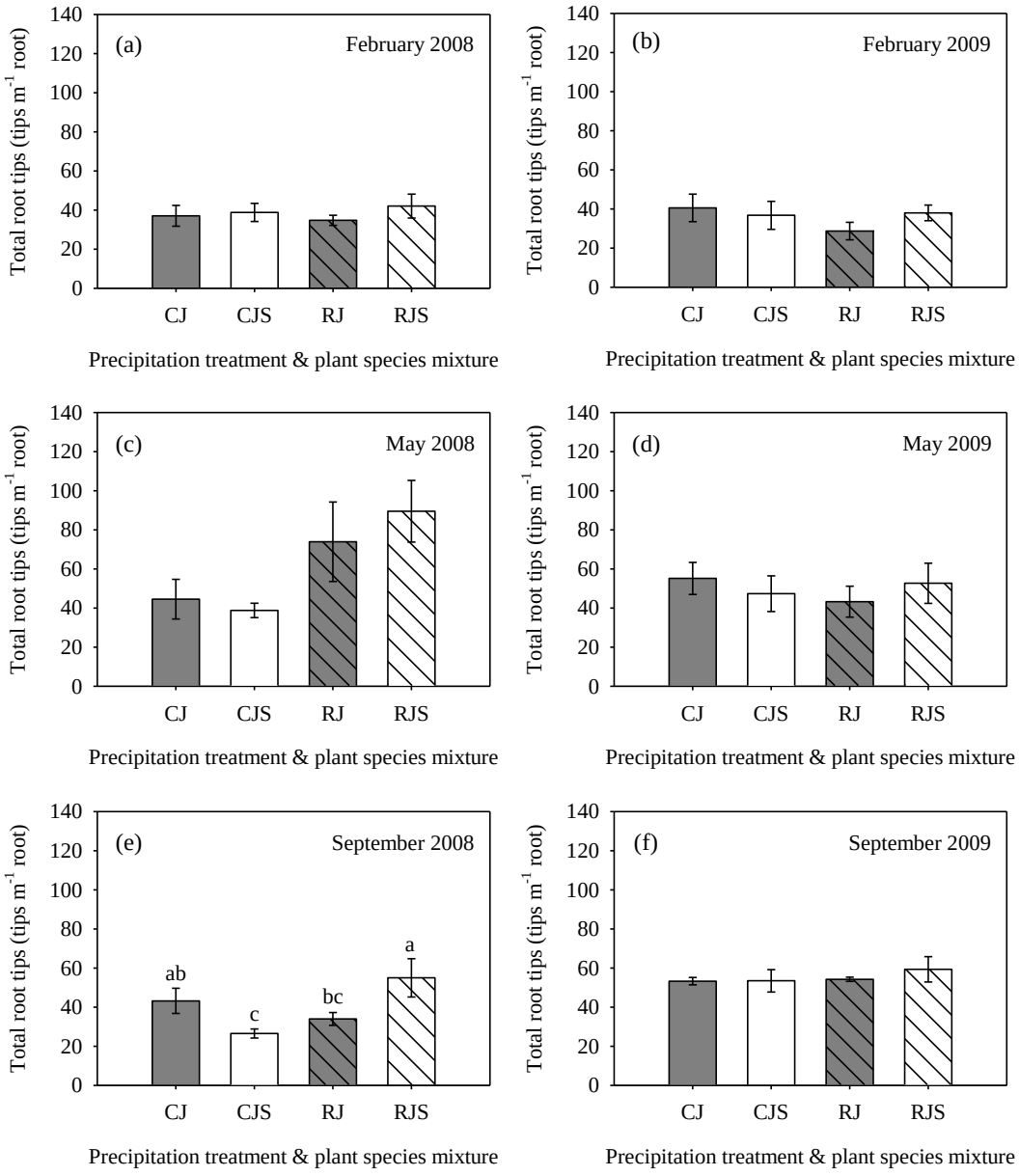

Figure A-5.9. Effect of precipitation distribution treatment on total root tips per root length (tips m^{-1} root) of *Juniperus virginiana* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

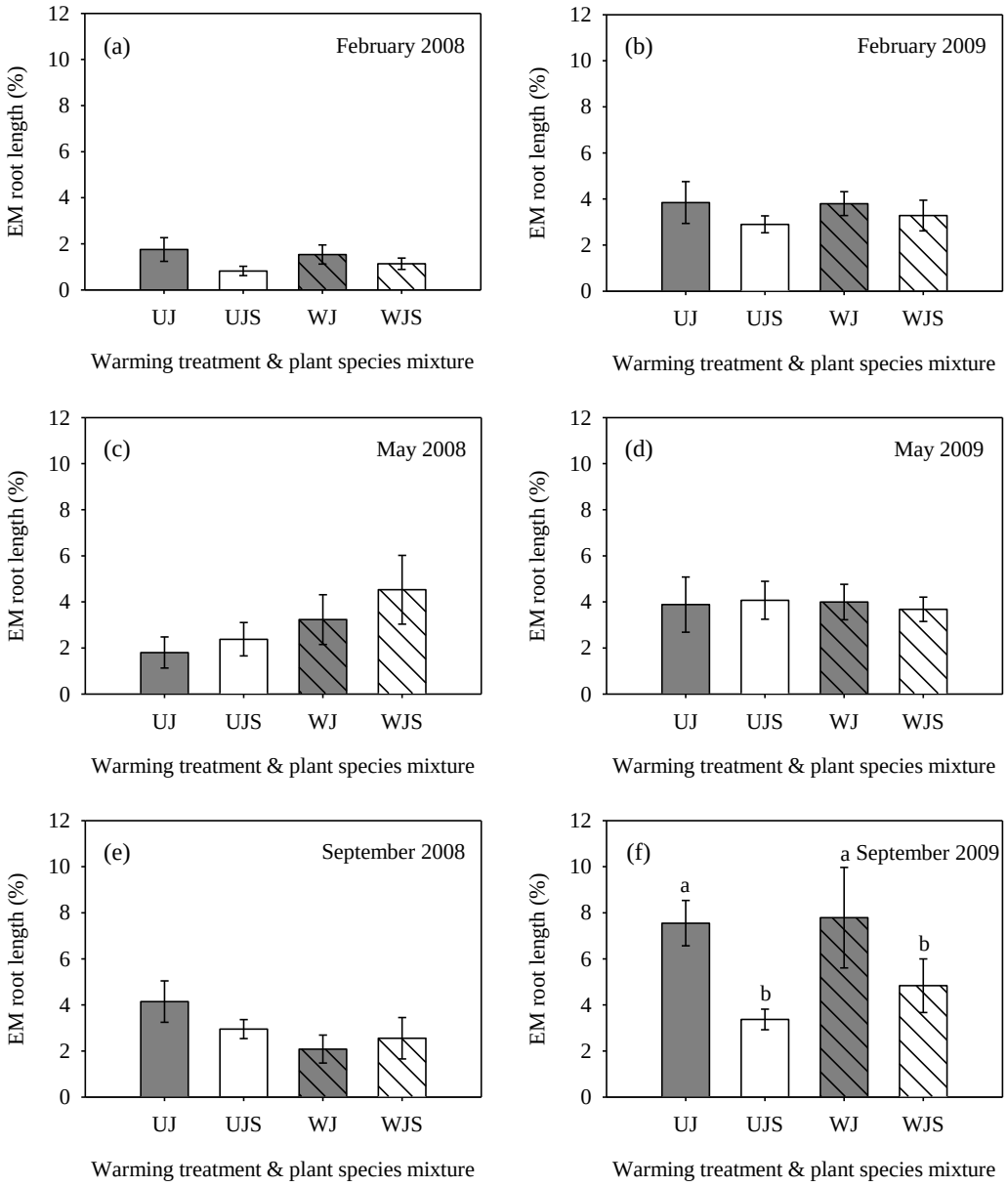

Figure A-5.10. Effect of warming treatment on percent ectomycorrhizal (EM) root length colonized of *Juniperus virginiana* averaged across precipitation treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

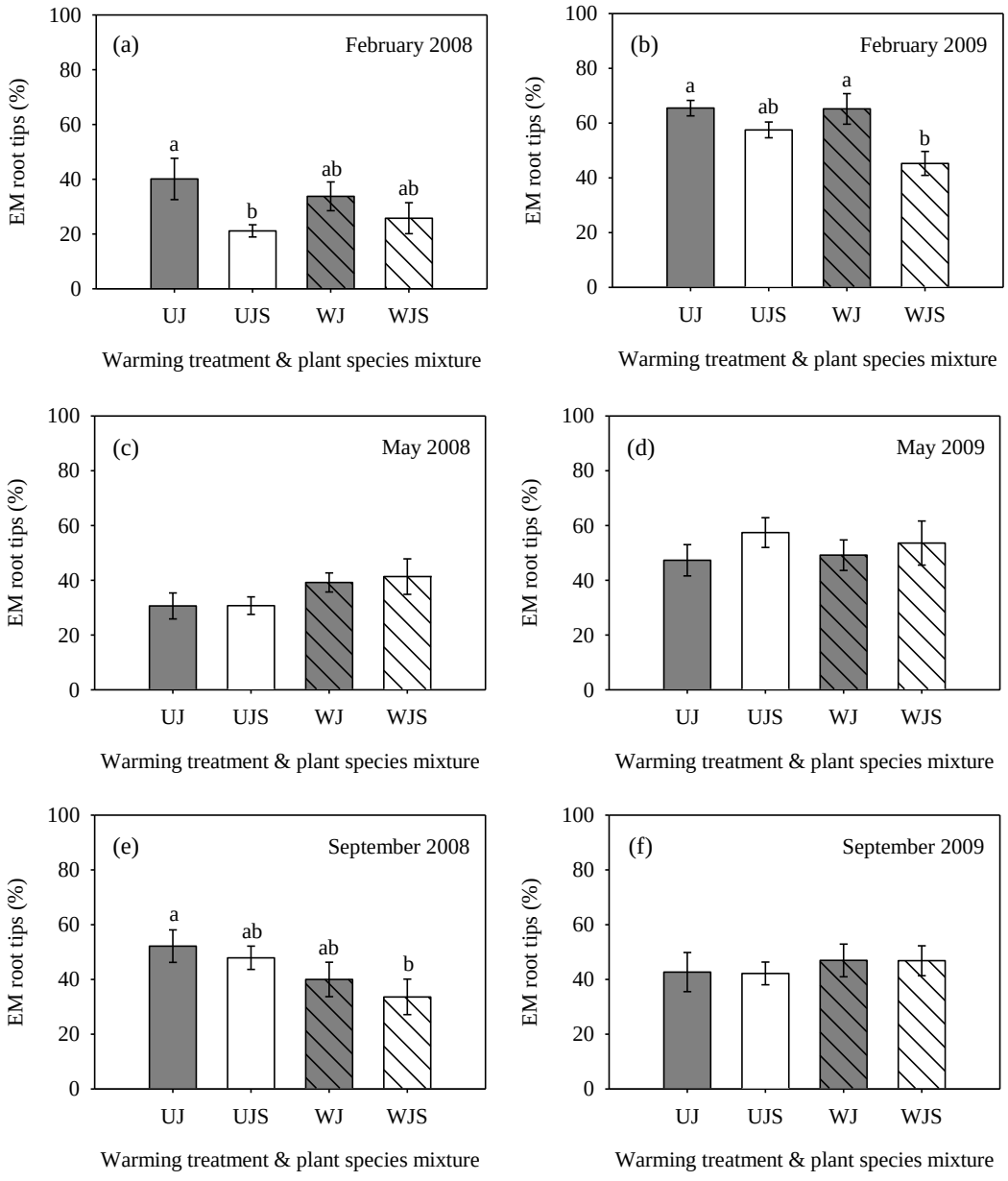

Figure A-5.11. Effect of warming treatment on ercent ectomycorrhizal (EM) root tips colonized of *Juniperus virginiana* averagedacross precipitation treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

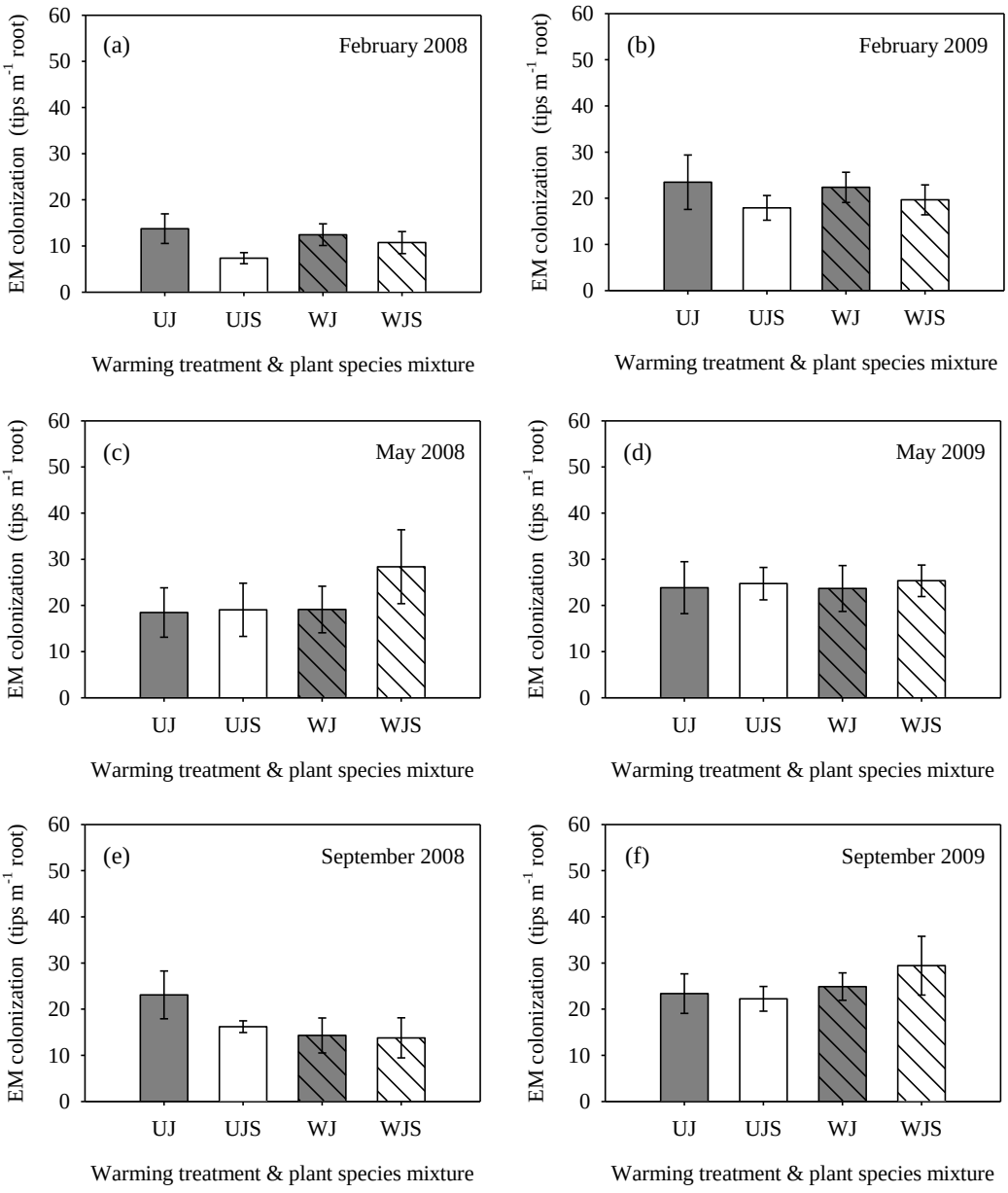

Figure A-5.12. Effect of warming treatment on percent ectomycorrhizal (EM) colonized root tips (tips m^{-1} root) of *Juniperus virginiana* averaged across precipitation treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

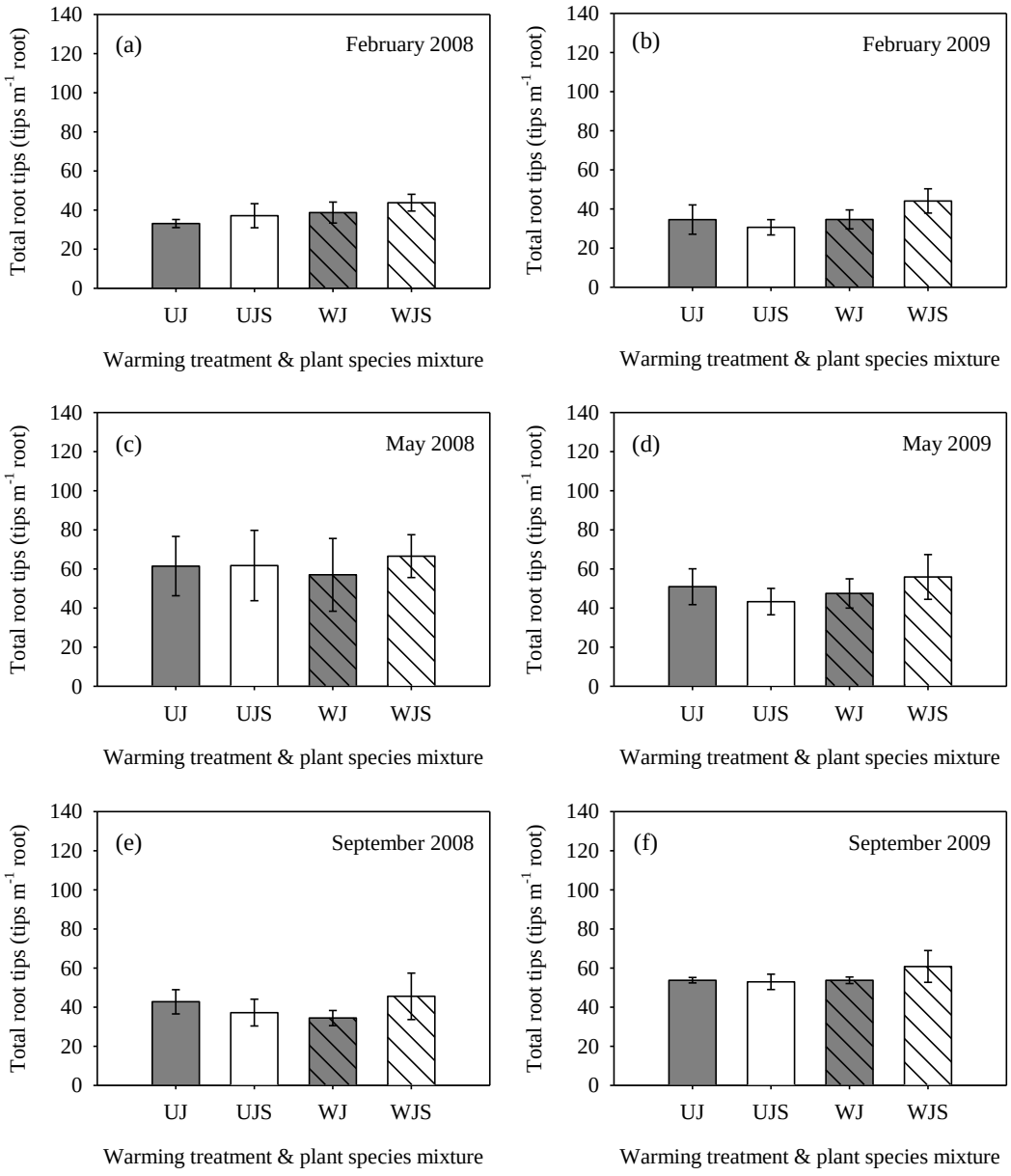

Figure A-5.13. Effect of warming treatment on total root tips per root length (tips m^{-1} root) of *Juniperus virginiana* averaged across precipitation treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

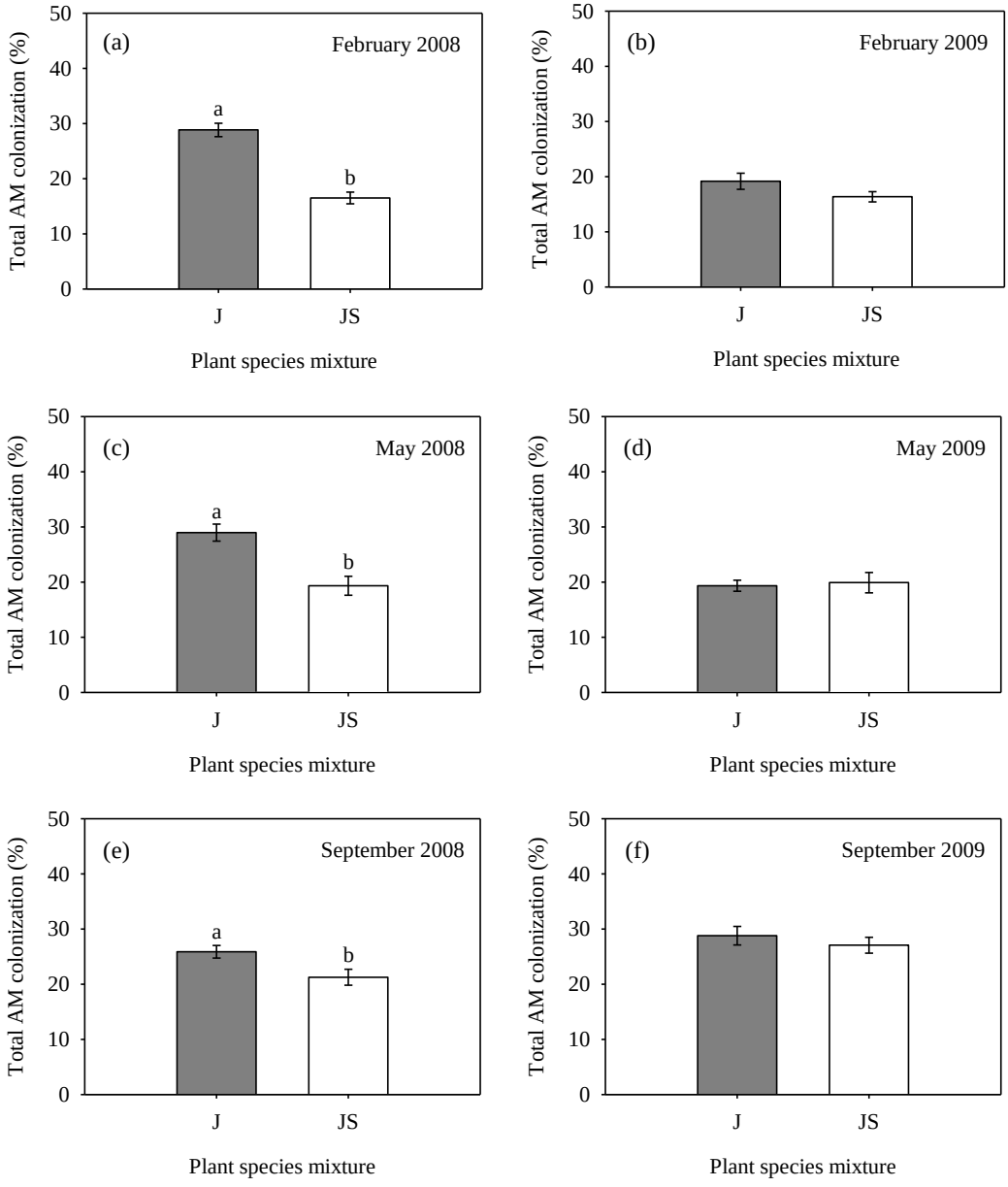

Figure A-5.14. Percent total arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

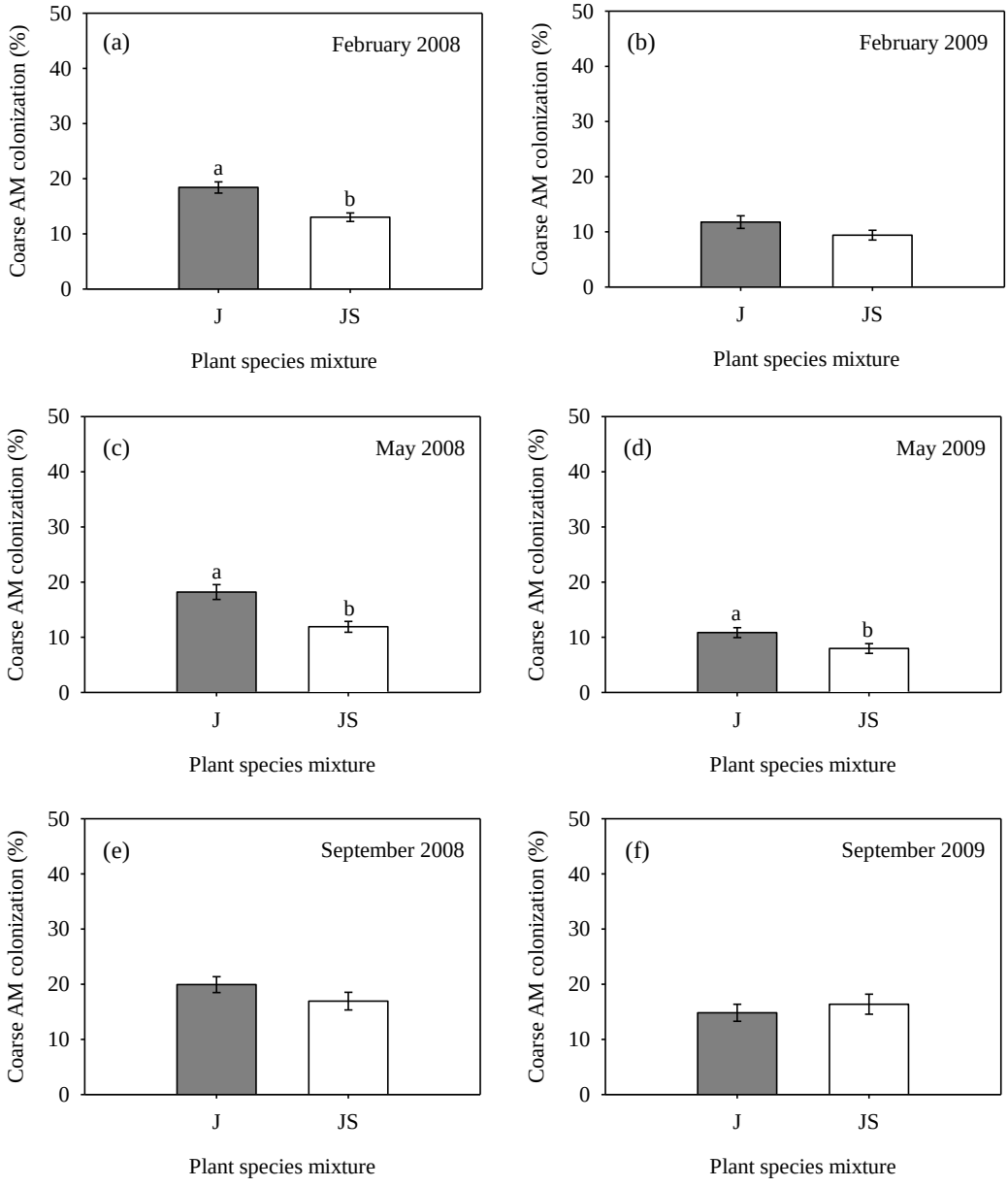

Figure A-5.15. Percent coarse arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

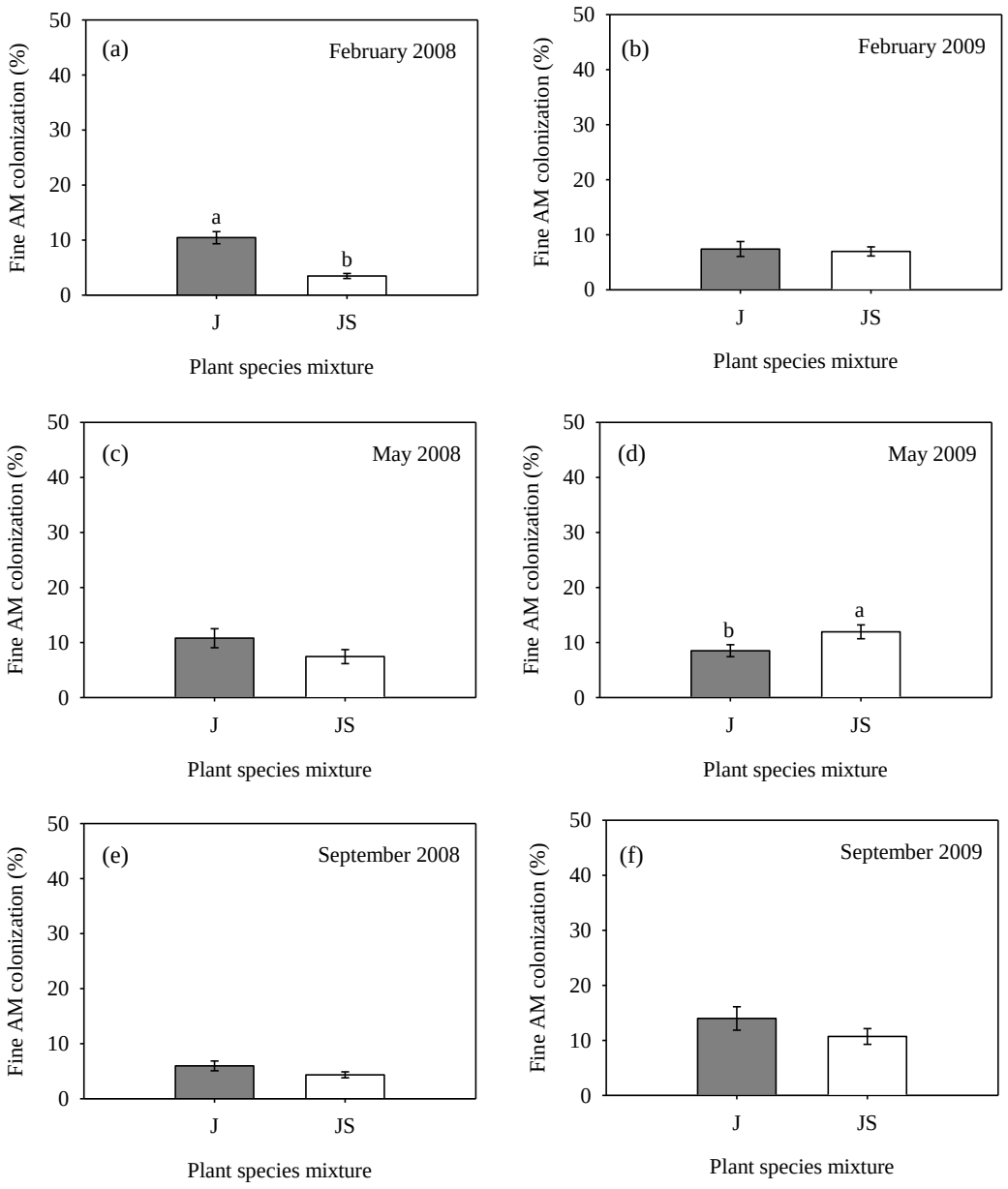

Figure A-5.16. Percent fine arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

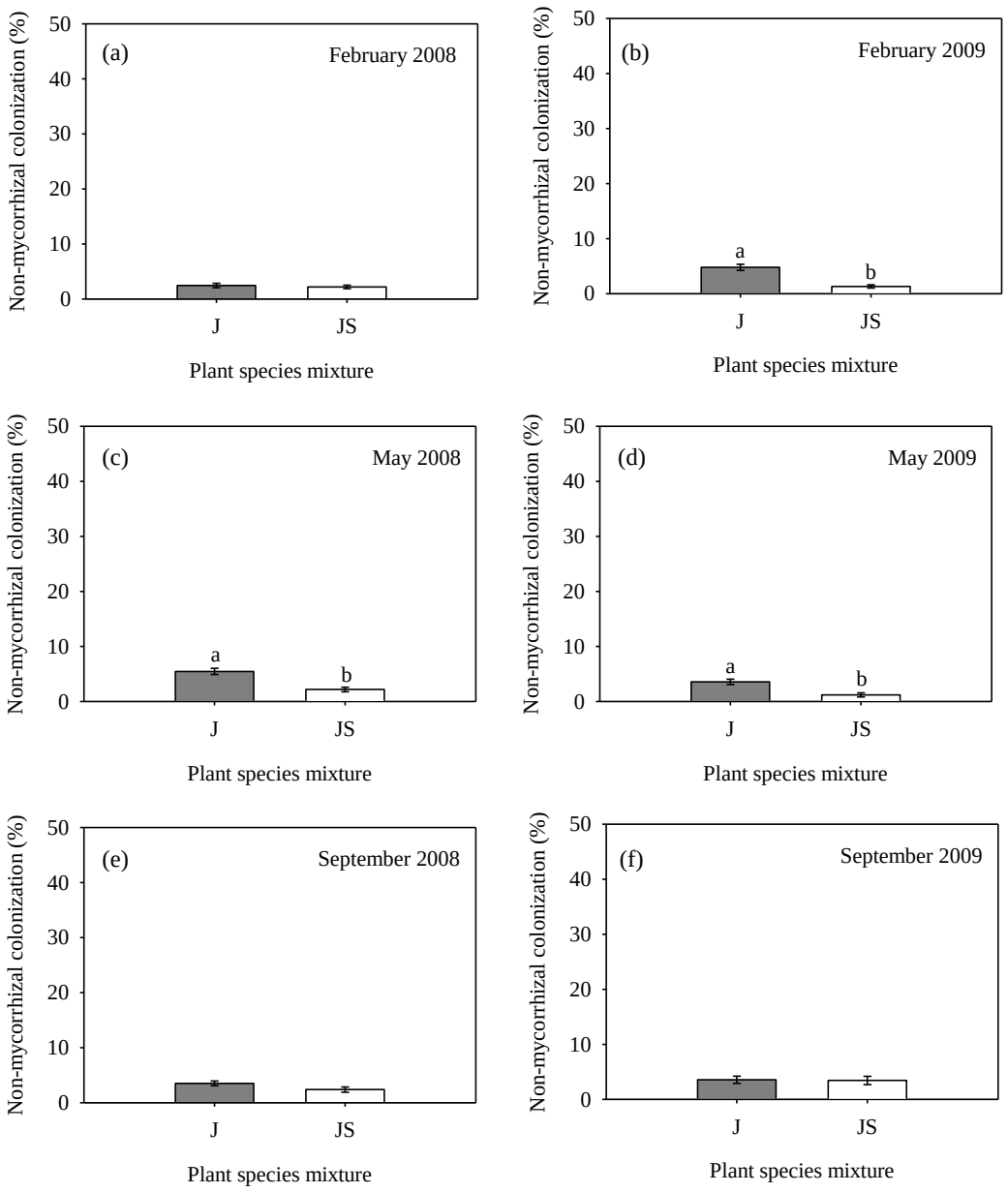

Figure A-5.17. Percent non-mycorrhizal root colonization of *Juniperus virginiana* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

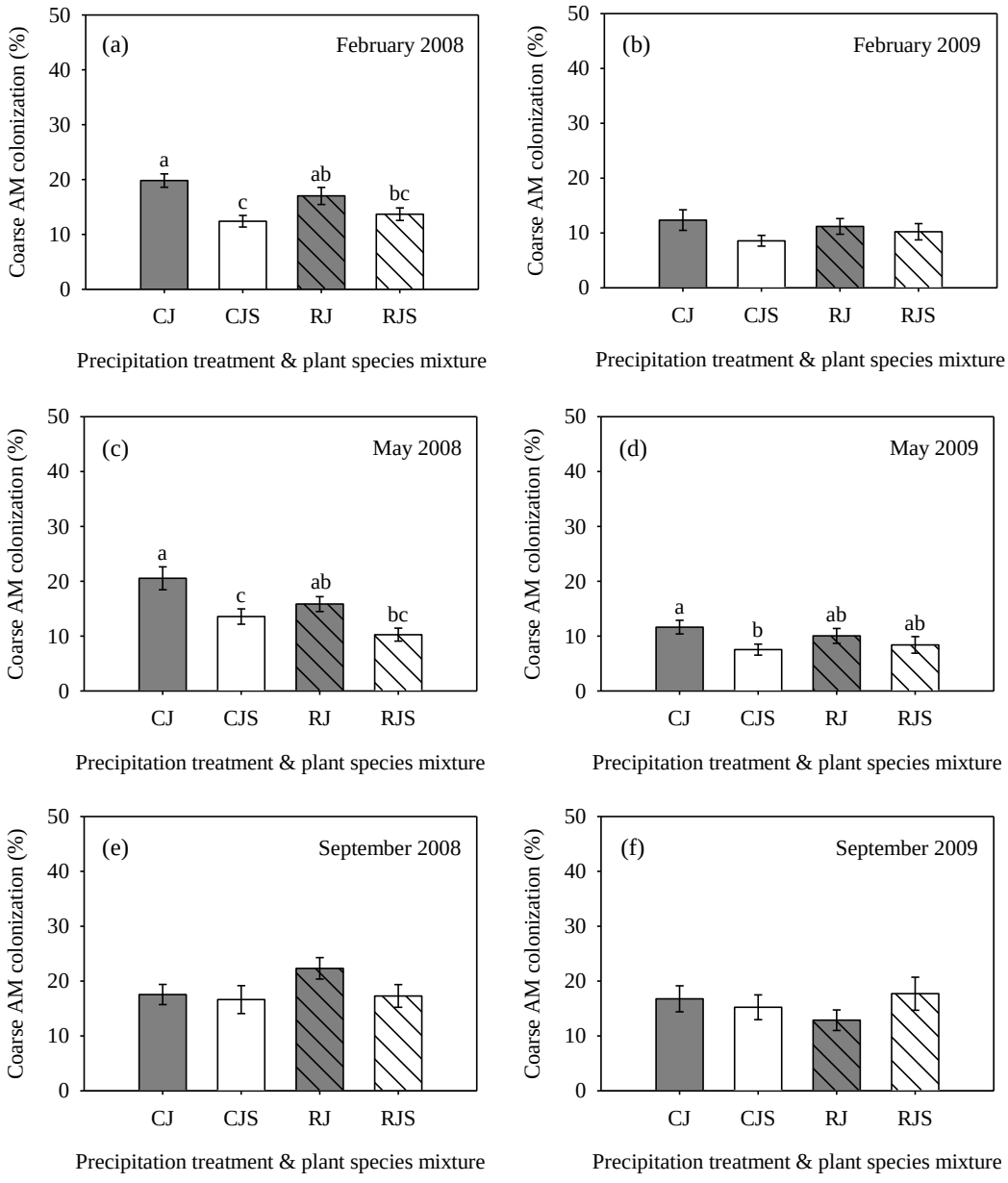

Figure A-5.18. Effect of precipitation distribution on percent coarse arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

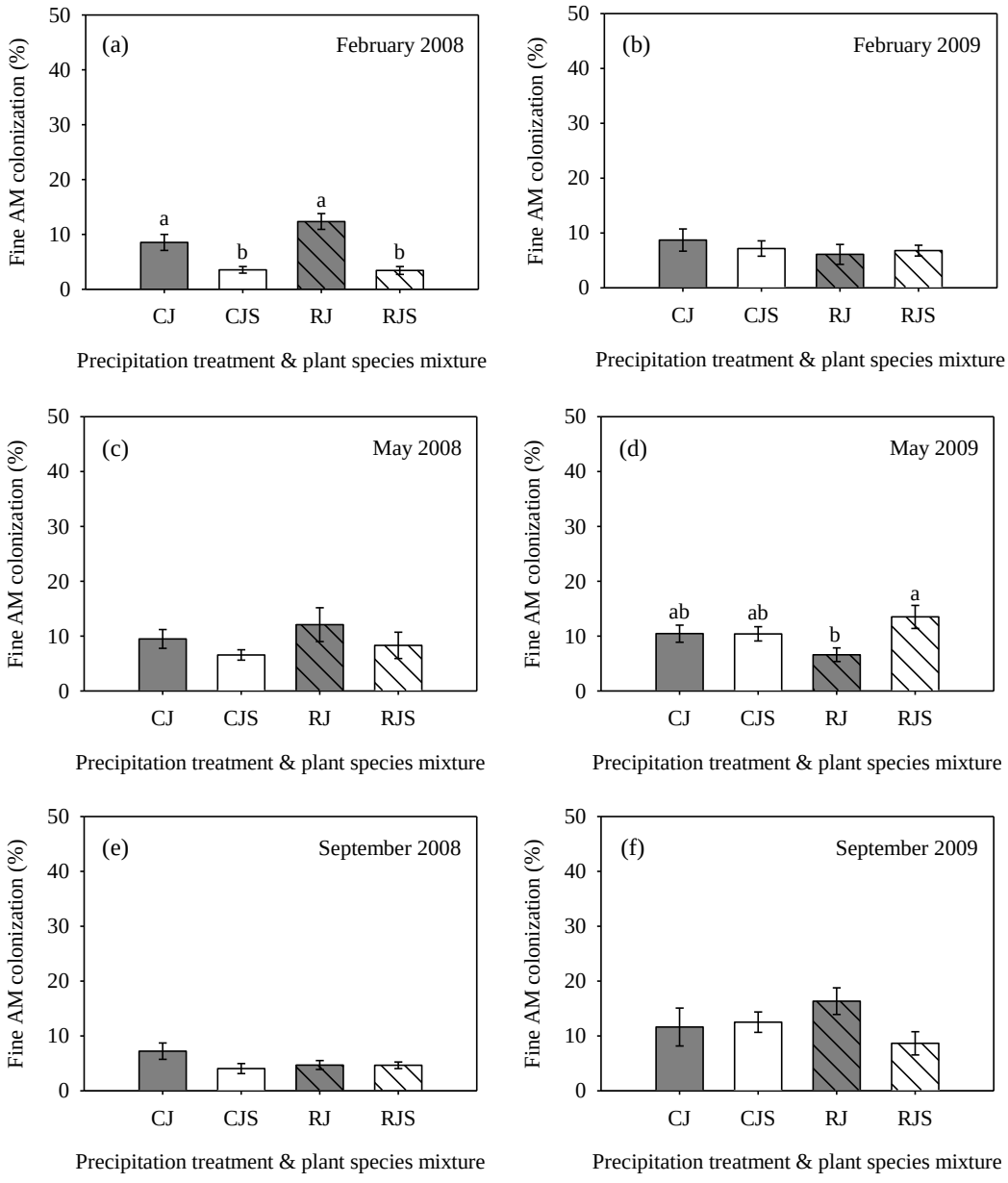

Figure A-5.19. Effect of precipitation distribution on percent fine arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

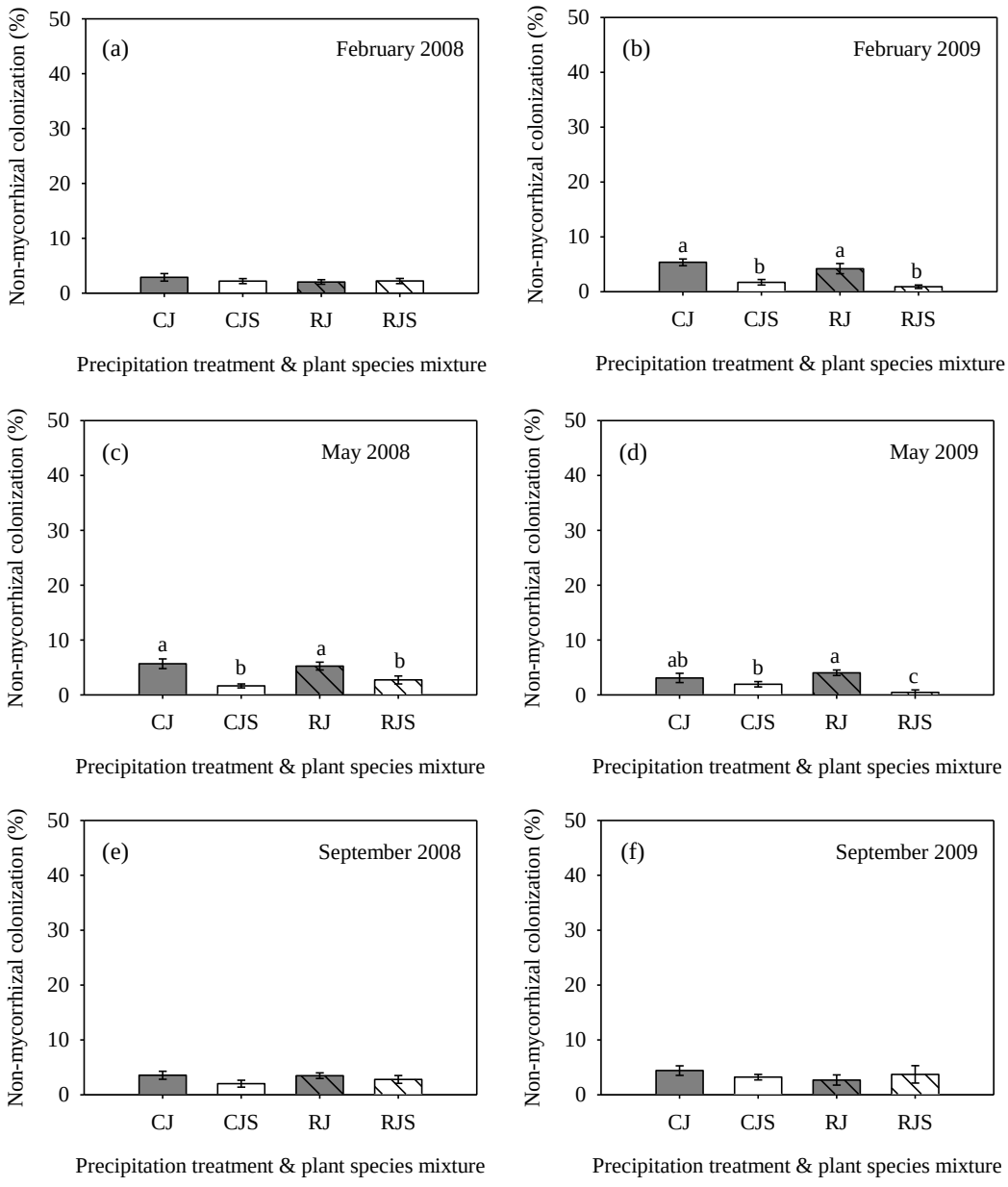

Figure A-5.20. Effect of precipitation distribution on percent non-mycorrhizal root colonization of *Juniperus virginiana* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

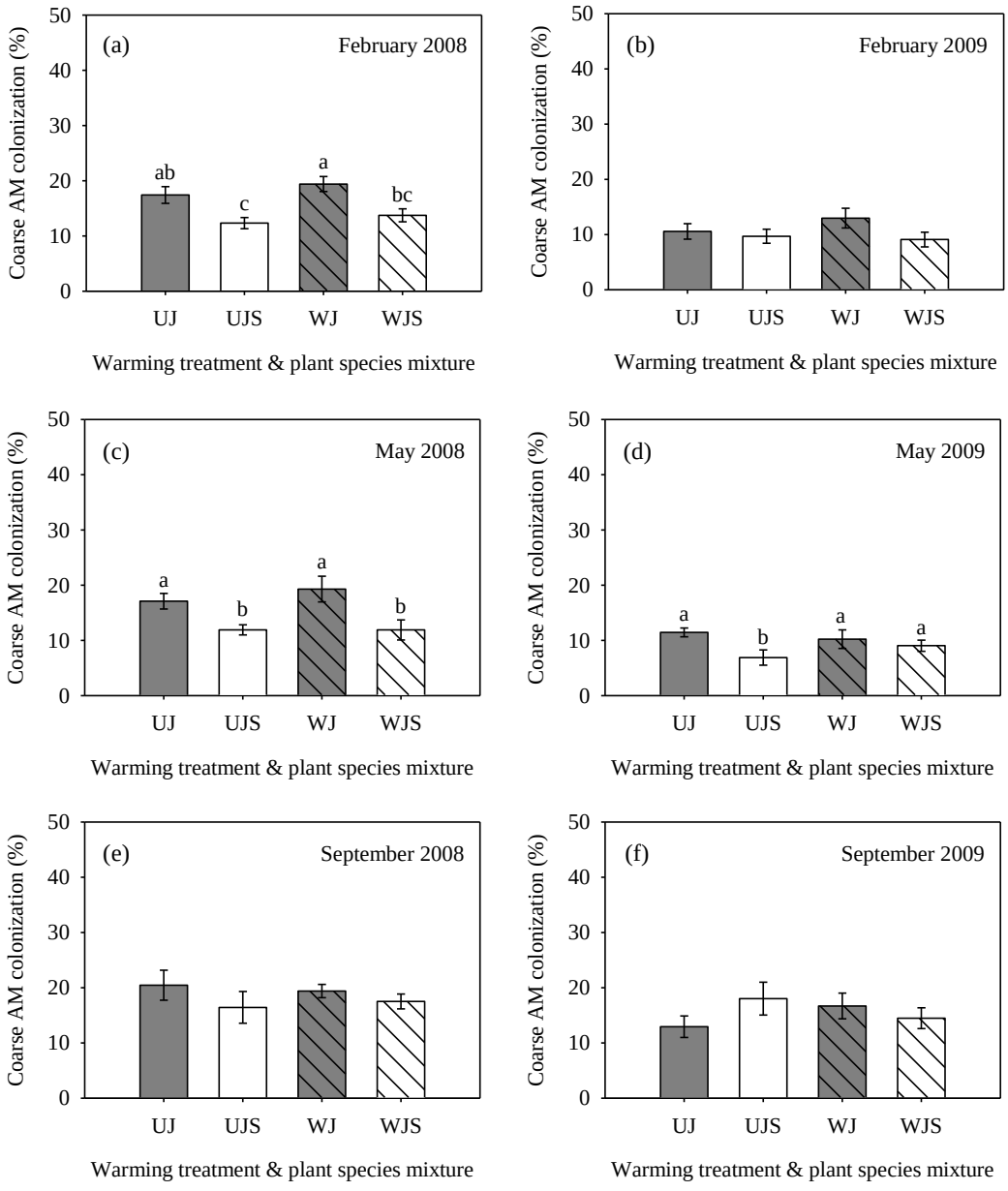

Figure A-5.21. Effect of warming treatment on percent coarse arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across precipitation treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

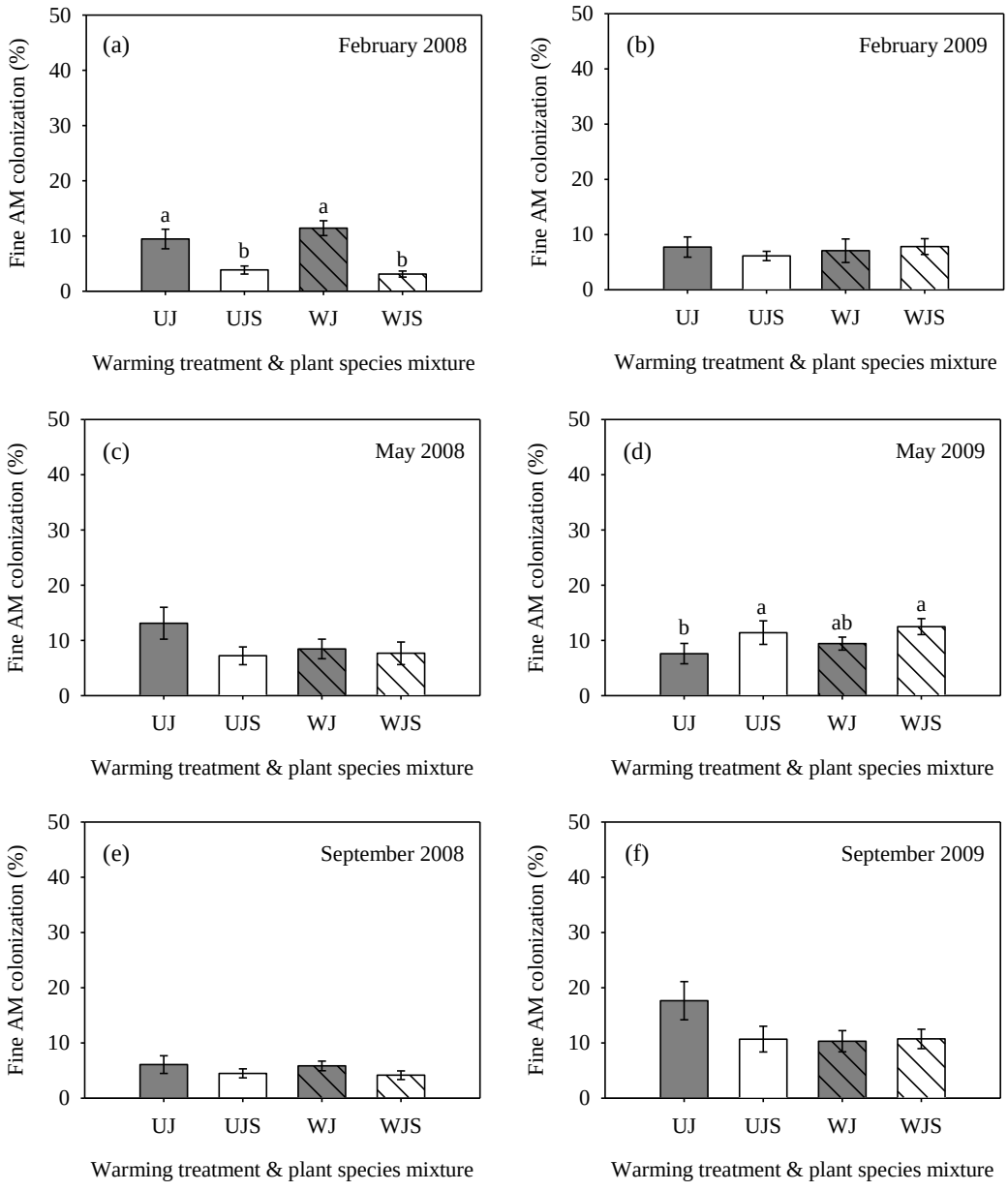

Figure A-5.22. Effect of warming treatment on percent fine arbuscular mycorrhizal (AM) root colonization of *Juniperus virginiana* averaged across precipitation treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

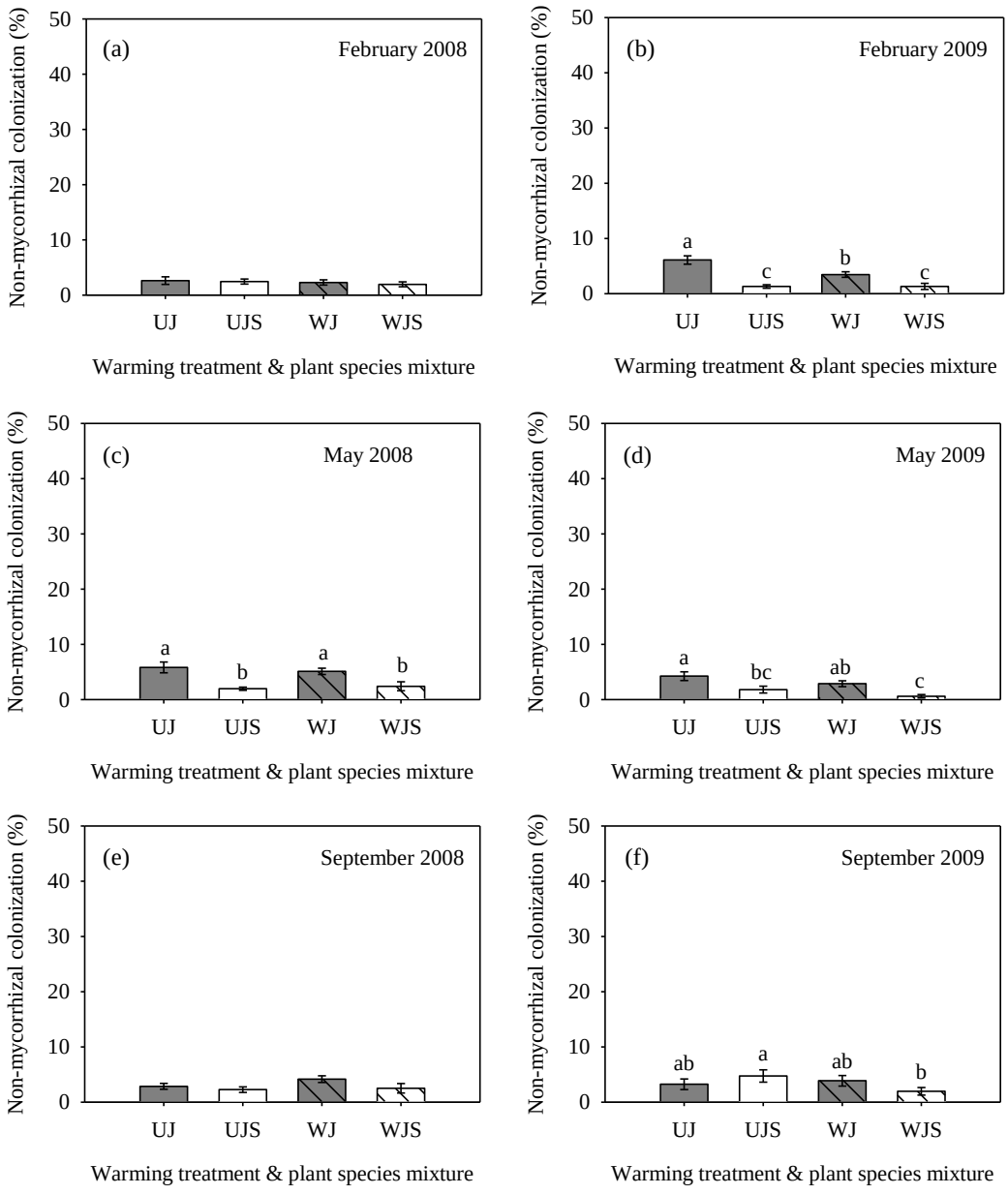

Figure A-5.23. Effect of warming treatment on percent non-mycorrhizal root colonization of *Juniperus virginiana* averaged across precipitation treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Filled bars depict *J. virginiana* grown in monoculture (J) and unfilled bars depict *J. virginiana* grown with *Schizachyrium scoparium* (JS). Diagonal hatches indicate warmed treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test.

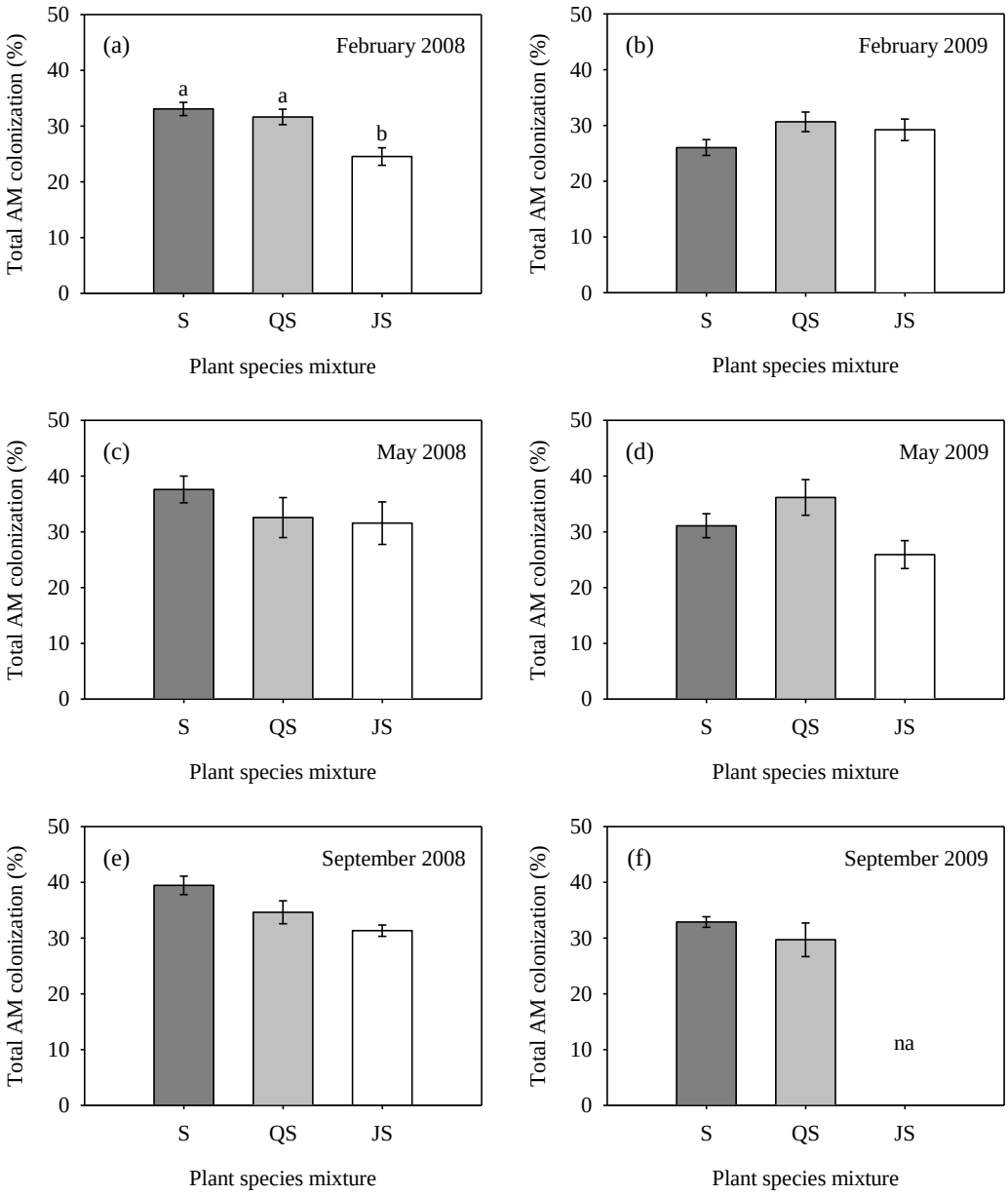

Figure A-5.24. Percent total arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

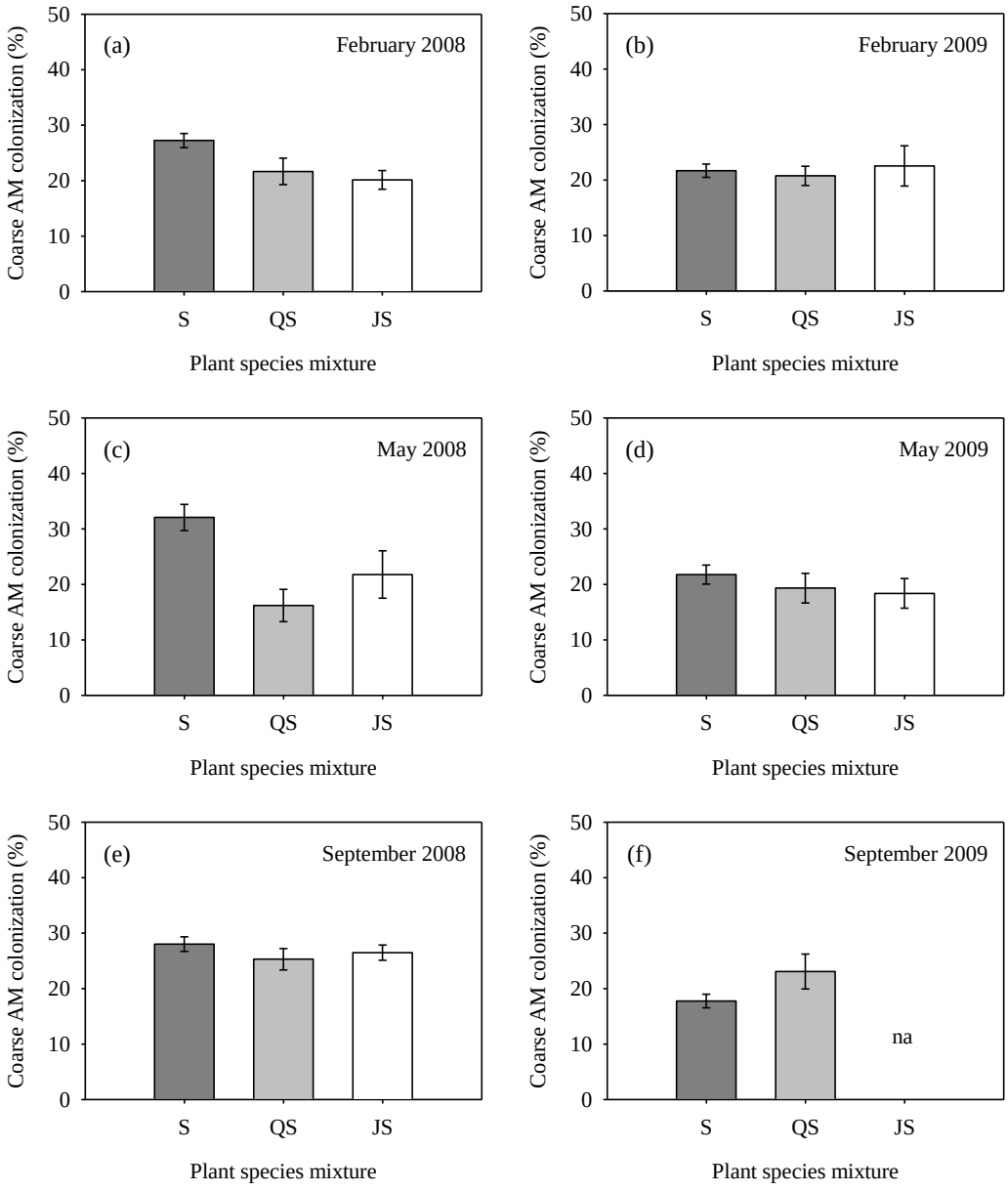

Figure A-5.25. Percent coarse arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

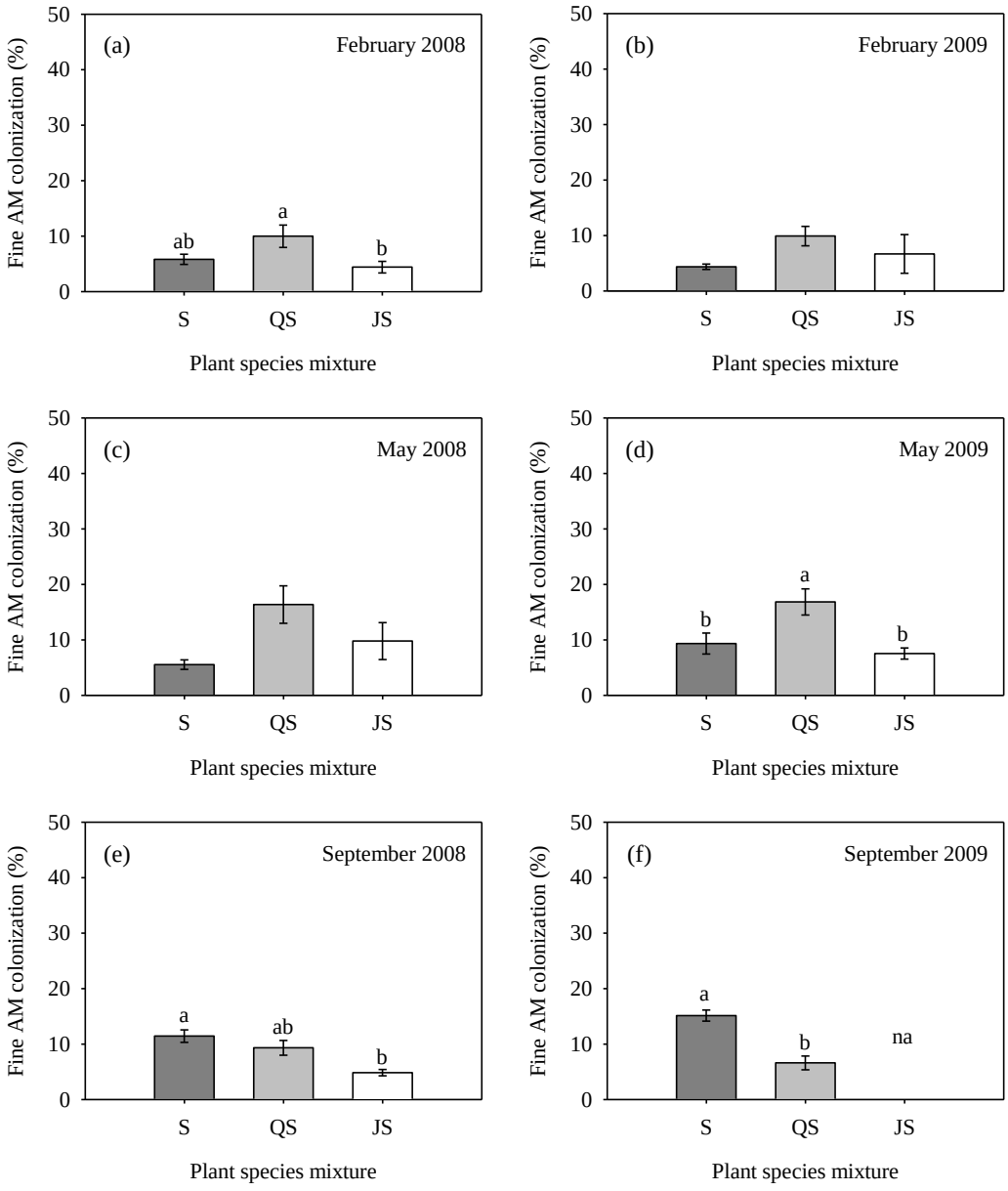

Figure A-5.26. Percent fine arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

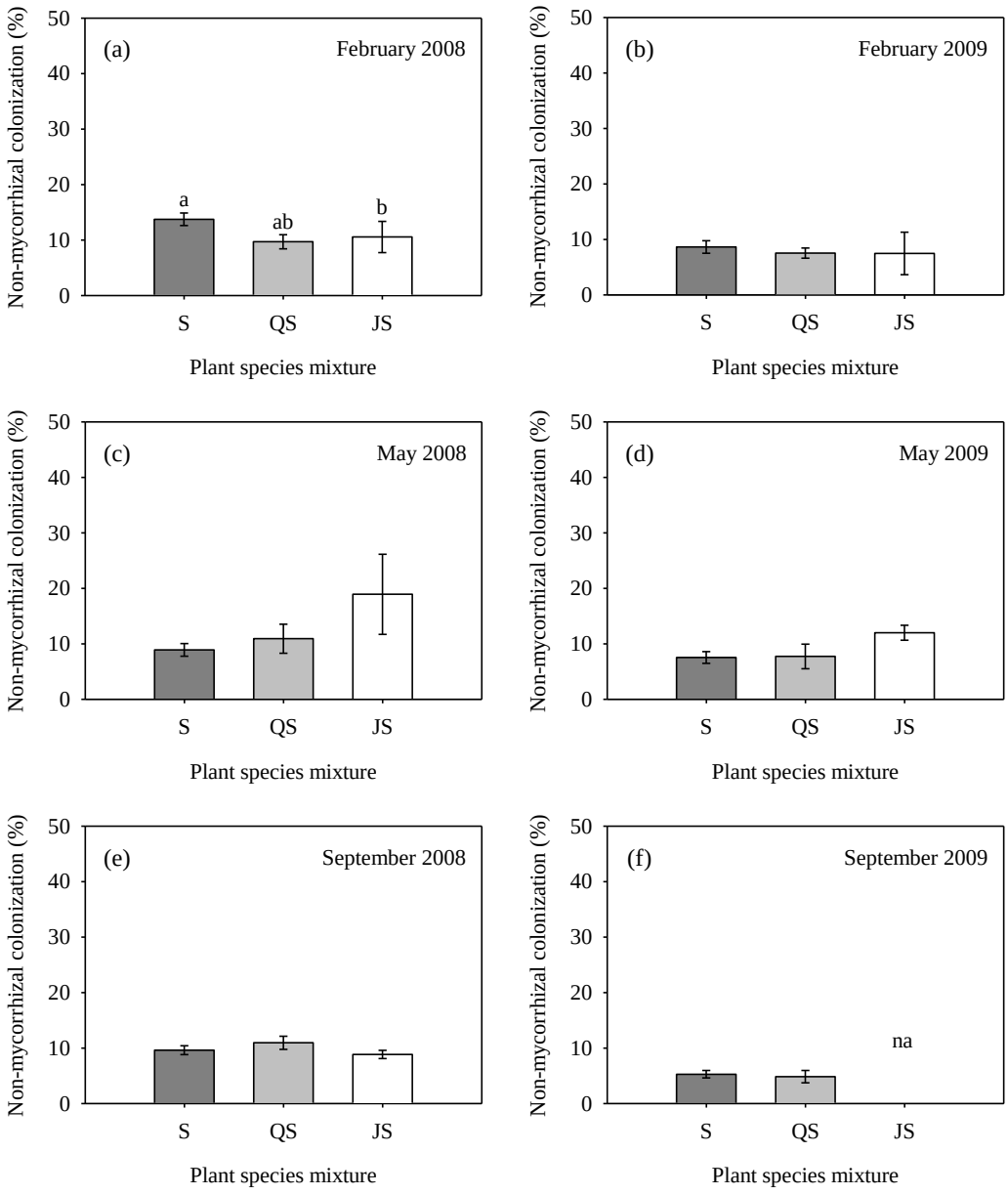

Figure A-5.27. Percent non-mycorrhizal root colonization of *Schizachyrium scoparium* averaged across warming and precipitation treatments in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

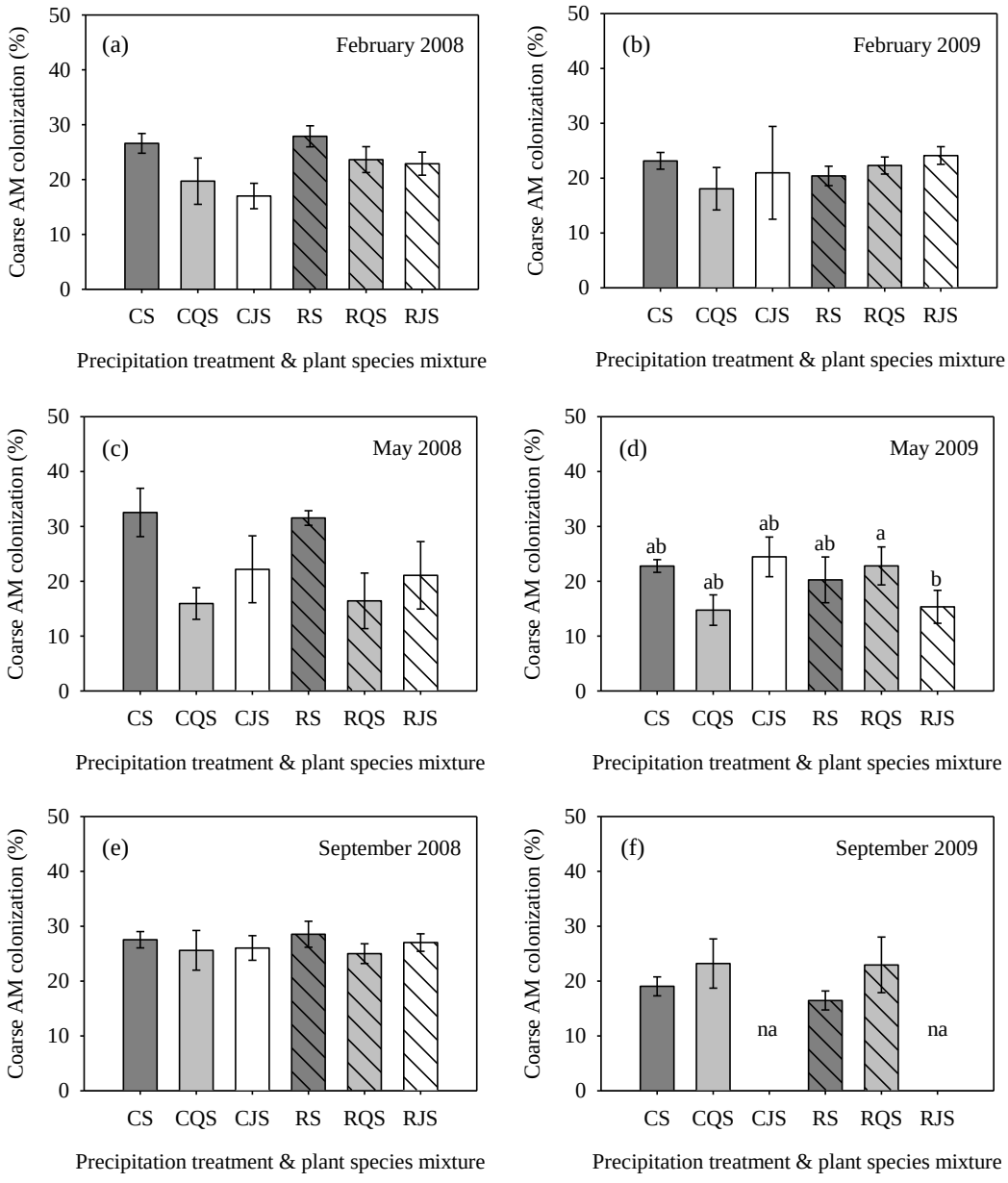

Figure A-5.28. Effect of precipitation distribution treatment on percent coarse arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

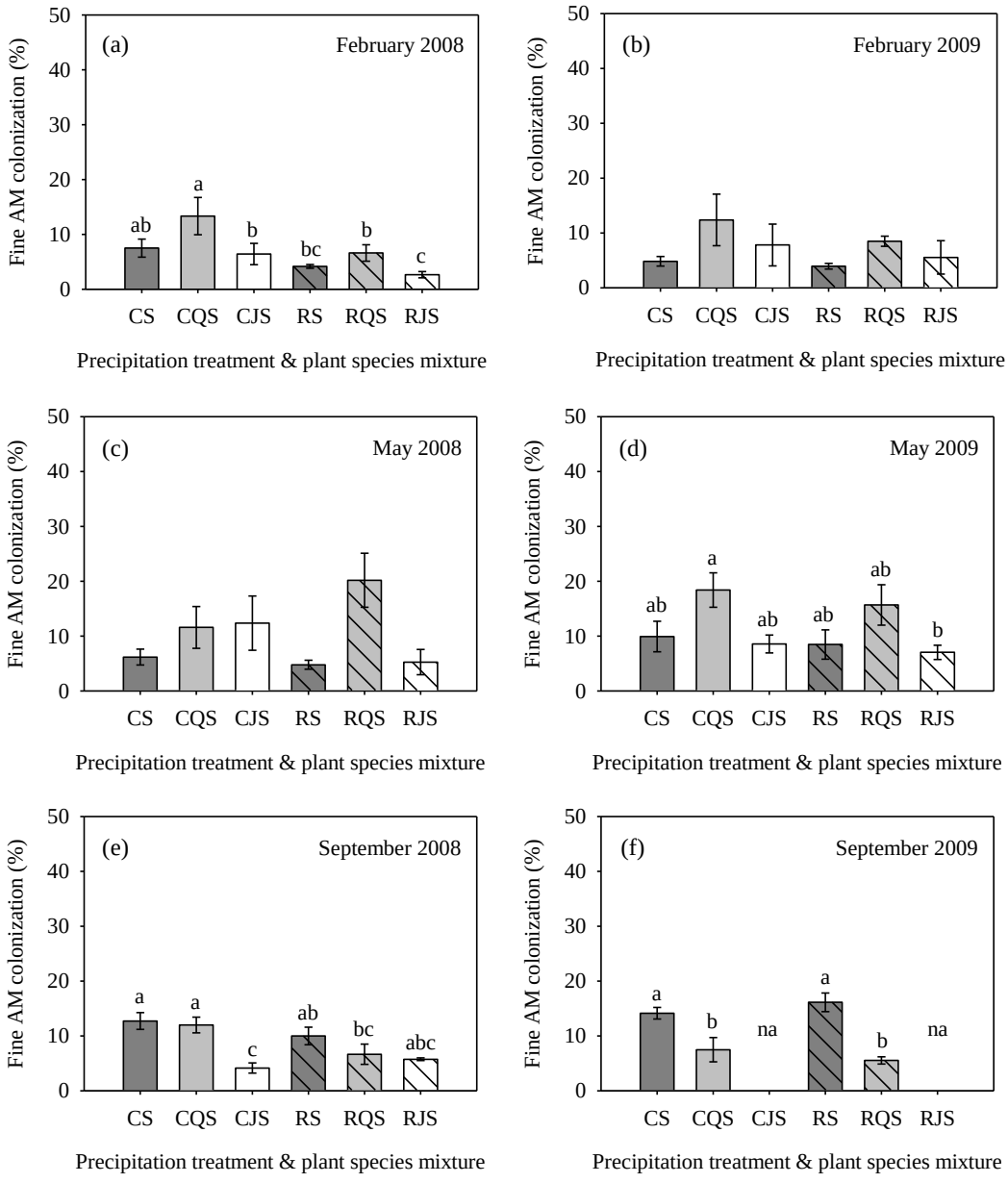

Figure A-5.29. Effect of precipitation distribution treatment on percent fine arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

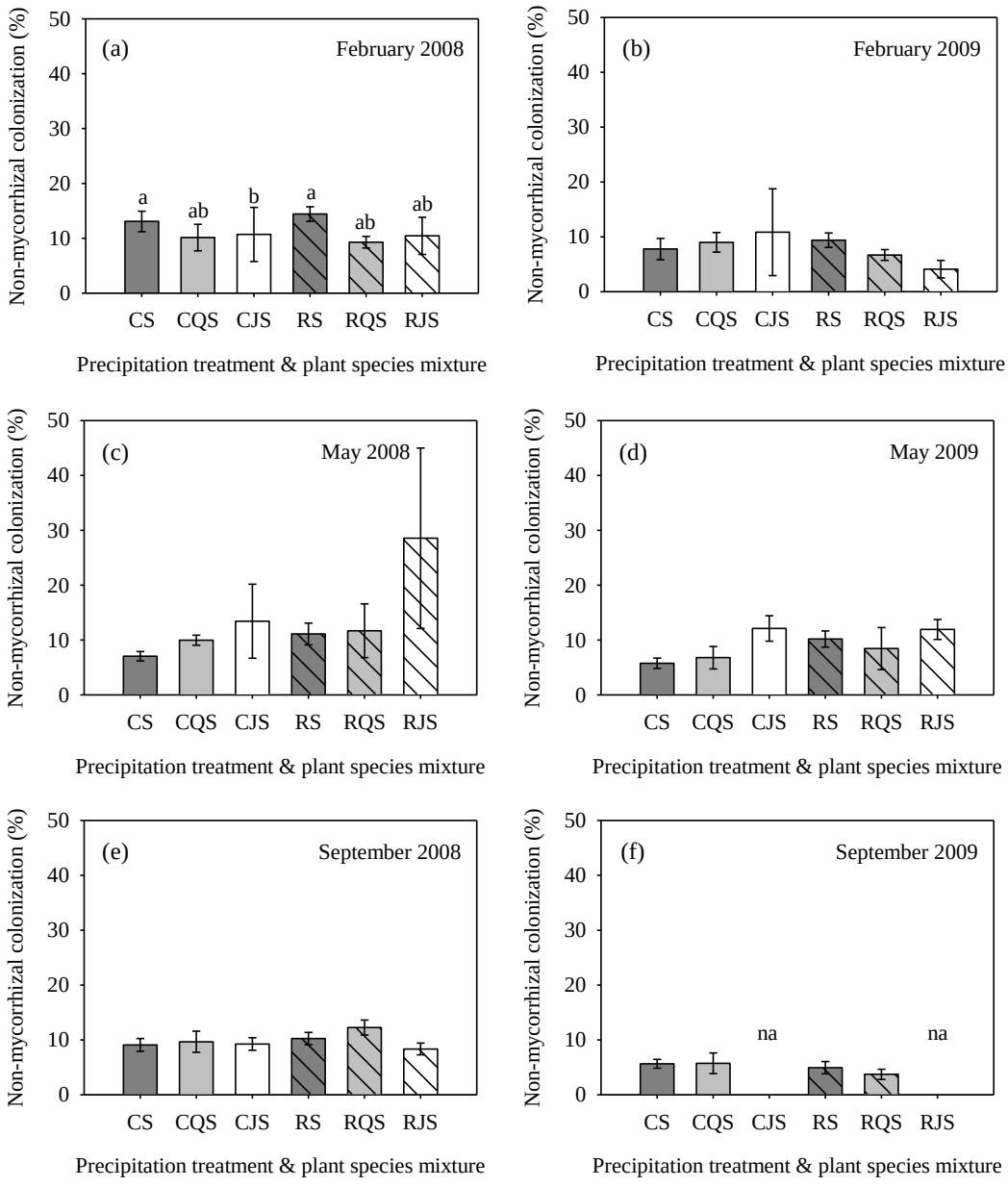

Figure A-5.30. Effect of precipitation distribution treatment on percent non-mycorrhizal root colonization of *Schizachyrium scoparium* averaged across warming treatment in (a) February 2008, (b) February 2009, (c) May 2008, (d) May 2009, (e) September 2008, and (f) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* in monoculture (S), light grey bars depict *S. scoparium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate redistributed precipitation treatment (R) and non-hatched bars indicate control precipitation treatment (C). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from JS in September 2009 (na).

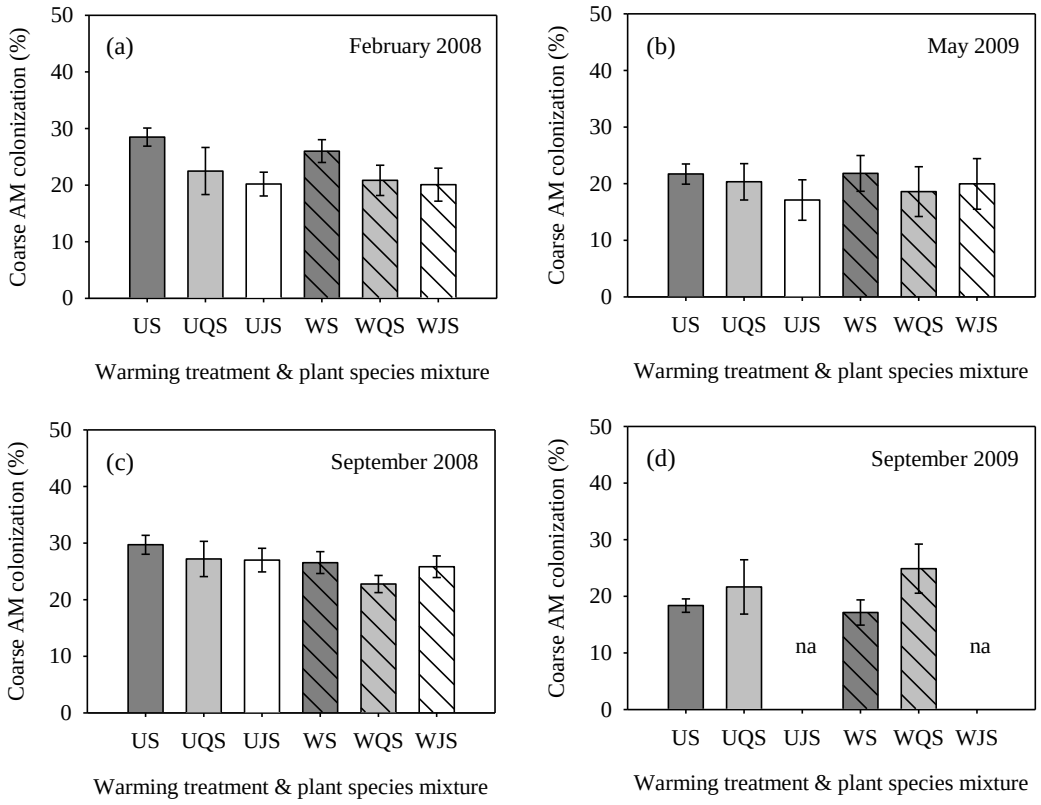

Figure A-5.31. Effect of warming treatment on percent coarse arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across precipitation treatment in (a) February 2008, (b) May 2009, (c) September 2008, and (d) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* grown in monoculture (S), light grey bars depict *S. scoaprium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate warming treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from warming treatments in May 2008, February 2009, and from JS in September 2009 (na).

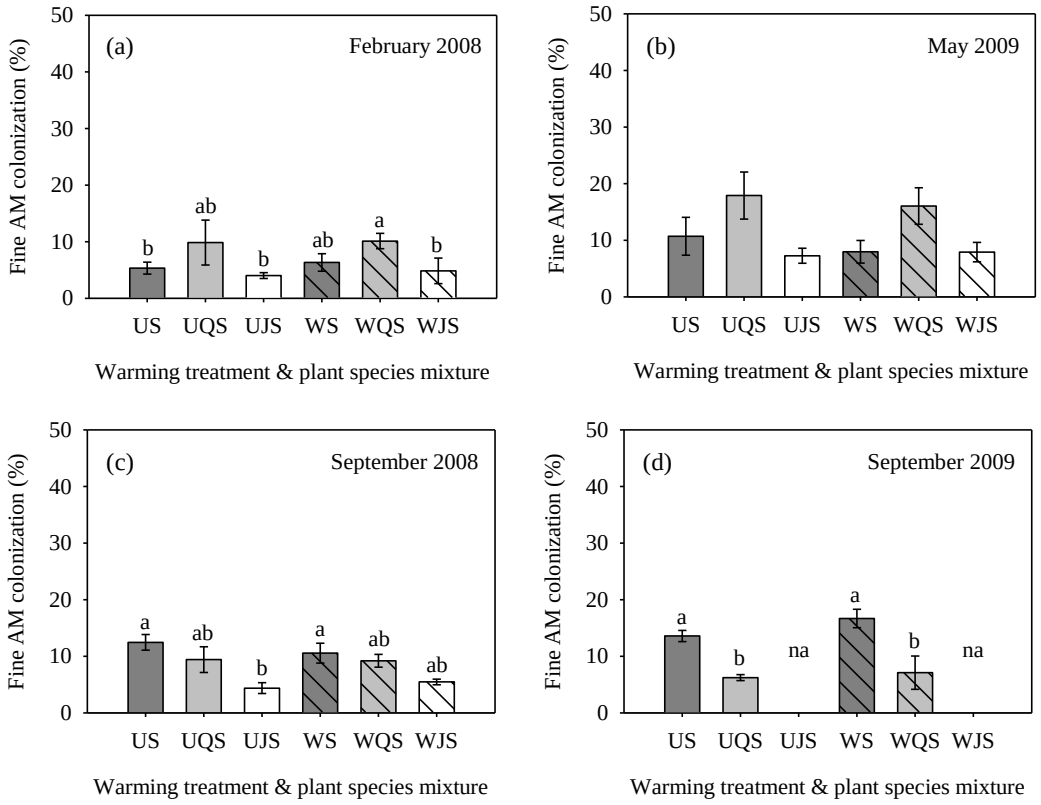

Figure A-5.32. Effect of warming treatment percent fine arbuscular mycorrhizal (AM) root colonization of *Schizachyrium scoparium* averaged across precipitation treatment in (a) February 2008, (b) May 2009, (c) September 2008, and (d) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* grown in monoculture (S), light grey bars depict *S. scoaprium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate warming treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from warming treatments in May 2008, February 2009, and from JS in September 2009 (na).

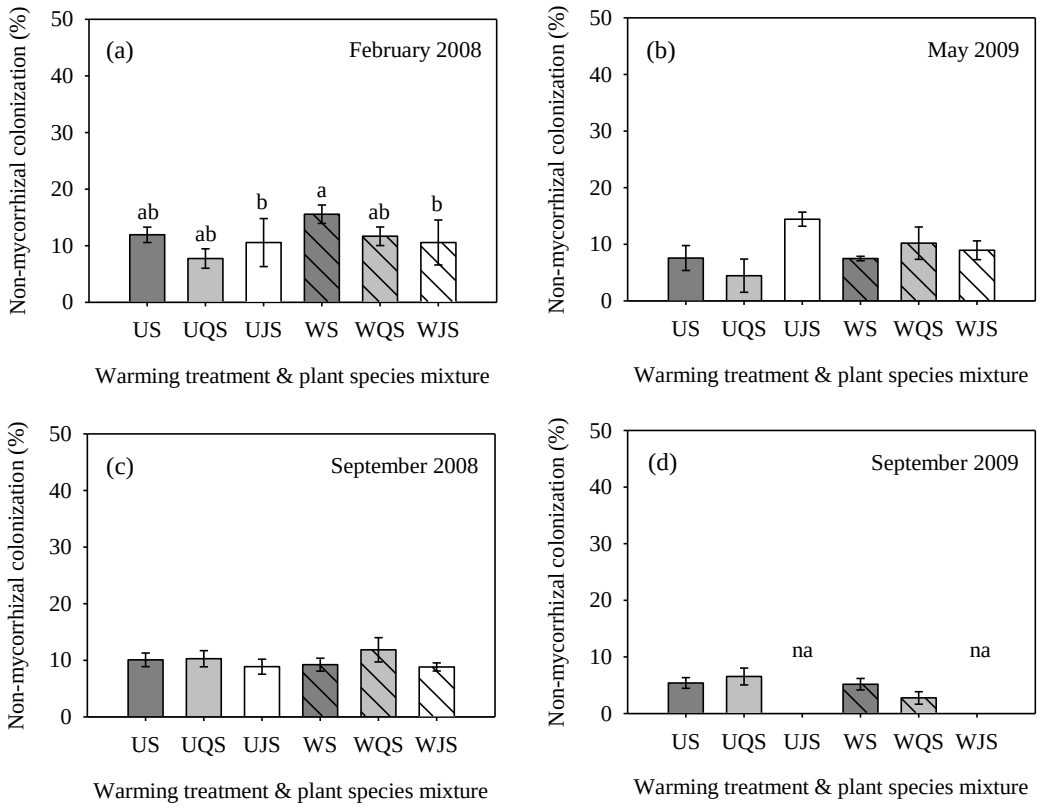

Figure A-5.33. Effect of warming treatment percent non-mycorrhizal root colonization of *Schizachyrium scoparium* averaged across precipitation treatment in (a) February 2008, (b) May 2009, (c) September 2008, and (d) September 2009 (means ± SE). Dark grey bars depict *S. scoparium* grown in monoculture (S), light grey bars depict *S. scoaprium* grown with *Quercus stellata* (QS), and unfilled bars depict *S. scoaprium* grown with *Juniperus virginiana* (JS). Diagonal hatches indicate warming treatment (W) and non-hatched bars indicate unwarmed treatment (U). Letters indicate significant ($P \leq 0.05$) differences in response according to student's t-test. Insufficient *S. scoparium* roots recovered from warming treatments in May 2008, February 2009, and from JS in September 2009 (na).

VITA

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During his time at Texas A&M University Andrew received several fellowships, scholarships and awards including The Tom Slick Graduate Research Fellowship, Louise B. Belsterling Scholarship, and the Garden Club of America Interchange Fellowship & Martin McLaren Scholarship. He has (co)authored six peer-reviewed publications.

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